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The use of social space with respect to rank : a look into female African elephant behavior (Loxodonta africana)

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The use of social space with respect to rank: a look into female African elephant behavior (*Loxodonta africana*)

A Thesis submitted in partial satisfaction of the requirements for the degree

Master of Science

in

Biology

by

Kelleen Leann Inglett

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Edwin Hutchins, Chair
James Nieh, Co-Chair
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David Woodruff

2014

The Thesis of Kelleen Leann Inglett is approved and it is acceptable in quality and form for publication on microfilm and electronically:

Co-Chair

Chair

University of California, San Diego

2014

DEDICATION

To my grandpa, Rocky Beebe, for always believing in me. He taught me so much, and now it is up to me to me to integrate those lessons into my life.

You will forever be missed.

EPIGRAPH

The student of behavior should seek to explain behavior, and not to prove that it cannot be explained.

Nikolaas Tinbergen

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I would like to wish a special thank you to Dr. Chris Johnson for all her support and guidance. She continually showed her belief in my capabilities and pushed me to do my best. In turn, I will continually be grateful for all she has done for me.

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ABSTRACT OF THE THESIS

The use of social space with respect to rank: a look into female African elephant behavior (*Loxodonta africana*)

by

Kelleen Leann Inglett

Master of Science in Biology

University of California, San Diego, 2014

Professor Edwin Hutchins, Chair

Professor James Nieh, Co-Chair

Female African elephants live complex lives that revolve around hierarchical group living, and the alloparenting of calves. However, how a female's rank may in turn affect her use of social space has not been fully examined; nor how the introduction of a newborn can affect the mother's use of social space. We addressed these questions by observing the elephants at the San Diego Zoo Safari Park. By integrating a video-annotation program *ChronoViz* with the *Anoto* digital pens, we traced out the paths of the subjects. Using the data provided by the program, we were able to determine the following rank-based findings: (1) low ranked elephants are more reactive than high ranked elephants upon being approached, (2) high ranked elephants are more likely to demonstrate "TO" behavior towards low ranked approachers, rather than vice versa, (3) reactions occur at a greater distance when a low ranked elephant approached a high ranked elephant, rather than vice versa, and (4) behavioral responses within a hot spot area were not significantly different than responses outside a hot spot area. We were also able to observe the following about changes that occur with the mother once the calf was born: (1) an increase in the mother's reactivity upon being approached, (2) an increase in the mother's TO behavior, and (3) an increase in the distance at which a high ranked elephant would react to the approach of the mother. These findings suggest that not only rank, but also the presence of a newborn, affects the way female elephants use their social space.

Introduction

Female African elephants (*Loxodonta africana*) present a particularly interesting subject in animal behavior due to their highly social behavior. They form and can maintain groups at multiple levels of organization. At the smallest family level, groups consist of 2-30 closely related females and their calves (Poole, 1996). These "family groups" can come together with other distantly related or allied family groups to form large communities, called "bond groups", which can include up to 5 different families of varied sizes (Ibid). This can lead to bond groups potentially as large as 150 elephants (Ibid). These bond groups can repeatedly divide back into the smaller family groups and then come together again, a process referred to as "fission-fusion" (Byrne, Bates & Moss, 2009; Poole, 1996; Wittemyer, Douglas-Hamilton & Getz , 2007a). Importantly, members of bond groups are capable of recognizing one another, indicating a high level of social intelligence (Byrne, Bates & Moss, 2009; Payne, 2003).

While male African elephants also sustain complex social structures, they spend their adolescent and adult lives primarily in all-male groups, or "bachelor groups", away from the female groups described. This means that these males do not regularly take part in female social interactions, except during times of musth when the males are primed for mating and seek out females (Hollister-Smith et al., 2007). Due to this, male social behavior is a subject in and of itself which we will not be investigating.

In addition to the female social characteristics discussed above, these animals are also capable of recognizing and following the eldest female elephant in their family group, called a matriarch (Payne, 2003; Wittemyer, Douglas-Hamilton & Getz, 2007a).

The matriarch's role is to lead the group to resources, help in defense, and support the overall survival and reproductive success of those under her guidance, while also maintaining overall dominance of the group (McComb et al., 2001; Payne, 2003). Depending on the matriarch's age and life experiences, she can handle and guide either larger or smaller family, and even bond groups (Wittemyer, Douglas-Hamilton & Getz, 2007a). The presence of a dominant, leading female, along with others of descending rank, has lead researchers to refer to elephant society as being hierarchical in nature (Byrne, Bates & Moss, 2009). A female elephant's rank can play a big role in her daily life, such as limiting or expanding the number of resources available to her through competition (Wittemyer, Douglas-Hamilton & Getz, 2007b).

It can be observed, both in the wild and in captivity, that distinct social ranks exist amongst female African elephants, ranging from dominant to subordinate (Adams & Berg, 1980; Freeman, Weiss & Brown, 2004; Friedman, 2011; Meeberg, 2010). Each rank has its own etiquette, or set of distinguishable behavioral characteristics, that sets them apart (Meeberg, 2010). Dominant females, for instance, tend to be more aggressive in their movements towards subordinate members, frequently making antagonistic gestures towards them such as shoving them, displacing them from a certain location, and flapping their ears while facing them (Ibid). Subordinate females, in turn, tend to heed the dominant members of the group and display subservient gestures towards them such as stepping aside or presenting their rear as they pass, accepting displacement by them to a given area, and occasionally running away from them (Ibid).

On top of visual social cues, other forms of communication also take part in this exchange of social information. For instance, elephants have a keen sense of smell, which they can use both during proximal inspections of one another's bodies, as well as from a distance (Byrne, Bates & Moss, 2009). They also produce both high frequency sounds, which are audible to humans, and low frequency sounds, which cannot be heard by humans but can be heard by other elephants, up to several kilometers away. In turn, they can use their ears, their trunk, and the padding at the bottoms of their feet to hear these sounds (O'Connell-Rodwell, 2007). While such communication is important for understanding the nuances of social behavior in these animals, a lot can still be gained just by observing the physical movements of the elephants and their use of space.

For example, in a study conducted by George Wittemyer and colleagues (2007b; 2008), it was found that rank plays a role in how a female elephant moves throughout the year, with respect to others, depending upon resource availability. In their study, they were able to discern that higher ranking females tend to walk shorter distances in comparison to lower ranking females during less productive seasons. This allows the higher ranking females to access closer, more desirable resources with less energy, ultimately staking out more valuable regions for themselves. They also found that high ranking females tend to use roughly the same daily paths of their choosing, at roughly the same times. Low ranking females used daily paths of their choosing as well, but the timing at which these paths were used was less consistent. It was determined that higher ranking females are able to be more choosey about their daily routines, while subordinate females had to alter their routines around the presence of dominant members, avoiding areas and times in which they could come into contact with one.

While Wittemyer and colleagues' provide some information on general differences in movements between dominant and subordinate elephants, not many other studies have been conducted on this matter. Because of this, while general rank etiquette is known, very little is known about paths and the different use of social space by female African elephants. Further research into the series of events that occur when a subordinate female comes into proximity of a dominant female, and how much space is afforded to a nearby subordinate female by a dominant one, has yet to be conducted. Exploring further into the topic of social space amongst female African elephants will be the focus of the current study. As a part of that focus, we will also examine the role these valuable, personally preferred regions - which we call "hot spots" - may contribute to the use of female African elephant social space. For our purposes, hot spot regions are defined as areas an elephant is frequently recorded in across the study period.

Another important part of a female African elephant's life involves the rearing of calves (Lee, 1987). In many cases other females will help care for and protect a calf that is not her own, called “alloparenting”, and a mother and her calf can potentially have multiple females carrying out this task at a single time (Ibid). However, an interesting part of this social interaction reveals that rank, again, plays a big role in determining who gains alloparents and who does not. A study conducted by Lee (1987) found that lower ranking females, particularly those that have just had their first calf, are more likely to have alloparents. Conversely, higher ranking females, particularly matriarchs, are less likely to have alloparents. Lee determined that this was likely due to the high-ranking mother's ability to become defensive of her young, therefore making alloparenting towards that calf unwelcoming or unappealing to others. In contrast, the low ranking female was unable to contest against potential alloparents, and consequently became a greater target for other females. This study established that a mother's sociality can be influenced by both her rank and the presence of a newborn. If a new mother is low ranking she is likely to come into contact with many more females, potentially more than average, in comparison to a high ranking mother. However, since most studies on alloparenting are focused on the calves, little is known about how this alteration in number of social interactions may temporarily, or permanently, alter a mother's use of social space, and how this could in turn affect her rank within a group as well. Since one of the subordinate subjects gives birth during the current study, we are able to take a unique look into fluctuations that may occur in that particular female's use of social space.

An additional part of our study also takes into consideration individual differences amongst the subjects. It has been noticed across several species, such as sticklebacks, tits, butterflies, dolphins, primates, bluebirds, mice, and rats, that constant differences in reaction types in response to various situations occur from individual to individual (Highfill & Kuczaj, 2010; Wolf, 2009; Wolf & Weissing, 2012). These differences can be referred to as “personalities” and, just like in humans, can alter slightly over time as life experiences and social contexts shape the individual (Wolf, 2009). These studies have discussed the evolutionary pressures and ecological functions for the presence of varied personalities, but one finding of interest is how personalities can affect the distribution of individuals across a given area. For example, Wolf and Weissing (2012) found that some male western bluebirds have an aggressive personality and some a passive personality. The more aggressive male bluebirds tended to aggregate around desirable territory areas and competed against other aggressive types. Meanwhile, the more passive male bluebirds tended to stray and make less desirable areas their territory, avoiding conflict.

In our study, differences in personality could be identified in the elephants we observed, from aggressive to passive and other small variations. We hypothesized that this could play a role in individual movements and the use of social space. Because of this, it was agreed that the study had to be broken down into two parts. The first part focuses on general differences between high and low ranking female African elephants, and the second part focuses on individual differences in the use of social space, specifically the subordinate mother's changes as her calf is introduced.

