The Social Relationships of Captive African Elephant (Loxodonta africana) Juveniles

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The Social Relationships of Captive African Elephant (Loxodonta africana) Juveniles

A Thesis

Presented to the Department of Psychology

College of Liberal Arts and Sciences

Butler University

Julia Machado

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Director, Honors Program  Date

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Departmental


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Abstract

*In situ* female African bush elephants (*Loxodonta africana*) live in a fission-fusion society comprised of “core groups” in which adult females associate with their dependent offspring (Archie, Moss, & Alberts, 2006). Most of the animals in a core group are related (Archie et al., 2006), but kinship is not the only contributor to elephant sociality.

Pre-reproductive females (allomothers) often assist in the care of calves and juveniles (Lee, 1987). The concept of inclusive fitness (Riedman, 1982) is the favored hypothesis for the evolution of allomothering. Zoological settings, with varied social groupings, provide the perfect opportunity to test this hypothesis (Schulte, 2000). During the winter of 2017-2018, four female elephants at the Indianapolis Zoo were grouped together temporarily (one hour per day) and given access to an outside yard. The group included an adolescent (Zahara), her juvenile sister (Nyah), another female juvenile (Kalina) and the (unrelated) dominant elephant at the facility (Sophi). Video recordings of the animals moving freely in the yard were examined to document proximity, changes in proximity, and behavioral observations. Zahara spent more time close to the calves than did Sophi. Zahara and each of the juveniles made and broke contact equally often; however, the juveniles were primarily responsible for maintaining proximity to Sophi. Zahara, surprisingly, associated more with Kalina than with Nyah. Finally, Zahara displayed far more agonistic behaviors towards Kalina than towards Nyah. These results suggest that Zahara was an allomother to both juveniles, favoring Nyah over Zahara, but also interacted with Kalina as a peer.
The Social Relationships of Captive African Elephant (Loxodonta africana) Juveniles

The African elephant (Loxodonta africana) displays a complex and unique social organization. In the wild (in situ), female elephants aggregate into “core groups” (or “family units”: Moss, Croze, & Lee, 2011) usually comprised of related adult females and their dependent offspring (Archie et al., 2006). After leaving their natal herd at between 10-15 years of age, male elephants rarely interact with females outside of breeding (Dublin, 1983). Over the course of hours or days, female core groups may come together to form “bond groups” or they may split apart into individual pairings. This social fluidity is characteristic of a fission-fusion society (Archie & Chiyo, 2011).

Strong, stable associations between individuals make up the heart of elephant sociality. Females rest, feed and travel close to one another, and display numerous affiliative behaviors towards other elephants in the group (Charif, Ramey, Langbauer, Payne, Martin, & Brown, 2007; Dublin 1983; Lee 1987; Moss, 1988; Poole, Payne, Langbauer, & Moss, 1988). The relationship between the mother elephant (cow) and her offspring is the most common and enduring relationship (Archie & Chiyo, 2011). Core groups can also include aunt-niece, sibling, first cousin and grandmother-granddaughter pairings (Archie et al., 2006). The exact way in which female associations form is unclear, but Archie and Chiyo (2011) proposed that young elephants develop relationships with core group associates and maintain these relationships into maturity.

Kinship is an important aspect of elephant sociality and a significant predictor of female social relationships. Archie and Chiyo (2011) found that pairings which spent 90% of their time together were most often first-order maternal relatives. This was the case even when individual pairs were not in the presence of their core group, indicating
that when family groups fission temporarily, maternal ties remain strong. Moreover, associativity is positively correlated with relatedness. Alberts et al. (2005) found that the oldest females in the core groups which comprised a bond group (the higher demographic classification) were closely related. This finding acts as strong evidence for long-term matrilineal impact and may represent the effects of historical matrilineal fissioning (Archie & Chiyo, 2011). The exact method by which distant relatives “stay in contact” is unknown, although auditory recognition has been implicated in the phenomenon and the oldest female in a population may be able to differentiate between 100 individual calls (Archie & Chiyo, 2011; McComb, Reby, Baker, Moss, & Sayialel, 2003).

