

Analysis of Intraspecific Communication Plasticity in Captive Female Orangutans (*Pongo pygmaeus*)

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Abstract: Social plasticity, the adjustment of social behavioral expression to the nuances of daily life, is an important facet of primate communication because it is a response to the selective pressures that make one form of communication more advantageous over another when utilized in specific social situations (Oliveira 2012). In this study examining social plasticity of orangutan communication as a function of sex, I compare the time budgets of communicative behaviors among female Bornean orangutans (*Pongo pygmaeus*) at the Lowry Park Zoo, Florida. Sex-based social plasticity was defined as a behavioral difference between same-sex and opposite-sex interactions. Data collection included 65 hours of video, recorded observations, and frame-by-frame analysis using focal animal sampling. Communicative behavior differed significantly between same-sex and opposite-sex interactions ($\chi^2=35.13$, $df=1$, $p<0.01$). When interacting with same-sex conspecifics, females spent most of their time utilizing tactile communication (86.8%), followed by visual communication (13.2%). When interacting with males, females spent most of their time utilizing visual communication (57.2%), followed by tactile communication (42.8%). No significant auditory communication was observed (<0.1%). I conclude that female orangutan communication exhibits sex-based social plasticity. I propose that this plasticity is a behavioral adaptation resulting from sex-specific social selective pressures.

Keywords Primatology, zoology, evolutionary anthropology, primate communication, animal cognition, primate social behavior

Introduction: Reconciling Biology and Culture

Consideration of the evolutionary trajectory of primate communication must emphasize a theoretical shift away from a traditional Neo-Darwinist framework. Neo-Darwinism posits that geographic variation in morphology and behavior are attributed to varying selection on local genotypes (van Schaik 2013). Experiments to test this concept have focused primarily on invertebrates and fish, organisms capable of expedited genetic evolution as a result of small brains and fast life histories (Holbrook et al. 2014; Krutzen et al. 2011; Oliveira 2012). Orangutans are large-brained animals with slow life histories as well as low population rates inhabiting rapidly changing physical and social environments. Genetic selection is therefore too slow to have a significant impact on their behavior (Krutzen et al. 2011; van Schaik 2013). An evolutionary approach to analyzing the adaptability of different communication strategies would not imply genetic adaptation. It would consider adaptation a function of social learning and behavioral plasticity.

A social approach to evolutionary theory implies consideration of the selective pressures that would make one form of communication more advantageous over another when utilized in specific social situations. My research aims

to question the differences in social bonding and therefore in selective pressures that manifest as a function of sex. If the maleness of a recipient necessitates a means of social bonding different from a female recipient in order to facilitate a successful interaction, then I hypothesize that a different communication modality will be employed as well.

Griebel and Oller (2008) suggest that as a social system becomes more complex, communicative flexibility, the ability to adjust communicative behavior to fit a situation, evolves as a means of breaking away from “fixed cues,” unspecialized involuntary states or actions that convey stereotypical information. Fixed cues limit the complexity of information that can be conveyed and would therefore become a disadvantage as the need for multifunctional and contextualized social signaling developed within a group. McComb and Semple (2005) apply a similar concept to vocal communication, suggesting that vocal repertoire size has a strong positive correlation to group size and time spent grooming. McComb and Semple’s work implies that communication modalities, in this case vocal communication, evolve as a function of social bonding in primates.

Changes in communicative strategy, from fixed cues to flexible signals, had a profound effect on neurological processing of social behavior. These changes can be observed on a gradient scale within the primate order. The simplest form of primate communicative flexibility is found among monkeys. Wild rhesus monkeys are known to exhibit within-group call similarity as well as population-specific vocal “dialects” (Hodun et al. 1982). Among Japanese macaques, populational differences have been found in use of food and contact calls (Green 1975; Sakura 1989).