Our overall hypothesis aims to reveal that differences in the use of social space occur across ranks and also after a female gives birth. The following questions about social rank and space still remain; these are the questions that will be addressed in our study. How do general rank differences affect the way a female African elephant moves and negotiates social space with other ranks? More specifically, (1) are low ranking elephants more reactive to the presence of others in comparison to high ranking elephants? We hypothesize that this will be true. (2) Is there a difference in the type of behaviors observed across low and high ranking group members when approached? We expect to see more aggressive behavior from high ranking elephants, and more submissive behavior from lower ranking elephants. (3) Is there a difference in mean reaction distance between low ranking and high ranking elephants? We hypothesize that the reaction distance will be greater when a high ranking elephant approaches a low ranking elephant, and for the opposite to be true if the ranks are swapped. (4) And lastly, does being within a personal hot spot region when approached influence the behavioral response observed? We hypothesize that approached elephants within their hot spot will be more likely to stay and defend their personal area rather than flee, no matter rank. Questions 1-3 will also be addressed in terms of individual differences between the elephants.

We will primarily look at the role of individual differences by examining the impact of the birth of a calf, in terms of how it may alter a subordinate mother's social space and potentially affect her rank. Specifically, we will ask if the increased level of social activity, due to alloparenting, changes the way a subordinate mother is able to react to more dominant group members. Plus, we will explore if the space allowed between the subordinate mother and a dominant group member is altered by the presence of the newborn. We hypothesize that the mother will become more reactive to others, that she may start to display more aggressive behavior , and that dominants will react to her at a further distance once the calf is born. In this study, observational data were collected in attempt to answer these questions and provide further insight into the complex social abilities of African elephants that has yet to be fully understood.

The way in which observational data are gathered during behavior studies has expanded with the development of new coding technologies. In the past, methods such as Focal Animal Sampling (FAS), in which a biologist focuses in on one subject out of a group and records any behaviors of interest at a set time interval (Meeberg, 2010), were commonly used. Today, more in-depth questions are being asked which require alternative data collection methods. Studying the use of social space in vertebrates and invertebrates has become an increasing popular subject in ecology and animal behavior. The most frequently used new tool for gathering information on an animal's location within a given area has been GPS - in which GPS collars, for example, are attached to wildlife and their movements tracked (Mabry & Pinter-Wollman, 2010). While this method is very accurate, it can be an expensive option.

The current study was set on developing a new method for taking spatial data, within a zoo enclosure, that was both informative and cost effective. In the development of a video-analysis program called *ChronoViz*, which we used to score our data, and its integration with new digital-pen technology, we hoped to develop an alternative method that could also be useful for future social space studies.

To carry out this study, video was taken of the African elephants at the San Diego Zoo Safari Park, whose ranks were already known by the keepers who worked with them. Using *ChronoViz,* developed by a UCSD graduate student in the Cognitive Science department (Fouse et al., 2013), and the *Anoto* digital pen, manipulated by a post-doc in the Cognitive Science department (Weibel et al., 2012), a protocol was created in which the paths and orientations adopted by the elephants could be traced onto a map of the enclosure. From there the program is able to turn out digital data on the orientations and locations each elephant occupies throughout the video. With this output we are able to calculate how far apart the elephants are, how one elephant orients or moves when another walks by, and so on. With this information it is possible to further investigate and understand the rank-based, and individual-based, use of social space.

Methods and Materials

Subjects & Setting

The adult African elephants (*Loxodonta africana*) observed in this study are located at the San Diego Zoo Safari Park, where they occupy an open, three-acre enclosure. This type of enclosure allows for free movement and interactions to be naturally carried out between elephants with no restraint, making behavioral studies possible (Adams & Berg, 1980; Berg, 1983; Friedman, 2011). There are eight adults in this group: two males (one adult, the other an adolescent), and six females estimated to be within a relatively close age range but occupying an array of rank levels (Table 1). All of these adults were originally born wild in Swaziland, Africa, and moved to the San Diego Zoo Safari Park. One of the subordinate females was pregnant and gave birth about midway through the recording period, providing a unique studying experience which allows us to look into the effects of a newborn on a mother's social space and behavior.

When I initially joined Dr. Christine Johnson's lab, another graduate student at the time was conducting a study to determine the relationship between food access and rank in these animals. As one of several interns working on this project, I was assigned the task of making weekly visits to the Safari Park in which I would videotape the elephants. Each intern, on our assigned days, would come equipped with a *Canon ZR200* video camera, a *GoPro HD Hero* video camera, a tripod which could hold both in place, and 16 GB memory cards for each camera. The importance of the two cameras was so that the *Canon* camera could focus in on a particularly interesting interaction or gathering, while the *GoPro* could continue recording a wide view of the enclosure and reduce the chances of missing a secondary interaction, as well as the approach or retreat of animals farther from the focal interaction. We would begin filming at 11:30am each trip, the time at which the keepers released the elephants into the enclosure after cleaning and placing food around the area. This time was ideal for recording elephant interactions because of the “rush”, as they all entered the enclosure at once - and because it was during this period that the most active negotiation for access to food piles occurred. We would end our recording session once the two 16 GB memory cards were full (roughly an hour worth of video).This process of gathering video continued between October 2010 to May 2011.

Once the recording process was over, Dr. Johnson took me on as a graduate student under the BS/MS program in Biology, under Dr. Ed Hutchins’ formal supervision. Our study would continue using these same videos from the previous study, but our focus would be on the negotiation of space amongst the different ranking elephants. A new group of interns were selected, and I supervised their training. These students were initially required to spend 4-6 hours a week at the Safari Park, getting used to identifying each elephant, recognizing patterns in their movements, and becoming more familiar with the layout of the enclosure itself. Since our study would require a form of mapping of the negotiation of space occurring amongst the subjects, being familiar with the enclosure itself was key to making this study successful.

Data Collection Development/Protocols

One goal of this study was to develop a way to efficiently take data on the relative locations and orientations of our subjects as they moved about their enclosure. In developing our data collection method, we worked closely with Dr. Adam Fouse, the creator of *ChronoViz*, and Dr. Nadir Weibel, whose work focuses on adaptations of the *Anoto* Digital pen. *ChronoViz* is a program which allows for time-linked notes to be associated with video and/or audio recordings. The *Anoto* pen is designed to turn written notes into digital notes. This is made possible by the use of special paper covered with a coordinate system of dots which the *Anoto* pen recognizes. This means the spatial location of a mark on this paper is used by the computer to create a digital version of that mark in the appropriate location on a digital map. Bringing these two technologies together permitted us to use *ChronoViz* to not only take temporal data, but spatial data as well. These properties made the updated version of *ChronoViz* an ideal program for the mapping of paths, which was exactly what our study required. While the technology was still new, Fouse and Weibel were up for the challenge of helping to mold their program to our specific study.

The first step in molding *ChronoViz* to our needs was to create an image to be printed on our notes sheet that the *Anoto* pen could be programmed to recognize. This image could be anything, depending on the purpose of your note taking, as long as the image could be fitted onto standard 11x8.5 inch printer paper. For our study, this meant acquiring an image of the enclosure and determining which part of the space should be the focus area. Working with a team of interns, a map area was agreed upon and selected, using *Google Earth*, to created a 2D version of the central area of the enclosure (Figure 1). The center of the enclosure was selected for three reasons: (1) Printing the entire enclosure area would mean reducing the level of magnification and thus reducing our ability to draw out details of the animals' movements, (2) social interactions frequently occurred within the central region, and (3) the clearest video collected was of this central region, where few viewing obstructions are present within the enclosure. Adaptations were made to the selected map area over time, after gradually becoming more familiar with the enclosure and the elephants, by coloring in pre-established dirt paths and landmark cues that were found to be helpful when taking data. Coloring-in these areas, while reducing the "realism" of the image, made viewing the selected map area and determining elephant locations easier, particularly when training new interns (Figure 2).

The second step in preparing *ChronoViz* for our study was deciding how to go about drawing the paths and which movements should be considered. From July 2011 through December 2011a team of interns, Dr. Johnson and I, through trial and consensus, determined the marks/movements to be considered and the protocol for drawing paths. Each decision we made was relayed to Fouse and Weibel, who translated our needs into computer code for *ChronoViz* and the *Anoto* Digital pen. This was a continuous, iterative process of editing, determining what could actually be programmed into *ChronoViz*, and finding other movements which needed to be accounted for in our study. Ultimately, a separate "Control Panel" sheet (Figure 3) was created which enabled us to select which subject out of eight possible choices we were drawing, and also select the type of movement/mark out of seven possible options we wanted to draw (Table 2). An official protocol sheet was also created, defining each movement of interest and listing the order/timing in which paths were to be drawn. The criteria for scoring the behaviors important to our study are listed below:

Forward Trajectory:	Elephant moves forward by more than half a body length, signified by the bending of the knee initiating the first step.
Backward Trajectory:	Elephant takes at least two steps back.
Veer:	During a trajectory when one of the four feet begins to shift off line of that trajectory, causing a change in path direction.
Change in Pace:	When an elephant begins to move slower/faster than before. Timemarkers need to be placed at the beginning and end of this speed change.
Stop:	Elephant has at least three feet on the ground, stationary, for three or more seconds.
Orientation:	The position/direction an elephant faces when it comes to a stop.
Pivot:	When an elephant is stopped and oriented and their orientation changes without the use of a trajectory, but rather the scooting of their feet.
Shuffle:	When an elephant makes an unusual movement that cannot be categorized by any of our other listed behaviors (ex. side-stepping). Must move by more than half a body length to be considered.