While kinship is a notoriously strong predictor of female elephant social behavior, interactions between non-kin are common. Unrelated females who live in a family grouping are termed “female immigrants.” As many as 10% of Amboseli elephants (a population from one of the longest field studies of the species) are female immigrants (Archie et al., 2006). It is likely that a good amount of female immigration is due to anthropogenic intervention. Namely, when an individual elephant’s core group is destroyed by poaching activities, a female might seek out unrelated associateships in order to retain the numerous adaptive benefits of sociality. The long-term impact of poaching on core groups may also be behind the finding of weak kinship effects on coordinated bond group movements (Charif et al., 2005). Non-anthropogenic female immigration has also been recorded. This rare occurrence may be due to natural demographic events like the birth of many male offspring (Archie et al., 2006).

Aside from the mothers, other females will often display caregiving behaviors towards young animals in the core group (Lee, 1987). This is a common mammalian
characteristic (Riedman, 1982). Generally, these “assistant mothers” are nulliparous females: however, older females have been known to display “allomothering” behavior (Dublin, 1983; Lee, 1987; Lee & Moss, 1999). When the mother is near, calves spend an average of 45% of their time in close proximity to an allomother. When the mother is not present that number increases to 52% (Moss et al., 2011). By maintaining proximity, allomothering behavior provides protection, herding, assistance, and comfort of the calf. Cases of allonursing have also been recorded: however, this behavior appears to be rare (Schulte, 2000).

Allomothering behavior is believed to promote calf survivorship (Schulte, 2000; Dublin, 1983), but the exact benefit for the allomother is harder to pin down. Several hypotheses have been explored in order to discover the evolutionary motive behind the seemingly maladaptive behavior of these females: (1) allomothers may receive better access to high-quality resources through assisting the calves of more dominant females; (2) allomothers may gain experience in handling young calves, thus developing maternal behaviors and potentially increasing survivorship of their own offspring; (3) an increased likelihood that the mother of the calf will “return the favor” when the allomother has her own calf; and (4) inclusive fitness (Dublin, 1983; Riedman, 1982). Inclusive fitness refers to the theory that an individual can increase its fitness indirectly by supporting the survival and reproduction of other related individuals in a population (Hamilton, 1964). Lee (1987) found that in situ allomothers are frequently siblings of the calves they are attending to, thus supporting the hypothesized importance of inclusive fitness. Others have additionally theorized that the contributions of allomothers may be correlated with the degree of relatedness of the calf (Archie et al., 2006).
Although elephants under human care in zoological facilities (*ex situ*) do not face many of the selective pressures faced by *in situ* animals (including predation, parasitism, and malnutrition), their range is significantly restricted, and their social groupings are small and artificially imposed, Schulte (2000) suggested studying them to explore the motives behind allomothering in African elephants. Despite the differences in context, *in situ* and *ex situ* elephants perform many similar behaviors (Adams & Berg, 1980). In addition, they also show strong dyadic relationships maintained in part through proximity (Bonaparte-Saller & Mench, 2018). This makes the zoological setting a perfect opportunity to investigate the effects of relatedness on individual behavior.