Arbib et al. (2008) hypothesize that mirror neuron activity, as observed in monkeys, is the evolutionary basis for language parity. In other words, all means of communicative ability are the result of brain mechanisms that expand upon the mirror neuron system responsible for perception of grasping actions. Within controlled laboratory studies, monkeys shown a video of a hand picking up an object and then shown another video of an object being placed behind an opaque screen, followed by a hand reaching behind the screen, will exhibit the same discharge of neurons indicative of perception of a grasping action in response to both videos (Fogassi and Gallese 2002). This identical set of responses indicates that the monkeys were recognizing that the hand in the second video, despite not being visible, still had the same goal action as the hand in the first video. However, mirror neurons only discharged during the second video if the monkey knew that an object was behind the screen. If the monkey did not know there was an object behind the screen, then no response was detected. Mirror neurons were activated only when the monkey had a concrete understanding of the trajectory of the action being performed by the hand. The monkey was able to use this information to create a motor representation of the action whether or not the action was visible. These results support Arbib et al.’s hypothesis by suggesting a correlation between mirror neurons and action understanding. Action understanding is fundamental to social assessment skills and subsequent development of proper behavioral responses (Rizzolatti and Craighero 2004).

The most effective means of testing the function of a neurological process is to study the effects of damage or developmental atrophy to the part of the brain responsible for said process. Monkeys reared in social isolation

have been shown to produce species-specific call types but lack the ability to produce their own new signals. This lack of ability suggests that socially isolated monkeys lack the communicative flexibility found in monkeys that learn how to communicate within their social group (Rizzolatti and Craighero 2004).

Concerning great apes, the involvement of a high degree of social learning in acquisition of communicative abilities is supported by studies that show enculturation with humans giving apes a different gestural repertoire from that exhibited by their wild counterparts (Premack and Premack 1972). Furthermore, apes add to the complexity of social ontogeny by exhibiting perception of psychological facts about conspecifics as opposed to just external behaviors (Brothers 1990). For example, DeWaal (1989) describes observing a captive bonobo becoming stranded at the bottom of a moat that is usually connected to the surface by a chain that had been pulled up by previous individuals. The mate of the stranded individual was seen dropping the chain back down the moat, allowing the stranded individual to climb up. DeWaal hypothesizes that this situation was an act of empathy and altruistic assistance by the mate. In the context of Brothers' argument, this implies that the mate constructed a psychological model of another individual, interpreted signs of distress within that individual, and responded accordingly. Such a response also implies that the psychological model of the stranded individual was constructed within an emotional context. If Arbib et al.'s mirror neuron hypothesis is correct, then the construction of a psychological model of another individual would begin with mirror neurons coding the intentions and dispositions of others through interpretation of present actions and learned social signals. Research tentatively suggests that these neuron firings are processed at least partly through limbic structures such as the amygdala and orbital frontal cortex, areas correlated with emotional response and in which brain lesions have been shown to cause deficits in social behavior (Kling and Steklis 1976).

Theoretical Approach

Analysis of social influences on neural mechanisms for social behavior as previously described requires a cohesive theoretical model that addresses the interdependent selective pressures that arise from both the physical environment and the social environment. In this section, I propose a model that combines aspects of social plasticity, niche construction, and evolutionary theory.

Social plasticity is the ability to adjust one's social strategy to fit the current situation or social influence. Such a broad definition allows social plasticity to be observed within the context of both the physical environment and the social environment. For example, as primates made the switch from nocturnal activity to diurnal activity, a greater reliance on visual communication than olfactory communication developed as shown by the disproportionate expansion of the visual system within the primate brain (Brothers 1990; MacKinnon and Fuentes 2012). Certainly, heightened vision was a great advantage in regards to basic survival, providing new means of finding food and avoiding predators. However, the addition of visual communication to the primate repertoire also allowed for a higher degree of temporal sequencing and brevity of signals that surpassed the efficacy of olfactory communication. This new communicative complexity preceded the evolution of more complex social struc-

tures (Brothers 1990). The evolution of visual communication began as a socially constructed exaptation of a response to a change in the physical environment.

The niche construction framework suggests that an organism is actively modifying its environment. In the context of communication, niche construction expands the meaning of communication from a simple transfer of information to an active manipulation of an individual's conspecifics in order to maximize inclusive fitness (MacKinnon and Fuentes 2012). Among orangutans, Knott et al. (2010) found that in response to high levels of forced copulation, females began to exhibit selective resistance as a function of their reproductive status. Near ovulation, females mated cooperatively only with prime flanged males. When conception risk was low, willingness to mate with lower ranked males increased. Knott et al. hypothesized that if a mating is unlikely to lead to conception, females may reduce resistance to avoid costs of male aggression such as personal harm or infanticide. The females are responding to a situation within their social environment by adjusting their social strategy through manipulation of their conspecifics.