These behaviors (except shuffle) were regularly displayed by the subjects and were necessary for the mapping-out of their daily movements. Also added to our scored data were "noteworthy" moments, in which a five-pointed star would be drawn to bring our attention to particularly unusual or interesting interactions. To draw out these behaviors in *ChronoViz*, the following order of path drawing was used:

1. Watch video and draw out preliminary paths in pencil
2. Once familiar with the paths, open *ChronoViz* and connect *ANOTO* pen
3. Select a single elephant path to work on
4. Draw entire path line (forwards and backwards parts) at time of elephant's appearance within the video
5. From beginning to end of video, draw timemarkers at the time of any behavioral change listed above besides pivot

6. From beginning to end of video, draw orientations at each stop time/location
7. Draw pivot arrows at appropriate times/locations
8. Draw in shuffle circles at appropriate times/locations and add a comment to describe the movement
9. Draw Noteworthy stars near times/locations of unusual interactions
10. Add comments to any other annotation marks where description of interaction is helpful
11. Watch path play out to ensure it runs smoothly and as desired
12. Close out of *ChronoViz* to save completed path
13. Continue repeating steps 2-12 for each elephant/path within the video

Inter-Observer Reliability test

Data collection officially began in December, 2011, once we had agreed on, and felt secure about, our protocol. Before initiating data collection, Inter-Observer Reliability (IOR) tests were required. Since this type of study does leave room for some idiosyncratic interpretation of the paths, but still requires a certain level of agreement across observers, we used two different methods to determine path likeness that took into account individual variations. First, we used a method that was visually based for initial determination of agreement. We came up with a way in which we would each draw the same series of paths and then overlay them. Due to my extensive experience in studying and drawing out paths, my map acted as the master key for all the others to be compared to. This would reveal to a certain extent the level of agreement across multiple observers. If the overlaid paths were too different from my own, then we would continue practicing and discussing how to draw certain scenarios/movements. Once the overlaid paths visually began to share more likeness in location, timing, and mark/behavior type to my own, we would allow data taking to proceed. This series of events (IDing the elephants, becoming familiar with the enclosure/map and elephant social movements, learning to use *ChronoViz*, and lastly visual path similarity) became the way in which new interns were trained to take data.

Because of delays in extracting the drawn data from *ChronoViz*, and not wanting to hold up data collection, our second quantifiable method of determining likeness had to be held off until after data taking began. As soon as the data spreadsheet was available to us, we ran an Index of Concordance test across behavioral agreements (i.e. orientation, timemarker, pivot, shuffle), time agreements, elephant ID agreements, orientation agreements (i.e. heading towards another, which we refer to as "TO", or heading away from another, which we refer to as "FROM"), and distance between elephants agreements. To begin, we again had each observer work on the same video. Once done, we calculated reliability (R) by taking the number of behaviors that were correct/agreed upon (N_a) and dividing it by that value again, plus the number of behaviors that were incorrect/not agreed upon (N_d) (Paterson, 2001):

$$R = N_a / (N_a + N_d)$$

For qualitative comparisons (i.e. Behaviors, elephant ID, and orientation), we counted the number of agreements and disagreements to conduct the test. However, for quantitative comparisons (i.e. Times and distances), we counted values correct only if they were within one standard deviation of the mean across all observers. In the end, the reliability amongst all variables came out to be an acceptable value of 0.802.

Data Collection

A little less than 200 videos worth of data (varying from 1 to 11 minutes long) were collected over the course of a little more than a year (December 2011-June 2013). These videos include interactions, which we define as an approach moments in which one subject walks closer to another, between all possible adult members, particularly focusing on the lowest and highest ranking females, T1, T3, T5, and T6. The analysis plug-in, created primarily by Dr. Nadir Weibel, turned our drawn data into a spreadsheet which contains information on the movements of each elephant at any given time, and the location (x-y coordinates) and orientation angle (0-360 degrees) of all other elephants at that time of action. This information is crucial in determining when an elephant may begin approaching or reacting to another during the course of a continuous video. For the purposes of our study, we define reacting/reactions as any change in orientation or position observed in the approachee upon an approach moment. These changes would appear in the data as one of our control panel behavior button options (i.e. pivot, orient, timemarker, etc). While these behavioral changes are likely due to the presence of the approacher, it is possible that other variables (i.e. nearby calves, food, keepers, etc.) may play a role as well.

Jeremy Karnowski, a graduate student of Dr. Edwin Hutchins and Dr. Christine Johnson, collaborated by creating a code that specifically found approach moments. This process included regular meetings between Karnowski and I in which I would describe how I would determine an approach or define specific moments, us agreeing upon the definition of these specific moments, and him writing code that captured this definition.

After testing the code across several different videos (roughly 18 minutes worth of video all together) and gaining 100% agreement between the code output and the videos, a final spreadsheet was provided. As a result, the following rules had to be met to be considered an approach moment and to determine which elephant was the "approacher" (i.e. the elephant doing the approaching), and which was the "approachee" (i.e. the elephant being approached) (J. Karnowski, pers. comm., January 11, 2014):

- Elephants separated by a distance of 32m or more were not considered as interacting. If an elephant left the region used for data collection, it was also considered to not be interacting.
- Approaches begin when the distance between two elephants decreases.
- At the start of an approach, the elephant that is moving is labeled the approacher. If both elephants are moving at this time, then the elephant that is more oriented towards the other is considered the approacher. The other elephant is then determined to be the approachee.
- The activity that follows will continue to be considered as part of the approach until one of three conditions is met: (1) If the distance between the elephants increases, then the end of the approach is the time point before the increase in distance. (2) If at any point during the approach, the distance between the elephants remains stable for 9.5 seconds or more, then the end of the approach is the time point before the period when the distance was stable. (3) If the distance between the elephants remains stable for less than 9.5 seconds, but the approachee faces away from the approacher by more than 90 degrees, the end of the approach is the moment before the approachee turned away.
- In addition to the above approach information, we were also interested in any responses that occurred immediately after the approacher passed the approachee. Therefore, 15.1 seconds were added to the end of approaches to capture any delayed reactions. This additional time was shortened if another approach activity started.

In the end, the spreadsheet Jeremy's code provided information on the complete time length of the interaction, distance between the approacher and approachee, the minimum distance reached, each reaction made by the approachee (including behavior such as walk and pivot, whether the behavior was a TO or FROM movement, the distance between the two, and the x-y coordinates of both the approacher and approachee at that moment). This was the spreadsheet we primarily used when conducting our statistical tests, which contained a total of 643 interactions between the four elephants of interest (i.e. T1, T3, T5, and T6).

For determining hot spots, we considered the areas in which each elephant frequented the most out of all the data collected to be their personal hot spot regions. Each ended up being a very different and unique region of the enclosure (Figure 4). The program *R Studio*, using a Kernel Density Estimator plug-in, was used to determine these frequented areas. Jeremy then collaborated again by helping me gain access to the actual x-y coordinates that made up each hot spot region. Once these x-y coordinates were gathered, it was possible to determine which approachee interactions occurred within their own hot spot regions by finding matches in coordinates via *Excel 2007*.

Rank-based Data Analysis

First we conducted analyses on general rank-based differences in the use of social space. For “reactivity” - that is, how likely the approachee was to react to the approacher - differences in the mean number of behaviors observed across different rank pair approach moments was determined using Tukey-Kramer Honestly Significant Difference Test (Tukey-Kramer HSD) via the statistical program *JMP 11*. Under all uses of Tukey-Kramer HSD, approachee was used to match columns across that variable for proper comparisons of approachee behavior, and an alpha of 0.05 was used.

Behavioral rank-based differences were split into two parts. The first behavioral analysis considered whether significant differences in TO/FROM behavior were observed across high and low ranking approachees, and whether high ranking approachees were more likely to exhibit TO or FROM behavior. In this case, we are looking at TO as being a primarily dominant behavior, though it could arise occasionally when one elephant faces another without an antagonistic purpose. Conversely, FROM is being considered a primarily subordinate behavior, though it could occasionally arise when one elephant faces away from another for a different purpose (i.e. food pile, calf, etc.). The second behavioral analysis considered the same questions, but instead focused more specifically on walk/pivot behavior. For this instance walk is being considered a complete displacement from a given area and therefore more submissive in nature, though one subject could potentially walk away for different reasons. Similarly, pivot is being considered an acknowledgement of the other elephant but not a full displacement, therefore a less submissive behavior, though it could again potentially occur for other purposes as well. Under both instances Fisher's Exact Test was used to answer these questions via *JMP 11*.

Differences in mean distance of reaction across high and low ranking appoachees was analyzed using the same Tukey-Kramer HSD methods performed for reactivity analysis.

Lastly, likelihood of walk/pivot behavior inside and outside personal hot spot areas were analyzed using Fisher's Exact Test, using the same methods as with the behavioral data analysis. For hot spot analysis, the test did not specifically take rank into consideration, but general behavior trends across all observed elephants.

Individual-based Data Analysis

Secondly we analyzed individual-based differences in the use of social space. Reactivity was determined using Tukey-Kramer HSD via *JMP 11*, using the same methods as rank-based comparisons mentioned previously.

Behavioral elephant pair differences were analyzed separately as TO/FROM and walk/pivot behavior. Both were tested using Pearson's Chi-Squared Test in *JMP 11*.

Difference in mean distance of approachee reaction across elephant pairs again used the same Tukey-Kramer HSD methods used previously.

All of the individual-based analyses were also split down from the total study period, into individual seasons: Fall 2010 (Oct-Dec), Winter 2011 (Jan-March), and Spring 2011 (April-May). This was done to better interpret how the birth of T3's calf may have altered her sociality. Given that the calf was born in January (Winter 2011), we expect changes in behavior to occur around that time. The same statistical tests were used for reactivity and distance across seasons. However, due to small sample sizes for TO/FROM and walk/pivot behavior across seasons, Pearson's Chi-Squared Test could not be relied upon. Instead, descriptive analysis was used. Differences that occur in T3's behavior over the seasons takes the main focus of our individual-based data analysis section. This is because she is the main one that goes through any personal changes in her use of social space.

Results

Rank-based

Mean number of reactions across rank pairs were significantly different ($q^* = 2.58$, $p < 0.05$). It was determined that when a high ranking elephant approached a low ranking elephant (mean = 1.93), a greater mean number of approachee reactions occurred in comparison to when the ranks were switched (mean = 1.08, Figure 5). Likewise, when a high ranking elephant approached a low ranking elephant, a significantly greater mean number of approachee reactions also occurred, in comparison to when a high ranking elephant approached another high ranking elephant (mean = 1.12). Interestingly, when a low ranking elephant approached another low ranking elephant (mean = 1.70) a significantly greater mean number of approachee reactions were observed, in comparison to when a low ranking elephant approached a high ranking elephant. This analysis across ranks was the only one in which same rank approach comparisons provided any significant differences; as a result, the following rank-based analyses will only consider opposite rank comparisons. Same rank analyses will resume when individual-based analysis is conducted, below.

Taking into account TO and FROM approachee behavior across rank pairs, it was determined that there was indeed a significant difference between which rank pairs tend to exhibit these behaviors ($p = 0.0444$). More specifically, a trend was observed in which the likelihood of exhibiting TO behavior was greater when a high ranking elephant was approached by a low ranking elephant (40.0%) versus when a low ranking elephant was approached by a high ranking elephant (27.2%, Figure 6). The reverse was not significant. Differences in walk/pivot behavior across rank pairs was also determined to be not significant.