In order to address the connection between relatedness and allomothering behavior, I collected observational data from an adolescent female African bush elephant at the Indianapolis Zoo between November 2017 and December 2018. As a nulliparous female, Zahara was a prime candidate to be an allomother (Lee, 1987). During observation times, Zahara was housed with two juveniles (Kalina and Nyah) and an unrelated dominant female (Sophi). Unpublished data collected by Dublin (1974-1976: Dublin, 1983) indicate that recently weaned juveniles like Kalina and Nyah are at an age in which significant allomothering is still common. This situation was particularly favorable to further exploring relatedness and allomothering due to the fact that Nyah was Zahara’s younger sister and raised with her, while Kalina was born to a different cow (Kubwa) and raised separately in Kubwa’s group. Prior to the current observations, Zahara and Nyah had spent relatively little time with Kalina. Kalina was not a member of Zahara’s and Nyah’s “core group,” but the three elephants had spent some time together (Years apart, and a few months together). Kalina and Nyah were both the result
of artificial insemination using semen from the same bull at another facility, but I did not expect this genetic relationship to be important. There is no evidence that paternal genetic relatedness plays a role in social behavior \textit{in situ}.

I analyzed three factors to quantify Zahara’s allomothering behavior. The first factor was Zahara’s and Sophi’s (baseline) social proximity to each accessible conspecific. The second factor was the degree to which Zahara and Sophi were responsible for maintaining proximity. The third factor was the amount of agonistic behavior performed by Zahara or Sophi to either calf.

Due to Zahara’s age and previous exposure to Kalina, I predict that the adolescent will display allomothering behavior to both juveniles. In particular, she should spend more time in proximity to the juveniles than Sophi and she should be primarily responsible for maintaining proximity to each of them. Due to the fact that Zahara and Nyah share a mother, have spent all of their time together, and have spent relatively little time with direct access to Kalina (Less than 0.5%), I hypothesize that Zahara will invest significantly more allomothering behavior into Nyah than Kalina. In particular, the adolescent should spend more time close to her sister, show a greater degree of responsibility in maintaining proximity, and display less agonistic behavior to Nyah than to Kalina.

\textbf{Method}

The following study was observational and noninvasive in nature. It was approved as Protocol 155 by Butler University’s Institutional Animal Care and Use Committee (IACUC) on 19 October 2017. The Indianapolis Zoo’s Research Committee approved the same protocol (17 November 2017).
Subjects

Members of our lab group recorded the behavior of an adolescent elephant at the Indianapolis Zoo while she had free access to two juveniles and an unrelated dominant female. Zahara, the adolescent, was born in 2006 to Ivory, an African bush elephant collected from Zimbabwe in 1984. Nyah, one of the juveniles, was born to Ivory in 2012. Zahara and Nyah were conceived through artificial insemination using genetic material from male elephants located in different facilities. As such, they are only half-siblings, related on the maternal side. This is commonly the case for in situ associates (Archie et al., 2011). Kalina was born in 2011 to Kubwa, a savannah African elephant collected from Mozambique in 1978. Kalina was conceived through artificial insemination using genetic material from the same elephant that sired Nyah. Thus, Nyah and Kalina were half-sisters, related on the paternal side. During our observations Kalina and Nyah were nearly equal in size, but much smaller than Zahara. The fourth elephant, Sophi, was the dominant (and unrelated) elephant at the facility, having been imported from Uganda in 1969.

For most of the year, Ivory, Zahara, and Nyah are not given free access to Kubwa and Kalina (they maintain the ability to initiate auditory, visual and, in the barn - tactile contact from adjacent stalls). During the coldest months the animals are housed in a heated barn; on warm-enough days (low wind speed and temperature above 10 °C), they are given access to separate yards adjacent to the barn. As a result, they tend to be much closer together during this time of the year. Between November 2016 and February 2017, Zahara, Nyah and Kalina were given free access to one another inside the barn for the first time. This occurred for about an hour a day everyday while the juveniles did not have free access to their mothers. After that, Zahara and Nyah were once again kept
separate from Kalina until the three were reintroduced (with Sophi) at the beginning of the current study. Video recordings of the group (Zahara, Nyah, Kalina and Sophi) were obtained between 20 November 2017 and 28 February 2018.

