2019

Behavioral assessment of social structure and guest provisioning program participation of zoo-housed giraffes (Giraffa camelopardalis) under varying spatial availability.

Fatima Ramis
University of North Florida, n01375630@unf.edu

Behavioral assessment of social structure and guest provisioning program participation of zoo-housed giraffes (*Giraffa camelopardalis*) under varying spatial availability.

Fatima Ramis

Committee Members: Dr. Terry Maple, Dr. Quincy Gibson, Dr. Gregory Kohn, Dr. Meredith Bashaw, Dr. Adam Rosenblatt.

A thesis submitted to the Department of Biology in partial fulfillment of the requirements for the degree of Master of Science in Biology

UNIVERSITY OF NORTH FLORIDA

COLLEGE OF ARTS AND SCIENCES

2019

CERTIFICATE OF APPROVAL

The thesis "Behavioral assessment of social structure and guest provisioning program participation of zoo-housed giraffes (*Giraffa camelopardalis*) under varying spatial availability."

Approved by the thesis committee:

Dr. Quincy Gibson Committee Chair Person — Date

Dr. Terry Maple — Date

Dr. Gregory Kohn — Date

Dr. Adam Rosenblatt — Date

Dr. Meredith Bashaw — Date

Accepted for the Department:

Dr. Matt Gilg — Date

ACKNOWLEDGEMENTS

I would like to express my gratitude to several individuals with whom this research would have been impossible without. Firstly, I would like to thank Dr. Terry Maple for believing in me and adding me on to your wellness lab even with my undeveloped ideas and naivety in the zoo field. Your support, words of inspiration, willingness to connect me to others and guidance has been essential throughout this period and I will be forever thankful. Secondly, I would like to thank Dr. Quincy Gibson for your indispensable advice, life lessons, guidance and emotional support throughout this process. To Kristy Brightwell, your willingness to make me a part of the Dolphin Ecology lab helped me feel integrated and supported through this process. To Dr. Gregory Kohn, thank you so much for all your support and insight into this project, without your help it would have been impossible to execute this analysis. To Dr. Meredith Bashaw, thank you all your help in designing this project and sharing your expertise in giraffe behavior, it would have been incredibly difficult to quantify the behaviors of such peculiar animals without you. Your passion for them is contagious. To Dr. Adam Rosenblatt thank you for your words of encouragement, statistical advice and overall positivity throughout this endeavor, they were much needed.

Next, I would like to thank the Jacksonville Zoo and Gardens staff for their support and willingness to entertain my ideas. To Dan Maloney, your support in carrying out this project and focus on the value it can provide to zoo management was crucial to shaping the goals of this project. To Valerie Segura and Megan Morris, thank you for your support in communication to zoo staff. I would like to thank Corey Neatrour and Travis McCullion and their team of animal care staff and exhibit guides for their interest, support, and facilitation of this project. Without your collaboration, this project would have never been possible. To Michaela Mohr, Kaileen Boccio, Lindsey Brown, and Meg Carmona, thank you for the hours spent helping collect these data, learning these animals, and most importantly for your emotional support, lightheartedness, and willingness to entertain my ideas.

Most importantly, I want to extend my wholehearted appreciation to my fellow lab-mate Emily Szott. These last two years would have never been possible without her support, countless hours of discussions, and timely inappropriate animal jokes. The friendship we developed will never be forgotten. To my future father in law, Keith Winsten, thank you for indispensable guidance in the zoo field, I am privileged to have you. To the rest of my family especially mom and dad, for their emotional support and encouragement. Finally, to my amazing fiancé, George Winsten I appreciate your unwavering support more than you will ever know. Thank you for believing in me and entertaining most if not all idiotic rambles and passion for this field. I am lucky to have you in my life.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

Close encounters with animals are considered integral for visitors and are trademark components of traditional educational engagement in zoological parks. As capacity for up-close encounters continue to increase with a simultaneous development in the field of animal welfare science, behavioral assessments on the role of common close encounters is timely. Giraffes (*Giraffa camelopardalis*) visitor feeding programs are established in approximately 57% of institutions accredited by Association of Zoos and Aquariums. Due to successful breeding and capacity building for zoological giraffe populations, this percentage will likely continue to increase. There is a great deal of variation in the environmental design of giraffe visitor feeding programs across institutions and limited understanding on the role of these variables on individual and group welfare for giraffes. The first chapter of this study behaviorally assesses the effects of space availability and observes the role of feed-type in the usage, interaction types, and measures of welfare in two different zoological institutions. Findings indicate that increased space availability increase sharing by individuals as well length of feeding bouts potentially influencing feeding comfort. Space also modulates aggression at the visitor station as displacement rates decreased with additional space and were overall lower in giraffes housed under large type feeding stations. Results show that individuals increase their displacement rate while at the visitor feeding station, potentially indicating that guest station significantly increases competition among conspecifics. The second chapter explores the role of social structure and dynamics on guest station interactions and usage. Though giraffes are thought to establish predominantly linear dominance hierarchy based on resource competition in zoological settings, the consequence of artificially concentrated resources for the purpose of guest interactions has not been investigated. Zoological studies and recent population studies provide a baseline

understanding for the role of pro-social feeding interactions and social structure in giraffe populations as it relates to food distribution, however, there is limited understanding of the role that social structure plays on the usage of guest feeding programs. Here we found that social structure metrics of centrality and importance of affiliative interactions play a role in sharing the guest station, though conspecific direct ties on exhibit are not transferable to ties at the guest station. Additionally, the study indicates that dominance structure as calculated by exhibit displacement interactions does not represent the dominance dynamics observed at the guest station. We suggest a variety of guest engagement opportunities which may better represent the social structure of these populations and suggest assessment of these programs to other institutions. This study validates the benefits of assessing animal behavior in zoological settings under context dependent interactions for the purpose of improving animal welfare enhancing guest engagement opportunities.

INTRODUCTION

Zoological programs that promote human-animal interactions can serve to influence human attitudes towards nature while promoting species appropriate behavior through empirical analysis of environmental design, the commonality and variability of giraffe provisioning programs across AZA institutions, makes them an appropriate animal to analyze. Zoological institutions accredited by the Association of Zoos and Aquariums are committed to improving animal care while emphasizing the importance of an entertaining family experience (M. D. Kreger & Hutchins, 2010). Zoo guests consider proximity and physical contact with animals an important component of their zoo visit which contribute to feelings of respect towards animal life (Kidd et al., 1995; Clayton et al., 2009). Proximity to animals has been associated to higher probability of supporting conservation efforts and building an environmental identity (Powell & Bullock, 2014; Swanagan, 2000; Clayton et al., 2011).

Visitor feeding stations have been historically common practice in zoos as a method of increasing close and active interactions with animals in a traditionally nourishing manner (M. Kreger & Mench, 1995). Until the 1970s, feeding stations were not only common, but often combined with showmanship by animals (M. Kreger & Mench, 1995). By the 1990s most feeding stations were reduced to petting-zoo animals and fish tank interactions due to high incidences of animal mortality caused by ingestion of foreign bodies potentially fed by visitors (M. Kreger & Mench, 1995; Hediger, 1969). With new regulations and modern practices in place due to the Animal Welfare Act of 1966 in the United States and other welfare related regulations worldwide, controlled feeding stations could serve as a form of education and attraction to visitors while simultaneously benefiting the animals (M. Kreger & Mench, 1995). Studies have indicated that close encounters with visitors can vary between negative, neutral, and positive experiences for the animals involved depending on species and even situation (Fernandez et al., 2009; Hosey, 2000). As human-animal interactions in zoos continue to be common world-wide, there is a need to empirically evaluate these by applying models of animal welfare (D'Cruze et al., 2019; Mellor, 2016). Animals whose social structure may be influenced by human- animal interactions due to their social structure composition should be the forefront of assessements as interactions could influence both individual welfare and group structure.

Giraffes form stable long-term relationships, that appear to be partially mediated by feeding interactions (Muller et al., 2918), therefore, guest provisioning programs should be analyzed to further understand the role of their design on giraffe usage and conspecific feeding interactions. The behavioral study of giraffes provides an opportunity to understand the role of modern-day public feeding on animal behavior, and the potential factors that modulate usage and effects of the station on giraffes. Giraffes are a popular megafauna commonly housed in zoos; they receive sufficient attention to allow for public feeding. Today, approximately 57% of AZA-accredited institutions provide giraffe feeding stations (Orban et al., 2016). However, there is a short list of literature that addresses this type of modern visitor feeding station's effect on animal welfare or empirically tested best practices.

A survey of AZA- accredited zoos conducted by Bashaw and colleagues (2001) found giraffes housed in zoos with visitor feeding programs exhibited a slight trend for lower probability of oral stereotypic behaviors, indicating that visitor feeding stations could positively affect giraffe welfare. A study by Orban (2016), found giraffes housed in zoos with visitor feeding stations with a continuous feeding schedule were more likely to spend time idle than those in zoos with scheduled feeding stations (Orban et al., 2016). Guest provisioning programs for giraffes likely promote positive attitudes towards giraffes, however, there is an existing knowledge gap in the role of environmental design on giraffe program usage and conspecific interactions, as well as welfare implications, indicating a need to analyze these variables.

CHAPTER 1

GUEST FEEDING PROGRAM DESIGN AND GIRAFFE STATION USAGE

ABSTRACT

Capacity and use of visitor-animal feeding programs in zoological institutions serve to foster human-animal connection. The growing establishment of animal welfare science places an emphasis on the assessment of the environmental design of human-animal interactions and behavioral effects of these inputs. The social complexity of giraffes and their commonality as participants in visitor-animal feeding programs makes this species a logical choice for behavioral assessment. This study assessed environmental design features of space and feed-type on giraffe participation and interactions in visitor feeding programs in two Florida zoological institutions. Space allotted at the visitor feeding station positively contributed to feeding bout lengths, percent of time sharing the visitor station, and reduced the rate of displacements at the visitor station. Cross-institutional comparisons indicate that visitor programs with larger space allocation have lower rates of conspecific displacement. Natural feed-types (wax myrtle) as opposed to vegetables (lettuce and sweet potatoes) was not associated with lower rates of oral stereotypy rates across institutions. Further assessments should quantify the role of a variety of environmental features such as food presentation, food type, space allocation, sound, and human interaction types across a larger number of accredited institutions.

INTRODUCTION

Animal Welfare in Environmental Design.

Zoological institutions provide guests the opportunity to engage with nature while promoting the wellbeing of animals under their care A considerable number of accredited zoological institutions place an emphasis on fostering a human-animal connection. This is often facilitated through close animal encounters and increasingly balanced with significant attention to animal well-being. The growing focus on animal well-being has been reflected in increased wellness-inspired designs that emphasize environmental complexity, space allocation, and active welfare monitoring (Browning & Maple, 2019; Carter et al., 2015; Ward et al., 2018; Von Fersen et al., 2018; Mellor et al., 2015).

The internal state or welfare of an animal is often defined as the integrated outcomes produced as consequence of the sensory and neural inputs from the animal's physiology (Mellor et al., 2009; Hill & Broom, 2009). The welfare or well-being of an animal ranges on a spectrum from "bad to great", and it is mainly governed by the five domains, four of which are governed by physical components of an environment: nutrition, environmental challenges, health, and ability to socially interact appropriately (Rushen & Passillé, 1992; Mellor et al., 2009). The fifth domain relates to the mental components of the animal that may be short- or long-lived, including anxiety, fear, pain, distress, helplessness, and frustrations among others (Rushen & Passillé, 1992; Mellor et al., 2009; Kagan et al., 2015; Mellor, 2016). These internal factors can be quantified through behavioral, endocrine, and physiological measures (Maple & Bloomsmith, 2018). In recent years, many zoos and scientists have promoted the implementation of aspects beyond the five domains, which are primarily related to survival and the absence of pain, to focus on positive welfare and create a "life worth living" for zoo animals, great welfare, or wellness (Meller, 2016; Maple & Perdue, 2013; Wolfensohn et al., 2018). This initiative places an emphasis on providing “agency”, control, and opportunity to “thrive” as an alternative measure from absence of negative indicators (Kagan et al., 2015; Mellor, 2016). Agency to animals has been defined under the five opportunities defined by Vicino and Miller, 2015. These relate to the opportunity for a well-balanced diet, to self-maintain, for optimal health, to express species-specific behavior, and for choice and control (Vicino & Miller, 2015). These opportunities can be measured on a balance of inputs and outputs which consider the individual or groups nutrition, environment, physical health, behavior and collectively contribute to the welfare or mental state of the individual or group (Mellor and Beausoleil, 2015).

One main component of promoting well-being of animals relates to the environmental design of a habitat as the provided environmental input for the animal to promote species-specific behaviors. Environmental design in zoos is devised with the intent of providing the animal or group with species appropriate experiences during the entirety of their day with the intention of encouraging species appropriate spectrum of behaviors (Kagan et al., 2015; Mellor, 2016). While zoos have historically used environmental enrichment to encourage species-appropriate behaviors, enrichments fail to provide animals with an enduring environment that provides species appropriate stimulus (Kagan et al., 2015). Environmental design requires considerably more commitment from zoos in both monetary investment and strategic planning. Environmental design requires an understanding of species natural history as well as sensory ecology, while recognizing that even the understanding and implementation of both do not ensure positive animal wellbeing (Kagan et al., 2015). As zoos continue to explore the balance between environmental design that stimulates species-appropriate behavior and innovative human-animal experiences, it is critical to assess the role of already existing human-animal interactive programs in promoting animal well-being.

Giraffe Ecology for Zoo Environmental Design

Environmental design for giraffes living in zoo environments should be carefully considered. As a prominent animal to zoological collections, giraffes provide a unique conservation story to guests as the tallest terrestrial living mammal, existing in a variety of African countries facing economic instability and ecological disruption. As a sentinel for large herbivore mammals with complex fission fusion social dynamics, zoological institutions should provide habitats which not only promote species appropriate behaviors but also provide guest engagement opportunities that facilitate the visibility of these ecological components.

Nutrition & Behavior

To understand the needs of giraffes in a zoological context, their feeding ecology must be interpreted, as it consumes most of their energetic budget. Studies conducted in the Serengeti (Seronera woodlands) show that females spend 72% of their day foraging for browse and males spend 55% (9.5 h -13 hours a day), with daily intakes of 1.6% and 2.1% of their body weights (Dagg & Foster, 1976). Their diet consists predominantly of *Acacia tortilis* (Males 33.3% and females 27.1% of annual diet) followed by *Grewia* and a few other types of Acacia (Pellew, 1984). These plant species contain high nutritional quality and many are armed plants that contain thorns with small leaves as well as stinging ants in the genus *Crematogaster*, and therefore require complex oral manipulation and relatively quick transition from tree to tree to efficiently forage (Madden & Young, 1992).

Captive feeding regimens have been linked to the occurrence of oral stereotypic behaviors in giraffes (Bashaw et al., 2001). Abnormal or stereotypic behaviors have been historically described as functionless, invariant, and repetitive behavior patterns, which commonly indicate a sign of compromised welfare (Mason, 1991; Mason 2010). However, stereotypies are complex in that the mere existence of a stereotypic behavior does not equate to a deficiency in the animal's welfare or consequence to their quality of life. Stereotypic behaviors can be a coping response to a stressor that no longer is present and can in some cases have not actual cost to the well-being of the animal. Due to their presence in animals housed in zoological institutions, they continue to serve as an initial indicator for animal well-being (Watters et al., 2009). A study by Bashaw (2001) surveyed 71 AZA-accredited institutions regarding giraffe stereotypic behaviors and found that 72.4% of surveyed giraffes regularly exhibited at least one type of stereotypic behavior. The most common oral stereotypies in giraffes are licking of non-food items and tongue playing, in which giraffes engage in rolling of the tongue inside and outside their mouth with no immediate feeding purpose (Bashaw et al., 2001). The third described oral stereotypic behavior is vacuum chewing, in which the animal repeatedly performs a chewing motion without ingestion of food item exclusively from rumination (Baxter & Plowman, 2001). Though abnormal behaviors in giraffes are not fully understood, the origin of oral stereotypic behaviors has been related to unsatisfied oral manipulation needed in more natural browse (Fernandez et al., 2018). Experimentally, it has been shown that closed top feeders in zoological institutions decrease the instance of oral stereotypies (Fernandez et al., 2008).

Sensory Ecology & Behavior

As inhabitants of the open African savannas, visual sensory modalities are important for both predator avoidance and social interactions (Bashaw, 2019 & Cameron & du Toit, 2005). Though a surprisingly short review of articles exists on the importance of visual and space acuity information for giraffe interaction, it is likely that it plays a large role in shaping their social environment (Kasozi & Montgomery, 2018). Giraffe's vision allows them to detect movement at a distance of 2 km (Foster & Dagg, 1976; Mitchell et al., 2013). This long-range visual sampling enables long distance interactions. For example, Seeber et al. (2012) described displacement behaviors between two bulls at distances between 40-100 meters. In the context of feeding, visual communication may be important between individuals. Muller et al. (2018) looked at social affiliation between 77 giraffes in the Great Rift Valley of Kenya and found that individuals showed consistent preferred affiliations independent of habitat type or complexity of habitat and displayed individual social preferences while foraging. Additionally, Bashaw et al., (2007) describes feeding within two neck lengths as an indicator of pro-social interactions between individuals, noting that social interactions between giraffes may be challenging to estimate as communication can potentially occur at large distances. Social feeding tendencies differ among sexes; females are more likely to establish long-term associations and are found in groups of 3-5 feeding as opposed to transient males, with the exception of young male bachelor groups who are found traveling and browsing together (Bercovitch et al., 2006; Bashaw et al., 2007; Bercovitch & Deacon, 2015; VanderWaal et al., 2014).

Environmental design for giraffes with consideration towards their feeding and social ecology commonly focuses on providing giraffes with opportunities to browse in a reasonably distributed environment of hay, concentrates, and varying browse that mimic wild counterparts' feeding ecology (Sullivan et al., 2010). Evenly distributed food resources encourage the expected feeding behaviors of giraffes in a zoo setting during normal feeding. Additionally, giraffe habitats are often built with large animal sensory in environment in mind, these encompass large visual fields, with ability to see other animal habitats, providing an opportunity for large established distances between conspecifics and others. In the case of visitor giraffe feedings, there is higher variability of food presentation and space allocation for giraffes. In a review by

Orban et al., (2016) an estimated 57% of AZA institutions provide guest provisioning programs, the structure of these varies in schedule, environmental design for giraffes, and food type offered.

*Visitor Feeding Stations **for** Giraffes*

Visitor feeding opportunities in giraffe habitats allow guests to interact with a large mammal in a secure environment while still promoting the basic principles of human-animal bonds through an inherently nurturing interaction (Kreger & Mench 1995). The design of such a feature in an animal habitat is complex, it must consider the guest experience while recognizing the inherent needs and motivations of the animals. Guest feeding programs vary greatly, many position guests at ground level with giraffes while others provide a platform to provide eye-level interaction between the two species. There is variation in their spatial structure as many provide multiple places for one or many giraffes to stand while others may only allow a restricted space for a single to a couple of giraffes to feed simultaneously. In the scenarios where giraffe feeding stations are designed to encourage a single giraffe to feed, this may result in the consolidation of resources, which may encourage food competition and discourage the species appropriate group feeding habits (Young & Isbell, 1991; Horova et al., 2015). Due to the potential importance of space in visual communication as well as preferred social affiliation during foraging interactions, it is possible that the amount of space allotted for giraffes to occupy at the visitor feeding station may influence their use of it in terms of total time spent consuming food, as well as total time sharing the food source. Additionally, if the visitor station is consolidated, it is possible that it creates a source of competition for food which may increase displacement at the visitor station as opposed to the rest of the exhibit. The existing variation in food presentation and feed type (browse, vegetables, and biscuits) may also contribute to the usage and nature of interactions at the visitor feeding station as well as engagement in stereotypical behaviors (Orban et al., 2016). Due to the existing variation across institutions, it is important to examine the role of these features on giraffe well-being in the context of feeding behavior and pro-social interactions. This type of evaluation should serve to better inform the design of human – giraffe interactions with a welfare framework that promotes species typical behavior.

This study makes observations on the potential role that design and feed type at the visitor station has on station use, interaction, and oral stereotypies through the analysis of interactions and station usage in two differently managed institutions. Due to the importance of visual communication and space acuity for social feeding in giraffes, it is expected that larger stations may diffuse competition for feed at the station and may encourage resource sharing. Additionally, feeding stations that offer natural browse may? Have lower rates of oral stereotypies by their users and may be a positive welfare input for giraffe environmental design.

METHODS

Study Site

This study observed the giraffe group of Jacksonville Zoo and Gardens (JZG). This population is housed in a 2.5 acre habitat with a visitor feeding station that is approximately 15ft in length allowing approximately one to two giraffes to use it simultaneously (rarely three), providing wax myrtle as well as other browse variety available seasonally, and allowing one visitor to provision at a time. This study also observed the Brevard Zoo's giraffe group which is housed in a 2.5 acre habitat with a visitor feeding station that is 75 ft long and 50ft feet wide (L shape) in which a combination of vegetables (sweet potato and lettuce) is offered at the station year-round. The structure of this visitor station allows virtually all giraffes to occupy it simultaneously, and provides the opportunity to feed for more than one feeding location, and more than one visitor at a time with unspecified limit. Table 3. provides comparison between guest feeding stations, figures 1 and 2 show google earth screenshots of both habitats.