Mean distances of reaction across rank pairs were again significantly different ($q^* = 1.97$, $p < 0.05$). This revealed that the distance at which a high ranking elephant responded to the approach of a low ranking one (median = 60mm, roughly equivalent to 16m within the enclosure) was greater than the distance at which a low ranking elephant responded to the approach of a high ranking one (median < 50mm, roughly < 13.4m within enclosure). The upper and lower quartiles, shown in Figure 7, for when a low ranking elephant approached a high ranking elephant, are also greater in comparison to high approaching low. While the minimum and maximum possible values are about the same for both rank pairs, more responses occurred at a greater distance when a low ranking elephant approached a high ranking elephant than vice versa.

For hot spot analysis, no significant differences in the behaviors observed were found, whether the approachee was inside or outside their personal hot spot area. However, when considering Figure 8, it appears that a trend occurs in which pivots seem to take place more frequently inside hot spot regions rather than outside.

Individual-based

Individual reactivity provided further evidence that when a high ranking elephant approached a low ranking one, interactions result in greater mean approachee reactivity than vice versa ($q^* = 3.28$, $p < 0.05$). Recall that animal T3 gave birth in the middle of this study (January, 2011). Also recall that T3 and T1 are lower ranking, while T5 and T6 are higher ranking. Taking a closer look into how T3's reactivity may have changed across the three seasons, it was found that no significant differences occurred between reactivity and different ranked elephant pairs in Fall 2010 (before the baby was born). However, in Winter 2011 T3 had a greater mean number of approachee reactions when approached by T6 (mean = 2.46) and T5 (mean = 2.42) in comparison to when the other low ranking animal, T1, was approached by T6 (mean = 0.68) and T5 (mean = 0.63, $q^* = 3.31$, $p < 0.05$, Figure 9). Again in Spring 2011 no significant differences occurred between the two measurements.

Behavioral data were analyzed across elephant pairs. Differences in TO/FROM behavior across elephant pairs for the entire study period were significant ($x^2 = 14.36$, $p = 0.0452$). Looking at TO/FROM behavioral data across the seasons in relation to T3, one trend revealed that T3 showed a sharp increase in TO behavior between Fall 2010 and Winter 2011 (18.46% of her reactions to 26.25% of her reactions). This TO behavior stays at an increased level in Spring 2011 (28.57%, Figure 10). Despite T3's lowest TO behavior period being in Fall 2010, her rates of turning TO an approacher are higher than any of the other animals tested: T1, T5, and T6 turn TO only 6.90%, 9.68%, and 0% of the time, respectively. In Winter 2011 T3 again demonstrates TO behavior the most, alongside T6 who did not exhibit any TO behavior in Fall 2010 (26.25% and 26.87%, respectively). In Spring 2011 T3 is observed doing her personal lowest amount of FROM behavior across all seasons (46.67% versus 55.06% in Fall and 60.0% in Winter). This comes with her TO behavior remaining elevated. T5 also showed an increase in her TO behavior (28.57% and 25.86%, respectively) during this period. The only elephant to show high levels of FROM behavior across all seasons was T1 (71.74% combined). However, differences in walk/pivot behavior across elephant pairs was found to be not significant and provided no clear descriptive trends to report.

Distance analyses conducted for elephant pairs across the entire study period again showed significant differences, consistent with previous rank-based findings. That is, in general, when a low ranked elephant approached each high ranked elephant, a larger reaction distance was observed compared to when high approached low ($q^* = 3.06$, $p < 0.05$). Taking a look at seasonal findings for the new mother, T3, no significant differences between mean distance of reaction and elephant pairs were determined for Fall 2010. However, in Winter 2011 a significantly greater mean distance of reaction occurred when T3 approached T5 (mean = 87.43mm, roughly equivalent to 23.8m within the enclosure), although only in comparison to when T6 approached T1 (mean = 43.86mm, roughly < 12.5m, $q^* = 3.13$, $p < 0.05$). In Spring 2011, a significantly greater mean distance of reaction continued to occur when T3 approached T5 (mean = 77.05mm, roughly 20.3m), except this time in comparison to when T6 approached T3 (mean = 44.54mm, roughly < 12.5m, $q^* = 3.09$, $p < 0.05$, Figure 11).

Discussion

Overview

In this study, by tracking the movements of the female African elephants, we found patterns in the way both different ranked subjects, and the individual new mother, negotiate and use social space. All together, the tendency of an animal to react, the sort of reaction it would make, and the distance at which it would react, differed in both rank-based and individual-based analyses, indicating that differences in the use of social space do occur. While these findings support the overall hypothesis of the study that differences in the use of social space do occur across ranks, and after a female gives birth, a closer look into the details of each finding reveal some of the complexity involved. Conversely, the “hot spot” analysis - in which we predicted that an approachee might react differently when in its preferred space, versus outside its preferred space - did not result in significant differences, although there may be reasons for this that I will discuss.

Perhaps one of the most interesting findings was that individual-based seasonal results also suggest that the presence of a newborn can alter the use of space by the mother. This occurred across all factors: reactivity, behavior type, and distance of reaction. Whether these changes across seasons were due to a change in T3's dominance, or other factors involving the calf, may be made more clear upon further inspection of the results.

The following will examine approachee reactivity, behavior type, distance of reaction, and hot spot results. The goal is to gain a deeper understanding of the use of social space by female African elephants by taking both rank-based and individual-based findings into consideration when discussing each subject.

Reactivity

Consistent with our hypothesis, the results for both rank-based and individual-based analyses suggested that low ranking elephants reacted more upon being approached, in comparison to high ranking elephants. Reactivity was at its maximum when high ranking elephants approached low ranking elephants, but still remained elevated when a low ranking approached another low ranking elephant. This reveals a level of submissiveness amongst the low ranking elephants, that does not occur at the same level amongst the high ranking elephants. This difference in submissive and dominant behavior across rank types was similarly demonstrated in the thesis conducted by Meeberg (2010) on wild African elephants. As in our study, Meeberg documented that high ranking, dominant individuals were more likely to approach low ranking, submissive individuals, resulting in a reaction. However, she also saw moments in which same ranked individuals approached one another, resulting in reactions as well. These approach moments provided insight into slight hierarchical differences amongst low ranking and high ranking individuals in her study, ultimately exposing the lowest ranked and highest ranked (matriarch) members.

Taking Meeberg's finding about same rank comparisons into consideration, and looking further into the details across seasonal data, in Winter 2011, when T6, the female which the keepers at the Safari Park considered the most dominant, approached either of the two presumed low ranking females, a greater mean number of reactions occurred in comparison to when T5, the female they ranked second, approached those same two animals. This provides additional support that T6 is indeed more dominant than T5. This also coincides with a jump in T3's reactivity, which occurred during the same season that T3 gave birth. As expected, this supports the idea that changes may have occurred in T3's use of social space and sociality due to the presence of the newborn. While a further look into the behavior displayed will be discussed later, it is likely that this change in behavior is not necessarily due to a change in T3's rank/dominance, but other factors involving the calf.

Behavior

TO/FROM behavior was found to differ significantly across rank pairs and individual pairs , while general walk/pivot behavior did not. Rank-based TO/FROM analysis concluded that not only are the behaviors different between low ranking and high ranking approachees, but specifically a trend in which TO behavior was more likely to occur as a response by a high ranking elephant when approached by a low ranking elephant. It follows that FROM behavior is more likely to occur as a response by a low ranking elephant in reaction to a high ranking approacher. This supports our hypothesis, consistent with the idea that the low ranking elephants should be more likely to demonstrate submissive behavior - like turning their rump to another - while high ranking members are more likely to demonstrate dominant behavior (Meeberg, 2010; Wittemyer et al., 2007b). While there is a chance that some of this TO/FROM behavior was not actually due to the rank of the approacher, but other factors (e.g. food pile, calves, keepers, etc.), enough data were collected during these approach moments that the general rank-based pattern was borne out. To further investigate this, a similar study could be run, this time documenting additional information such as whether a food pile or calf may be in the general direction that the approachee turns to face.

Individual-based analysis of TO/FROM behavior again supported the idea that differences do occur across elephants. Descriptive analysis of seasonal changes revealed that high rankingT6 had increased levels of TO behavior in Winter (when the calf was a factor), while second rankingT5 did not increase her levels of TO behavior until Spring. This distribution of dominance behavior agrees with their consecutive ranks. T1 , the only female without an infant, consistently showed the most FROM behavior across all seasons, demonstrating her low rank. Even before T3's calf was born, T1 had higher rates of FROM behavior than T3, which indicates that T1 is even lower ranking than T3.

T3, likely due to her new calf, had changes across the seasons in TO/FROM behavior. In keeping with our hypothesis, an increase in her TO behavior began after the calf was born and decreased only slightly in Spring. However, this change in TO behavior under such circumstances may not reveal a switch from subordinate to dominant behavior in T3, instead, social interactions could well have been driven by the new calf. Upon observation, it was seen that T3's calf frequently left his mother's side and ventured out towards other elephants. In this process, T3 would come following after her calf, forcing her to also approach others more frequently. This agrees with the findings by Lee

(1987), who also observed calves leaving their mothers in search of other elephants to interact with. While we did not score the data for any signs of alloparenting from other female elephants, T3's behavior, approaching potential alloparents that the calf was spending time with, is consistent with this idea. Due to the fact that T3 is a subordinate mother, her chances of gaining alloparents is increased (Lee, 1987), making it a likely scenario. This could also explain why T3 had a jump in reactivity in Winter, since this was also when she was observed doing the most TO behavior. However, further analysis, including scoring alloparenting behavior towards T3's calf, would be essential to determine whether alloparenting is indeed a factor in T3's change in behavior.

We further hypothesized that if an elephant reacted to an approach with a more energy-demanding walk away, rather than a mere pivot in place, this could indicate a greater discrepancy in their ranks. However, differences between reactions - in terms of whether the approached animal did a "walk" or just a "pivot" - were not found to be significant in either rank pair or individual pair analyses. This too may be due to other factors not documented in this study. Animal behavior can depend on many external factors. Perhaps if the study was conducted again, but this time considering whether a food pile worth defending (or at least not abandoning) was located nearby, or if there was an area to which the approachee could easily relocate, a clearer trend in these behaviors would be revealed.