**Exhibit**

Observations were made in the “cow yard” (see Figure 1). This off-exhibit yard is about 270 square meters in size and is adjacent to the elephant barn. The cow-yard is entirely sand-filled. Enrichment devices such as large tires, sand piles, wooden logs, and browse were placed throughout the habitat on a varying basis. Usually, several bales of hay were thrown into this yard just before the animals were introduced and given access to the area. During the one-hour observation periods, the animals could move freely between the outdoor yard and an “indoor area” consisting of three adjacent stalls. The indoor area was approximately 170 square meters large and was adjacent to separate stalls where Ivory and Kubwa were held. Between November 2017 and February 2018, 25 observation sessions were conducted. Access to the cow yard was weather-dependent and, as a result, 13 indoor/outdoor observations occurred on warmer days (typically when the temperature was above 10 °C). The remaining sessions monitored only the indoor area. The data presented here were obtained in the outdoor arena (cow yard) during the sessions in which the animals had both inside and outside access.

**Materials**

My colleagues and I used Sony digital video cameras to record Zahara’s allomothering behavior. The raw video was uploaded digitally onto two independent digital hard drives (dual Western Digital 8TB “mirroring” drives). The data were analyzed on Macintosh computers using QuickTime Media Player, so that the video
could be manipulated (fast-forward, rewind, slow-motion) to improve accuracy. The analyzed data was stored on a University owned Google drive in Google-sheet and Microsoft Excel formats.

**Procedures**

Between November 2017 and February 2018, 13 video records of the four animals interacting in the cow yard were collected and analyzed. Due to the weather getting colder as the winter progressed, most of the data was obtained in 2017. All video was recorded from the same location to ensure consistency (Figure 1). Most observation sessions were about 50-60 min long, though some were shorter. During a few recording sessions, cameras or batteries failed and backup cameras had to be used. As a result, single sessions were sometimes split into several recordings. When there were multiple videos for an observation session, all videos were entered into one scoring sheet with pauses clearly marked.

Scoring proximity was conducted using instantaneous sampling at 30 second-intervals (Martin & Bateson, 2007). Every 30 s, beginning with the first appearance of the animals, a record was made of each animal’s proximity to all conspecifics. For example, Nyah could be alone, proximal to one other elephant, proximal to any two of them, or proximal to all three. Social proximity was operationalized as within an adult elephant body length (shoulders to rear, about 5m) from another individual. Proximity was judged on a pair-wise basis: for example, if Kalina, Zahara and Nyah were standing side-by-side – in that order - it would be possible for both Kalina and Zahara and Zahara and Nyah to be proximal, whereas Kalina and Nyah might not be so. In addition, “Pass-bys,” in which one animal was close to another for only a few seconds while moving past that animal to a different location, were not recorded as “proximal.” An index of
association was constructed to quantify the proximity results (Martin & Bateson, 2007). On this index, a score of 1.0 would indicate that the two animals were always seen together, a score of 0.0 would indicate that they were never seen together, and a score of 0.5 would indicate that the two animals were together as often as they were apart. The probabilities with which Zahara and Sophi were in contact with each of the two calves were compared using the z-score test for the significance of the difference between two independent proportions (Ferguson & Takane, 1989), assuming that Zahara and Sophi made their choices independently.

All-occurrence sampling was used to score changes in proximity for the four animals. Within each 30 s interval we recorded whether an animal initiated or broke proximity to another (proximity = within one body length/5m). There were sometimes multiple changes in proximity within each sampling period. If two animals approached or left one another at the same time, that observation was not included in the analysis (the alternative being a double approach). When an individual animal approached a pair of animals or a pair approached an individual, the data was entered as though all animals were separate. For instance, if Zahara and Nyah approached Kalina, two data points would be entered. One would represent Zahara approaching Kalina and one would represent Nyah approaching Kalina.

In any dyadic relationship, one animal may make contact (approach) more frequently than it breaks contact (leaves), or leave more than it approaches, or leave and approach the other equally often. The Hinde index (Hinde & Atkinson, 1970; Silk, Cheney, & Seyfarth, 2013) is used to quantify this behavior. The Hinde Index varies between -100 and +100: A score of 100 indicates that the focal animal always approaches
and never leaves, a score of -100 indicates that the focal animal always leaves and never
approaches, and a score of 0 indicates that the focal animal makes contact as often as it
breaks contact.