Subjects

Nine giraffes classified as reticulated housed in Jacksonville Zoo and Gardens (JZG) and 7 classified as Masai, 1 reticulated giraffe housed in Brevard Zoo were observed. The JZG population has one adult male, two non-reproductive adult females, two adult reproductive females, two sub-adult females and two individuals who were under the age of one during observations and were therefore excluded from analysis due to natal interactions and physical inability to access station. The Brevard Zoo population has two adult males, two juvenile males, three adult females, and one individual under the age of one who was also excluded from analysis. Characteristics of individual animals can be found in table 2.

Data Collection

A total of 186.5 hours of interaction data were collected between May 19 and July 28, 2018. A total of 84.92 hours of social interaction and station usage collected at Jacksonville Zoo and Gardens, 44.92 hours during phase 1 of the study and 40 hours during phase 2 of the study, and 37.58 hours at Brevard Zoo. An additional total of 45.5 hours of feeding and stereotypy observations were collected at Jacksonville Zoo, and 18.5 hours at Brevard Zoo using instantaneous minute scans to collect the presence of foraging type or stereotypy. At both locations, animals were observed Monday through Friday between the hours of 9:00 and 15:00 for one hour and twenty-five-minute observations in which the first fifty-five minutes observed station usage and interactions, and the following thirty minutes observed feeding behaviors and stereotypies. During observations, the observer was positioned on the visitor platform adjacent to the feeding stations. Therefore, giraffes were only observed when on public display. All data collection was approved by JZG and Brevard Zoo's IACUC committees. This method was used to reliably collect interaction information and station usage. A single observer collected all of Jacksonville Zoo and Garden's data, and a different single observer collected the data for Brevard Zoo. Inter Observer Reliability was obtained four times for each population for the entirety of the session, once weekly.

Behavioral Observations

An ethogram was established by combining published work by Seeber et al. (2012) and Bashaw (2003) (Table 2.) Station usage, duration, and interactions were collected as all-occurrence behaviors, and feeding or oral stereotypic behaviors were recorded at one-minute instantaneous scans (Altmann, 1974). Preliminary observations indicated that one-minute intervals are sufficient to scan the nine individuals in Jacksonville Zoo. The use of the station is categorized in table 2. as "Use of Station Behaviors". Use of station behaviors, regardless of sociality or dominance involved, were recorded separately from other social behaviors, to avoid circular measurements. Individuals were considered to be using the visitor station if they were within a neck's length of the platform for both institutions. In the Jacksonville group, using the station was counted if the individual was within a neck's length of the platform and they were within the rock structure in which a visitor could feed them. Because the study could not control for the presence of a visitor being present, we counted use of the station whether there was a visitor present or not. Approach to an occupied station was counted if a giraffe becomes proximate or within one neck's length of the platform while there is another giraffe within one neck's length of the platform. Individual time sharing the station was counted as the total seconds of overlap between one giraffe and other(s). Displacement at the station was recorded as both contact and non-contact displacement if it occurred within proximity of the platform (one neck's length of the giraffe). All observations were recorded using Zoo Monitor's interactive ethograms (Ross et al., 2016).

Manipulation of Environment

The first phase of the study observed the Jacksonville Zoo and Garden's population when there was only one feeding station available, allowing for one or two individuals to access it simultaneously. Phase two of the study involved the addition of a secondary feeding station which allowed for two more individuals to access the visitor feeding platform. These two stations were adjacent to each other and allowed individuals to interact. The addition of a secondary station was accomplished by modifying the internal rock structure of the exhibit to allow giraffes to approach the platform from a secondary point from the first station at Jacksonville Zoo. Data collection for each treatment was done for one month continuously with a week period of acclimation after the second station was inserted. The Brevard population was observed without any manipulations to their station structure. Ethogram and data collection protocols were the same as that used in Jacksonville Zoo and Gardens.

Because not all individuals were observed during the same amount of time, either due to phase 1 and phase 2 observation differences or individual management differences (giraffes chose to stay in barn or were out of view from observer), visitor station approach was converted to rate per minute of total observed time for each animal. Additionally, percentage of time at station was calculated as the percentage of time an individual used the visitor station out of total time visible. Bouts of station usage was calculated as the average amount of time an individual spent at the station each time they approached. Since individuals spent unequal amounts of time at the visitor station, displacement rate per minute was calculated out of the total time an individual spent at station each session.

Statistical Analysis

To look at the differences between station usage between phase 1 and phase 2 in the JZG population a paired t-test or Wilcoxon signed ranked test, was conducted according to data normality, for the Jacksonville group by comparing mean values of each individual for percent time using station, rate of station approach, average station usage bout, and rate of displacement. To look at group differences for station use between JZG and Brevard Zoo an Independent T-test, or Mann-Whitney U test was conducted, according to normality, to compare phase 1 and Brevard Zoo and phase 2 and Brevard Zoo for percent time using station, rate of station approach, average station usage bout, and rate of displacement. To compare differences in displacement rates between males and females a Mann Whitney U test was conducted due to non-normal distribution using the mean displacement rate of all males ($n = 4$) and all females ($n = 8$). To compare the difference in average percent of scans of browse consumption and stereotypies between the two populations, an Independent T-test were conducted due to normal distribution. To assess the relationship between oral stereotypies and browse consumption, Pearson correlation was conducted due to normal distribution.

Hypothesis 1. Because co-feeding is an affiliative behavior in giraffes, visitor feeding stations that require giraffes to be in proximity while feeding will be less used than those that allow large space gaps between giraffes due to consolidated resource allocation. Therefore, the more space allotted at the visitor feeding station, the more use it will receive by individuals with a lower rate of displacement.

Predictions 1:

Effects of modifying platform at Jacksonville

1. The visitor feeding station will receive more use during phase 2 than phase 1.
2. Individuals will feed for longer averaged bouts during phase 2.
3. On average, individuals will spend a larger percent of time sharing the station during phase 2 than phase 1.
4. Due to increased space availability, individuals will exhibit a lower average rate of displacement while using the visitor feeding station during phase 2 than phase 1.

Differences Between Zoos

5. Due to the larger space availability of Brevard Zoo's visitor station, on average individuals will spend a larger percentage of their time at the station than both phase 1 and phase 2 of the Jacksonville population.
6. Due to larger space availability of Brevard Zoo's visitor station, on average individuals will spend a larger amount of time sharing the visitor station than both phase 1 and phase

7. Due to larger space availability of Brevard Zoo's visitor station, individuals will exhibit lower average displacement rate at the station than in JZG's phase 1 and phase 2.
8. Space consolidation at the Jacksonville Station creates food competition, therefore there is an average higher rate of displacement/minute at the visitor station than on exhibit. This should not be observed during phase 2 or in the Brevard group.

Hypothesis 2. Browse consumption encourages natural oral locomotion by giraffes and therefore giraffes that consume more browse will be less likely to engage in oral stereotypies.

Prediction H2.

1. There will be a negative correlation between average percent scans of browse consumption and average percent scans engaging in stereotypies.

Hypothesis 3. Visitor stations that offer browse will have a population who consumes more browse while on exhibit than those who are only offered browse throughout exhibit.

Prediction H3.

1. Brevard Zoo's population will on average consume less browse than JZG's population.

RESULTS

H 1.1 Station usage was normally distributed for average percent station usage for phase 1 (SW = 0.69) and phase 2 observations (SW = 0.52). Therefore, a paired samples T-test was used to assess the difference between average usage of the visitor station between phase 1 and phase 2 observations. No significant difference was identified between phase 1 (M = 11.81, SD= 8.01) and phase 2 (M = 16.95, SD = 11.29) average station usage (t(6) = -1.66, p = -0.148).

H1.2 The difference between phase 1 and phase 2 average feeding bout length was calculated conducting a Wilcoxon Related Samples Signed Ranked test due to non-normal distribution of feeding bouts (phase 1 SW < 0.0001, phase 2 SW = 0.003). **Results indicate that on average individuals fed for longer bouts during phase 2 (M = 341,95, SD = 156.56) than when they fed in phase 1 (M = 192.33, SD =71.27; Z(6) = 2.197, p = 0.028).** (Figure 6.)

H1.3 Values for percent sharing for phase 1(SW = 0.901, p = 0.337) and phase 2 (SW = 0.857, p = 0.143) were normally distributed, therefore a Paired Samples T-test was used to assess the difference between average percent of sharing between phase 1 (M = 27.28,SD= 17.90) and phase 2 (M = 53.96,SD = 22.5). **Results indicate that on average group members spent more time sharing the station during phase 2 (t(6) = -7.761, p < 0.0001).** (Figure 4.)

H1.4 Average displacement rate/minute was normally distributed in phase 1 (SW = 0.914, p = 0.422) and phase 2 (SW = 0.948, p = 0.713), therefore a Paired Samples T-test was used to assess the difference between average rate/minute of displacement at the visitor station during phase 1 (M = 0.25 , SD = 0.16) and phase 2 (M = 0.096, SD = 0.082). **Rate of displacement was significantly lower during phase 2 than phase 1 interactions (t(6) = 0.257, p = 0.042).** (Figure 5.)

H1.5 A Mann-Whitney U Test was used to assess the difference between Brevard's average percent station usage and JZG phase 1 (SW = 0.782, p = 0.003) and Brevard and phase 2 (SW =

0.827, p = 0.011).Results indicate no significant difference between Brevard (Mdn = 30.51) and JZG’s phase 1 (Mdn = 11.75;U = 11.00, p = 0.097 r = 0.46) or JZG’s phase 2 (Mdn = 11.79; U = 15.00, p = 0.259, r = 0.32).

H1.6 Due to the normal distribution of JZG’s phase 1 and Brevard’s values sharing the station (SW = 0.923, p = 0.241), and the normal distribution of JZG’s phase 2 and Brevard’s values sharing the station (SW = 0.962, P = 0.757) an Independent T- test of unequal variance (F = 5.58, p = 0.036) was used to calculate the difference between average percent of time sharing the station for JZG phase 1 and Brevard and independent T-test of equal variance (F = 2.46 , p = 0.143) was used to assess the difference between JZG phase 2 and Brevard. **Results indicate that on average individuals in the Brevard population (M = 73.55,SD = 31.96) spent a larger amount of time sharing the station than individuals in phase 1 (M= 27.29, SD = 17.90; t(9.4) = 3.341 , p = 0.008)** (Figure 4.). Results indicate no significant difference between average percent of time sharing the station in Brevard (M= 73.55,SD = 31.96) and JZG’s phase 2 (M = 53.96, SD = 22.50; t (12) = 1.33, p = 0.209).

H1.7 A Mann Whitney U test was used to assess the difference of average displacement rates between phase 1 and Brevard (SW = 0.764, p = 0.002) and phase 2 and Brevard (SW = 0.732, p = 0.001). **Results indicate that on average, the Brevard population (Mdn = 0.00) has a lower rate/minute of displacement while using the station than phase 1 (Mdn = 0.31; U = 0.00 , p = 0.001, r = 0.84) and phase 2 (Mdn = 0.093; U = 5.00, p = 0.011, r = 0.68)** (figure 5.).

H1.8 Average rate of displacement on exhibit (SW= 0.943, p = 0.665) and at the station (SW = 0.959, p = 0.808) during phase 1 observations was normally distributed. Therefore, a Paired Samples T-test was calculated to assess the average difference in rate of displacement between individuals while interacting on exhibit and at the station. **There was a significant difference**

between average displacement rate on exhibit (M = 1.94 E-06, SD = 1.11 E-06) and at the visitor station (M = 0.25, SD = 0.16; t(6) = 4.09, p = 0.006), indicating that on average, individuals were more likely to displace others at the visitor station than they were on exhibit during phase 1. Average rate of displacement on exhibit (SW = 0.964, p = 0.852) and at the station (SW = 0.948, p = 0.713) during phase 2 observations was normally distributed, therefore a Paired Samples T-test was calculated to assess the average difference in rate of displacement between individuals while interacting on exhibit and at the station. **There was a significant difference between average displacement rate on exhibit (M = 1.42 E-06 , SD = 6.09 E-07) and at the visitor station (M = 0.09, SD = 0.08; t(6) = 3.081 , p = 0.022), indicating that on average, individuals were more likely to displace others at the visitor station than they were on exhibit during phase 2.** Average rate of displacement on exhibit (SW = 0.700, p = 0.004) and at the station (SW = 0.838, p = 0.95) during Brevard observations were not normally distributed. Therefore, a Wilcoxon Signed Ranked Test was calculated to assess the average difference in rate of displacement between individuals while interacting on exhibit and at the station. There was no significant difference between average displacement rate on exhibit (Mdn = 0.00-7) and at the visitor station (Mdn = 0.000; Z (6) = -0.943 , p = 0.345).

H2.1 Due to normal distribution of browse consumption samples (SW = 0.931, p = 0.559) and stereotypy (SW = 0.29, p = 0.539), a Pearson correlation was calculated to measure the relationship between browse consumption and oral stereotypies, the Brevard and JZG populations were combined. There was no significant relationship between average percent browse consumed (M = 12.70, SD = 9.69) and average percent of scans engaged in stereotypic behaviors (M = 9.63, SD = 7.90; r (14) = -0.144, p = 0.312).

Males' and females' average difference for percent station usage, average percent sharing, average rate per minute of received displacement, and average rate per minute of initiated aggression were assessed for Brevard and phase 1 (JZG) and Brevard and phase 2 (JZG). Mann Whitney U tests were conducted for phase 1 and Brevard (SW = 0.782, p = 0.003) and phase 2 and Brevard (SW = 0.827, p = 0.011) average percent of time at station values. There was no significant difference between males (Mdn = 30.51) and females (Mdn = 11.79; U = 13.00, p = 0.205, r = 0.34) average use of the station for phase 1 and Brevard comparisons. There was also no significant difference between males (Mdn = 30.51) and females (Mdn = 11.79; U = 12.00, p = 0162, r = 0.04) average use of the station for phase 2 and Brevard comparisons. Independent T-tests of equal variance were calculated for phase 1 and Brevard (SW = 0.923, p = 0.241; F= 2.13, p = 0.17) and phase 2 and Brevard (SW = 0.962, p = 0.757, F = 2.23, p = 0.16) average percent of time sharing the station values. There was no significant difference between males (M = 29.88, SD = 23.15) and females (M = 42.30, SD = 29.62; t(12) = -1.198 , p = 0.254) average sharing of the station for phase 1 and Brevard comparisons. There was also no significant difference between males (M = 70.93, SD = 59.76) and females (M = 59.76, SD = 24.98; t(12) = 0.690, p = 0.503) average sharing of the station for phase 2 and Brevard comparisons. Mann Whitney U test was conducted to assess the difference in rates of received displacement at the station between males and females between phase 1 and Brevard (SW = 0.76, p = 0.002) and phase 2 and Brevard (SW = 0.39, p <0.0001). There was no significant difference between males (Mdn = 0.007) and females (Mdn = 0.15; U = 10.50, p = 0.11, r = 0.43) average received displacement rate for phase 1 and Brevard comparisons. There was also no significant difference between males (Mdn = 0.007) and females (Mdn = 0.21; U = 9.00, p = 0.07, r = 0.48) average received displacement rate for phase 2 and Brevard comparisons. Mann Whitney U test was calculated to assess the difference in rates of initiated displacement at the station between males and females between phase 1 and Brevard (SW = 0.76, p = 0.002) and phase 2 and Brevard (SW =0.66, p =0.003). **There was a significant difference between males (Mdn = 0.00) and females (Mdn = 0.16; U = 5.50, p = 0.022, r = 0.61) average initiated displacement rate for phase 1 and Brevard comparisons.** There was no significant difference between males (Mdn = 0.00) and females (Mdn = 0.04; U = 9.00, p = 0.66, r = 0.49) average initiated displacement rate for phase 2 and Brevard comparisons.

H3.1 An Independent T-test of equal variance was calculated to measure the difference between average percent of scans engaged in browse consumption between the JZG group and the Brevard population (SW = 0.931, p = 0.559; F = 0.828, p = 0.381). There was no significant difference between percent of scans engaged in browse consumption between the JZG population (M = 15.72, SD = 8.41) and Brevard (M = 9.67, SD = 10.54; t(12) = -1.187, p = 0.258).

DISCUSSION

This study provides support for the importance of environmental design modeled after species feeding and social ecology as a factor to promote animal well-being and guest engagement programs that promote species appropriate behavior. The overall behavioral comparisons between treatments and populations show that space availability at the visitor feeding station positively contribute to conspecific interactions as defined by co-feeding behaviors and lower displacement rates while engaging with a guest program. Though space did not increase total use of the station, it likely provided feeding comfort to individuals as mean feeding bout increased.

This study does not indicate that naturalistic browse at the feeding station plays an important role in total browse consumption for individuals given that there is opportunity to browse throughout the habitat. Additionally, this study does not provide support for the station usage as tool to reduce stereotypical oral behaviors.

Station Usage

The addition of a secondary station to the Jacksonville population did not result in individuals using the station more, however, their interactions with the station were longer on average. Longer feeding bouts by giraffes potentially contribute to longer interaction between guests and animal, and likely influence guest attitude towards animal (Kreger & Mench, 1995; Clayton 2009). Despite the larger size and dimension of Brevard's guest feeding station (table 3. & figure 1.), their population did not significantly use the station more than the Jacksonville population in either treatment, indicating that space alone does not predict usage of the station from giraffes.

It is likely that station usage on an individual scale is modulated by intrinsic factors such as hunger, amenability towards guests, relationship to the staff or volunteers present, preference for diet offered at the feeding station or potentially other unmeasured values. While JZG offered a natural species of browse, wax myrtle, this species is not similar to *Acacia tortilis* types or

Grewia, the more naturally consumed browse types for giraffes (Pellew, 1984). It is possible that browse type contributes to motivation to interact with station and guests. In the case of Brevard, adult female Johari, used the station the most, it is possible she found a preference for the food type offered as opposed to others.

Station Sharing

This study provides evidence for the importance of space allocation in human-giraffe feeding programs in relation to giraffe co-feeding interactions and resource distribution. The Brevard population significantly spent more time sharing the station with conspecifics than phase 1 of the Jacksonville population. The addition of a secondary station to the Jacksonville population significantly increased sharing among individuals, making this treatment statistically similar to the Brevard population. As strict natural browsers with overlapping home ranges, and social system mediated by food distribution (Foster and Dagg 1972; Muller 2018;Vandewaal et al., 2014), a large (~75 ft long) guest feeding platform provides the opportunity for multiple giraffes to feed simultaneously at distances that appropriately represent their overall large sensory range (Kasozi & Montgomery, 2018; Mitchell et al., 2012). It is possible that during the phase 1 treatment, individuals were less likely to share the station due to the proximity the station demands of conspecifics, always closer than two neck lengths, and often in contact with each other (Bashaw, 2007). This small distance was not normally observed during co-feeding bouts on exhibit, therefore, this design reduces the opportunity for giraffes to feed at a distance that is normally appropriate. When the secondary station was installed, average sharing increased by almost every individual, indicating that individuals were more likely to engage in the new required conspecific distance for co-feeding while feeding at the visitor station.

Consolidated Feeding Opportunities Contribute to Displacement Interactions

This evaluation provides evidence for the importance of space and displacement interactions among giraffes. Displacement rates at the visitor feeding station were significantly higher in phase 1 than phase 2 of the study, indicating that resource consolidation at the visitor station may promote competition and result in higher aggression rates and likely contributes to a more linear than expected hierarchy among giraffes (Horova et al., 2015). Brevard's population exhibited significantly lower rates of displacement compared to both phase 1 and phase 2 in the Jacksonville population. However, during all observations including Brevard, displacement rates were highest at the visitor feeding station than the rest of the exhibit. This indicates that any kind of consolidation, no matter how small, positively contributes to displacement rates among individuals. Male giraffes have been observed engaging in dominance and submissive interactions at distances approximating 40-100 meters (Seeber et al., 2012), while this has not been observed in females who made up the majority of the sample size, this consolidated area could amplify competition merely due to the proximity it requires. It is also possible this increased rate in displacement may exist due to restricted opportunities at the feeding station (one available guest to provide food). Future environmental design should focus on creating ample space for guest feeding interactions and potentially a variety of food disbursement opportunities likely supported by guests. These structured challenges at the visitor feeding station could dilute the possibility of amplified competition among conspecifics in restricted spaces.

Browse Consumption & Stereotypes in Relation to the Visitor Station.

The comparison of browse consumption between the Brevard population and the Jacksonville population independent of treatment did not indicate a significant difference, this indicates that despite the absence of browse in the Brevard visitor feeding station, individuals consume browse from other features of the habitat (feeders and natural browse). The absence in relationship between browse consumption and oral stereotypies may potentially indicate that oral stimulation does not always come from browse interaction. This study did not find a relationship between oral stereotypy rates and station usage in agreement with Orban et al., (2016)'s findings, indicating that at the very least, the guest feeding stations do not contribute to welfare compromise for individuals.