Distance

In striking contrast to our original hypothesis, it was determined that reactions occurred at a greater mean distance when a low ranking elephant approached a high ranking elephant than vice versa. This was again supported when looking at individual differences in reaction distance.

The original thought was that since low ranking elephants are less dominant, they would react the moment they detected an approach movement occurring, particularly from a high ranking approacher. Thus, we predicted a greater mean distance of reaction when dominants approached. Since the opposite was found, this may be due to a couple factors. First, it may be that submissive individuals engage in conflict avoidance behavior by freezing in place until they are certain the approacher is targeting them. This type of behavior is most commonly documented in primates. In a study by Coss (1978), behavior exhibited between dominant and subordinate mouse lemurs was recorded across multiple groups. When a dominant lemur began to approach a subordinate lemur, the subordinate was observed freezing in place. This stance was taken until the dominant got close or attacked, which would cause the subordinate to abandon its frozen stance and either be forced to protect itself, or retreat. In the case of our study, attack and defense behavior was never observed, but the freezing in place could help explain the lower mean distance of reaction when a low ranking elephant is approached by a high ranking elephant.

Secondly, this may be due to the fact that IOR scores across observers were the lowest for distance, with an average of only 0.67. Due to the idiosyncratic interpretations that occurred while using *ChronoViz* and the *Anoto* pens to gather data, it was difficult to get all observers to draw things the exact same way, particularly the distance between subjects. This disagreement on distance could have altered our final results, making our findings less accurate. Perhaps if a single person, rather than a group of interns, took all the data in *ChronoViz*, this error would be less likely to occur. It could also be that, indeed, our original hypothesis was correct, but the method we chose was not precise enough to gather proper information about inter-animal distances. For example, perhaps using technology such as GPS trackers (Mabry & Pinter-Wollman, 2010) would have produced more accurate and reliable distance results. While I feel our final results are not likely made inaccurate by the IOR score, and that *ChronoViz* is fully capable of recording accurate distance data, obtaining the data through a different method may be a good choice to ensure its validity.

Looking closer into the new mother, T3's seasonal changes, for the most part our results were consistent with our hypothesis. T3 began to generate significantly greater mean distances of reaction, upon approaching a dominant group member, after the calf was born. This was particularly true when she approached second-ranked T5, and continued to stay this way from Winter into Spring. Interestingly, this was only the case in which T5, rather than the top-ranked T6, showed the most significant results. While this, again, may be affected by the relatively low IOR score for distance discussed above, it does suggest that perhaps T6 is the highest ranking elephant and potentially the matriarch, causing T3 to not exhibit the same approacher behavior towards her as she would towards T5. However, in the case of T5, an increase in distance before reacting to T3 makes sense based upon Lee's (1987) study. If indeed a lower ranking mother is more likely to attract alloparents, particularly those that are insistent or more dominant than the mother herself, then T5 would be the ideal candidate to demonstrate this behavior. Because the calf was still only a few months old by the time Spring arrived, T5 therefore would be expected to continue on with this behavior, as supported by the data. In contrast, T1, being apparently less dominant than T3, and having no calves of her own, would be less likely to have the ability to demonstrate alloparent behavior towards T3's calf. This may account for why the distance at which T1 reacted to T3 was not as great, and also the consistency in her FROM behavior. As mentioned previously, another study in which alloparent behaviors toward T3's calf are recorded would be necessary in order to confirm whether T5 is indeed acting as an alloparent.

Hot Spots

It was determined that differences in behavior inside versus outside a hot spot area were not significant, while we had hypothesized that it would be significant. However, Figure 8 indicates a trend in which pivot behavior inside hot spot areas is more likely to occur than outside hot spot areas. Again, for this question we were not interested in rank-based or individual-based differences, but in whether any animal would react differently if approached while in its personally preferred spot. The thought was that, given that their hot spot is somewhere they tend to frequent, it must be of value to them (e.g. as a place of food access, water access, vantage point, etc.). If this is indeed the case, then we expected that they would be more willing to stay within their hot spot if approached (i.e. pivot in response), rather than be displaced from the area (i.e. walk in response). While the results were not significant, there were some trends in this direction.

One factor that may have played into this was that not many documented interactions took place within the approachee's hot spot (about 1/3 fewer than observed outside their hot spots). Since all compiled data were used to map these regions - whether the elephant was being approached or not - it is a possibility that there are many more situations in which an elephant is within her hot spot and not being approached. If true, this suggests there could be some kind of avoidance by approachers while an approachee is within their hot spot. If this is the case, our method of only looking at approach moments within the hot spot regions may be underestimating the effects. Perhaps a more informative test would be to look at all moments an elephant is in her hot spot, and then document how other elephants in the vicinity behave. This may provide some evidence for the hot spot avoidance hypothesis.

Conclusion

Ultimately, this study does support the idea that differences in the use of social space occur, on both a rank-based level and an individual-based level. While some changes and additions to the study may provide more solid support for our hypotheses, the findings presented answer questions that have not yet been scientifically explored. While some may find the questions addressed here trivial, we do not. As early ethologist Nikolaas Tinbergen (1952) once wrote, "Much so-called 'random behavior' is not random at all, but steered from step to step by outside stimuli....In these and many similar cases it is our lack of knowledge of the influential outside stimuli that makes the movements appear random." By taking a deeper look into behaviors that most deem "random", or have observed but not scientifically studied, we further our understanding of the factors that shape those behaviors.

While this study only considered captive African elephants, it provides important knowledge, which zoos could use to better understand their animals and the dynamics occurring between them. This could contribute to the better management of captive populations. I further suggest that conducting a similar study on wild African elephants is crucial in expanding our knowledge of the species. Such studies could also enable us to document any differences that occur between captive and wild populations, and better understand the potential reasons for those variations in behavior.

Due to the fact that we observed some behaviors in these captive elephants that have been documented in wild African elephants, I feel that this provides evidence that the enclosure at the San Diego Zoo Safari Park is of decent size. With an animal that is use to living in large, open areas in Africa, ensuring an enclosure is large enough for healthy behavior to still exist is very important. We also did not observe any overtly aggressive, attack/defense behavior, which I feel further supports the idea that the enclosure at this zoo is of healthy size. I would postulate that if the enclosure was too small, lack of space would lead to potential attack/defense behavior, which could be detrimental to the health of the captive elephants. Because this is not the case, I believe that conducting studies on African elephant behavior at this particular zoo is a legitimate and valuable option.

Additionally, the video-annotion program *ChronoViz*, in conjunction with the

Anoto digital pens, was developed and worked successfully for our purposes. This addition to the tools which scientists can pull from was an important facet of this project. Developing and using these tools was a feat in and of itself, and working as a team with other scientists from different fields, for one combined purpose, was a major learning experience. Being able to communicate successfully and agree upon various functions of the program, spreadsheet layouts, and ultimately data analysis, was an invaluable experience. In the end, we are able to present this technological development as a possible option for future ethologists and ecologists studying animals' use of social space.

Figures

Figure 1: Original 2D *Google Earth* image of entire enclosure area is depicted at top. The central enclosure area, boxed in green, is expanded below. This central region was used as our data collection map.

Figure 2: Final colored map image, printed on coordinate paper.

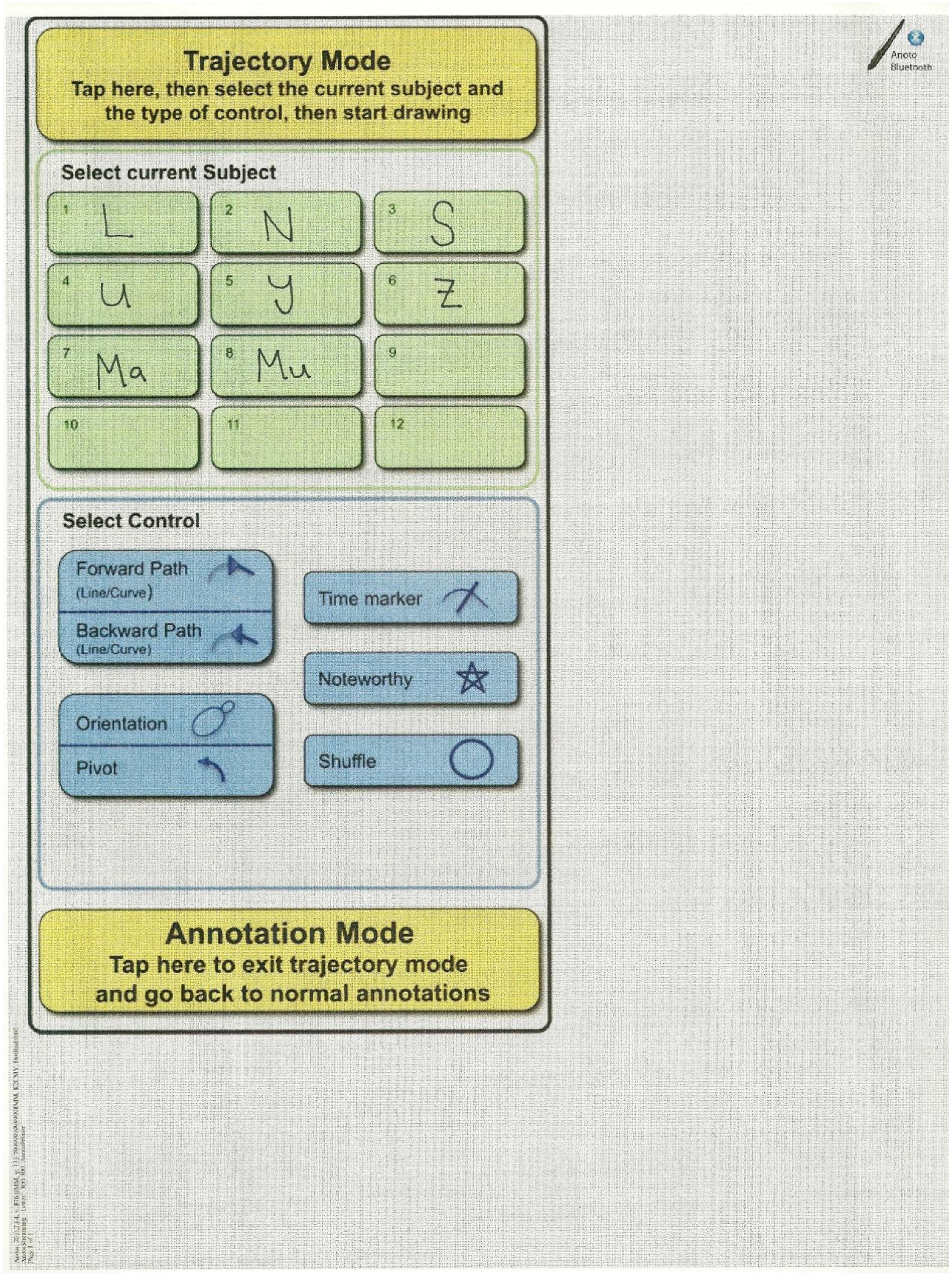

Figure 3: Control panel used to select subjects and behaviors, printed on coordinate paper.