Secondly, *one animal may be responsible for the majority of changes in proximity*
(that is, do most of the approaching and leaving). The Brown Index (Brown, 1981; Silk et
al. 2013) is used to quantify this behavior. The index varies between 0 and 100, with a
score of 100 indicating that the focal animal was responsible for all of the changes in
proximity, a score of 0 indicating it was responsible for none of them, and a score of 50
indicating the two animals shared the responsibility for changing proximity equally.

Because making contact (approaching another) and breaking contact (leaving
another) were not statistically independent events, the relative probabilities with which
two animals in a dyad made and broke contact were analyzed separately, using the Chi-
square statistic (Siegel, 1956).

At the beginning of the study, observations were made to determine how to
classify agonistic behaviors (Figure 2). The behavioral terms and definitions in Table 1
were taken from Olson (2002). All-
occurrence sampling, coded within 30 s intervals, was
used to record behavioral observations.

**Results**

Social proximity data revealed that Zahara spent about three times as long as
Sophi with each of the juveniles (see Table 2: for Kalina, 28.0% vs. 7.6%; for Nyah,
23.7% vs. 9.0%). Both differences were statistically significant (for Kalina, $z = 10.66$, $p
< 0.01$; for Nyah, $z = 7.66$, $p < 0.01$). However, an index of association (Table 3: Martin
& Bateson, 2007) indicated that both Zahara and Sophi were with the calves only for a
small proportion of the available time. On this index, a score of 0.0 would indicate that
two animals were never together, a score of 0.5 would indicate that they were together as
often as they were apart, and a score of 1.0 would indicate that they were always
together. Zahara’s scores were 0.15 and 0.18 for Nyah and Kalina, respectively; Sophi’s
corresponding scores were 0.06 and 0.05.

In contrast, the index of association for Nyah and Kalina (Index = 0.51: Table 3)
suggested that Nyah and Kalina were together as often as they were apart, whereas
Zahara and Sophi were rarely together (Index = 0.05)

Changes in social proximity were assessed with the Hinde and Brown Indices,
and with separate Chi-square one-sample tests for the likelihoods of one animal
approaching or leaving the other animal in the dyad. The Hinde Index results (Table 4)
showed that Zahara and Sophi were each equally likely to make or break contact with
Kalina (Hinde Indices of 0.001 and 0.03, respectively) and that Sophi was equally likely
to make or break contact with Nyah (Index = -0.04). However, the index suggested that
Zahara was slightly more likely to make, rather than break, contact with Nyah (Hinde
Index = 0.153). In contrast, the Hinde Index for Sophi and Zahara (0.44) suggested that
Sophi was much more likely to make, rather than break, contact with Zahara.

The Brown Index, suggesting which animal in a dyad was responsible for most of
the changes in proximity to the other animal, indicated that both Nyah (0.49) and Kalina
(0.49) changed contact with Zahara as often as Zahara changed contact with them (Table
3). Consistent with this suggestion, the Chi-square tests showed that there were no
statistically significant ($p < 0.05$) differences in how often Zahara and Nyah either
approached or left each other, or in how often Zahara and Kalina approached or left one another (largest $\chi^2 (1) = 2.33$. n.s.)

On the other hand, given the Brown Indices for Sophi and Nyah (0.25) and for Sophi and Kalina (0.23), it seemed that the juveniles were responsible for most of the proximity changes with Sophi (Table 4). Again, the results of the Chi-square test supported this: Kalina and Nyah both approached and left Sophi more often than the reverse (smallest $\chi^2 (1) = 5.54, p < 0.02$)

Finally, Zahara displayed different levels of aggression towards the two juveniles (see Table 1 for the forms of aggression). During almost 10 hours of observation, Zahara was aggressive towards Kalina 15 times and towards Nyah once ($\chi^2 (1) = 12.25, p < 0.01$). Most of these aggressive behaviors occurred when Zahara interrupted sparring (play fighting) between Nyah and Kalina. In 15/16 cases, Zahara pushed Kalina away from Nyah, rather than the reverse.