Future Guest Feeding Program Design

Visitor feeding programs can exist as a tool to promote human animal connection and engage guests with the conservation stories of giraffes in a manner that promotes ecologically appropriate behaviors. This study indicates that stations should be built to allow a multitude of giraffes to occupy it at the same time while maintaining at least neck-length distance between each other. Because giraffes often feed in groups of three and habitats often allow for various viewing areas, it is possible that a successful design could involve a variety of engagement pods. Programmatically, this would likely reduce waiting time for guests while increasing possibility of engagement. Ecologically, it would provide giraffes to use the visitor feeding station while maintaining an ecologically appropriate distance from conspecifics and potentially feed alone based on their social position (chapter 2.). Additionally, because giraffe stations had higher rates of displacement than the rest of the exhibit/habitat, it is possible that multiple feeding opportunities facilitated by guest could ameliorate this factor. Potentially feeding enrichment devices similar to those facilitated in barns could be adapted for guest engagement. This would not only promote natural feeding behavior by giraffes but may also provide an educational opportunity for guests regarding giraffe wellness.

Giraffe Guest Engagement Environmental Design Should be Further Explored

The existing variation of visitor feeding opportunities in giraffe habitats should be further assessed. An in-depth review of environmental design features or inputs of both giraffe and human environment could quantify the existing variation in more detail across AZA institutions. The usage of station, sharing, and displacement at the visitor station should also be assessed across varying programs to create a better understanding of the role of these environmental features on giraffe behavior and social interaction. Other factors such as guest derived noises as well as program related noises could also influence station usage and should be considered (Orban et al., 2016). The role of human interaction features on giraffes should also be assessed in terms of temporal effects and welfare. Though current literature on giraffe feeding programs does not indicate that their existence is a hinderance towards welfare, there are indications of higher levels of idleness (Orban et al., 2016). Here we indicate that stations increase competition among individuals, however, this should be further explored to analyze the role of competition among giraffes on other welfare indicators.

Study Design Improvements

Though the study observed different giraffes during the same seasons and time frame, the influence of season likely affects the types of interactions giraffes have with the visitor station both in the context of nutritional needs and as a result of visitor densities. The study took place during the summer months, reflecting a relatively active period for guest presence which does not reflect guest densities throughout the year. Additionally, these traditionally hotter months likely positively contributed to giraffe activity compared to winter months as giraffes are most efficient in dissipating heat (Mitchell and Skinner, 2004). This study strictly focused on animal behavior components and could have expanded by incorporating guest attitudes and reflection regarding guest feeding experiences and preferences to get a clear understanding of both sides of engagement. Alterations to the stations impacted both the giraffes' perception of the station and guest usage, quantifying this factor could improve the validity of the results. Guest and staff interactions were not controlled during this study, this component is difficult to control but likely affected the results of the study. Observations of two different institutions were compared during this study, while this provided a reasonable understanding about the effects of space on giraffe station usage, it also introduced biases related to design as these stations not only differed in size but also in purpose. In the Brevard habitat, the feeding station's first level is a keeper location, therefore, throughout the day keepers walk in and out of this area, likely affecting the motivation for usage of this space. In the Jacksonville population, the visitor feeding station also has a water feature for giraffes to drink, though drinking behaviors were excluded from the data set, this likely contributed to individual motivation for approaching the station. Sample size is a persistent challenge in zoo studies, the small sample size observed in this study is likely not an accurate representation of behaviors across institutions especially when considering the multitude of external factors in a habitat.

Conclusion

This study demonstrates that space allocation in visitor feeding program contributes to displacement rates, conspecific sharing, and bouts of feeding. Further research should focus on the role of visitor feeding programs and giraffe oral stereotypy to assess the role of oral manipulation at the station and engagement in oral maladaptive behaviors. Environmental design features across AZA institutions should be assessed in relation to input variations for both giraffes and visitors. Behavioral assessment in relation to conspecific sharing, displacement at the visitor station and group cohesion should be analyzed across varying visitor feeding programs and designs to better understand the role of visitor feeding programs on individual welfare and group cohesion.

Institution	Name	Sex	Age	Sub-Species
	Duke	Male	20 Years	Reticulated
	Sir Isaac	*Male*	*2 Months*	*Reticulated*
	Naomi	Female	11 Years	Reticulated
Jacksonville	Luna	Female	10 Years	Reticulated
	Lily	Female	1 Year	Reticulated
	Ivy	*Female*	*2 Months*	*Reticulated*
	Spock	Female	16 Years	Hybrid
	Faraja	Female	12 Years	N/A
	Willow	Female	2 Years	*Reticulated*
	Raffiki	Male	19 Years	Masai
	Doc	Male	15 Years	Hybrid
	Floyd	Male	1 Year	Masai
Brevard	Greg	Male	2 years	Masai
	Sprinkles	*Male*	*9 Months*	*Masai*
	Milenna	Female	16 Years	Masai
	Johari	Female	18 Years	Masai
	Kumi	Female	5 Years	Masai

Table 1. Individuals Observed
Individuals italicized under one year at the time of observation were not included in analyses of habitat or station usage. These individuals were unable to physically reach the station and relied on maternal milk during the time of observations.

Table 2. Ethogram Modified from (Bashaw, 2003; Seeber et al., 2012)	
Stereotypic Behaviors	**Description: Recorded at 1-minute intervals**
Pacing	The animal walks a definite short path without immediate purpose. Locomotes from point A to point B back to A in repetitive fashion.
Object Licking	The animal uses tongue on an object that is not feed or mineral block. Licking is exhibited repeatedly.
Sucking Wood	The animal places mouth on wood item. Mouth is often partially open and drawing motion can be detected from mouth.
Tongue Twisting	A persistent motion of the tongue outside the animal's mouth. The animal is not engaging in feeding behavior shortly prior to or after behavior. The animal's tongue is not in contact with any object.
Mane Biting	Biting or chewing the mane of conspecific. The behavior is repetitive and not used to grooming.
Vacuum Chewing	The animal repeatedly performs a chewing motion without ingestion of food item. This behavior is exclusive from rumination.
Feeding Behaviors	**Description: Recorded at 1-minute intervals**
Feeding Stationary	Animal is either standing not moving or lying (sternally or laterally recumbent), and foraging (Note food type: Grass, pellets, hay, browse surrounding exhibit).
Ruminate Stationary	Animal is either standing or lying (sternally or laterally recumbent) not moving and chewing cud.
Feeding Locomotion	Animal is walking or running while foraging (Note the food type)
Ruminate Locomotion	Animal is walking or running while chewing cud
General Behaviors	**Description: Recorded at 1-minute interval**
Orient	Animal is standing still with face and ears towards a stimulus. Animal is not engaging in any other behavior. (Note Stimulus)
Locomoting	Animal is either walking or running not performing any other behavior
Self-Directed Behavior	Animal is self-grooming, scratching, or engaged in any other self-directed behavior.
Stationary	Animal is lying (sternally or laterally recumbent) or standing not engaged in any other behavior.
Maintenance	Animal is defecating or urinating.

Not Visible (Out of View)	Observer cannot see animal. Indicate if (Holding yard, obstacle, or night house).
Agonistic Behaviors	**Description: Recorded all-occurrence**
Avoid	Animal moves away at the approach of other, but no resource is involved.
Displace	One animal takes away resources from other (food, water, shade).
Displaced	Animal that loses resources (food, water, shade).
Sparring	Animal stands next to another animal and repeatedly throws head and neck towards the body or neck of the other. Note actor and recipient.
Non-Contact Yield	Receiver of non-contact aggression.
Non-Contact Aggression	Any threatening or attempts of aggressive behavior which does not result in contact. Examples: Chasing with ears back, lunging, feigning to bite, kick, or attempting to bite/ kick.
Contact Yield	Receiver of contact aggression
Contact Aggression	Aggressive behavior that results in contact. Examples: Head butting, kicking, biting.
Bumping	Strikes at head, neck, or any part of recipient including rump.
Use of Station Behaviors	**Description: Recorded all-occurrence / 1-minute Interval**
Sharing Station Feeding	Two or more animals stand at feeding station simultaneously within neck length of each other. Animal is taking food from visitors/ staff or standing idle. Indicate individuals sharing station and individual who initiated sharing interaction.
Stating Usage Alone	Animal is receiving food from visitor/ staff at the feeding station or standing. Individual is alone at station. Indicate which station.
Displaced at Station	Animal loses access to feeding station by any of the displacement interactions.
Station Approach	Individual is one neck length or less from the barrier.
Displacement at Station	Animal takes away access to feeding station engaging in any of the "aggressive" behaviors.

Table 2. Shows variety of behaviors measured. Ethogram adapted from Seeber et al., (2012) & Bashaw et al., (2007).

Table 3. Guest Feeding Station Qualities by Institutions

Guest Feeding Station Qualities		
Facility	Jacksonville Zoo and Gardens	Brevard Zoo
Habitat (acres)	~2.5	~2.5
Length of Guest Feeding Station (length ft.)	~15	75
Length of Guest Feeding Station (width)	~10(Phase 1) ~30(Phase 2)	50
Number of giraffes that can occupy	Two to three (Phase 1) Three to Five (Phase 2)	Five to nine
Diet Fed	Wax myrtle	Sweet potato and lettuce

Table 3. Displays differences in qualities of feeding stations based on size, dimensions, number of total giraffes that can occupy and the diet fed.

Table 4. Descriptive Values of Station Usage and Interactions

Descriptive Values of Station Use and Interaction for individuals

	Average % Station Use	Average % Station Sharing	Average % of Approaches to Occupied Station	Average Rate/ minute of Received Approaches	Average Rate/ minute of Initiated Aggression	Average Rate/ minute of Received Aggression
Individuals						
Duke	5.96	3.02	0.00	0.01	0.01	0.01
Faraja	3.81	4.41	1.85	0.04	0.35	0.04
Naomi	4.54	48.87	58.59	0.25	0.31	0.25
Luna	11.79	39.49	46.20	0.27	0.48	0.27
Spock	11.75	28.26	39.38	0.14	0.11	0.14
Willow	24.52	41.17	45.21	0.19	0.16	0.19
Lily	20.36	25.78	26.00	0.30	0.32	0.30
Duke	23.54	32.55	6.25	0.11	0.03	0.00
Faraja	2.94	14.28	11.90	0.88	0.00	1.49
Naomi	9.80	74.63	91.47	0.64	0.16	0.11
Luna	11.79	75.34	93.60	0.38	0.09	0.09
Spock	10.92	59.56	59.21	0.31	0.04	0.10
Willow	23.59	61.33	71.35	0.32	0.13	0.13
Lily	36.13	60.00	67.81	0.25	0.23	0.02
Raffikki	30.51	117.00	39.85	0.25	0.00	0.01
Doc	31.67	54.12	47.13	0.13	0.00	0.03
Johari	16.57	61.85	73.41	0.14	0.01	0.01
Milenna	88.93	30.88	11.89	0.13	0.01	0.00
Kumi	1.56	100.00	100.00	0.16	0.00	0.00
Floyd	14.78	51.00	45.69	0.22	0.00	0.00
Greg	66.50	100.00	100.00	0.26	0.00	0.00

Table 4. Displays average values of station usage and interactions for JZG's phase 1 and phase 2 observations and Brevard's observations.

Figure 1. Brevard Zoo's Giraffe Habitat. This habitat is approximately 67,583 ft^2, the orange line displays the area for visitor feeding opportunities.

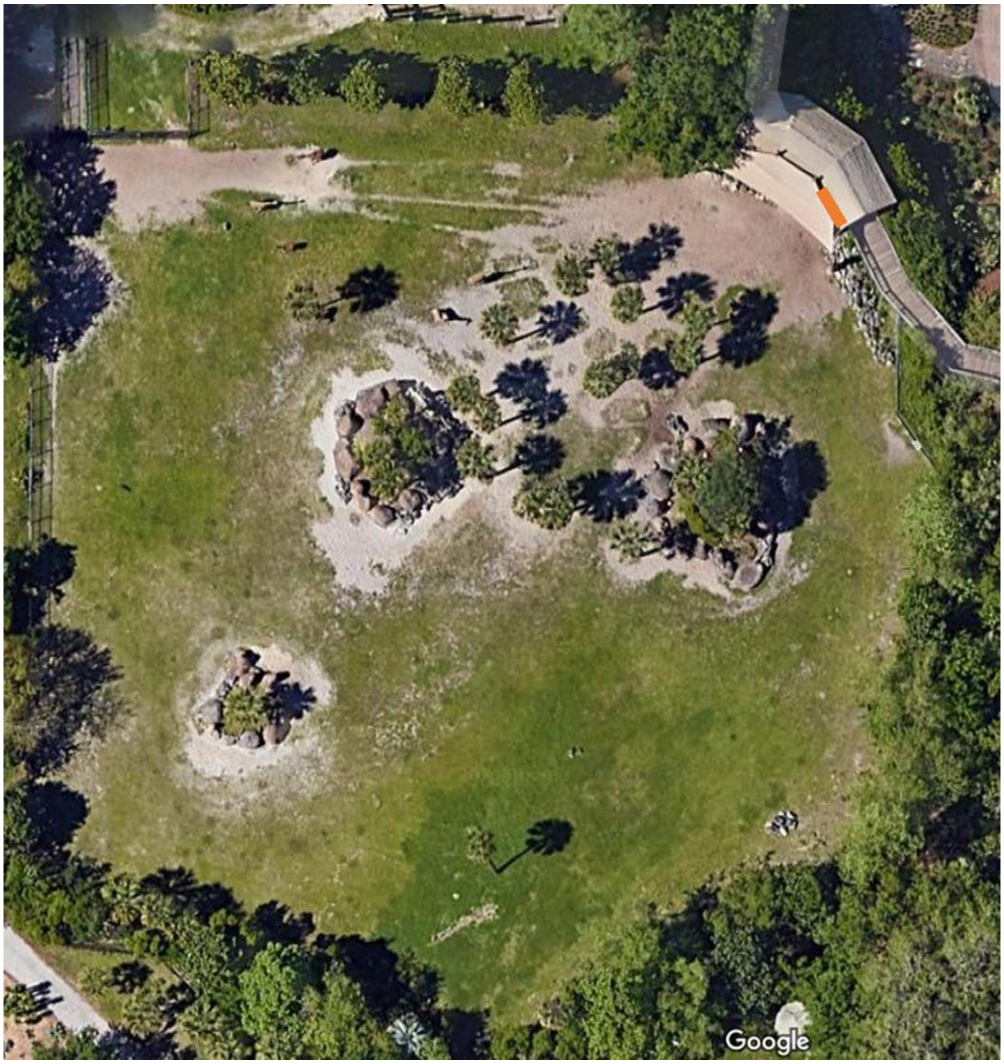

Figure 2. Jacksonville Zoo and Garden's Giraffe Habitat. This habitat is approximately 56,028 ft^2, the orange line represents the space allotted for visitor feeding opportunities.

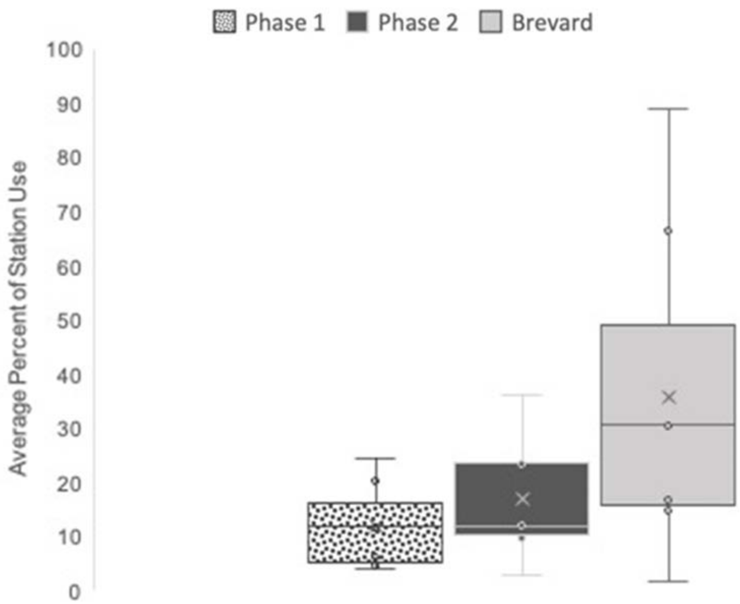

Figure 3 Differences in average percent station usage.
No statistical difference between average percent station use by individuals in phase 1 (M = 11.81, SD= 8.01) and phase 2 (M = 16.95, SD = 11.29; t (6) = -1.66, p = -0.148). No statistical difference of average station uses by Brevard's population (Mdn = 30.51) and phase 1 (Mdn = 11.75; U = 11.00, p = 0.097 r = 0.46) or phase 2 (Mdn = 11.79; U = 15.00, p = 0.259, r = 0.32).

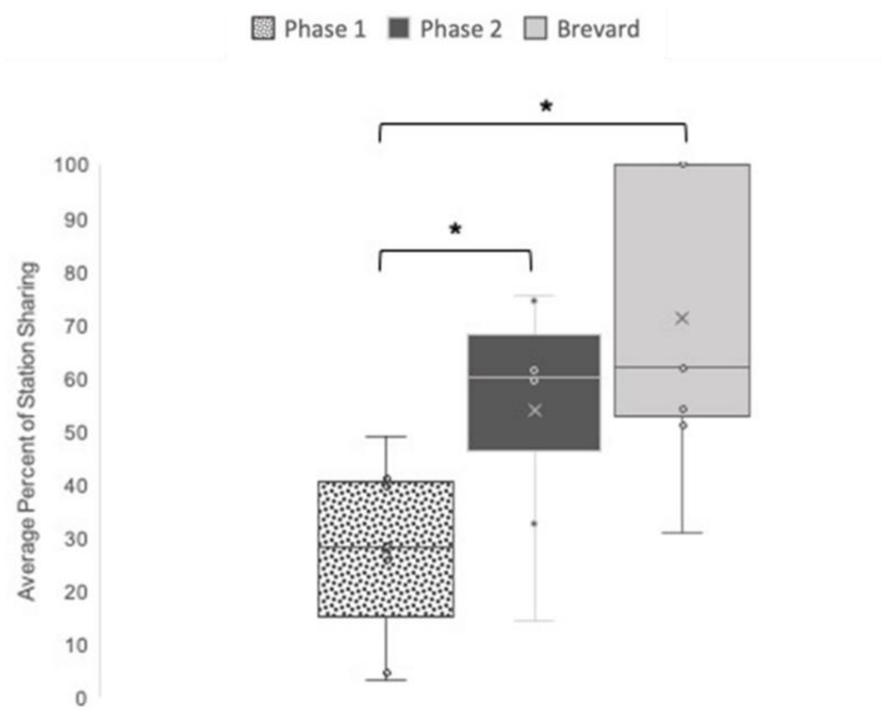

Figure 4. Differences in average percent sharing.
Statistical difference between Jacksonville Zoo and Garden's individual average percent sharing of the station during phase 1 (single available stations) (M = 27.28,SD= 17.90), and phase 2 (secondary station) (M = 53.96,SD = 22.5; t(6) = -7.761, p < 0.0001). Statistical difference between Brevard (M = 73.55, SD = 31.96) and Jacksonville Zoo and Garden's phase 1 (M= 27.29, SD = 17.90; t(9.4) = 3.341 , p = 0.008). No statistical difference between Brevard population's individual average percent sharing (stat.) and Jacksonville Zoo and Garden's phase 2 (M = 53.96, SD = 22.50; t (12) = 1.33, p = 0.209).

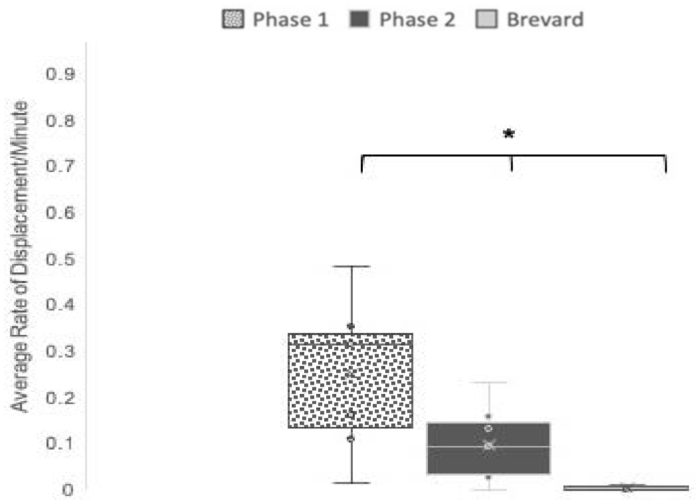

Figure 5. Differences in average rates of displacement

Statistical difference between Jacksonville Zoo and Garden's (JZG) phase 1 (M = 0.25, SD = 0.16) and phase 2 average rate of displacement (M = 0.096, SD = 0.082; t (6) = 0.257, p = 0.042). Brevard's population (Mdn = 0.00) and JZG's phase 1 average rate of displacement (Mdn = 0.31; U = 0.00 , p = 0.001, r = 0.84), and Brevard's population and JZG's phase 2 average rate of displacement (Mdn = 0.093; U = 5.00, p = 0.011, r = 0.68).