Niche construction integrates social theory into an evolutionary framework by expanding Darwinian evolution beyond the physical environment. In opposition to the Neo-Darwinist perspective of evolution, this model posits that among social species, the ability to construct a niche through social manipulation is evolutionarily advantageous. Organisms are responding to their environment as well as using their ability to adapt to a situation in order to manipulate aspects of said environment to their advantage. Concerning long-lived and large-brained animals, geographic influence on local genotypes is statistically insignificant particularly within a micro-evolutionary analysis (Kuze et al. 2005). Instead, social evolution both in response to and in spite of the physical environment must be emphasized. The ability to construct complex social strategies that take into consideration both physical and social context in order to convey desired information is the most advantageous means of survival for an organism, such as the orangutan, that inhabits a consistently and rapidly changing environment.

Methods

Animals

The group of animals, described in Table 1, was comprised of an adult male, Goyang, two adult females, Josie and DeeDee, and two juvenile females, 9-year-old Hadiyah, an offspring of Josie, and 6-year-old RanDee, an offspring of DeeDee.

Setting

This study was conducted at the Lowry Park Zoo in Tampa, Florida. Lowry Park Zoo is a 63-acre nonprofit zoo. The ground level of the enclosure (Figure 1) had a grass-covered floor with palm fronds and moss on raised platforms of rock. This level was almost entirely hidden from the vantage point of the visitors' area unless a visitor observed the level from the edge of the barrier separating the visitors' area from the enclosure.

Table 1: *Bornean orangutans (Pongo pygmaeus)* observed at Lowry Park Zoo, FL.

Name	Sex	Age (years)	Year introduced to group	Known history
Josie	Female	Early 30s	1988	Source: San Diego Zoo; Mother of Hadiah
DeeDee	Female	Mid-30s	1986	Source: Dallas Zoo; Mother of RanDee
Goyang	Male	Mid-teens	2013	Source: Pittsburgh Zoo; Reported copu-
Hadiah	Female	9	2005	Source: Born in Lowry Park Zoo;
RanDee	Female	6	2008	Source: Born in Lowry Park Zoo; Offspring of Dee-Dee and Rango (deceased)

An artificial pool and waterfall provided a constant supply of water. One wall of the exhibit had an entrance from which zookeepers provided food and care for the orangutans on a daily basis. The second level of the enclosure (Figure 2) had a hay-covered floor upon which a series of raised wooden platforms and columns was erected. Wooden logs and rope bridges connected the structures and provided walkways between the levels of the enclosure. Blankets and enrichment items were distributed among the platforms. Spectators could observe the second level from an open air sidewalk or a glass protected sidewalk that led visitors on a path through each of the primate habitats. The third level of the enclosure (Figure 3) consisted of large wooden platforms connected by rope nets and wooden logs atop 50-foot columns in the center of the habitat.



Figure 1: First level of enclosure.



Figure 2: Second level of enclosure.



Figure 3: Third level of enclosure.

Observation Procedures

Data collection was conducted using a series of duration recording sessions. Duration recording monitors the percentage of time a behavior occurs during an observation period. The percentage is calculated by dividing the duration a behavior occurs by the total interaction time (Defler 1993). This type of behavioral recording is the most advantageous method for multimodal communication research because it can account for behaviors of varying duration without distorting statistical significance.

Sessions occurred in 40-minute intervals with 15-minute interludes between each interval. One individual, and all resulting interactions involving said individual, was the focus of observation per session. The target individual was decided upon beforehand using a fixed schedule to ensure that equal time was spent observing each individual. Six duration recording sessions occurred per day. Two individuals were observed per day in alternating sessions. This ensured that each individual was observed for an adequate amount of time at least every other day. Morning and afternoon intervals were alternated between pairs of individuals to ensure that each individual was observed at different times of the day.