**Discussion**

As expected, Zahara spent far more time with the calves than did Sophi. In addition, Zahara and the calves shared responsibility for maintaining contact, whereas the calves took primary responsibility for maintaining contact with Sophi. Both of these results are consistent with the idea that Zahara was allomothering both juveniles, whereas Sophi was monitoring the juveniles much less often.

Zahara also displayed a significant amount of discrimination in her treatment of Kalina and Nyah. Almost all of Zahara’s aggressive behavior (94%) was directed towards Kalina, suggesting that she was more tolerant of Nyah than of Kalina. This would be expected, since she was much more familiar with Nyah (who had spent virtually all of her
life in direct contact with Zahara) than she was with Kalina (who had spent very little
time in direct contact with Zahara).

Allomothering is an energetically costly activity and thus there must be
significant adaptive benefits for the allomother (Dublin, 1983; Lee, 1987; Riedman,
1982). Zahara’s preferential treatment of Nyah during the Nyah-Kalina sparing bouts
supports the hypothesis that her behavior constitutes allomothering, and that it is
motivated by inclusive fitness.

Limitations

There were several limitations to this study. For some periods, it was not possible
to observe accurately the distance between animals and/or their individual behaviors. To
some degree this was because of the shape of the exhibit, limitations on where the camera
could be placed, and the restriction that only one recording location (area) was permitted.
Sometimes the larger animals (Sophi and Zahara) were close to the camera location and
blocked the view of the other animals. At the beginning of data collection, 10-15-year-old
cameras with relatively poor-quality images were used. These cameras were soon
replaced with new, superior cameras. In addition, the location of the outside camera made
proximity scoring especially difficult. We had intended to have two outside cameras,
perpendicular to one another, allowing more effective estimation of inter-animal
distances. However, because of concerns that the second camera would be too distracting
to the elephants, at the last minute the zoo staff permitted us to have only one camera.

Another limitation to this study was the amount of video we collected. Due to the
poor weather and the limited time period during which the elephants were together, only
13 tapes of the animals in the cow yard were obtained. This was particularly problematic in analyzing agonistic behaviors because those behaviors were relatively infrequent.

Finally, the exact nature of Zahara’s relationships with Nyah and Kalina is unclear. On the one hand, Zahara, Nyah, and Kalina had almost constant auditory and olfactory contact with each other for the entirety of their lives. On the other hand, Zahara and Nyah had much more direct contact with one another than Kalina had with either of them. It is not clear whether the difference between the ways Zahara interacted with Nyah and Kalina reflected differences in familiarity or differences in genetic relatedness.

**Future directions**

A valuable way to proceed with this research would be to examine different elements of allomothering in relation to relatedness. For instance, much *in situ* research on allomothering describes group-defense and traveling-related behaviors (Lee, 1987). These behaviors are inherently unlikely to be performed *ex situ*. A much more likely way that allomothering might be displayed is through resource-guarding. An allomother should be more likely to share precious resources with a juvenile or calf if that animal’s fitness directly contributes to its own. Thus, if allomothering is purely driven by inclusive fitness, a related allomother should allow a juvenile greater access to resources like food and enrichment than would an unrelated allomother.

Whichever avenues may be pursued in the future, the information obtained in the current project should contribute to our understanding of elephant sociality and the role relatedness plays in behavior.
Acknowledgements

I would like to thank the Indianapolis Zoological Society for allowing me the opportunity to work with African bush elephants. In particular, this thesis would never have gotten off the ground without the help of Jill Sampson and Niki Kowalski. I am extremely grateful for their assistance to this project through the devotion of both their time and knowledge.