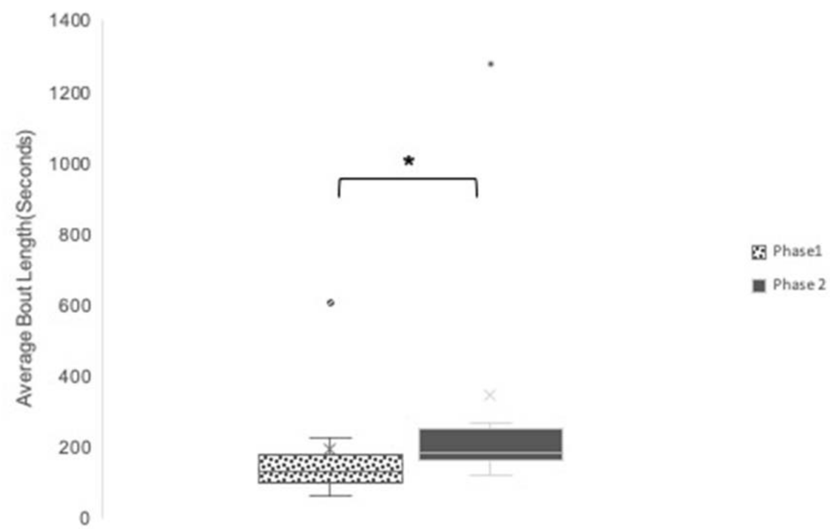

Figure 6. Differences in average feeding bout length.
Statistical difference between average feeding bout length in the Jacksonville Zoo and Garden's population during phase 1 (M = 192.33, SD =71.27) and phase 2 (M = 341,95, SD = 156.56; Z (6) = 2.197, p = 0.028).

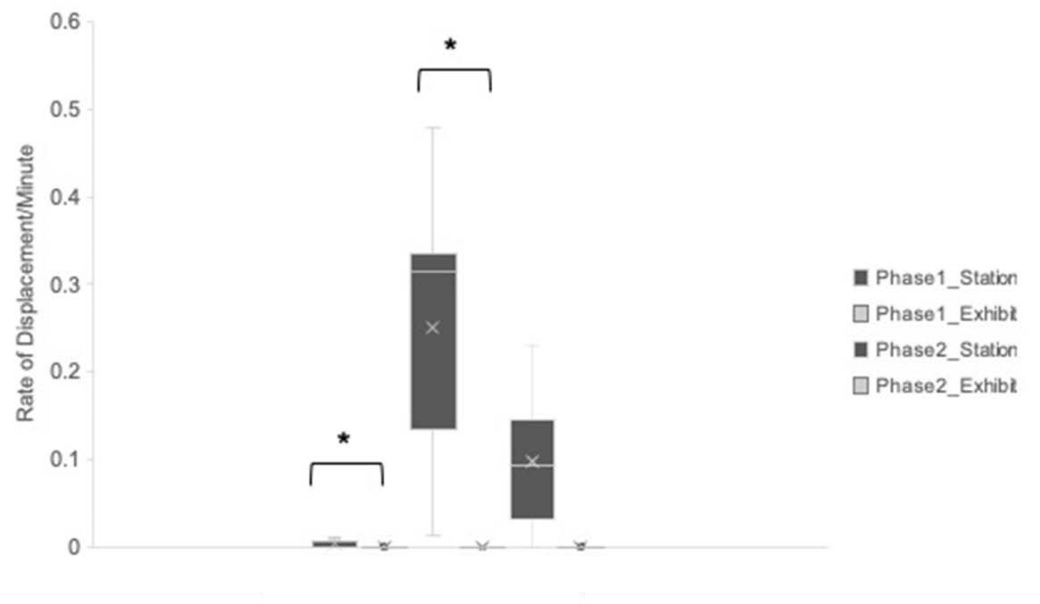

Figure 7. Differences in average displacement rates on exhibit and visitor station.

Statistical differences between average displacement rates in the Jacksonville Zoo and Garden's phase 1 exhibit interactions (M = 1.94 E-06, SD = 1.11 E-06) and visitor station interactions (M = 0.25, SD = 0.16; t(6) = 4.09, p = 0.006). Statistical differences between average displacement rates in the Jacksonville Zoo and Garden's phase 2 exhibit interactions (M = 1.42 E-06 , SD = 6.09 E-07) and visitor station interactions (M = 0.09, SD = 0.08; t(6) = 3.081 , p = 0.022). No statistical differences between average displacement rates in the Brevard population exhibit (Mdn = 0.00-7) interactions and visitor station interactions (Mdn = 0.000; Z (6) = -0.943 , p = 0.345).

CHAPTER 2

ASSESSMENT OF GIRAFFE SOCIAL STRUCTURE AND ITS ROLE ON GUEST PROGRAM STATION USAGE AND SHARING.

ABSTRACT

Zoological institutions use social and ecological theories for the purpose of designing species appropriate habitats and opportunities for guest engagement. Research has only begun to assess the role of design on social dynamics and structure in relation to guest and animal interactions. Here we assessed the social structure of two zoo housed giraffe populations under a variety of social contexts with a focus on their interactions and usage of guest provisioning programs. We found that measures of social position of centrality and influence from affiliative interactions with conspecifics on exhibit plays a role in dictating sharing interactions at guest provisioning programs under varying management protocols and guest engagement designs. Our findings also suggest that interactions and significant ties among conspecific are context and potentially temporally dependent. Finally, this study provides insight into the role of dominance interactions at the guest feeding station, disproving customary belief of male monopolization at guest engagement points for the studied population, and highlighting the role of female resource displacement instead. We propose the use of pliable and multiple guest engagement stations for future design in order to facilitate feeding opportunities for central and peripheral members of giraffe groups. This proposed shift would provide variable feeding opportunities for giraffes that represents their group composition following ecological theory while maximizing points of engagements for guests.

INTRODUCTION

Social Systems

Animal social systems have evolved from exceeding benefits of group living in the form of higher vigilance, predator avoidance, and collective resource defense among others over the cost of living in close proximity to conspecifics, presented in the form of resource competition, disease risk and visibility among others (Alexander, 1974; Silk, 2014). Social systems and relationships among kin and non-kin group members have shown to have meaningful reproductive and survival fitness consequences for individuals in wild population (Schülke et al., 2016; Cameron et al., 2009) In societies that exist in fission fusion dynamics where group composition and size vary over short timescales, preferential bonds and familiarity during non-breeding season present benefits during the breeding season in the form of reproductive output (Kohn, 2017).

Understanding of social systems from field studies has provided a framework for the design of zoo habitats and enabled appropriate monitoring of social systems in zoo environments. (Coe et al., 2003; Maple & Perdue, 2013; Holdgate et al., 2016). Environmental design of great-ape habitats has benefitted from field studies and their interpretation of great-ape social systems (Ross et al., 2005; Coe et al., 2009; Maple et al., 1982; Clark, 2011). As social systems and their relationship to ecology are further understood in various taxa, zoological institutions can continue to use this as a framework to evaluate the environmental inputs we present to zoo species, and the roles these play on their social organization. Giraffes along with their extant relative Okapi are the only species in the family Giraffidae. These tall mammals are commonly housed in zoos all through the United States and present a critical conservation story as their populations face threats related to poaching, land fragmentation, and human-animal conflict which vary according to species and are intricately tied to their social organization (Kideghesho 2016; Muller, 2008; Fennessey et al, 2016). As zoos continue to enhance their wellness and conservation missions, understanding the social systems and environmental effects of this animal will enhance zoo management along with messaging provided for guests.

Social Structure and Usage of the Visitor Feeding Station

Initial descriptions of giraffe behavior and ecology in the wild stated giraffe herds form loose associations with no definite leader (Innis, 1958). Foster and Dagg (1972) characterized random association between individuals with a lack of social structure, and even loose mother-offspring bonds as mothers and offspring were not always observed at close proximity after their first six weeks. This publication speculated that there may be a large difference in weaning time between wild giraffes and those in captivity (Foster & Dagg, 1972). Later studies characterized giraffe societies as having loose fission-fusion social systems with temporary separation of individuals (Pellew, 1984), and close bonds were limited to early development between mother and calves (Langman, 1977). Young & Isbell (1991) observed a sex-biased niche separation in giraffes, in which males occupy the taller vegetation and females occupy the open field. This publication speculates that access to the tall vegetation may be restricted by a strong male dominance hierarchy based on size which prevents females from using this vegetation. However, the results indicated that dietary restriction was more likely attributed to offspring care and necessity to stay in open areas. This niche separation was later related to higher tannin levels in shrubby plants which nursing females may avoid due to distaste to offspring (Caister et al., 2003). Other studies showed that groups in wild populations were determined to be stable for females, whereas males immigrate and emigrate seasonally (Jeugd & Prins, 2000). Additionally, Pratt & Anderson (1985) concluded that nursery groups (females with dependent calves) established a more consistent membership than others. A captive study by Tarou et al., (2000) conducted a social separation study of two adult female giraffes following the separation of an adult male and found increased stress related behaviors by the females, suggesting that individuals were socially bonded at least in the context of captivity.

Bashaw (2003)'s dissertation on social structure among captive female giraffes found patterns of social preference among adult female giraffes based on proximity/contact measurements, nearest-neighbor distance, social and feeding behaviors. She discussed that one of the major reasons why giraffe association may have been previously regarded as random may be the proximity and affiliative measurements used. She noted that social preference can be established by proximity measurements of two neck lengths between two giraffes, as affiliative behaviors are rarer among giraffes than other taxa such as primates. Additionally, she noted that group sizes may be within a larger range than what was previously measured due to giraffes' potentially larger sensory range. She noted that although all females interact with each other, proximity and nearest neighbor distances were not randomly distributed. Later, Bercovitch & Berry (2013) compiled 34 years of data on 52 recognized Thornicroft's giraffe (*G.g thornicrofti*) and found that giraffe herd structure is characterized by long-term social associations mainly determined by kinship with mother-offspring relationships having strongest and longer-lasting associations. More recent literature suggests that giraffes' association patterns are part of a structured social network with multiple levels of organization (VanderWaal et al., 2014). Both males and females contribute to the social network, though only females establish long term stable relationships, and maturity affects contribution to social structure (Shorrocks & Croft, 2009). Consequently, their fission-fusion dynamics are mediated by their social structure, females show nonrandom association to each other and association is related to spatial overlap as well as kinship, though these factors do not fully explain association (Aureli et al., 2008, VanderWaal et al., 2014, Carter et al., 2013). It is important to note that patterns of non-random association among adult male and females have not been identified in field studies. Additionally, associations between adult male and adult female giraffes are affected by the female's estrus cycle (14.7 days long), as males are more likely to investigate females that were cycling and association between a male and female was higher during her potential fertile stage (Bercovitch & Berry, 2013).

In the last two years a variety of field observations have further refined the understanding of giraffe social systems and organizations. Muller et al., (2018)'s Rothschild observations in Great Rift Valley of Kenya analyzed two populations under varying predator density and human disturbance. This study suggests that giraffes mainly display social preferences during foraging events, and not during travel or resting. This indicates that giraffe fusion-fission social systems are highly flexible and dynamic displaying preference during feeding and foraging bouts. Prehn et al., (2019) examined social network stability over five data collection periods between 2012 and 2016 in Pilanesberg National Park, South Africa. This study found non-random patterns of association between individuals with stable association patterns across seasons but higher social connectivity, particularly among females during the wet seasons. Additionally, a shift in group size occurred during the dry season, potentially indicating a higher degree of competition during the dry season and more sub-grouping. In contrast, males did not show difference in numbers of same-sex associate, or overall social connectivity. A six-year study of Masai giraffes in Tanzania by Bond et al., (2019) examined the nature of fission-fusion dynamics in relation to human settlement proximity, predator density, and resource abundance. This study's findings support the idea of flexible group sizing based on resource distribution and abundance, indicating that small group sizes were observed during the drier seasons. Lewton & Rose (2019)'s observations of 13 zoo housed giraffes during two study periods reaffirmed the existence of significant consistent preferred and avoided relationships due to non-random distribution of association with males having a more peripheral role in the social network. Additionally, their study shows that sociality for individual's changes over time, reaffirming the assumption that gregariousness for giraffes is flexible over time.

Though social structure in giraffes is beginning to be broadly understood, translation to captive animal management has not yet been fully explored. Social affiliations between females and potentially males on exhibit, may be an accurate predictor of likelihood to share the visitor feeding station. Because co-feeding is itself an affiliative action, predictive of sociality (Bashaw et al., 2007; Muller et al., 2018), and the station is a limited resource due to space limitations, it is possible that closely bonded individuals are more likely to share the station than those who are not. If this is the case, it is likely that solitary individuals (not affiliated to individuals) would be more likely to use the station at the same time as others if the size of the feeding station is doubled or does not require proximity.

Dominance and Use of Visitor Feeding Station

Competition for resources often leads to the formation of dominance and subordinate interactions which ultimately establish dominance hierarchies based on winner and loser effects (Dugatkin, 1997; Horova, 2015). Dominance in groups possibly arises to avoid direct and potentially harmful contact with one another (Hand, 1986). The dominance hierarchy of wild giraffes was initially described and based on sexual and physical dominance, which was only observed in males (Coe, 1967). Stability in these groups was thought to arise to avoid serious injuries due to intense necking behaviors. Foster & Dagg (1972) described dominance behavior by males based on access to females. Male dominance was described as linear and a consequence of competition for food and reproductive resources (Pratt & Anderson, 1985). It is expected that strong male dominance grants benefits including predator protection as the presence of bulls influence vigilance in both bulls and cows. Therefore, dominance may be a social influence of vigilance on giraffes (Cameron & du Toit, 2005). It is important to note that though these studies described dominance in males, females were not considered to be part of the dominance hierarchy. It has been argued that dominance among female ungulates follows the socio-ecological theory framework and is related to food competition rather than mating opportunity as observed in males (Fournier & Festa-Bianchet, 1995). Bashaw (2003) described female social relationships in giraffes as egalitarian, classified by an even win/loss ratio between each dyad. She suggested that in the case of females, giraffes may use other forms of conflict resolution to reduce resource competition, such as co-feeding or avoidance of feeding at the same site. Additionally, she suggested that dominance in females may be related to transient statuses such as reproductive status or even hunger.

Dominance in Captive Habitats

Dominance is often related to patchy distribution of resources and territoriality (Stamps & Krishnan, 1999). Giraffes are non-territorial and depend on widely distributed resources (Foster & Dagg, 1972; Leuthold, 1979). Therefore, it is likely that behaviors which suggest dominance are more likely to be observed in captivity (Bashaw, 2003). In captive environments, food resources are often aggregated in both space and time and managed by humans. In the case of visitor feeding stations, high value food is often concentrated at the station, potentially contributing to an increase in competition among the herd. Another artifact of captivity, is the increase in social density, and consequently, in social interactions between individuals which may more easily reflect the ranking status of the herd (Horová et al., 2015). Horova et al. (2015) was first to establish a clear stable linear dominance hierarchy in captive giraffes based on resource holding potential over limited resources by creating dominance matrices. This study observed three herds in captivity and concluded that position in the hierarchy was strongly influenced by age, possibly more than body mass. Males were ranked highest in the herd independent of height or age; this could be attributed to the common management practice of only including one male in the herd. In the case of juveniles, males ranked higher than females. Female dominance was attributed to herd residency time and was stable when observed during varying seasons. Additionally, dominant behaviors were expressed as displacement contact and non-contact aggression for the purpose of accessing food resources. This study indicates that once dominance structure is established among females, it remains stable.

Currently, there is one visitor feeding station at both Jacksonville and Brevard Zoo that allows for virtually all giraffes to participate simultaneously. The Jacksonville feeding station is more confined allowing up to two, rarely three individuals to simultaneously use it. Due to the limitations of space and availability of resources at the visitor feeding station (as only one visitor is allowed to feed giraffes at a time), it is possible that understanding the potentially linear and stable dominance order of these herds can establish predictability for the use of the station. Additionally, it is possible that distributing the resource at the station more evenly (by creating multiple sites for feeding), may relieve the potential source of competition among both males and females; consequently, this change may result in a higher rate of feeding station use. Brevard Zoo contains an open station model that has the spatial capability of allowing all herd members (8) to use the station at once. This study observes the role of social ties during exhibit interactions on guest program station feeding, sharing, and interactions by conspecifics in two different facilities with variable guest feeding program protocols. The goal of the study is to identify if interactions on exhibit shape the nature of interactions at the point of human-animal interface, and to further understand the role of space with relation to feeding for giraffes housed in zoological environments.

Hypotheses and Questions

Hypothesis 1 Because the guest provisioning programs present a resource in a consolidated fashion, giraffes' patterns of conspecific interactions on exhibit will be consistent with station interactions and sharing behaviors. Therefore, individuals with more social ties on exhibit will likely be more important to station sharing interactions than more socially isolated individuals.

Questions and Predictions

1. Do giraffes associate randomly on exhibit and at the visitor feeding station?

Chi-square goodness of fit test will show a non-random distribution of interactions for all exhibit behaviors (proximity, cofeeding, interactions) and station sharing rate.

2. Do giraffes rank each other similarly during exhibit interactions?

Individuals will rank each other in the same order for all exhibit interactions, indicated by Kr Rank Matrix Correlations. This pattern will be observed across all observations.

3. Do giraffes rank and each other similarly during exhibit interactions and station interactions?

Individuals will rank each other in the same order on exhibit (based on affiliative interactions as well as by separate co-feeding interactions) and at the visitor feeding station (indicated by approach at the visitor feeding station), this will be indicated by Kr Rank Matrix Correlations.

4. Do exhibit network metrics of centrality and importance (in-degree, out-degree, affinity and eigenvector centrality, and social index), and cliqueness (clustering coefficient) relate to the amount of time giraffes spend at the visitor station?

High network metrics of in and out degree, centrality, and cliqueness will be predictors of higher average station usage as indicated by lmp model.

5. Do exhibit network metrics of centrality and importance (in-degree, out-degree, affinity and eigenvector centrality, and social index), and cliqueness (clustering coefficient) relate to station sharing and interactions at the visitor station?

Individuals with high in-degree and/or social index are likely to have a high rate of received approaches from others while at the visitor station. Individuals with high in-degree, clustering coefficient, social index, and eigenvector centrality will be more likely to share the visitor station and initiate interactions at the visitor station.

Hypothesis 2. If the visitor feeding station is a spatially restricted resource and of potential value, higher ranking individuals will have access to the station most frequently and will be more likely to have priority to food at the visitor feeding station.

1. *Does dominance order on exhibit relate to access priority at the visitor feeding station?*

   Individuals with higher modified David's Scores will be more likely to use the station, less likely to share the station, and less likely to receive approaches while using the station. If space available affects dominance and station usage, then these relationships will be strongest during phase 1 observations but not phase 2 or in the Brevard habitat.

2. *Is dominance on exhibit related to displacement interactions at the visitor station?*

If dominance on exhibit is related to displacement interactions at the visitor station, Modified David's Scores will be positively correlated to average rate/minute of initiated displacement at the visitor station.

METHODS

To investigate alternative protocols of a giraffe feeding station to determine which ones increase attendance by giraffes as well as promote welfare, this study collected behavioral observations in two different institutions: Jacksonville Zoo and Gardens and Brevard Zoo. Jacksonville Zoo and Gardens has a population of nine individuals, one adult male, two adult non-reproductive females, two adult reproductive females, two sub adult females and two individuals who were under the age of one during observations, and were therefore excluded from analysis due to natal interactions and their inability to physically access the station. Brevard Zoo has a population of eight individuals with two adult males, two juvenile males, three adult females, and one individual under the age of one who was also excluded from analysis. Characteristics of individual animals can be found in table 2. This study observed the giraffe group of Jacksonville Zoo and Gardens (JZG) population is housed in a 2.5 acre habitat with a visitor feeding station that is approximately 15ft in length allowing approximately one to two giraffes to use it simultaneously (rarely three), providing wax myrtle as well as other browse variety available seasonally, and allowing one visitor to provision at a time. This study also observed the Brevard Zoo's giraffe group which is housed in a 2.5 acre habitat with a visitor feeding station that is 75 ft long and 50ft feet wide (L shape) in which a combination of vegetables (sweet potato and lettuce) is offered at the station year-round. The structure of this visitor station allows virtually all giraffes to occupy it simultaneously and provides the opportunity to feed for more than one feeding location, and more than one visitor at a time with unspecified limit. A total of 122.5 hours of social interaction were collected between May 19 and July 28, 2018. A total of 84.92 hours were collected at Jacksonville Zoo and Gardens, 44.92 hours during phase 1 of the study and 40 hours during phase 2 of the study. A total of 37.58 hours were collected at Brevard Zoo. Animals were observed Monday through Friday between the hours of 9:00 and 15:00 for two to three daily fifty-five-minute observations at both locations. A single observer collected all of the data at Jacksonville Zoo and a different single observer collected the data for Brevard Zoo. Inter Observer Reliability was obtained four times for each population at about weekly intervals. During observations, the observer was positioned on the visitor platform adjacent to the feeding stations either at the visitor level or underneath the platform. Therefore, giraffes were only observed when on public display. All data collection protocols were approved by the institutions' IACUC and Research Review Committee.