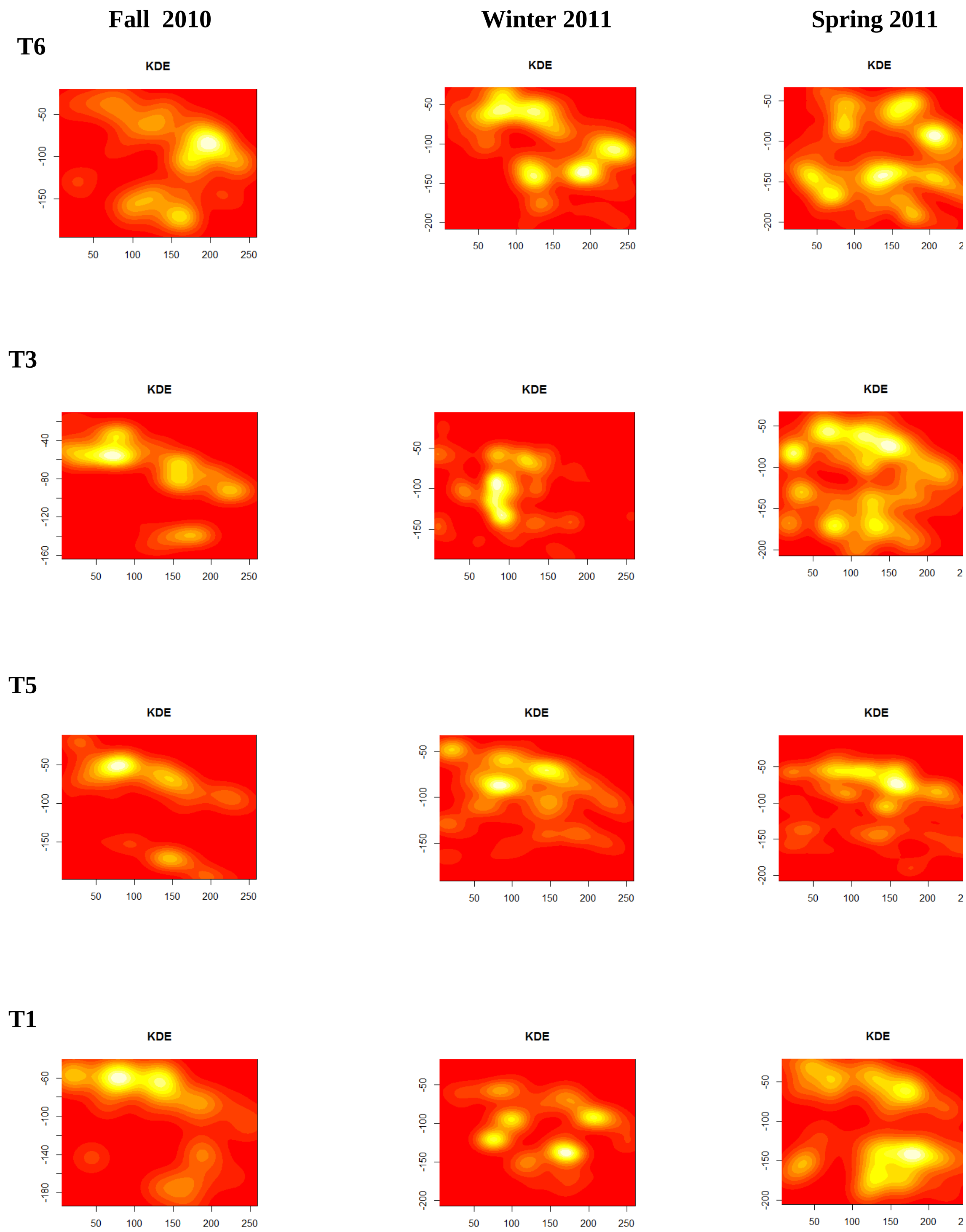

Figure 4: Hot spot images for T6, T3, T5, and T1 across all three seasons.

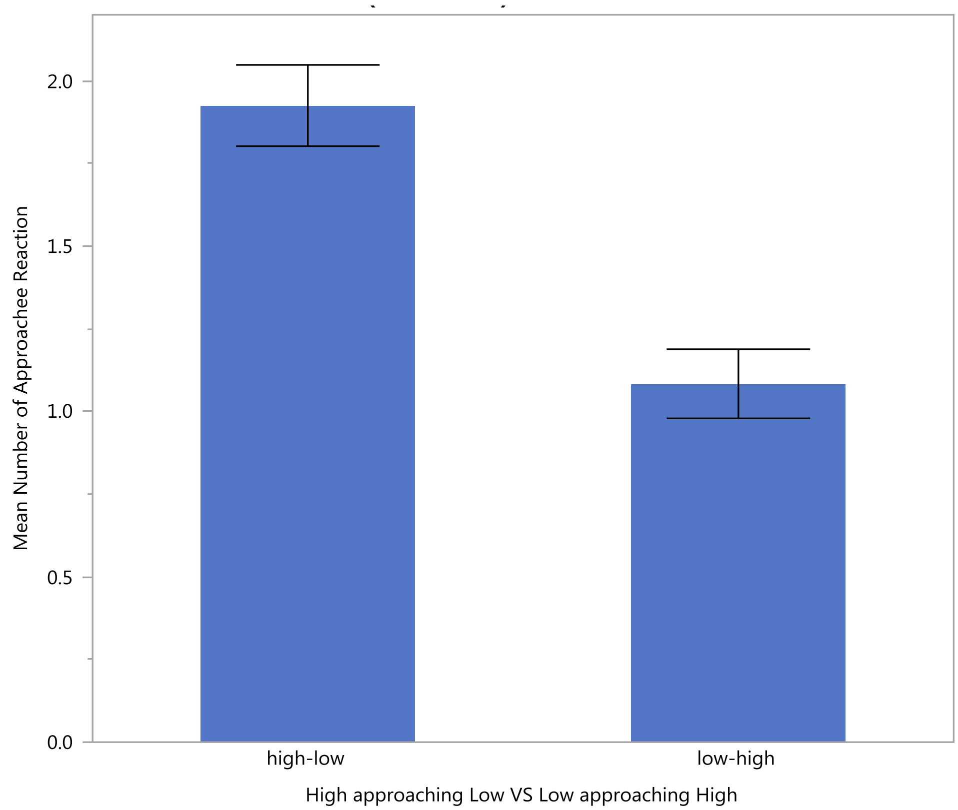

Figure 5: Mean number of approachee reactions when the approacher is of the opposite rank. A greater amount of reactions are seen when a low ranking elephant is approached by a high ranking elephant. Error bars represent 1 standard error from the mean.

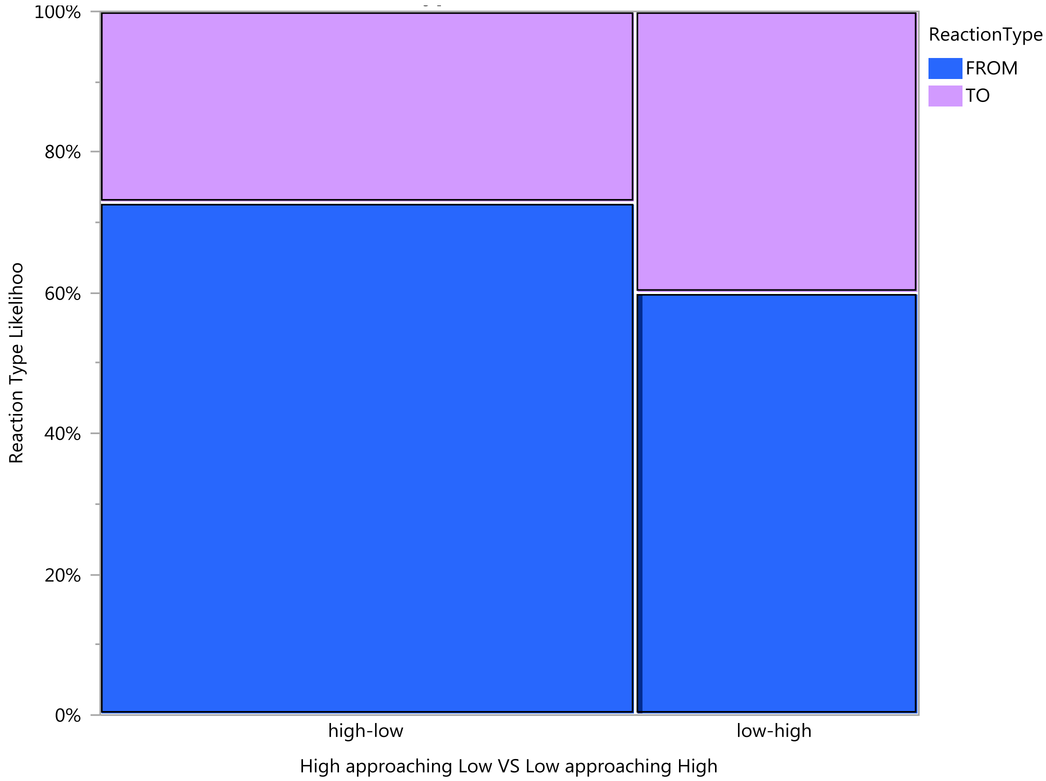

Figure 6: Likelihood of approachee reaction type (TO or FROM) versus opposite ranked pairs. A trend in which high ranking elephants are more likely to TO when being approached by a low ranking elephant, than vice versa, is observed.