My fellow student lab members, Chelsea Patton, Brandon Knepper and Sammy Ruppert were hugely assistive in my research efforts. They helped collect and analyze observational data samples throughout the entire year and without their help, this thesis would never have been completed.

I would also like to thank my thesis reader, Dr. Jennifer Berry. She showed amazing patience as I pieced together the different elements of my study. I greatly appreciate the time and consideration she put into critiquing my work.

And finally, I would like to thank my advisor, Dr. Robert Dale. His constant support, encouragement, and counsel on all things elephant have been a blessing while developing, conducting, and analyzing this project. I am extremely thankful for the opportunity to work with such a fantastic advisor. Lastly, thank you Butler University for this amazing opportunity.
References


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Table 1: Behavioral ethogram of focal agonistic behaviors

<table>
<thead>
<tr>
<th>Behavior</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Driving</td>
<td>Uses head, tusks or trunks to push the rear of another elephant, maintaining contact while both elephants move at least one body length</td>
</tr>
<tr>
<td>Push</td>
<td>Head-to-head, head-to-body or body-to-body forceful contact that results in the target elephant moving. Not using tusks.</td>
</tr>
<tr>
<td>Slap</td>
<td>Strikes another elephant (or other animal) with trunk.</td>
</tr>
<tr>
<td>Tusking, social</td>
<td>Pushes or strikes another elephant (or other animal) with tusks. Usually strikes the target elephant’s rump. May be a forward strike or a “sideswipe.”</td>
</tr>
</tbody>
</table>

[Table 1: Behavioral ethogram of focal agonistic behaviors. Preliminary observations were conducted to determine which agonistic behaviors should be included in the observations. All-occurrence sampling was used to record the performance of each behavior at 30-second intervals. Which animal displayed each behavior, and to whom the behavior was directed, were also recorded. Behavior names and definitions taken from Olson, 2002].
Table 2: Proximity to juveniles: Zahara and Sophi

<table>
<thead>
<tr>
<th>Focal Animal</th>
<th>Kalina only</th>
<th>Nyah only</th>
<th>Both Kalina and Nyah</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zahara</td>
<td>11.1%</td>
<td>6.5%</td>
<td>16.9%</td>
</tr>
<tr>
<td>Sophi</td>
<td>2.7%</td>
<td>4.1%</td>
<td>5.0%</td>
</tr>
</tbody>
</table>

[Table 2: Proximity percentages compared for Zahara and Sophi. Observations of social proximity were made at 30-second intervals. Percentages were computed using all observations for which Kalina (N = 804) and Nyah (N = 799) were visible].
Table 3: Index of Association for Zahara, Sophi and the Juveniles

<table>
<thead>
<tr>
<th>Animals (Older &amp; Younger)</th>
<th>NOY</th>
<th>NO</th>
<th>NY</th>
<th>Index of association</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zahara &amp; Nyah</td>
<td>188</td>
<td>486</td>
<td>611</td>
<td>0.15</td>
</tr>
<tr>
<td>Zahara &amp; Kalina</td>
<td>225</td>
<td>449</td>
<td>579</td>
<td>0.18</td>
</tr>
<tr>
<td>Sophi &amp; Nyah</td>
<td>72</td>
<td>472</td>
<td>727</td>
<td>0.06</td>
</tr>
<tr>
<td>Sophi &amp; Kalina</td>
<td>61</td>
<td>483</td>
<td>743</td>
<td>0.05</td>
</tr>
<tr>
<td>Kalina &amp; Nyah</td>
<td>539</td>
<td>265</td>
<td>260</td>
<td>0.51</td>
</tr>
<tr>
<td>Sophi &amp; Zahara</td>
<td>55</td>
<td>489</td>
<td>619</td>
<td>0.05</td>
</tr>
</tbody>
</table>