Behavioral Observations

An ethogram was established by combining published work by Seeber et al. (2012) and Bashaw (2003; Table 2). Social, agonistic interactions, station usage duration, and co-feeding duration were collected as all occurrence behaviors. Proximity and contact were recorded at one-minute instantaneous scans (Altmann, 1974). Proximity measurements were made by recording individuals nearest neighbor at the one-minute interval. Giraffes were considered proximate when individuals were two neck lengths from each other and were recorded in contact when they were touching (Bashaw, 2007). Preliminary observations indicated that one-minute intervals are sufficient to scan the nine individuals in Jacksonville Zoo. The use of the station is categorized in table 1 as "Use of Station Behaviors". Use of station behaviors, regardless of sociality or dominance involved, were recorded separately from other social behaviors, to avoid circular measurements. All observations were recorded using Zoo Monitor's interactive ethograms (Ross et al., 2016).

Manipulation of Environment

The first phase of the study observed the Jacksonville population when only one feeding station was available that allowed for one or two individuals to access it simultaneously. Phase two of the study involved the addition of a secondary feeding station directly adjacent to the station which allowed for two more individuals to access the visitor feeding platform. The addition of a secondary station was accomplished by modifying the internal rock structure of the exhibit to allow giraffes to approach the platform from a secondary point from the first station at Jacksonville Zoo. Data collection for each treatment was be done for one month continuously with a week period of acclimation after the second the station was inserted.

The Brevard population was observed without any manipulations to their station structure. Ethogram and data collection protocols were the same as that used in Jacksonville Zoo and Gardens with the exception of proximity measures which were not obtained for Brevard. Because not all individuals were observed during the same amount of time, either due to phase 1 and phase 2 observation differences or individual management differences (giraffes chose to stay in barn or were out of view from observer), visitor station approach was converted to rate per minute of total observed time for each animal. Additionally, percentage of time at station was calculated as the percentage of time an individual used the visitor station out of total time visible. Bouts of station usage were calculated as the average amount of time an individual spent at the station each time they approached. Since individuals spent unequal amounts of time at the visitor station, displacement rate per minute was calculated out of the total time an individual spent at station each session.

Social Network Analysis

Social network analysis was developed in the field of sociology and math theory and has been thoroughly explored in social economics and social ecology. The use of social network analysis in captivity is limited but provides a framework for the use of social position and influence of individuals to inform management and husbandry decisions. (Asher et al., 2009; Coleing, 2009;

Schel et al., 2013; McCowan et al., 2008; Rose & Croft, 2015). In this study we used social network metrics to characterize affiliative interactions on exhibit (both social interactions and co-feeding interactions), co-feeding on exhibit, sharing at the visitor station, displacement interactions on exhibit, and station displacement interactions by creating a matrix for each type of interaction as done for captive elephants in Coleing (2009) and with cattle (Foris et al., 2019).

Matrices

Asymmetrical square matrices were made for three types of interactions: affiliative interactions in rate per hour on exhibit (not including station), proximity/contact percent of minute scans on exhibit (not including station), and co-feeding (not including station) interactions/ hour. A matrix was made for three types of interactions during phase 1 and phase 2 of the study. In order to account for variation in sample time and unequal visibility due to individual variation, rates of interactions per hour were created for matrices (Whitehead, 2008). Gephi was used to visualize all matrices using ForceAtlas2 layout for network spatialization. This layout is useful for small-world/scale-free networks. Tolerance speed was set to 0.02, approximate repulsion was left un-checked, approximation was set to 1.2, scaling was set between 50-100, stronger gravity was left un-checked, gravity was set to 35.00. Behavior alternatives were set to prevent overlap and include maximum edge weight influence, these settings were used as recommended for small-world/scale-free networks (Bastian et al., 2009).

Analyzing Characteristics of Networks

Network metrics are statistical measures used to characterize properties of individual nodes or entire networks (Krause et al., 2015; Borgatti, 2002). Asymmetric weighted networks from interaction rates described in the matrix section to calculate a network matrix for affiliative interactions on exhibit, co-feeding interactions on exhibit, and station sharing interactions. For each network, in and out degrees were measured to represent the total incoming and outgoing interaction rates for each node in each network. Eigenvector centrality was calculated to represent the sum of centralities of an individual's neighbors. High eigenvector values can be achieved by either having a high degree value or by having associates with high degree centrality. This measure is important to capture the overall importance or influence of the individual in a network as the value assigns relative scores to all nodes in the network based on the concept that connections to high-scoring nodes contribute more to the score of the node in question than equal connections to low-scoring nodes (Borgatti et al., 2002, Whitehead et al., 2005). Affinity is a measure of strength of an individual's associates weighted by the association index of its associates. High affinity values therefore represent individuals who are highly associated with individuals who have overall high strength values. Clustering coefficient is clique value or a representation of how connected the node's connections are (Whitehead, 2015). Directed measures of in and out degree/strength and clustering coefficient were calculated for each network with UCINET (Borgatti et al., 2002). Symmetrical measures of eigenvector centrality and affinity were calculated using SOCPROG 2.7 software (Whitehead et al., 2005). To look at the relationship between matrix measures, in-degree, out-degree, clustering coefficient, affinity, and eigenvector centrality of exhibit interactions and station usage and sharing values were calculated using the lmp model of maximum likelihood estimators as a multiple regression carrying out 10,000 permutations per test using the exact method to produce permute the values exactly (Mineo, 1995).

Social Index Scores

To look at the relationship between overall social experience on exhibit and station interactions an index was created based on affiliative interactions on exhibit following the methods used in Parr et al. (1997) and Foris et al. (2019). In this calculation, the number of interactions received (in-degree) is subtracted by the number of interactions initiated (out-degree), this value is then subtracted by the total number of interactions. Positive index scores indicated that more interactions were performed than received and negative interaction scores indicated the reverse. These index scores were calculated for social interaction matrices based on affiliative and co-feeding interactions for phase 1, phase 2, and Brevard's herd.

Assessing Preference and Avoidance in a Directed Network

The vutard test is based on the procedure to asses significance of transitions in Morkov chains but is applied to social network matrices. The test using a row and column-based permutation procedure where a null distribution is created by resampling 10,000 times. From this resampled distribution Z scores are calculated for each interaction cell, and compared to the observed interactions cells. Observed cells that occur above specific Z score associated with 2 SD above the mean for that cell are considered to be preferred associations, whereas observed cells that fall below a Z score associated with 2 SD below the mean for that cell are considered to be avoided associations.

Measuring Relationship Between Networks

Random association between giraffes was assessed by calculating chi-square goodness of fit for interaction rates in all matrices separately (affiliative, cofeeding, and station sharing matrix). Relationship between exhibit interactions (proximity/contact, co-feeding rate/hour, and affiliative interactions), Kendall's rank order matrix was used to correlate these three matrices. To look at the relationship of individual rank order of individuals on exhibit and station sharing interactions, Kendall's rank order matrix was used to correlate these three matrices to station sharing interactions. The Kr matrix test measures correlation between two matrices with the relative ranks of frequency data in each cell, controlling for differences in frequency with which different individuals perform a behavior by calculating only within-row comparisons (Hemelrijk, 1990). Kendall's rank correlation coefficient (Tau Kr test) is calculated from within-row comparisons between corresponding cells in two matrices. This function considers individual variation in social interactions by exclusively calculating within rows of the actor and receiver matrices and not among all pairs. This test represents a ranked value of preferred partners in each matrix and creates a correlation. The one-tailed probability value reported is the percentage of all permutations from correlation in the right half of the distribution that yield a value as large or larger than that calculated in the observed data. (Hemelrijk, 1990). Kr matrix correlations were calculated using 10000 permutations or sub-samples through matrix tester 3.0.2, (Hemilrijk, 2018).

Relationship of Exhibit Network Characteristics and Station Usage/Interactions.

The relationship between exhibit network metrics (in-degree, out-degree, eigenvector centrality, clustering coefficient, affinity, and social index) and usage of visitor station (average percent of time using the station, average percent of station sharing, average rate of approach to an occupied station, average rate of received interactions while using the station) was assessed using using the lmp model of maximum likelihood estimators as a multiple regression carrying out 10,000 permutations per test using the exact method to produce permute the values exactly (Mineo, 1995).

Dominance & Priority Access

To determine whether a hierarchy order existed in both captive giraffe herds, we created dominance matrices based on agonistic interactions recorded on exhibit (with the exclusion of behaviors associated with the visitor feeding station). Additionally, two matrices were created in the Jacksonville Zoo population to discriminate between phase 1 and phase 2 of the study. For each agonistic encounter, the initiator and receiver were recorded. Only interactions in which receiver responded to initiator without contest were recorded. Loss and win tables were analyzed using SOCPROG software (Whitehead, 2009). To assess linearity, we calculated Landau's index of linearity. Landau's h' value varies from 0 to 1, with 0.8- 1.0 indicating strongly linear hierarchies. If values are highly linear, data would be compiled with I&SI methods developed by DeVries (1998). In this method the order that is most consistent with a linear hierarchy is identified by the minimizing number of inconsistencies I, (the number of dyads in which the lower-ranked individuals dominates the higher ranked individual) and then (without increasing inconsistencies) the total strength of inconsistencies SI (the sum of distances of inconsistencies from the matrix diagonal (Schmid & DeVries, 2013; Horova, 2015). Because dominance hierarchies were not highly steep, we used David's score as this is a better measure for hierarchies that are not extremely steep (Foris et al., 2019; S.nchez-T.jar et al., 2017). Modified David's score was used as the dominance index. This method calculates dominance indices in the case where interactions do not occur randomly across the hierarchies and deals with repeated interactions between group members (Gammell et al., 2003). In the analysis we used modified David's score suggested by De Vries et al., (2006) for count data. Modified David's score values were then related to average rate/minute of initiated displacements at the visitor station, average rate/minute of received displacements at the visitor station, and average percent of time spent at the station, average percent of time sharing the station, average rate/minute of received approach at the station, similar to methods used in Ficken et al. (1990). We used Spearman rank correlations to compare David's modified score and each of these measures for all individuals. Correlations with a $P < 0.05$ were considered significant. Additionally, lmp model was used to look at the effect of MDS, age and sex, on station usage and interactions (Mineo, 1995).

RESULTS

Summary

A total of 737 exhibit interactions were recorded during phase 1, 294 during phase 2, and 743 in Brevard. A total of 72 co-feeding interactions were recorded during phase 1, 43 during phase 2, and 22 in Brevard. A total of 10.68 hours of station sharing and 415 interactions were recorded during phase 1, 25.03 hours of station sharing, and 756 interactions were recorded during phase 2, and 26.65 hours of station sharing and 454 interactions during Brevard observations. A total of 174 displacement interactions on exhibit were recorded during phase 1, 83 during phase 2, and 223 in Brevard observations. A total of 365 station displacement interactions were recorded during phase 1, 219 during phase 2, and 26 during Brevard observations. During phase 1 animal visibility ranged between 38.37 and 41.54 hours, 30.24 and 34.52 during phase 2, and 5.03 and 30.67 during Brevard observations.

*H1.1.*Chi-Square goodness of fit tests indicate that giraffes do not associate randomly. In both phase 1 and phase 2 of the study, distribution of social interactions was not random, therefore giraffes did not randomly aggregate spatially, did not interact randomly, and did not co-feed randomly on exhibit, or at station. All chi-square goodness of fit tests for phase 1 indicate non-random association (proximity/contact: X^2 (71, N = 2052) = 2,764, $p < 0.001$; affiliative interactions: X^2 (71, N=1,487) = 4,405.62 $p < 0.001$; cofeeding: X^2 (34, N= 227) =330 $p < 0.0001$; station sharing X^2 (71, N = 209) = 1,425.64 $p < 0.001$). All chi-square goodness of fit tests for phase 2 also indicate non-random association (proximity/contact: X^2 (71, N = 2,517) = 5277, $p < 0.001$; affiliative interactions: X^2 (71, N=978) = 2,850 $p < 0.001$; cofeeding: X^2 (15, N= 43) = 32, $p < 0.005$; station sharing (Count of interactions) X^2 (71, N= 580) = 1,155, $p < 0.001$). There was also non-random association in the Brevard population as indicated by chi-square goodness of fit (affiliative interactions: X^2 (37, N = 1163) = 1001, $p < 0.0001$; co-feeding: X^2 (7, N= 21) = 3, $p < 0.0001$; and station sharing: X^2 (29, N = 419) = 927, $p < 0.0001$).

Vutard Test of Significant Ties

Significance in relationship among group members. The Vutard significance test (Vutard et al., 1990), indicates that significance in relationship among herd members varied according to context of interaction. Of the existing significant ties in the affiliative network during phase 1, 2/3 were directed towards Naomi, 1/3 in the proximity network, 2/2 in the co-feeding network, while none in the station sharing network (Figure 1.). During phase 2 the pattern was similar indicating that Naomi was part of 2/3 significant relationships in the affiliative network and 2/2 in the co-feeding network, while Lily, Willow, and Luna formed the significant ties at the feeding station. (Figure 2.). In the Brevard population Greg and Kumi formed had a significant tie in the affiliative network, while Floyd to Milenna and Doc to Kumi formed a significant tie in the co-feeding network (Figure 3.). During station sharing there was a shift to 3/3 ties involving Johari. In all observations no avoided ties were identified.

H1.2. Exhibit networks of proximity, co-feeding, and affiliative interactions were partially correlated in both phase 1 and phase 2 of the study indicating that individuals ranked each other similarly in various types of exhibit interactions in Jacksonville Zoo and Gardens. Phase 1: Proximity and affiliative interactions ($TauK_r = 0.757$, N = 7, p = 0.0006), and proximity and co-feeding ($TauK_r = 0.472$, N = 7, p = 0.019). Phase 2: Proximity and affiliative interactions ($TauK_r = 0.512$, N = 7, p = 0.001), proximity and co-feeding ($TauK_r = 0.539$, N = 7, p = 0.002).

H1.3 . Exhibit networks of proximity, co-feeding, and affiliative interactions were not correlated to the station sharing interaction network in either phase 1; affiliative and station sharing ($TauK_r = 0.116$, N = 7, p = 0.319), cofeeding and station sharing ($TauK_r = 0.443$, N = 7, p = 0.0411), proximity and station sharing ($TauK_r = 0.282$, N = 7, p = 0.071), phase 2; affiliative and station sharing ($TauK_r = 0.242$, N = 7, p = 0.127), cofeeding and station sharing ($TauK_r = 0.168$, N = 7, p = 0.209), proximity and station sharing ($TauK_r = 0.321$, N = 7, p = 0.053), or in the Brevard population; affiliative and station sharing ($TauK_r = 0.147$, N = 7, p = 0.238), cofeeding and station sharing ($TauK_r = 0.285$, N = 7, p = 0.117). Multiple regression quadratic assignments indicated that affiliation (-0.03), co-feeding (0.586), and proximity (0.00) did not explain station sharing during phase 1 (*Adjusted* $r^2 = -0.054$, S.E = 0.405, F = 0.302, p =0.823). This was also observed during phase 2, affiliation (0.21), co-feeding (0.035), proximity (0.002) (*Adjusted* $r^2 = 0.013$, S.E = 0.583, F = 1.181, p =0.329). Additionally, MRQAP indicated no relationship between affiliation (-0.061), co-feeding (0.019) and station sharing (*Adjusted* $r^2 = -0.040$, S.E = 0.772, F = 0.208, p =0.813).

H1.4 Descriptive network metrics of mean half-weight index, in-degree, out-degree, eigenvector centrality, clustering coefficient, affinity, and social index for individuals can be seen in table 3 for the affiliative networks and in table 4. For the co-feeding networks. Figure 4. Shows a visual representation of ties between individuals using in and out-degrees. Average station usage represented by average percent of time spent utilizing the guest feeding station was not associated with social network metrics for the Brevard population or for JZG's population in either phase 1 or phase 2. Lmp model incorporated Brevard and phase 1 metrics of affiliative in-degree (M = 3.75 SD = 2.78), affiliative eigenvector centrality (M = 0.37 SD = 0.03), affiliative affinity(M = 6.98, SD = 0.57), affiliative clustering coefficient (M = 0.29, SD = 0.07), affiliative mean half-weight index (M = 1.11, SD = 0.15), affiliative outdegree (M = 3.75, SD = 3.31), and affiliative social index (M = 0.01, SD = 0.52) as a predictor of station use did not indicate a significant association (F = 0.3181, $R^2 = -0.580$ p = 0.9202). Table 6. displays relationship for each individual variable. Lmp model incorporated Brevard and phase 2 metrics of affiliative in-degree (M =3.12 , SD = 3.19), affiliative eigenvector centrality (M = 0.38 , SD = 0.01), affiliative affinity (M = 7.03, SD = 0.60), affiliative clustering coefficient (M = 0.30, SD = 0.08), affiliative mean half-weight index (M = 1.13, SD = 0.16), affiliative outdegree (M = 3.12, SD = 3.18) and affiliative social index (M = -0.01, SD = 0.49) as a predictor of station use did not indicate a significant relationship (F = 0.263, Adjusted R^2 = -0.515, p = 0.937) . Table 6. displays the relationship for each individual variable.

H1.5 Sharing by giraffes, represented by average percent of time sharing the guest feeding station was positively associated with measures of social position and importance for the Brevard population as well as phase 1 and phase 2 of the JZG population. Lmp model incorporated Brevard and phase 1 metrics of affiliative in-degree (M = 3.75 SD = 2.78), affiliative eigenvector centrality (M = 0.37 SD = 0.03), affiliative affinity(M = 6.98, SD = 0.57), affiliative clustering coefficient (M = 0.29, SD = 0.07), affiliative mean half-weight index (M = 1.11, SD = 0.15), and affiliative outdegree (M = 3.75, SD = 3.31) as a predictor of average percent station sharing (M = 50.42, SD = 34.58) indicated a significant association (F = 4.463 , adjusted R^2 = 0.615 p = 0.035). Table 6. displays relationship for each individual variable. This relationship was also present in JZG's phase 2 and Brevard observations using the Lmp model for affiliative in-degree (M =3.12 , SD = 3.19), affiliative eigenvector centrality (M = 0.38 , SD = 0.01), affiliative affinity (M = 7.03, SD = 0.60), affiliative clustering coefficient (M = 0.30, SD = 0.08), affiliative mean half-weight index (M = 1.13, SD = 0.16), and affiliative outdegree (M = 3.12, SD = 3.18) (F = 22.56 , adjusted R^2 = 0.909 p = 0.0003*).

Assessment for the relationship between network metrics and average percent of approaches to an occupied feeding station using the lmp model did not indicate a relationship between network metrics of affiliative indegree, clustering coefficient, eigenvector centrality, and mean half-weight index, for phase 1 and Brevard (M = 45.37, SD = 30.95); (F = 1.24 , adjusted R^2 = 0.10,p = 0.388) but was significant for phase 2 and Brevard (M = 45.37, SD = 30.95); (F = 6.29, adjusted R^2 = 0.709 , p = 0.015).

Assessment for the relationship between network metrics and average rate per minute of initiated aggression while at station using the lmp model indicated a significant relationship for phase1 and Brevard (M = 0.13, SD = 0.17); F = 3.905, adjusted R^2 = 0.573,p = 0.049, mainly due to clustering coefficient values (p = 0.026). This pattern was also observed for phase 2 and Brevard (M = 0.049, SD = 0.074); F = 3.905, adjusted R^2 = 0.573, p = 0.049; clustering coefficient (p = 0.023), see table 6 for individual network results.

Assessment for the relationship between network metrics and average rate per minute of received aggression while at station using the lmp model indicated a significant relationship for phase1 and Brevard (M =0.09, SD = 0.0.11); F = 4.64, adjusted R^2 = 0.627,p = 0.032, mainly due to clustering coefficient values (p = 0.04). This pattern was also observed for phase 2 and Brevard (M = 0.14, SD = 0.39); F = 4.64, adjusted R^2 = 0.627,p = 0.032, clustering coefficient (p = 0.03) see table 6 for individual network results.

Assessment for the relationship between network metrics and average rate per minute of received approaches while at station using the lmp model did not indicate a significant relationship for phase1 and Brevard (M = 0.178, SD = 0.085); F = 0.972, adjusted R^2 = -0.013 ,p = 0.506, or phase 2 and Brevard (M = 0.300, SD = 0.218); F = 0.662, adjusted R^2 = -0.184 ,p = 0.684, see table 6 for individual network results.

H2.1 Modified David's scores (MDS) were correlated to average percent of station usage, average percent of station sharing, and average percent of received approaches for all observations. In phase 1 observations, MDS (M = 0.001, SD = 4.45), was not correlated to average percent of station usage (M =11.82, SD = 8.01; r (7) = -0.266, p = 0.282), or average percent of time sharing (M = 6.77,SD = 17.9); r (7) = -0.352, p = 0.219, or average rate/minute of received approach (M = 0.17 , SD = 0.12; r (7) = 0.077 p = 0.435). Similarly, in phase 2 observations, MDS (M = 0.001, SD = 5.16), was not correlated to average percent of station usage (M = 16.96, SD = 11.30; r (7) = 0.558, p = 0.096), average percent of time sharing (M= 53.96, SD = 11.30; r (7) = 0.07, p = 0.441) or average rate/minute of received approach (M = 0.41, SD = 0.26; r (7) = -0.634 p = 0.063). In the Brevard observations, MDS (M = -0.0014, SD = 1.65) was also not correlated to average percent of station usage (M = 35.79, SD = 31.07; r (7) = 0.12, p = 0.41), average percent of time sharing (M = 73.55, SD = 31.96;r (7) = 0.34, p = 0.23), or average rate/minute of received approach (M = 0.18, SD = 0.058; r (7) = -0.29 p = 0.475). Lmp model was used to correlate sex, age, and MDS to average percent of station usage, average percent of station sharing, and average percent of received approaches for all observations, no relationships were identified in either phase or Brevard's population(see table 8).