Primate communication studies are vulnerable to observation bias through projection of human traits onto nonhuman primates. Operationalization of each concept studied is of particular pertinence. Only behaviors that exhibited intentionality, as opposed to fixed cues, were considered within the scope of this study. Fixed cues were defined as involuntary actions that conveyed stereotypical information thereby limiting its use to only one particular function (Griebel and Oller 2008). Bard defines communication by intentionality and operationalizes intentionality as behaviors that include direct manipulation of an animate or inanimate object in order to accomplish a specific goal (Bard 1992). This is a useful concept for evaluation of tactile communication. However, Bard's definition must be expanded when studying three types of communication modalities to include all behaviors utilized to accomplish a

specific goal. In the context of communication, this means all behaviors utilized to convey information to a recipient. Therefore, a behavior was coded as an intentional communicative gesture if it was performed to capture and maintain the attention of another individual as well as convey desired information in a manner that the recipient understands. Recipient understanding was operationalized as an active attentional state to the interaction, particularly in the form of bodily or facial orientation towards the instigator. Additionally, the instigator must have exhibited a lack of repetition of the communicative behavior to ensure that said behavior did not fail in conveying desired information (Russon and Andrews 2010). Only behaviors that contributed to a mutual interaction, in which the communication recipient responded to the instigator with a communicative behavior, were coded for. Otherwise, recipient understanding, and therefore the signal's efficacy, remained unclear and considered beyond the scope of the study.

Communication modality was defined as a particular way in which communication is expressed. Communication modalities were categorized into three different groups: visual, auditory, and tactile. Visual communication was defined as conveyance of information that could be looked upon by the communication recipient. Auditory communication was defined as conveyance of information that relied on vocalizations. Tactile communication was defined as conveyance of information that relied on physical touch. If an individual utilized more than one modality at a time, then all observed modalities were separately coded for. The purpose of this study is to gain an understanding of the social advantages of each communication modality category (visual, auditory, and tactile). If a single modality contributed to the efficacy of a multimodal signal, then it exhibited an advantage within a particular social environment. Therefore, coding multimodal signals as single modalities does not contribute to statistical overrepresentation of multimodal signals.

All observed behaviors were organized in an ethogram and categorized by modality. Five days of preliminary observation were conducted to become acquainted with individual orangutans and to identify specific behaviors utilized by the group. A behavior was added to the ethogram when observed more than once. These preliminary sessions were not included in the study analysis.

Each interaction was timed from start to finish. Communicative behaviors, as previously defined, were individually timed and recorded for the selected individual. An interaction was considered instigated when an individual's communicative strategy captured the attention of another individual. An interaction was considered completed when the individuals did not utilize communicative strategies towards each other for a period of more than 2 minutes. Any further interaction past this timeframe was considered a new bout.

Due to the subtle nature of many orangutan behaviors, all interactions were video recorded on an Apple iPad using iMovie, a high-speed video recording and video editing software application. Data collection was conducted through frame-by-frame analysis of the video recordings. A separate audio tape recorder was utilized for observation notes. Recordings were transferred to a computer file after data collection.

Analytical Procedures

Utilization of duration recording sessions allowed for analysis of data using a modified time budget approach focusing only on communicative behaviors as previously defined. Time budgeting, calculation of an individual's distribution of time expenditure as a function of implemented behaviors, has been a common form of analysis for behaviors such as feeding, sleeping, and grooming. The significance of the time budget in previous studies is that the results suggest prioritization among the behaviors observed (Defler 1995; McFarland et al. 2014). Within an evolutionary context, preference for a specific behavior implies that said behavior is most conducive to fitness. I propose that preference for a specific communicative behavior implies that said behavior is most conducive to social efficacy. Among social species such as primates, social efficacy implies a higher level of fitness. Social efficacy was defined as the ability to produce a communicative behavior that conveys desired information in a manner that the recipient understands.

Data was analyzed for correlations between type of interaction, same-sex or opposite-sex, and communication modality frequency. Tests of independence were conducted using Pearson's chi-square test, calculated by hand. The chi-square test evaluates the likelihood that observed differences between multiple sets of data arose by chance. Chi-square tests were conducted for same-sex interactions and for opposite-sex interactions to evaluate behavioral frequency for each type of interaction. If the chi-square test showed an insignificant likelihood of differences between same-sex interactions and opposite-sex interactions, then it was possible to conclude that there were no differences between same- and opposite-sex interactions. If the likelihood of differences between same-sex interactions and opposite-sex interactions was shown to be significant, then the most frequent modality in each set was considered the preferred modality for that type of interaction. Frequency of a modality was determined by longest average time among all interactions within a set.