[Table 3: Index of Association: the proportion of time for which two elephants are together in the yard. Observations of social proximity were made at 30-second intervals. An index of association was constructed comparing the number of observations in which the two animals were separate or together. NOY indicates the number of observations in which the older (O) focal animal and the younger (Y) target animal were together, NO indicates the number of observations in which the older animal was alone or with animals other than the younger animal and NY indicates the number of observations for which the younger animal was alone or with animals other than the older animal. For the index of association, 0.0 indicates that the animals were never together, 0.5 indicates that the animals were together as much as they were apart and 1.0 indicates that the animals were always observed together].
<table>
<thead>
<tr>
<th>Animals (Older &amp; Younger)</th>
<th>Ao</th>
<th>Ay</th>
<th>Lo</th>
<th>Ly</th>
<th>Hinde Index (Approach vs. Leave Bias)</th>
<th>Brown Index (Proximity Change Frequency)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zahara &amp; Nyah</td>
<td>49</td>
<td>37</td>
<td>35</td>
<td>49</td>
<td>15</td>
<td>49</td>
</tr>
<tr>
<td>Zahara &amp; Kalina</td>
<td>48</td>
<td>49</td>
<td>38</td>
<td>40</td>
<td>1</td>
<td>49</td>
</tr>
<tr>
<td>Sophi &amp; Nyah</td>
<td>7*</td>
<td>23*</td>
<td>7*</td>
<td>19*</td>
<td>-4</td>
<td>25</td>
</tr>
<tr>
<td>Sophi &amp; Kalina</td>
<td>8*</td>
<td>29*</td>
<td>10*</td>
<td>30*</td>
<td>-3</td>
<td>23</td>
</tr>
<tr>
<td>Kalina &amp; Nyah</td>
<td>84</td>
<td>70</td>
<td>41*</td>
<td>94*</td>
<td>24</td>
<td>43</td>
</tr>
<tr>
<td>Sophi &amp; Zahara</td>
<td>14</td>
<td>11</td>
<td>3*</td>
<td>21*</td>
<td>44</td>
<td>35</td>
</tr>
</tbody>
</table>

Table 4: Control of Changes in Proximity: Hinde and Brown Indices

[Table 4: Hinde Index and Brown Index comparing approaches (A) and leaves (L). All-occurrence sampling was used to record changes in proximity at 30-second intervals. Ao indicates the number of observations in which the older animal approached the younger animal. Ay indicates the number of observations in which the younger animal approached the older animal. Lo indicates the number of observations in which the older animal left the younger animal. Ly indicates the number of observations in which the younger animal left the older animal. A Hinde Index of “0” indicates that the older animal approached and left the younger animal equally often: an index of “+100” indicates that the older animal always approached, and never left, the younger animal; an index of “-100” indicates that the older animal never approached, but always left the younger animal. Positive scores indicate that the older animal was more likely to approach than leave the younger animal. A Brown Index of “0” indicates that the older animal was not responsible for any changes in proximity; an index of “50” indicates that the older animal and the younger animal were equally responsible for changes in proximity; a score of “100” indicates that the older animal was responsible for all of the changes in proximity. Scores below 50 indicate that the younger animal was responsible for most of the changes in proximity].

*Chi-square scores: statistically significant at the p =0.05 level (two-tailed)
[Figure 1: African elephant habitats at the Indianapolis Zoo. During observation times animals were given access to the cow yard as well as three indoor barn stalls. The red “x” marks the location of observers. By moving East or West along the gate between the exercise and cow yards, observers could view any part of the cow yard—though not all of the cow yard from all locations. Satellite image obtained from Google Maps.]
Examples of agonistic encounters

[Figure 2: Examples of agonist encounters. Agonistic encounters involving Zahara, Kalina, Nyah, and Sophi were monitored. Pictured is an example of a “Tusk, social” when one animal moves quickly to press its tusks into the body of another.]