H1.2 There were no significant correlations between MDS value and average rate of received displacements (M = 0.17,SD = 0.11; r (7) = 0.077, p = 0.43), or average rate of initiated displacements (M = 0.25, SD = 0.16; r (7) = -0.449, p = 0.156) during phase 1 observations. There was no significant correlation between MDS and average rate of received displacements (M = 0.01, SD = 0.083; r (7) = -0.578, p = 0.09), or average rate of initiated displacements (M= 0.28, SD = 0.54; r (7) = 0.20, p = 0.33) during phase 2. There was also no significant correlation between MDS and average rate of received displacements (M = 0.02, SD= 0.058; r (7) = -0.087, p = 0.43) or average rate of initiated displacements (M = 0.0035, SD = 0.005; r (7) = 0.40, p = 0.19) during Brevard observations. Lmp model was used to correlate sex, age, and MDS to average rate of received aggression and to average rate of initiated aggression. No relationships were identified in either phase or Brevard's population for received aggression or initiated aggression, though a pattern for higher rates of initiated aggression by females was identified in all observations (see table 8).

DISCUSSION

This study provides support for studying social interactions in zoological environments as for the purpose of understanding animal use of environmental features. Here we found that giraffes who are central and influential to their network spent more time sharing the station under varying management strategies. Additionally, we found that relationships among conspecific are context dependent and do not relate to relationships at the visitor feeding station. Dominance on exhibit was not a predictor for station usage or displacement at the visitor station, indicating that individuals should be managed differently under varying contexts. Environmental design can serve to promote socially appropriate behaviors during guest engagements by providing a variety of opportunities that allow for variable social feeding interactions.

Giraffe Social Ties are Context and Time Dependent

Giraffes displayed non-random interactions in all interaction types (affiliative, co-feeding, proximity, and station sharing) and across different times (phase 1 and phase 2), this was also observed in the Brevard population. Non-random association patterns in giraffes have been repeatedly observed in both zoological environments and field observations (Bashaw et al., 2007; VanderWaal 2014; Carter 2013; Muller et al., 2018; Prehn et al., 2019; Lewton & Rose, 2019). The study suggests that though network interaction rank was similar among exhibit interactions it was not similar to station sharing interactions, indicating that direction and rank order of co-feeding and affiliative interactions are not transferable to guest provisioning programs. Furthermore, vutard test indicates that significant ties among individuals are not consistent under varying contexts and times (figures 1- 3). This indicates that interactions among conspecifics may be context dependent and that specifically station sharing interactions vary more than exhibit affiliative interactions. While Perhn et al., (2019)'s study indicated social preferences during feeding and foraging bouts, this study suggests that feeding preferences may be context dependent according to the foraging opportunity and design.

Importance on Exhibit Influences Sharing Behavior at Guest Station

Giraffe network metrics from affiliative interactions (half-weight index, out-degree, in-degree, eigenvector centrality, clustering coefficient, and affinity) were predictive of sharing at the visitor station by individuals during phase 1 and phase 2 (maintaining Brevard constant). This indicates that sharing of the visitor station is positively associated with metrics related to social importance, centrality, and influence in the network. Additionally, during phase 2, these measures were also indicative of approaches to an occupied station. The co-feeding network's metrics were not indicative of station sharing, confirming that though station sharing is a co-feeding interaction, there does not appear to be transferability between co-feeding on exhibit (mainly consisting of sharing a feeder or browse) and occupying/ using a guest feeding station. This indicates that though ties between conspecifics are context dependent, the overall position and centrality of individuals does play a role in their interactions while using the guest feeding station.

Social Position and Aggression at Guest Feeding Station

Clustering coefficient values or cliquishness (Watts & Strogatz, 1998) were positively related to received and initiated aggression while at the guest feeding station in both scenarios and including the Brevard dataset. Potentially, this could indicate that individuals who are part of a clique on exhibit are less tolerant while at the guest feeding station of non-clique members. Further assessment of the role cliques in zoo habitats should be explored to understand their role in various feeding contexts.

Exhibit interactions and social position in relation to guest feeding station usage.

Network metrics from affiliative interactions or co-feeding interactions did not predict station usage by individuals in either phase or in Brevard (table 6. & table 7.). This indicates that usage may be modulated by space (See chapter 1) as well as other potential factors unmeasured in this study such as personality, leniency towards human interactions, motivation, hunger, and personal preference for food type at the visitor station.

Dominance does not relate to Station Use

Modified David's Scores is not indicative of station usage, or of station displacement interactions (table 8.). This could mean that dominance rank order on exhibit does not transfer to the guest feeding programs, further highlighting differences between exhibit and station usage interactions. In both phase 1 and phase 2, females appeared to be more likely to displace at the visitor station, independent of dominance (table 5 & table 8). This challenges prior believes of males and their role in monopolizing the guest feeding station and supports the idea that female dominance for giraffes follows socio-ecological theory framework and is related to food competition (Fournier & Festa-Bianchet, 1995). Findings from chapter 1 suggest that displacement rates are higher at the guest feeding station than the rest of the exhibit, with space allotment playing a role in displacement rates by individuals. These two findings combined indicate that though displacement is highest at the station, it is not executed by individuals with the highest MDS values, potentially indicating that individuals who are not dominant on exhibit modulate their behavior for access to the feeding station due to the constricted nature of the feeding station. Further information should be collected on the nature of displacement interactions at the guest feeding station in order to understand the role these displacement interactions play on the overall dominance hierarchy of the group. Because displacement rates were highest in this context, it is possible that these interactions should be accounted for when calculating MDS (Horova, et al, 2015).

Social Structure Implications for Environmental Design

Findings from this study suggest that guest provisioning programs could be an opportunity to provide individuals with variable guest feeding and interaction opportunities that better represent their social structure on exhibit. Because station sharing appears to be influenced by social position related to centrality, importance, and cliqueness, individuals who are more central to the network spend more time sharing with others though not necessarily feeding more. To provide opportunities to more peripheral members to engage with feeding programs, a variety of guest engagement opportunities with optimal space facilitation between individuals could improve the likelihood of simultaneous engagement with guest programs.

Further Analysis

Because sociality varied over short periods of time, as seen in Lewton & Rose (2019), it would be beneficial to observe potential changes in station usage and dynamic according to season, visitor density, as well as exhibit resource distribution especially for habitats which depend on naturally present browse. It is possible that station usage can be mediated by browse distribution as well as temperature. Lastly, individuals under one were excluded from this analysis, however, it would beneficial to understand how individuals begin to shape their interactions with others in relation to guest feeding opportunities. Due to the variability of guest engagement designs across AZA institutions, further analysis should focus on the role of social importance and influence on station interactions in a variety of guest feeding designs which may vary in space, height, schedules, and encompass varying group compositions.

Conclusion

The study of social structure and group dynamics is an important tool for understanding social animals housed in zoological environments, especially when accounting for modifications to provide guest experiences. Here we found that giraffe social position from affiliative interactions with conspecifics on exhibit plays a role in dictating sharing interactions at guest provisioning programs under varying management protocols and guest engagement designs. This study provided insight to context dependent ties and interactions in a zoological environment. Finally, it disproved the customary belief of male monopolization at guest engagement points for the studied population, highlighting the role of female resource displacement instead. As guest engagement opportunities continue to increase, this type of analysis is helpful to design animal opportunities that appropriately serve the existing group dynamics while providing educational and engaging guest experiences.

Table 1. Individuals Observed

Institution	**Name**	**Sex**	**Age**	**Sub-Species**
Jacksonville	Duke	Male	20 Years	Reticulated
	Sir Isaac	*Male*	*2 Months*	*Reticulated*
	Naomi	Female	11 Years	Reticulated
	Luna	Female	10 Years	Reticulated
	Lily	Female	1 Year	Reticulated
	Ivy	*Female*	*2 Months*	*Reticulated*
	Spock	Female	16 Years	Hybrid
	Faraja	Female	12 Years	N/A
	Willow	Female	2 Years	*Reticulated*
Brevard	Raffiki	Male	19 Years	Masai
	Doc	Male	15 Years	Hybrid
	Floyd	Male	1 Year	Masai
	Greg	Male	2 years	Masai
	Sprinkles	*Male*	*9 Months*	*Masai*
	Milenna	Female	16 Years	Masai
	Johari	Female	18 Years	Masai
	Kumi	Female	5 Years	Masai

*Individuals italicized under one year at the time of observation were not included in analyses of habitat or station usage. These individuals were unable to physically reach the station and relied on maternal milk during the time of observations.

Table 2. **Ethogram** (Bashaw, 2003; Seeber et al., 2012)

Table 2. Ethogram Modified from (Bashaw, 2003; Seeber et al., 2012)

Agonistic Behaviors	**Description: Recorded all-occurrence**
Avoid	Animal moves away at the approach of other, but no resource is involved.
Displace	One animal takes away resources from other (food, water, shade).
Displaced	Animal that loses resources (food, water, shade).
Sparring	Animal stands next to another animal and repeatedly throws head and neck towards the body or neck of the other. Note actor and recipient.
Non-Contact Yield	Receiver of non-contact aggression.
Non-Contact Aggression	Any threatening or attempts of aggressive behavior which does not result in contact. Examples: Chasing with ears back, lunging, feigning to bite, kick, or attempting to bite/ kick.
Contact Yield	Receiver of contact aggression
Contact Aggression	Aggressive behavior that results in contact. Examples: Head butting, kicking, biting.
Bumping	Strikes at head, neck, or any part of recipient including rump.
Use of Station Behaviors	**Description: Recorded all-occurrence & Duration**
Sharing Station Feeding	Two or more animals stand at feeding station simultaneously within neck length of each other. Animal is taking food from visitors/ staff or standing idle. Indicate individuals sharing station and individual who initated sharing interaction. (Duration)
Stating Usage Alone	Animal is receiving food from visitor/ staff at the feeding station or standing. Individual is alone at station. Indicate which station. (Duration)
Displaced at Station	Animal loses access to feeding station by any of the displacement interactions.
Station Approach	Individual is one neck length or less from the barrier.
Displacement at Station	Animal takes away access to feeding station enagaging in any of the "agonistic" behaviors.
Social/ Interactive Behaviors	**Description: Recorded all-occurrence**
Approach	Animal moves to proximity or contact with another animal. Animal must appear to be moving directly towards another animal.

Social Play	Animal frolics with other animal (Bucking, throws head, or runs in circles). Animal's ears are forward. Note actor and recipient.
Necking	Animal rubs neck with another giraffe. Note actor and recipient.
Head Rub	Animal rubs head on any part of the other animal's body other than head or neck. (If head, score muzzle, if neck, score necking).
Co-Feeding	Two animals in proximity or contact feed at the same time. From same feeder or bush.
Sentinel	One animal approaches another animal that is lying down and stands in proximity to that animal (Note actor and recipient).
Anogenital Exam	Animal sniffs or licks the anogenital area of another. (Note actor and recipient).
Urine Testing	Animal licks the urine of another animal (Note actor and recipient).
Flehmen	Animal inhales while lifting upper lip, usually lifts head and flares nostrils. Usually in response to scent and usually following urine testing.
Attempted Mount	This animal rocks onto back feet and lifts front feet off the ground, attempts to place sternum on the back of recipient while standing behind the animal. This action does not result in mounting. (Note actor and recipient).
Mount	Animal rocks onto back feet and lifts front feet off the ground to place sternum on the back of another animal, while standing behind the animal. (Note actor and recipient).
Mate Guard	One animal stands directly behind the other in either contact or close proximity and performs no other behavior. (Note actor and recipient).
Copulation	Animals engage in sex (Note actor and recipient).
Nursing	One animal is suckling the udders of another (Note actor and recipient).

Proximity Measures	**Description: Recorded 1-minute interval**
Nearest Neighbor	Indicated closest neighbor
Proximate	All animals within two neck lengths of the scanned animal, but not in contact with the scanned animal
Contact	Two or more animals make contact

Table 3. Affiliative Network Metrics

Individuals	Affiliative Network: Mean Half Weight Index	Out-Degree	In-Degree	Eigenvector Centrality	Clustering Coefficient	Affinity	Social Index
				Phase 1			
Duke	1.07	7.79	0.41	0.35	0.34	7.10	-0.89
Faraja	1.07	0.52	0.15	0.36	0.35	7.13	-0.57
Naomi	1.22	1.31	5.97	0.40	0.37	6.91	0.64
Luna	1.08	1.04	3.02	0.36	0.38	7.06	0.48
Spock	1.24	2.16	7.01	0.39	0.28	6.65	0.51
Willow	1.19	1.14	0.88	0.39	0.35	6.86	-0.12
Lily	1.20	4.25	0.79	0.39	0.36	6.92	-0.69
				Phase 2			
Duke	1.24	2.49	0.26	0.42	0.40	7.21	-0.81
Faraja	1.13	0.38	0.16	0.40	0.44	7.64	-0.38
Naomi	1.14	0.76	3.81	0.36	0.36	7.05	0.68
Luna	1.13	1.28	2.33	0.34	0.34	6.72	0.30
Spock	1.39	0.63	1.66	0.45	0.35	6.89	0.44
Willow	1.05	1.55	0.47	0.32	0.36	6.89	-0.54
Lily	1.07	2.29	0.68	0.33	0.38	6.92	-0.56
				Brevard			
Raffikki	0.86	1.99	2.37	0.34	0.32	8.50	0.67
Doc	1.16	3.97	5.96	0.37	0.20	6.48	0.05
Johari	1.01	1.77	2.67	0.34	0.23	7.17	0.01
Milenna	1.03	2.53	6.79	0.36	0.28	7.18	0.52
Kumi	1.03	5.80	8.84	0.36	0.26	7.32	0.24
Floyd	1.19	5.81	3.42	0.39	0.23	6.55	-0.22
Greg	1.52	12.46	4.27	0.47	0.16	5.91	-0.53

Table 3. Displays measured network metrics for affiliative interactions (including co-feeding) for phase 1, phase 2 of the JZG population and the Brevard Zoo population.

Table 4. Co-feeding Network Metrics

	Co-Feeding Network						
	Mean Half Weight Index	**Out-Degree**	**In-Degree**	**Eigenvector Centrality**	**Clustering Coefficient**	**Affinity**	**Social Index**
Individuals				*Phase 1*			
Duke	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Faraja	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Naomi	1.65	0.20	1.19	0.57	0.26	3.60	0.72
Luna	0.78	0.20	0.15	0.37	0.60	6.20	-0.14
Spock	0.77	0.36	0.10	0.37	0.60	6.22	-0.58
Willow	0.85	0.22	0.22	0.39	0.60	5.91	0.00
Lily	1.36	0.78	0.10	0.50	0.39	4.01	-0.78
				Phase 2			
Duke	1.22	0.00	0.03	0.63	0.00	10.60	1.00
Faraja	1.73	0.10	0.00	0.69	0.00	7.03	-1.00
Naomi	1.18	0.13	0.65	0.11	0.15	5.88	0.68
Luna	0.90	0.16	0.25	0.07	0.20	6.83	0.23
Spock	1.05	0.06	0.22	0.30	0.06	8.46	0.56
Willow	0.93	0.40	0.09	0.09	0.20	6.75	-0.63
Lily	1.16	0.49	0.10	0.11	0.14	5.93	-0.68
				Brevard			
Raffikki	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Doc	1.36	0.00	0.39	0.45	0.12	5.24	1.00
Johari	1.08	0.20	0.00	0.39	0.00	6.17	-1.00
Milenna	0.96	0.11	0.24	0.37	0.32	6.75	0.43
Kumi	0.88	0.05	0.09	0.36	0.25	7.17	0.33
Floyd	1.09	0.05	0.20	0.39	0.17	5.93	0.67
Greg	1.48	0.52	0.00	0.48	0.18	5.10	-1.00

Table 4. Displays measured network metrics for co-feeding interactions for phase 1, phase 2 of the JZG population and the Brevard Zoo population.

Table 5. Station Interactions and Exhibit Dominance

Individuals	Modified David's Score	Average % Station Use	Average % Station Sharing	Average % of Approaches to Occupied Station	Average Rate/ minute of Received Approaches	Rate/ minute of Initiated Aggression	Rate/ minute of Received Aggression
				Phase 1			
Duke	4.97	5.96	3.02	0.00	0.01	0.01	0.01
Faraja	-1.60	3.81	4.41	1.85	0.04	0.35	0.04
Naomi	-0.94	4.54	48.87	58.59	0.25	0.31	0.25
Luna	3.34	11.79	39.49	46.20	0.27	0.48	0.27
Spock	-3.51	11.75	28.26	39.38	0.14	0.11	0.14
Willow	-6.80	24.52	41.17	45.21	0.19	0.16	0.19
Lily	4.55	20.36	25.78	26.00	0.30	0.32	0.30
				Phase 2			
Duke	9.01	23.54	32.55	6.25	0.11	0.03	0.00
Faraja	-5.98	2.94	14.28	11.90	0.88	0.00	1.49
Naomi	0.75	9.80	74.63	91.47	0.64	0.16	0.11
Luna	0.94	11.79	75.34	93.60	0.38	0.09	0.09
Spock	-4.24	10.92	59.56	59.21	0.31	0.04	0.10
Willow	-3.64	23.59	61.33	71.35	0.32	0.13	0.13
Lily	3.17	36.13	60.00	67.81	0.25	0.23	0.02
				Brevard			
Raffikki	0.00	30.51	100.00	39.85	0.25	0.00	0.01
Doc	-0.54	31.67	54.12	47.13	0.13	0.00	0.03
Johari	2.38	16.57	61.85	73.41	0.14	0.01	0.01
Milenna	-0.54	88.93	30.88	11.89	0.13	0.01	0.00
Kumi	0.00	1.56	100.00	100.00	0.16	0.00	0.00
Floyd	-2.81	14.78	51.00	45.69	0.22	0.00	0.00
Greg	1.50	66.50	100.00	100.00	0.26	0.00	0.00

Table 5. Displays exhibit dominance values indicated by Modified David's Score (MDS) and station interactions for phase 1, phase 2 of the JZG population and the Brevard Zoo population.

Table 6. lmp Model Affiliative Interaction. Metrics for phase 1 & Brevard, and phase 2 Brevard population

Measures of Station Usage/ Interaction	Coefficients p-values: Mean Half Weight Index	Out-Degree	In-Degree	Eigenvector Centrality	Clustering Coefficient	Affinity	Model Statistics: Residual Standard Error	df	Multiple R squared	Adjusted R squared	F statistic	p-values
Phase 1 & Brevard												
Average % Station Use	0.311	0.894	0.874	0.241	0.537	0.511	27.03	7	0.375	-0.16	0.7012	0.6593
Average % Station Sharing	0.876	1	0.449	0.412	**0.0492***	0.2	21.45	7	0.793	0.615	4.463	**0.035***
Average % of Approaches to Occupied Station	0.792	0.919	0.319	0.951	0.275	0.59	29.36	7	0.515	0.1	1.24	0.388
Average Rate/ minute of Received Approaches	0.752	0.552	0.929	0.376	0.937	0.817	0.009	7	0.454	-0.013	0.972	0.506
Average Rate/ minute of Initiated Aggression	0.682	0.247	0.764	0.57	**0.026***	0.422	0.11	7	0.77	0.573	3.905	**0.049***
Average Rate/ minute of Received Aggression	0.348	0.252	0.481	0.553	**0.04***	0.637	0.069	7	0.799	0.627	4.639	**0.032***
Phase 2 & Brevard												
Average % Station Use	0.627	0.592	1	0.664	0.947	0.633	29.56	7	0.216	-0.456	0.322	0.906
Average % Station Sharing	**< 2 e-16***	**0.001***	**0.0436***	**< 2 e-16***	**0.0004***	**< 2 e-16***	8.593	7	0.951	0.909	22.56	**0.0003***
Average % of Approaches to Occupied Station	**0.003***	0.218	0.082	**0.002***	0.129	**0.005***	17.67	7	0.843	0.709	6.29	**0.015***
Average Rate/ minute of Received Approaches	0.693	0.98	0.821	0.777	0.435	0.723	0.237	7	0.362	-0.184	0.662	0.684
Average Rate/ minute of Initiated Aggression	0.655	0.234	0.755	0.553	**0.023***	0.399	0.11	7	0.77	0.573	3.905	**0.049***
Average Rate/ minute of Received Aggression	0.326	0.238	0.493	0.545	**0.03***	0.606	0.07	7	0.799	0.627	4.64	**0.032***

Table 7. lmp Model Co-feeding Interaction Metrics for phase 1 & Brevard, and phase 2 Brevard population.