Results

Female orangutans spent a total of 214.38 minutes out of the 65-hour observation period engaging in communicative interactions. A repertoire of 23 communicative behaviors, as defined in the Methods section, was observed, containing 7 visual behaviors and 16 tactile behaviors. One auditory behavior was observed for a statistically insignificant amount of time (<0.01%) and was not considered in the final analysis. Table 2 shows all observed communicative behaviors categorized by modality in association with a short description.

When interacting with same-sex conspecifics, females spent most of their time utilizing tactile communication (86.8%) followed by visual communication (13.2%). When interacting with the one male subject, females spent most of their time utilizing visual communication (57.2%) followed by tactile communication (42.8%) (Figure 4). The difference in time budgets between same-sex and opposite-sex interactions was shown to be statistically significant ($\chi^2=35.13$, $df=1$, $p<0.01$) (Table 3). These results imply that females exhibited an adjustment in social strategy, through changes in communication modality preference, in response to the sex of the individual with whom they were interacting.

Table 2: Observed orangutan behaviors categorized by modality in association with a short description.

Modality	Behavior	Definition
<i>Visual</i>		
	Eye-gaze/stare	Instigator looks steadily and intently at recipient
	Baring of teeth	Instigator opens mouth slightly with corners of mouth pulled back and teeth visible
	Arm wave	Instigator extends arm and waves it horizontally in front of own body
	Move away	Instigator gazes at recipient within a distance of 3 feet or less then moves away from recipient
	Present genitals	Instigator sits in front of recipient, facing forward or backward, and presents genitals
	Chase	Instigator pursues recipient engaging in "Move away"
	Smile	Slight turning of the corners of the lips with mouth closed; all open mouthed variants are coded as "baring of teeth"
<i>Tactile</i>		
	Bite	Instigator bites recipient on any body part
	Hold tight	Instigator seizes hand or foot of recipient
	Put hand on head	Instigator puts flat hand on head or back of recipient and remains there
	Give object	Instigator gives object to recipient
	Grab object	Instigator seizes object in recipient's possession, usually followed by attempt to take object away from recipient
	Throw object	Instigator throws object at recipient
	Suckle	Instigator suckles recipient's nipple
	Social grooming	Instigator removes dead skin or parasites from recipient

Table 2 cont.

Modality	Behavior	Definition
<i>Tactile</i>		
	Grab	Instigator forcefully grasps body part of recipient
	Embrace	Instigator puts one or two arms around body of recipient
	Gentle touch	Gentle touch with hand or foot
	Lip touch	Instigator touches recipient's lips with own lips
	Pull	Instigator grasps and forcefully moves body part of recipient
	Push	Instigator forcefully shoves recipient
	Slap	Instigator forcefully touches recipient with a flat hand
	Mate	Instigator engages in sexual intercourse with recipient

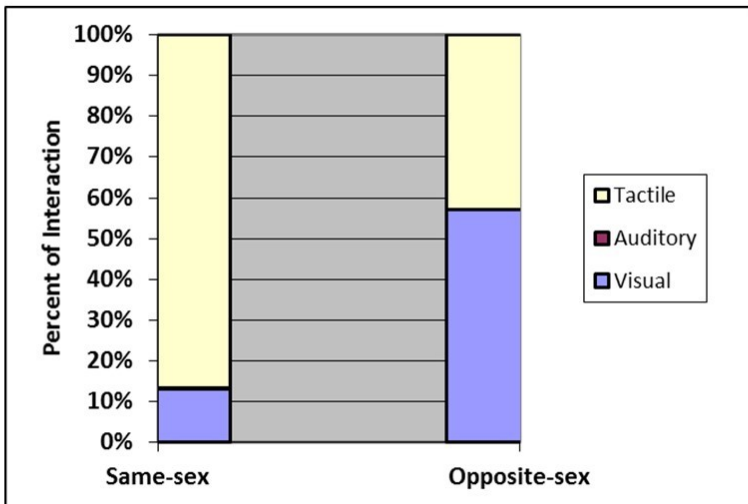


Figure 4: Bar graph depicting time budget percentages for same-sex and opposite-sex interactions.

Table 3: Chi-square test variables for same-sex and opposite-sex interactions.

Interaction Type	Modality	Percentage	Observed (minutes)	Expected (minutes)
Same-sex	Tactile	86.8	155.53	142.56
Same-sex	Visual	13.2	23.58	36.55
Opposite-sex	Tactile	42.8	15.1	28.07
Opposite-sex	Visual	57.2	20.17	7.2

Results: $\chi^2=35.13$, $df=1$, $p<0.01$

Limitations

Multimodal communication research is inherently limited because attention must be divided between the modalities. Due to site and sample size limitations, the findings of this study may be highly contextualized.