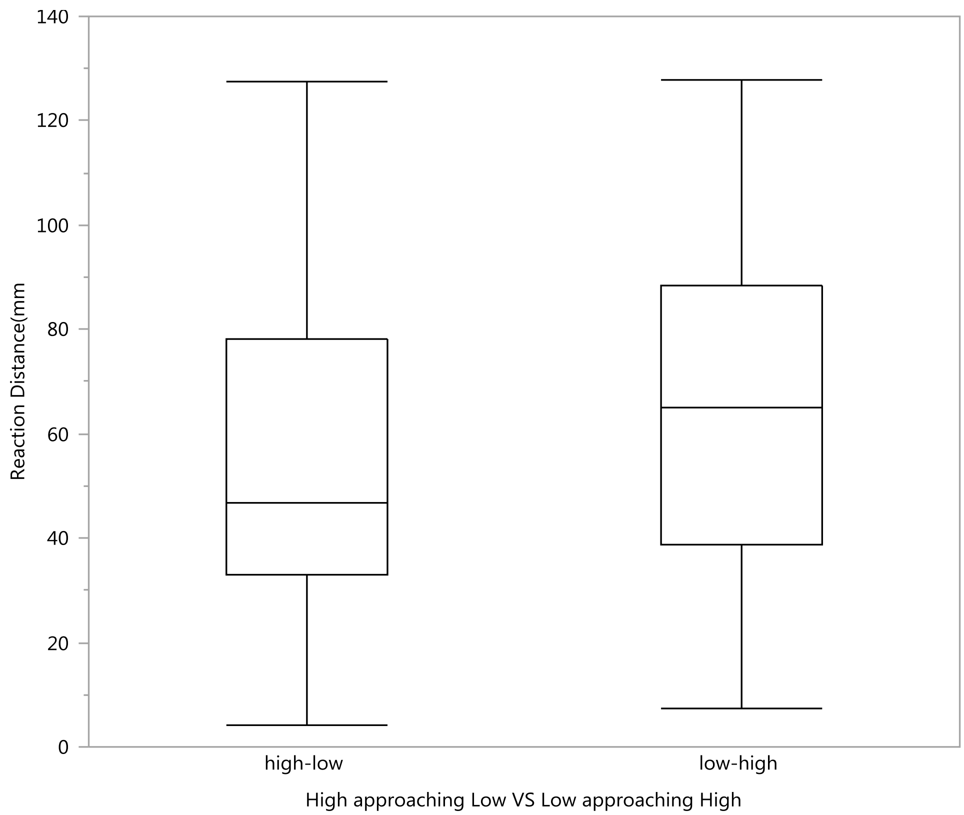

Figure 7: Reaction distance (in map millimeters) versus rank pair is depicted. A greater distance of reaction is seen when a low ranking elephant approaches a high ranking elephant. A millimeter on the map is roughly 3.75m within the enclosure.

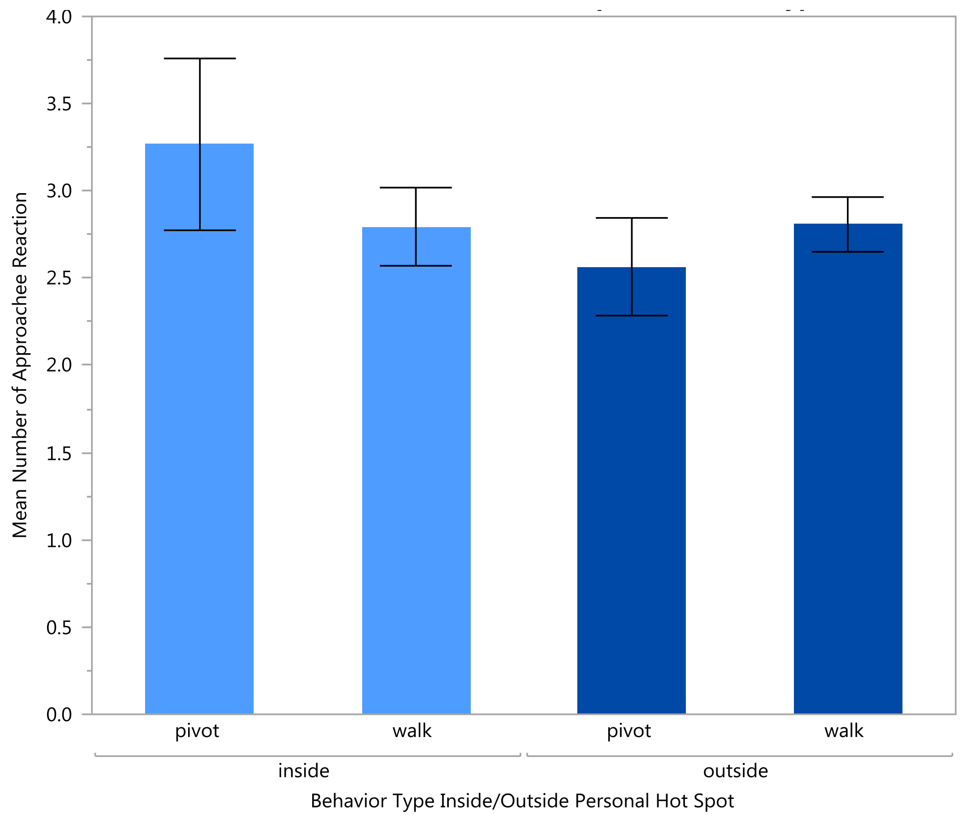

Figure 8: Inside hot spot behavior (pivot or walk) and outside hot spot behavior is depicted. Darker bars represent outside hot spot behaviors, lighter bars represent inside hot spot behaviors. Though the differences were not significant, these data indicate a trend in which pivot behavior occurs more frequently inside hot spot areas versus outside. Error bars represent 1 standard error from the mean.

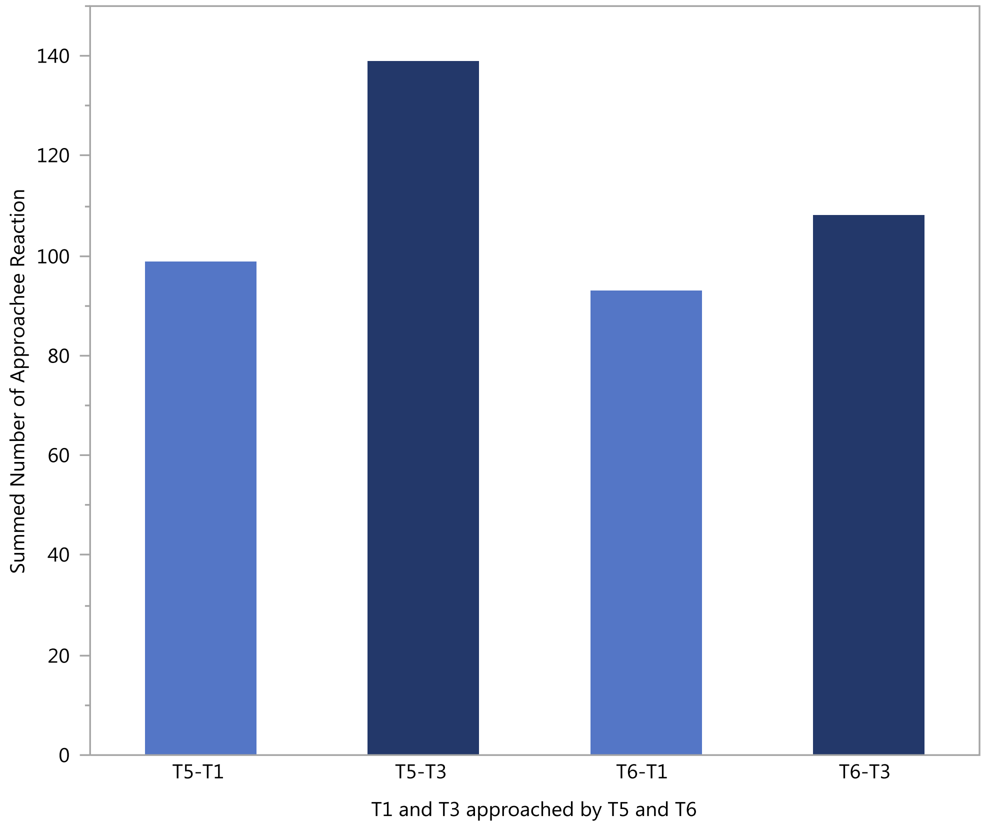

Figure 9: Summed number of reactions by subordinates T1 and T3 towards dominants T5 and T6 in Winter 2011. Darker bars represent when T3 acted as the approachee, lighter bars represent when T1 acted as the approachee. T3 reacted more to the high ranked elephants in comparison to T1.

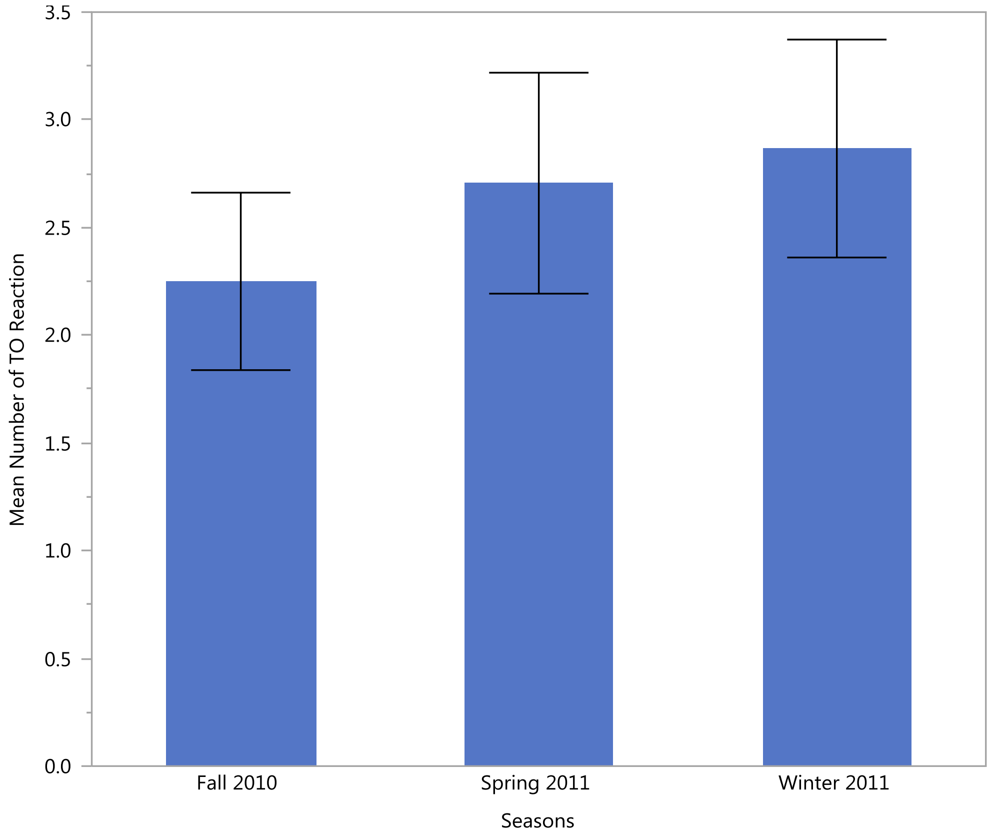

Figure 10: T3's mean number of TO reactions across each season, displayed by increasing value rather than seasonal order. A sudden increase in TO behavior occurs between Fall and Winter/Spring, with Winter having the highest of all TO behavior. Error bars represent 1 standard error from the mean.