Measures of Station Usage/ Interaction	Coefficients p-values						Model Statistics					
	Mean Half Weight Index	Out-Degree	In-Degree	Eigenvector Centrality	Clustering Coefficient	Affinity	Residual Standard Error	df	Multiple R squared	Adjusted R squared	F statistic	p-values
Phase 1 & Brevard												
Average % Station Use	0.0246	0.126	0.179	0.023	0.03	0.037	18.37	7	0.712	0.465	2.881	0.096
Average % Station Sharing	0.822	0.956	0.904	0.871	0.92	0.86	42.53	7	0.19	-0.513	0.266	0.936
Average % of Approaches to Occupied Station	0.776	0.816	0.713	0.7	0.536	0.976	30.89	7	0.463	0.003	1.007	0.488
Average Rate/ minute of Received Approaches	0.909	0.859	0.653	0.74	0.787	0.567	0.085	7	0.461	-0.001	0.997	0.493
Average Rate/ minute of Initiated Aggression	0.284	0.712	0.743	0.294	1	0.272	0.152	7	0.559	0.18	1.476	0.309
Average Rate/ minute of Received Aggression	**0.007**	0.357	0.289	**0.006**	0.876	**0.0036**	0.039	7	0.936	0.881	17.15	**0.0007**
Phase 2 & Brevard												
Average % Station Use	**0.05**	0.036	0.098	**0.025**	0.455	0.53	19.37	7	0.662	0.375	2.3	0.15
Average % Station Sharing	0.368	0.439	0.639	0.373	0.935	0.388	25.62	7	0.563	0.188	1.502	0.302
Average % of Approaches to Occupied Station	0.811	0.75	0.949	0.617	0.725	0.937	33.94	7	0.422	-0.073	0.852	0.57
Average Rate/ minute of Received Approaches	0.08	0.205	0.311	0.137	0.862	0.342	0.207	7	0.514	0.097	1.23	0.391
Average Rate/ minute of Initiated Aggression	0.419	0.503	0.796	0.074	0.074	0.305	**0.041**	7	0.835	0.694	5.907	**0.017**
Average Rate/ minute of Received Aggression	**0.029**	0.084	0.077	0.091	0.7	0.255	0.305	7	0.673	0.392	2.397	0.139

Table 8. Lmp model using Modified David Scores, Age, Sex and station usage and interactions.

Measures of Station Usage/ Interaction	Coefficients p-values: MDS	Sex	Age	Model Statistics: Residual Standard Error	df	Multiple R squared	Adjusted R squared	F statistic	p-values
Phase 1 & Brevard									
Average % Station Use	0.869	0.609	1	28.07	10	0.037	-0.251	0.131	0.939
Average % Station Sharing	0.858	0.273	0.569	36.55	10	0.331	0.129	1.647	0.241
Average % of Approaches to Occupied Station	1	0.843	0.211	32.38	10	0.158	-0.095	0.627	0.616
Average Rate/ minute of Received Approaches	0.508	1	**0.049**	0.079	10	0.331	0.13	1.647	0.241
Average Rate/ minute of Initiated Aggression	0.352	**0.03**	0.431	0.149	10	0.4	0.22	2.225	0.148
Average Rate/ minute of Received Aggression	0.439	0.057	0.241	0.101	10	0.392	0.21	2.153	0.157
Phase 2 & Brevard									
Average % Station Use	0.659	0.622	0.904	26.95	10	0.069	-0.21	0.247	0.862
Average % Station Sharing	0.735	0.565	0.453	30.84	10	0.095	-0.176	0.351	0.79
Average % of Approaches to Occupied Station	0.439	0.331	0.079	30.02	10	0.354	0.161	1.829	0.205
Average Rate/ minute of Received Approaches	0.168	0.468	0.915	0.208	10	0.301	0.091	1.435	0.29
Average Rate/ minute of Initiated Aggression	0.108	**0.033**	0.086	0.059	10	0.5	0.35	3.331	0.065
Average Rate/ minute of Received Aggression	0.087	0.87	0.752	0.371	10	0.307	0.1	1.48	0.28

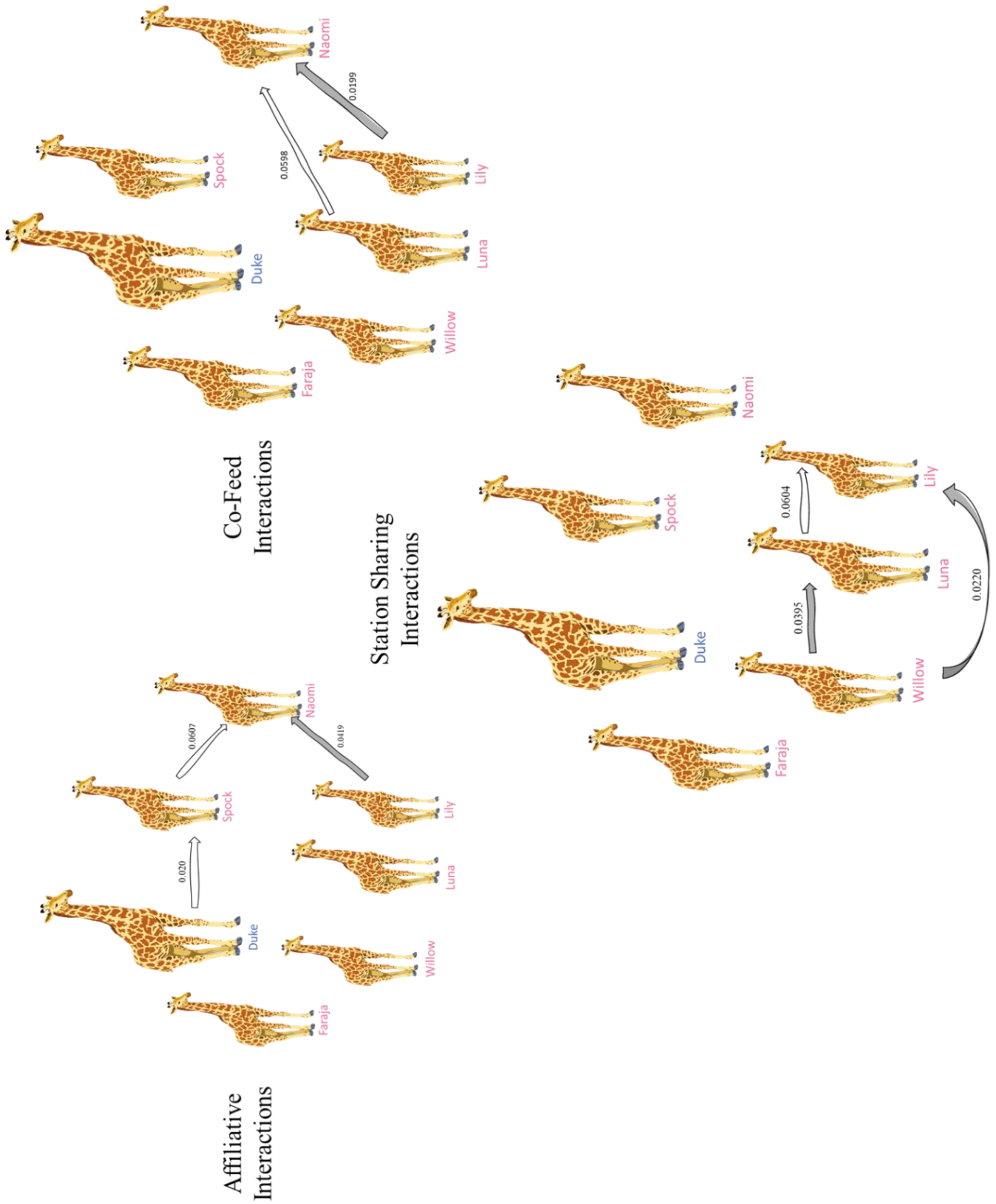

Figure 1. Vutard significant ties Phase 1 JZG.
Displays significant directional relationships during phase 1 observations for affiliative exhibit interactions, co-feeding exhibit interactions, and station sharing interactions as indicated by vutard test. Gray arrows indicate statistically significant relationships, white arrows indicate non-significant trends.

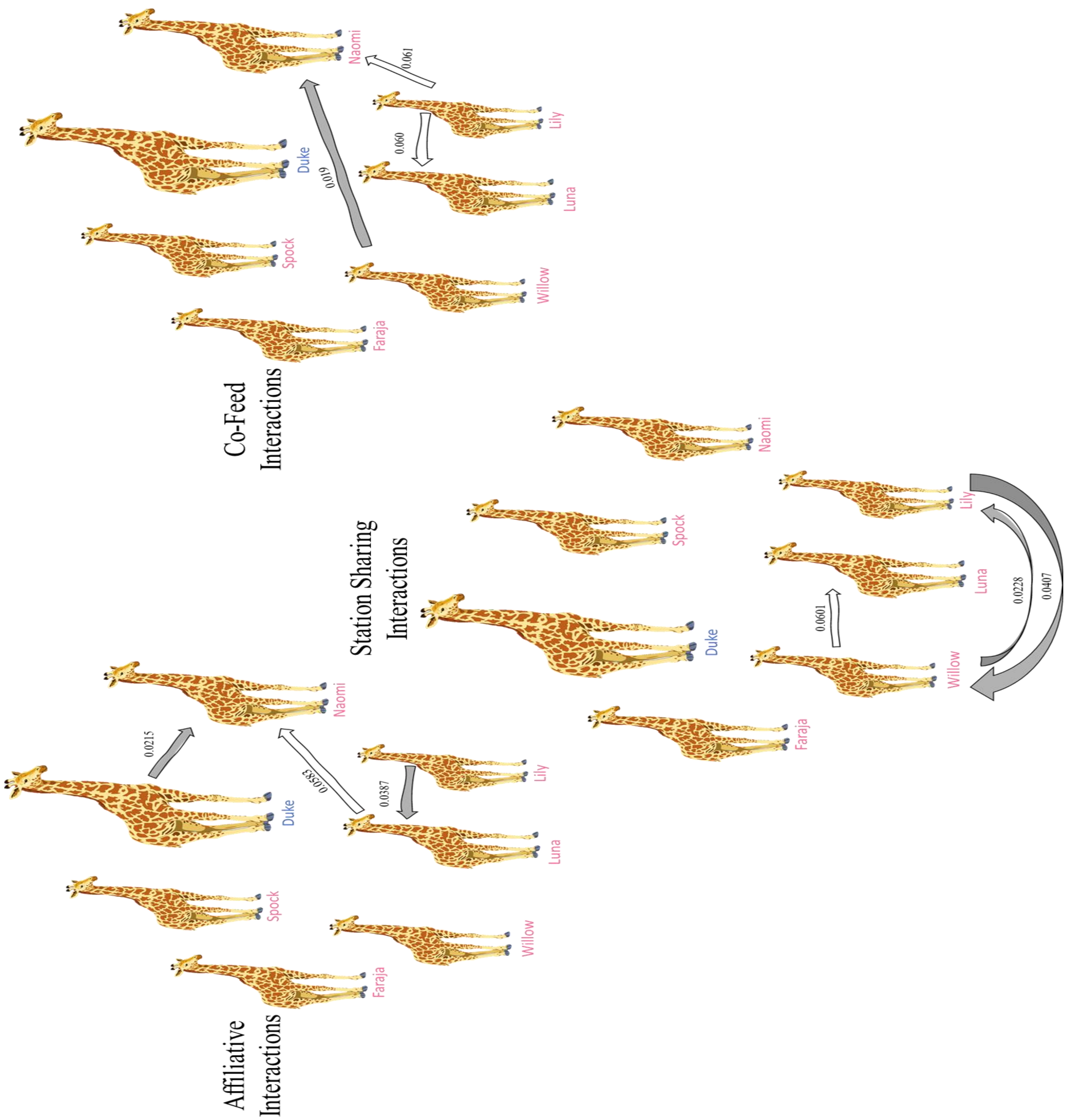

Figure 2. Vutard significant ties Phase 2 JZG.
Displays significant directional relationships during phase 1 observations for affiliative exhibit interactions, co-feeding exhibit interactions, and station sharing interactions as indicated by vutard test. Gray arrows indicate statistically significant relationships, white arrows indicate pattern (>0.05 – 0.069).

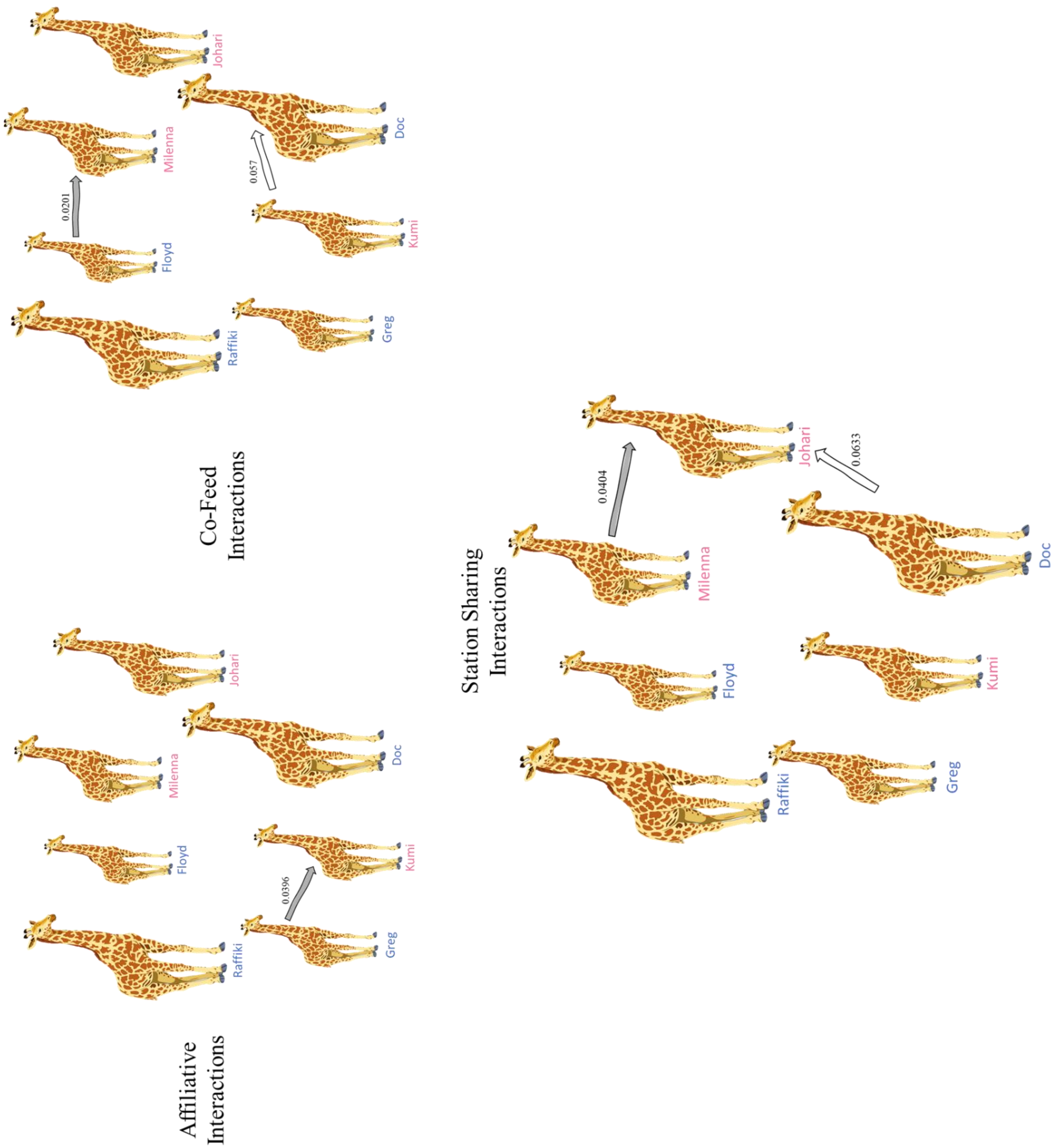

Figure 3. Vutard significant ties Brevard.
Displays significant directional relationships during phase 1 observations for affiliative exhibit interactions, co-feeding exhibit interactions, and station sharing interactions as indicated by vutard test. Gray arrows indicate statistically significant relationships, white arrows indicate pattern (>0.05 – 0.069).

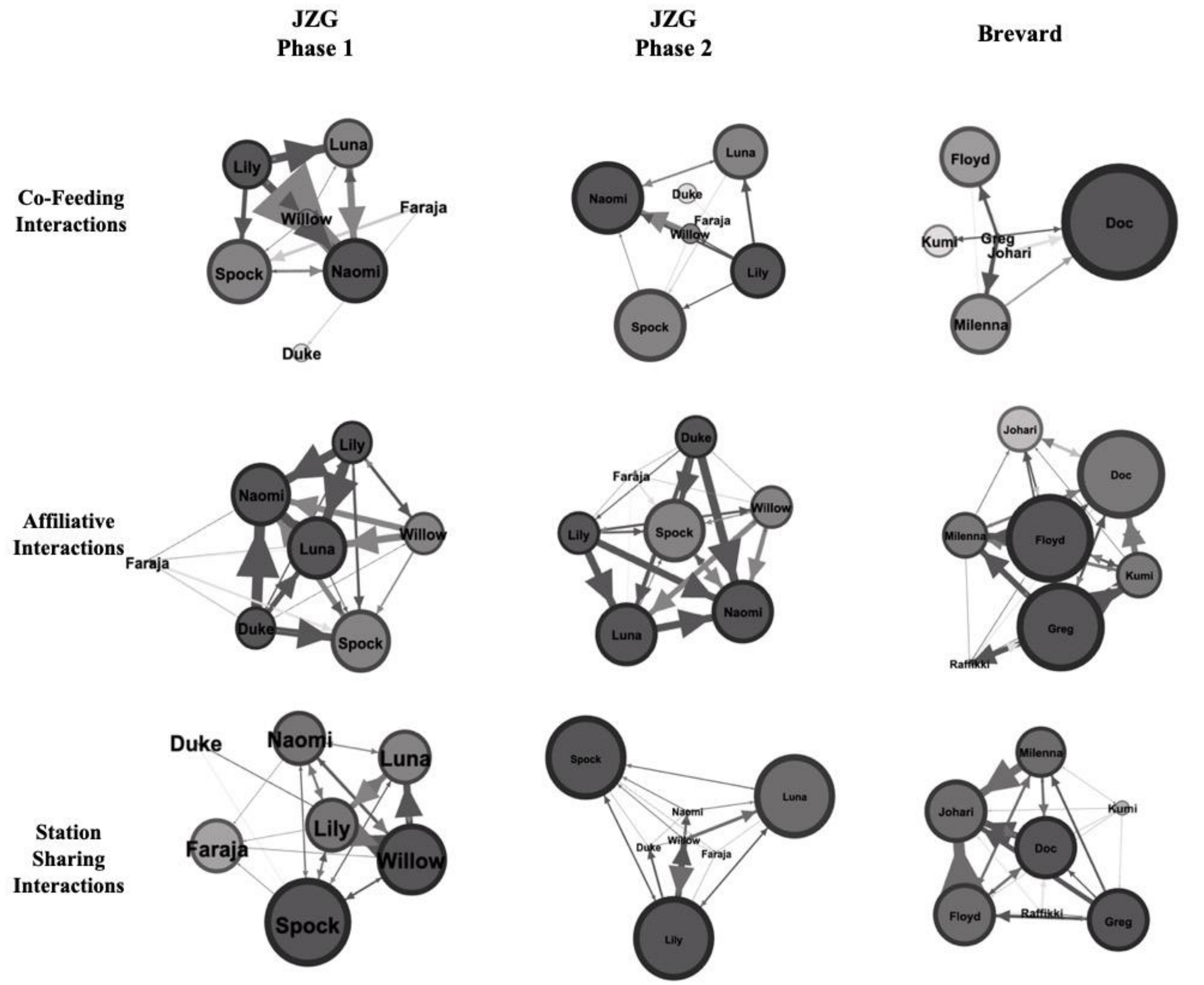

Figure 4. Visual network representation of affiliative, co-feeding, and station sharing networks for JZG Phase 1 observations, JZG Phase 2 observations, and Brevard observations. The size of the arrow displays the relative value of the out-going and in-coming interactions, the shade of the node indicates the relative size of the overall degree value for the individual, and the size of the node indicates the relative strength of the individual's in-degree.

LITERATURE CITED

Alexander RD (1974) The evolution of social behavior. Annu Rev Ecol Syst 5:325–383

Altmann, J. (1974). Observational study of behavior: sampling methods. Behaviour, 49(3), 227–266.

Antle, M. C., & Silver, R. (2009). Neural basis of timing and anticipatory behaviors. European Journal of Neuroscience, 30(9), 1643–1649.

Asher, L., Collins, L. M., Ortiz-Pelaez, A., Drewe, J. A., Nicol, C. J., & Pfeiffer, D. U. (2009). Recent advances in the analysis of behavioural organization and interpretation as indicators of animal welfare. Journal of the Royal Society Interface, 6(41), 1103-1119.

associations and age-related sociability of wild giraffes. Anim. Behav. 2013, 86, 901–910.

Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., ... & Holekamp, K. (2008). Fission-fusion dynamics: new research frameworks. Current Anthropology, 49(4), 627-654.

Bang, A., Deshpande, S., Sumana, A., & Gadagkar, R. (2010). Choosing an appropriate index to construct dominance hierarchies in animal societies: a comparison of three indices. Animal Behaviour, 79(3), 631–636.

Bashaw, M. J. (2003). Social behavior and communication in a herd of captive giraffe. Georgia Institute of Technology.

Bashaw, M. J., Bloomsmith, M. A., Maple, T. L., & Bercovitch, F. B. (2007). The structure of social relationships among captive female giraffe (Giraffa camelopardalis). Journal of Comparative Psychology, 121(1), 46.

Bashaw, M. J., Tarou, L. R., Maki, T. S., & Maple, T. L. (2001). A survey assessment of variables related to stereotypy in captive giraffe and okapi. Applied Animal Behaviour Science, 73(3), 235–247.

Bashaw, M.J. (in press). Creating a giraffic park: Design and management ideas for optimal giraffe wellness. In V. D. Segura, D. L. Forthman, T. L. Maple (Eds.): Wellness for Elephants. Fernandina Beach, FL: Red Leaf Press.

Bashaw, M.J. (in press). Creating a giraffic park: Design and management ideas for optimal giraffe wellness. In V. D. Segura, D. L. Forthman, T. L. Maple (Eds.): Wellness for Elephants. Fernandina Beach, FL: Red Leaf Press.

Bastian M., Heymann S., Jacomy M. (2009). Gephi: an open source software for exploring and manipulating networks.International AAAI Conference on Weblogs and Social Media.

Baxter, E., & Plowman, A. B. (2001). The effect of increasing dietary fibre on feeding, rumination and oral stereotypies in captive giraffes (Giraffa camelopardalis). Animal Welfare, 10(3), 281–290.

Bercovitch, F. B., & Berry, P. S. (2013). Herd composition, kinship and fission–fusion social dynamics among wild giraffe. African Journal of Ecology, 51(2), 206–216.

Bercovitch, F. B., & Deacon, F. (2015). Gazing at a giraffe gyroscope: where are we going? African Journal of Ecology, 53(2), 135–146.

Bercovitch, F. B., Bashaw, M. J., & del Castillo, S. M. (2006). Sociosexual behavior, male mating tactics, and the reproductive cycle of giraffe (Giraffa camelopardalis). Hormones and Behavior, 50(2), 314–321.

Bond, M. L., Lee, D. E., Ozgul, A., & König, B. (2019). Fission–fusion dynamics of a megaherbivore are driven by ecological, anthropogenic, temporal, and social factors. Oecologia, 191(2), 335-347. (Need access)

Borgatti, S.P., Everett, M.G. and Freeman, L.C. 2002. Ucinet for Windows: Software for Social Network Analysis. Harvard, MA: Analytic Technologies.

Browning, H., & Maple, T. L. (2019). Developing a Metric of Usable Space for Zoo Exhibits. Frontiers in Psychology, 10, 791.

Caister, L. E., Shields, W. M., & Gosser, A. (2003). Female tannin avoidance: a possible explanation for habitat and dietary segregation of giraffes (Giraffa camelopardalis peralta) in Niger. African Journal of Ecology, 41(3), 201–210. https://doi.org/10.1046/j.1365-2028.2003.00422.x

Cameron, E. Z., & du Toit, J. T. (2005). Social influences on vigilance behaviour in giraffes, Giraffa camelopardalis. Animal Behaviour, 69(6), 1337–1344.

Cameron, E. Z., Setsaas, T. H., & Linklater, W. L. (2009). Social bonds between unrelated females increase reproductive success in feral horses. Proceedings of the National Academy of Sciences, 106(33), 13850-13853.

Carter, K.D.; Brand, R.; Carter, J.K.; Shorrocks, B.; Goldizen, A.W. (2013) Social networks, long-term

Carter, K.D.; Seddon, J.M.; Frere, C.H.; Carter, J.K.; Goldizen, A.W (2013). Fission-fusion dynamics in wild giraffes may be driven by kinship, spatial overlap and individual social preferences. Animal Behav., 85, 385–394.

Clark, F. E. (2011). Great ape cognition and captive care: Can cognitive challenges enhance well-being?. Applied Animal Behaviour Science, 135(1-2), 1-12.

Clauss, M., Franz-Odendaal, T. A., Brasch, J., Castell, J. C., & Kaiser, T. (2007). Tooth wear in captive giraffes (giraffa camelopardalis): mesowear analysis classifies free-ranging specimens as browsers but captive ones as grazers. Journal of Zoo and Wildlife Medicine, 38(3), 433–445. https://doi.org/10.1638/06-032.1

Clayton, S., Fraser, J., & Burgess, C. (2011). The role of zoos in fostering environmental identity. Ecopsychology, 3(2), 87-96.

Clayton, S., Fraser, J., & Saunders, C. D. (2009). Zoo experiences: Conversations, connections, and concern for animals. Zoo Biology: Published in affiliation with the American Zoo and Aquarium Association, 28(5), 377-397.

Clutton-Brock, T. H., Albon, S. D., & Guinness, F. E. (1984). Maternal dominance, breeding success and birth sex ratios in red deer. Nature, 308(5957), 358.

Coe, J. C. (2003). Steering the ark toward Eden: design for animal well-being. Journal of the American Veterinary Medical Association, 223(7), 977-980.

Coe, J. C., Scott, D., & Lukas, K. E. (2009). Facility design for bachelor gorilla groups. Zoo Biology: Published in affiliation with the American Zoo and Aquarium Association, 28(2), 144-162.

Coe, M. J. (1967). "Necking" behaviour in the giraffe. Journal of Zoology, 151(3), 313–321.

Coimbra, J. P., Hart, N. S., Collin, S. P., & Manger, P. R. (2013). Scene from above: retinal ganglion cell topography and spatial resolving power in the giraffe (Giraffa camelopardalis). Journal of Comparative Neurology, 521(9), 2042–2057.

Coleing, A. (2009). The application of social network theory to animal behaviour. Bioscience Horizons, 2(1), 32-43.

D'Cruze, N., Khan, S., Carder, G., Megson, D., Coulthard, E., Norrey, J., & Groves, G. (2019). A Global Review of Animal–Visitor Interactions in Modern Zoos and Aquariums and Their Implications for Wild Animal Welfare. Animals, 9(6), 332.

Dagg, A. I., & Foster, J. B. (1976). The giraffe: its biology, behavior, and ecology. Van Nostrand Reinhold Company.

De Vries, H. (1998). Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. Animal Behaviour, 55(4), 827–843.

De Vries, H., Stevens, J. M., & Vervaecke, H. (2006). Measuring and testing the steepness of dominance hierarchies. Animal Behaviour, 71(3), 585-592.

Dugatkin, L. A. (1997). Winner and loser effects and the structure of dominance hierarchies. Behavioral Ecology, 8(6), 583–587.

Farine, D. R., & Whitehead, H. (2015). Constructing, conducting and interpreting animal social network analysis. Journal of Animal Ecology, 84(5), 1144-1163.

Fennessy, J., Bidon, T., Reuss, F., Kumar, V., Elkan, P., Nilsson, M. A., ... & Janke, A. (2016). Multi-locus analyses reveal four giraffe species instead of one. Current Biology, 26(18), 2543-2549.

Fernandez, E. J., Tamborski, M. A., Pickens, S. R., & Timberlake, W. (2009). Animal–visitor interactions in the modern zoo: Conflicts and interventions. Applied Animal Behaviour Science, 120(1), 1–8.

Fernandez, L. T., Bashaw, M. J., Sartor, R. L., Bouwens, N. R., & Maki, T. S. (2008). Tongue twisters: feeding enrichment to reduce oral stereotypy in giraffe. Zoo Biology, 27(3), 200–212. https://doi.org/10.1002/zoo.20180

Foris, B., Zebunke, M., Langbein, J., & Melzer, N. (2019). Comprehensive analysis of affiliative and agonistic social networks in lactating dairy cattle groups. Applied Animal Behaviour Science, 210, 60-67.

Foster, J. B., & Dagg, A. I. (1972). Notes on the biology of the giraffe. African Journal of Ecology, 10(1), 1–16.

Fournier, F., & Festa-Bianchet, M. (1995). Social dominance in adult female mountain goats. Animal Behaviour, 49(6), 1449–1459.

Fowler, M. E. (1978). Z00 and Wild Animal Medicine. WB Saunders Company, Philadelphia, Pa.

Gammell, M. P., Vries, H. D., Jennings, D. J., Carlin, C. M., & Hayden, T. J. (2003). David's score: a more appropriate dominance ranking method than Clutton-Brock et al.'s index. Animal behaviour, 66(3), 601-605.

Hand, J. L. (1986). Resolution of social conflicts: dominance, egalitarianism, spheres of dominance, and game theory. The Quarterly Review of Biology, 61(2), 201–220.

Hediger, H., Vevers, G.A., 7 Reader, W. (1970). Man and Animal in the Zoo; Zoo Biology.

Hemelrijk, C. K. (1990). Models of, and tests for, reciprocity, unidirectionality and other social interaction patterns at a group level. Animal Behaviour, 39(6), 1013–1029.

Hill, S. P., & Broom, D. M. (2009). Measuring zoo animal welfare: theory and practice. Zoo Biology: Published in affiliation with the American Zoo and Aquarium Association, 28(6), 531-544.

Holdgate, M. R., Meehan, C. L., Hogan, J. N., Miller, L. J., Soltis, J., Andrews, J., & Shepherdson, D. J. (2016). Walking behavior of zoo elephants: associations between GPS-measured daily walking distances and environmental factors, social factors, and welfare indicators. PloS one, 11(7), e0150331.

Horová, E., Brandlová, K., & Glonekova, M. (2015). The First Description of Dominance Hierarchy in Captive Giraffe: Not Loose and Egalitarian, but Clear and Linear. PLOS ONE, 10(5), e0124570. https://doi.org/10.1371/journal.pone.0124570

Hosey, G. (2000). Zoo Animals and Their Human Audiences: What is the Visitor Effect? (Vol. 9).

Hummel, J., Clauss, M., Baxter, E., Flach, E. J., & Johansen, K. (2006). The influence of roughage intake on the occurrence of oral disturbances in captive giraffids. Zoo Animal Nutrition, 3, 235–252.

IBM Corp. Released 2016. IBM SPSS Statistics for Windows, Version 24.0. Armonk, NY: IBM Corp.

Innis, A. C. (1958). The behaviour of the giraffe, Giraffa camelopardalis, in the eastern Transvaal. Journal of Zoology, 131(2), 245–278.

Kagan, R., Carter, S., & Allard, S. (2015). A universal animal welfare framework for zoos. Journal of Applied Animal Welfare Science, 18(sup1), S1-S10

Kaufman, A. B., Bashaw, M. J., & Maple, T. L. (Eds.). (2019). Scientific foundations of zoos and aquariums: Their role in conservation and research. Cambridge University Press.

Kearney, C. C., & Ball, R. L. (2001). Body scoring system for captive giraffe (Giraffa camelopardalis). In Joint Conference-American Association of Zoo Veterinarians (pp. 358–359).

Kidd, A. H., Kidd, R. M., & Zasloff, R. L. (1995). Developmental Factors in Positive Attitudes toward Zoo Animals. Psychological Reports, 76(1), 71–81. https://doi.org/10.2466/pr0.1995.76.1.71

Kideghesho, J. R. (2016). Reversing the trend of wildlife crime in Tanzania: challenges and opportunities. Biodiversity and conservation, 25(3), 427-449.

Kohn, G. M. (2017). Friends give benefits: autumn social familiarity preferences predict reproductive output. Animal behaviour, 132, 201-208.

Krause, J., James, R., Franks, D. W., & Croft, D. P. (Eds.). (2015). Animal social networks. Oxford University Press, USA.

Kreger, M. D., & Hutchins, M. (2010). Ethics of keeping mammals in zoos and aquariums. Wild Mammals in Captivity: Principles and Techniques for Zoo Management, 3–10.

Kreger, M., & Mench, J. (1995). Visitor-Animal Interactions at the Zoo (Vol. 8). https://doi.org/10.2752/089279395787156301

Langman, V. A. (1977). Cow-calf Relationships in Giraffe (Giraffa camelopardalis giraffa). Ethology, 43(3), 264–286.

Laule, G. (2005). The role of fear in abnormal behavior and animal welfare. In Proceedings of the seventh international conference on environmental enrichment (pp. 120–125).

Leuthold, B. M. (1979). Social organization and behaviour of giraffe in Tsavo East National Park. African Journal of Ecology, 17(1), 19–34.

Madden, D., & Young, T. P. (1992). Symbiotic Ants as an Alternative Defense against Giraffe Herbivory in Spinescent Acacia drepanolobium. Oecologia, 91(2), 235–238.

Maple, T. L., & Bloomsmith, M. A. (2018). Introduction: The science and practice of optimal animal welfare. Behavioural processes, 156, 1.

Maple, T. L., & Perdue, B. M. (2013). Wellness as welfare. In Zoo Animal Welfare (pp. 49-67). Springer, Berlin, Heidelberg.

Maple, T. L., & Perdue, B. M. (2013). Zoo animal welfare (p. 22). Berlin, Germany:: Springer.

Maple, T. L., & Stine, W. W. (1982). Environmental variables and great ape husbandry. American journal of Primatology, 3(S1), 67-76.

Markham, A. C., Gesquiere, L. R., Alberts, S. C., & Altmann, J. (2015). Optimal group size in a highly social mammal. Proceedings of the National Academy of Sciences, 112(48), 14882-14887.

Mason, G. J. (1991). Stereotypies: a critical review. Animal Behaviour, 41(6), 1015–1037.

Mason, G. J. (2010). Species differences in responses to captivity: stress, welfare and the comparative method. Trends in ecology & evolution, 25(12), 713-721.

McCowan, B., Anderson, K., Heagarty, A., & Cameron, A. (2008). Utility of social network analysis for primate behavioral management and well-being. Applied Animal Behaviour Science, 109(2-4), 396-405.

Mellor, D. (2016). Updating animal welfare thinking: Moving beyond the “Five Freedoms” towards “a Life Worth Living”. Animals, 6(3), 21.

Mellor, D. J., Hunt, S., & Gusset, M. (2015). Caring for wildlife: the world zoo and aquarium animal welfare strategy. WAZA Executive Office.

Mellor, D., Patterson-Kane, E., & Stafford, K. J. (2009). The sciences of animal welfare. John Wiley & Sons.

Mineo, A.M. (1995) Stima dei parametri di regressione lineare semplice quando gli errori seguono una distribuzione normale di ordine p (p incognito). Annali della Facolt\`a di Economia dell'Universit\`a di Palermo (Area Statistico-Matematica), pp. 161-186.

Muller, Z. (2008). Quantifying giraffe poaching as population threat. The Rothschild’s Giraffe Project.

Muller, Z., Cantor, M., Cuthill, I. C., & Harris, S. (2018). Giraffe social preferences are context dependent. Animal behaviour, 146, 37-49.

Orban, D. A., Siegford, J. M., & Snider, R. J. (2016). Effects of guest feeding programs on captive giraffe behavior. Zoo Biology, 35(2), 157–166.

Parr, L. A., Matheson, M., Bernstein, I. S., & De Waal, F. B. (1997). Grooming down the hierarchy: allogrooming in captive brown capuchin monkeys, Cebus apella. Animal behaviour, 54(2), 361-367.

Pellew, R. A. (1984). Food Consumption and Energy Budgets of the Giraffe. Journal of Applied Ecology, 21(1), 141–159. https://doi.org/10.2307/2403043

Potter, J. S., & Clauss, M. (2005). Mortality of captive giraffe (Giraffa camelopardalis) associated with serous fat atrophy: a review of five cases at Auckland Zoo. Journal of Zoo and Wildlife Medicine, 36(2), 301–307.

Powell, D., & V. W. Bullock, E. (2014). Evaluation of Factors Affecting Emotional Responses in Zoo Visitors and the Impact of Emotion on Conservation Mindedness (Vol. 27). https://doi.org/10.2752/175303714X13903827488042

Pratt, D. M., & Anderson, V. H. (1985). Giraffe social behaviour. Journal of Natural History, 19(4), 771–781.

Prehn, S. G., Laesser, B. E., Clausen, C. G., Jønck, K., Dabelsteen, T., & Brask, J. B. (2019). Seasonal variation and stability across years in a social network of wild giraffe. Animal Behaviour, 157, 95-104.

Rose, P. E., & Croft, D. P. (2015). The potential of Social Network Analysis as a tool for the management of zoo animals. Animal Welfare, 24(2), 123-138.

Ross, M.R., Niemann, T., Wark, J.D., Heintz, M.R., Horrigan, A., Cronin, K.A., Shender, M.A., Gillespie, K. (2016). ZooMonitor (Version 1) [Mobile application software].

Ross, S. R., & Lukas, K. E. (2005). Zoo visitor behavior at an African ape exhibit. Visitor Studies Today, 8(1), 4-12.

Rushen, J., & Passillé, A. M. B. D. (1992). The scientific assessment of the impact of housing on animal welfare: a critical review. Canadian Journal of Animal Science, 72(4), 721-743.

Schel, A. M., Rawlings, B., Claidiere, N., Wilke, C., Wathan, J., Richardson, J., ... & Slocombe, K. (2013). Network analysis of social changes in a captive chimpanzee community following the successful integration of two adult groups. American Journal of Primatology, 75(3), 254-266.

Schmid, V. S., & de Vries, H. (2013). Finding a dominance order most consistent with a linear hierarchy: an improved algorithm for the I&SI method. Animal Behaviour, 86(5), 1097-1105.

Schülke, O., Bhagavatula, J., Vigilant, L., & Ostner, J. (2010). Social bonds enhance reproductive success in male macaques. Current Biology, 20(24), 2207-2210.

Seeber, P. A., Ciofolo, I., & Ganswindt, A. (2012). Behavioural inventory of the giraffe (Giraffa camelopardalis). BMC Research Notes, 5, 650. https://doi.org/10.1186/1756-0500-5-650

Shorrocks, B., & Croft, D. P. (2009). Necks and networks: a preliminary study of population structure in the reticulated giraffe (Giraffa camelopardalis reticulata de Winston). African Journal of Ecology, 47(3), 374–381.

Sosa, S., Puga-Gonzalez, I., Feng, H. H., Zhang, P., Xiaohua, X., & Sueur, C. (2018). A multilevel statistical toolkit to study animal social networks: Animal Network Toolkit (ANT) R package. BioRxiv, 347005.

Stamps, J. A., & Krishnan, V. V. (1999). A Learning-Based Model of Territory Establishment. The Quarterly Review of Biology, 74(3), 291–318. https://doi.org/10.1086/393163

Swanagan, J. S. (2000). Factors Influencing Zoo Visitors' Conservation Attitudes and Behavior. The Journal of Environmental Education, 31(4), 26–31. https://doi.org/10.1080/00958960009598648

Tarou, L. R., Bashaw, M. J., & Maple, T. L. (2000). Social attachment in giraffe: response to social separation. Zoo Biology, 19(1), 41–51.

Van der Jeugd, H. P., & Prins, H. H. (2000). Movements and group structure of giraffe (Giraffa camelopardalis) in Lake Manyara National Park, Tanzania. Journal of Zoology, 251(1), 15–21.

VanderWaal, K. L., Wang, H., McCowan, B., Fushing, H., & Isbell, L. A. (2014). Multilevel social organization and space use in reticulated giraffe (Giraffa camelopardalis). Behavioral Ecology, 25(1), 17–26.

Von Fersen, L., Encke, D., Hüttner, T., & Baumgartner, K. (2018). Establishment and implementation of an animal welfare decision tree to evaluate the welfare of zoo animals. Aquatic Mammals, 44(2), 211-220.

Ward, S. J., Sherwen, S., & Clark, F. E. (2018). Advances in Applied Zoo Animal Welfare Science. Journal of Applied Animal Welfare Science, 21(sup1), 23-33.

Watters, J. V. (2014). Searching for behavioral indicators of welfare in zoos: uncovering anticipatory behavior. Zoo Biology, 33(4), 251–256.

Watters, J. V., Margulis, S. W., & Atsalis, S. (2009). Behavioral monitoring in zoos and aquariums: a tool for guiding husbandry and directing research. Zoo Biology: Published in affiliation with the American Zoo and Aquarium Association, 28(1), 35-48.

Wey, T., Blumstein, D. T., Shen, W., & Jordán, F. (2008). Social network analysis of animal behaviour: a promising tool for the study of sociality. Animal behaviour, 75(2), 333-344.

Whitehead, H. (2009). SOCPROG programs: analysing animal social structures. Behavioral Ecology and Sociobiology, 63(5), 765-778.

Wolfensohn, S., Shotton, J., Bowley, H., Davies, S., Thompson, S., & Justice, W. (2018). Assessment of welfare in zoo animals: Towards optimum quality of life. Animals, 8(7), 110.

Young, T. P., & Isbell, L. A. (1991). Sex differences in giraffe feeding ecology: energetic and social constraints. Ethology, 87(1–2), 79–89.