Captive subjects may exhibit different behaviors from their wild counterparts due to the nature of their environment and upbringing. The social system of orangutans in the wild is considered to be semi-solitary. However, captive orangutans are kept in groups for long periods of time (Tajimi and Kurotori 2010). The difference in environment and upbringing can have a significant effect on their behavior that must be considered when conducting a captive study. Frequency of social interactions increases as a function of closer proximity (Tajimi and Kurotori 2010). Tobach et al. (1989) found that in a close-quarters setting orangutans behave similarly to chimpanzees in that associative behaviors revolve around the behavior of the females and infants. However, Tobach et al. defined associative behavior strictly by tactile association. Rather than dictating the associative behavior of the group, perhaps females were exhibiting a preference for tactile communication when interacting with each other or their infants.

Observation of varied opposite-sex interactions was limited because only one male inhabits Lowry Park Zoo. The male is an adult so observation of interactions with male infants and juveniles was impossible.

Discussion and Conclusions

Analysis of the collected data indicated a difference in female communicative behavior between same-sex and opposite-sex interactions. Females preferred tactile communication when interacting with other females and visual communication when interacting with the male. These results indicate that female orangutan communication exhibits sex-based social plasticity. I propose that, by budgeting their interaction time in preference of a particular communication modality, females deemed said modality most advantageous in achieving a successful social interaction. This social success is indicated by the mutual participation of both instigator and recipient in a communicative bout as well

as observation of recipient understanding as defined in the Methods section of this study.

Congruent with the niche construction framework, the behavioral discrepancy between same-sex and opposite-sex interactions indicates consideration as well as intentional response to the sex of the communication recipient. Intentionality requires conveyance of information in a manner that the recipient understands. The results of this study indicate that sex was recognized as a variable that required a change in a female's manner of information conveyance. In other words, females had to adapt their social strategy to fit the particular social situation. Requirement of adaptation in order to successfully navigate the social environment categorizes sex as a social selective pressure.

Further study is required to understand the implications of sex as a social selective pressure. These results simply indicate the presence of said pressure. It can also be tentatively concluded that female orangutans exhibit an ability to recognize social selective pressures through their plastic response to this particular change in the social environment (sex of communication recipient). Further study is required to ascertain whether this evaluative ability extends to other social pressures, such as familial relation and resource possession. Such studies could lead to a better understanding of communication plasticity as a means of social adaptability.

This study was a pilot study of time budget analysis for strictly communicative behaviors. Time budgeting has been a common form of analysis for behaviors such as feeding, sleeping, and grooming. According to Defler (1995) and McFarland et al. (2014), the significance of the time budget is that the results suggest prioritization among the behaviors observed. Within an evolutionary context, preference for a specific behavior implies that said behavior is most conducive to fitness. When communication is included in a time budget, it is usually placed under the umbrella category of social activity. For example, Defler (1995) conducted a time budget analysis of wild woolly monkeys that included categorizing behaviors as either "resting," "moving," "foraging," or "social behavior." "Social behavior" was operationalized as any interaction between two individuals. Such a vague definition implies that any form of association could be considered social. This disregards the need for context and cognitive processing of said context, which separates a social situation from a simple spatial relation. Similar categorization can be found within a study on orangutan social behavior conducted by Mitani et al. (1991) in which the terms "association" and "social behavior" were utilized interchangeably and operationalized as two animals approaching within 30 meters of each other.

Time budget analysis has the potential to integrate social behavior into an evolutionary framework but only if communication is considered a separate and more complex category than that of spatially defined associative behaviors. As preference for a specific type of behavior implies that said behavior is most conducive to fitness (Defler 1995; McFarland 2014), I propose that preference for a specific communicative behavior implies that said behavior is most conducive to social efficacy. Among social species such as primates, social efficacy implies a higher level of fitness.

Acknowledgments

I would like to thank Lorena Madrigal and Daniel Lende for their guidance. I also thank Lowry Park Zoo for allowing me to conduct research at their facility.

Notes

1. The author completed the research for this article at the University of South Florida and will be enrolling as a master's student at the University of Roehampton.

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