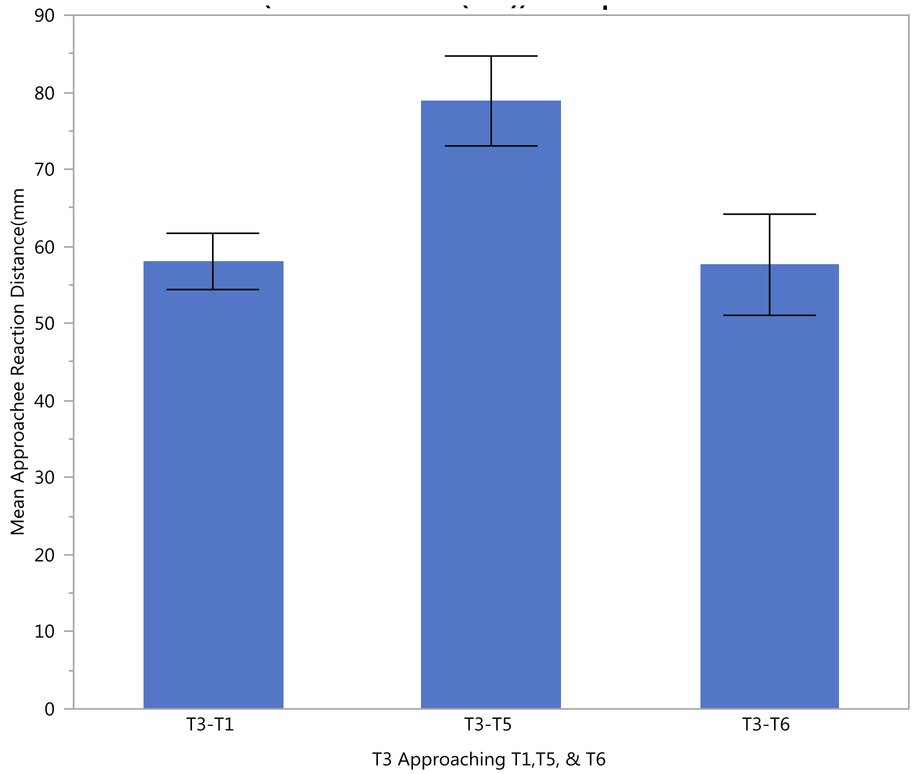

Figure 11: Mean approachee distance of reaction when T3 approaches all other elephants (T1, T5, &T6) across all seasons. T5 reacts to the approach of T3 at the farthest distance. Error bars represent 1 standard error from the mean.

Tables

Table 1: Adult African elephants at the San Diego Zoo Safari Park.

Name (Sex)	Abbreviations	Rank	Nursing Calf (Yes/No, YOB)
Mahbu (Adult male)	Ma, T7	N/A	N/A
Musi (Juvenile male)	Mu, T8	N/A	N/A
Lungile (Adult female)	L, T1	Low	No
Semba (Adult female)	S, T3	Low	Yes, 2010
Umngani (Adult female)	U, T4	Mid	Yes, 2009
Ndula (Adult female)	N, T2	Mid	Yes, 2010
Moya (Adult female)	U, T5	High	Yes, 2010
Swazi (Adult female)	Z, T6	High	Yes, 2010

Table 2: List of *ChronoViz* marks/movements and definitions.

***ChronoViz* Mark**	**Definition**
Forward Path (path-fw)	Elephant moves forwards
Backward Path (path-bw)	Elephant moves backwards
Timemarker	A mark made to indicate where an elephant is at a given time. Can denote the onset of a trajectory, the onset of a stop/orientation, change in trajectory direction, change in pace, etc.
Orientation	The angle in which an elephant is facing with regards to the 2D map (0-360, moving counter-clockwise) when fully stopped.
Pivot	Elephant does not begin a trajectory forwards or backwards, but instead moves either its front or back end changing its orientation angle.
Shuffle	Rare instances in which a movement cannot be defined by any pathline or pivot movement. Creates blank data with only a commented description available to relay what movements were made.
Noteworthy	A continuous 5-point star is drawn on the map near the time and location of an interesting or unusual social encounter. A comment is made along with that star to describe the event and its potential significance.

References

Adams, J., & Berg, J.K. (1980). Behavior of female African elephants (*Loxodonta africana)* in captivity. Applied Animal Ethology *Volume 6*, 257-276.

Berg, J.K. (1983). Vocalizations and associated behaviors of the African elephant (*Loxodonta africana*) in captivity. Ethology, *Volume 63*, 63-79.

Byrne, R.W., Bates, L.A., & Moss, C.J. (2009). Elephant cognition in primate perspective. Comparative Cognition & Behavior Reviews *Volume 4*, 65-79.

Coss, R.G. (1978). Perceptual determinants of gaze aversion by the lesser mouse lemur (*Microcebus murinus*), the role of two facing eyes. Behaviour *Volume 64*, 248-270.

Fouse, A., Weibel, N., Johnson, C., & Hollan, J. (2013). Reifying social movement trajectories. In Proceedings of CHI '13, ACM Conference on Human Factors in Computing Systems, Paris, France.

Freeman, E.W., Weiss, E., & Brown, J.L. (2004). Examination of the interrelationships of behavior, dominance status, and ovarian activity in captive Asian and African elephants. Zoo Biology *Volume 23*, 431-448.

Friedman, W.R.G. (2011). Assessing the socio-cognitive ecosystem of eight captive elephants (Thesis). University of California, San Diego.

Highfill, L.E., & Kuczaj, S.A. (2010). How studies of wild and captive dolphins contribute to our understanding of individual differences and personality. International Journal of Comparative Psychology *Volume 23*, 269-277.

Hollister-Smith, J.A., Poole, J.H., Archie, E.A., Vance, E.A., Georgiadis, N.J., Moss, C.J., & Alberts, S.C. (2007). Age, musth, and paternity success in wild male African elephants, *Loxodonta africana*. Animal Behavior *Volume 74*, 287-296.

Lee, P.C. (1987). Allomothering among African elephants. Animal Behaviour *Volume 35*, 278-291.

Lee, P. (1996). Studying the behaviour of elephants. In *Studying Elephants*, Kadzo Kangwana eds., (Kenya: African Wildlife Foundation) pp.98-110.

Mabry, K.E., & Pinter-Wollman, N. (2010). Spatial orientation and time: methods. Encyclopedia of Animal Behavior *Volume 3*, 308-314.

McComb, K., Moss, C., Durant, S.M., Baker, L., & Sayialel, S. (2001). Matriarchs as repositories of social knowledge in African elephants. Science *Volume 292*, 491-494.

Meeberg, G. (2010). Assessing focal animal sampling (FAS) as a mean of categorizing dominance behaviour and determining group hierarchy in an African elephant herd (*Loxodonta africana*) (Thesis). Utrecht University, the Netherlands.

O'Connell-Rodwell, C.E. (2007). Keeping an "ear" to the ground: seismic communication in elephants. Physiology *Volume 22*, 287-294.

Paterson, J.D. (2001). Inter-observer reliability testing: do two people see the same things? In *Primate Behavior: An Exercise Workbook*, 2nd edition, (Prospect Heights, IL: Waveland Press, Inc.) pp.165-172.

Payne, K. (2003). Sources of social complexity in the three elephant species. In *Animal Social Complexity: Intelligence, Culture, and Individualized Societies*, Frans, B.M., de Waal, Tyack, P.L. eds., (Cambridge, MA: Harvard University Press) pp.57-85.

Poole, J. (1996). The African Elephant, In *Studying Elephants*, Kadzo Kangwana eds., (Kenya: African Wildlife Foundation) pp.1-8.

Tinbergen, N. (1952). "Derived" activities; their causation, biological significance, origin, and emancipation during evolution. Quarterly Review of Biology *Volume 27*, 1-32.

Weibel, N., Fouse, A., Emmenegger, C., Friedman, W., Hutchins, E., & Hollan, J.D. (2012). Digital pen and paper practices in observational research. In Proceedings of CHI '12, ACM Conference on Human Factors in Computing Systems, Austin, Texas.

Wittemyer, G., & Douglas-Hamilton, I., & Getz, W.M. (2007a). The socioecology of elephants: analysis of the processes creating multitiered social structures. Animal Behaviour *Volume 69*, 1357-1371.

Wittemyer, G., Getz, W.M., Vollrath, F., & Douglas-Hamilton, I. (2007b). Social dominance, seasonal movements, and spatial segregation in African elephants: a contribution to conservation behavior. Behavioral Ecology and Sociobiology *Volume 61*, 1919-1931.

Wittemyer, G., Polansky, L., Douglas-Hamilton, I., & Getz, W.M. (2008). Disentangling the effects of forage, social rank, and risk on movement autocorrelation of elephants using Fourier and wavelet analyses. PNAS *Volume 105*, 19108-19113.

Wolf, M. (2009). Adaptive individual differences: the evolution of animal personalities (Thesis). University of Groningen, the Netherlands.

Wolf, M., & Weissing, F.J. (2012). Animal personalities: consequences for ecology and evolution. Cell Press *Volume 27*, 452-461.