

The Role of Touch in the Social Interactions of Asian Elephants (*Elephas maximus*)

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In order to successfully engage in social interactions, it is necessary to recognize and respond to the communicative cues provided by the other participants in these interactions. Communicative signals can occur in a variety of sensory modalities, including vision, sound, olfaction, and touch. In this study, we focus on the role of touch in the social interactions of elephants. Both aggressive and nonaggressive tactile behaviors were examined. In all cases, the body parts used to initiate tactile behaviors as well as the body parts that received these tactile behaviors were analyzed. Significant differences were seen in the overall frequency of tactile behaviors initiated and received by each elephant, as well as in the frequency of aggressive and nonaggressive tactile behaviors initiated and received by each elephant. The trunk was the body part most commonly used to initiate and receive tactile behaviors. The influence of several factors on the observed tactile behavior patterns are discussed, including the influence of social rank and movement in the social hierarchy.

Group living has many advantages, such as group foraging, group defense, and group care of offspring (Croney & Newberry, 2007). But understanding one's role in a group and behaving appropriately are essential for group members. Social dominance hierarchies are thought to facilitate group cohesion, and are reflected in both cooperative and competitive social interactions (Whitehead, 1997). As a result, an increase in social complexity is oftentimes accompanied by an increase in cognitive demands, including the need to recognize and respond to communicative cues. These cues may involve a variety of sensory modalities, including vision, sound, olfaction, and touch. Of these modalities, vocal and visual signals have been studied in the greatest detail. However, the use of touch is salient in the interactions of many social species, including primates (Chevalier-Skolnikoff, 1973; Cooper & Bernstein, 2000; Franz, 1999; Goosen & Ribbons, 1980; Lazaro-Perea, Arruda, & Snowdon, 2004; Leinfelder, Deleu, & Nelisson, 2001; Matheson & Bernstein, 2000; Matsumura, 1996; Nakamura, 2003; Nelson & Geher, 2007; O'Brien, 1993; Schaffner & Aureli, 2005; Schino, 2001; Seyfarth, 1977; Weber, 1973) and dolphins (Connor, Mann, & Watson-Capps, 2006; Dudzinski, 1998; Dudzinski, Gregg, Ribic, & Kuczaj, 2009; Kaplan & Connor, 2007; Paulos, Dudzinski, & Kuczaj, 2008; Sakai, Hishi, Takeda, & Kohshima, 2006; Tamaki, Tadamichi, & Michihiro, 2006; de Waal & van Roosmalen, 1979).

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In this paper, we add to the literature on the use of touch in the social interactions of Asian elephants (*Elephas maximus*).

Elephants are known to use vocalizations, touch, olfaction, and visual signals during their social interactions (Berg, 1983; Langbauer, 2000; Payne, 2003; Poole, 1994; Spinate, 1994; Vidya & Sukumar, 2005). For example, Payne (2003, pp. 59–60) described the interactions of family members after separations of several hours:

The gathering animals run together rumbling and screaming, circling, clashing tusks if they have them, entwining trunks, sniffing, stroking, shoving, bumping rumps – expressing excitement in social behaviors that range from affectionate to aggressive – while individually secreting from their temporal glands, and urinating and defecating.

Tactile signals involve a variety of body parts, including the trunk, tail, head, legs, and sometimes the entire body. These behaviors may be directed towards virtually any part of another elephant's body, including the trunk, genitalia, mouth, rear, tail, back, head, and legs (Adams & Berg, 1980; Berg, 1987; Gadgil & Nair, 1984; Langbauer, 2000; Vidya & Sukumar, 2005). The use of the trunk during tactile interactions is especially salient (Vidya & Sukumar, 2005). This is not surprising given that the trunk is an extremely sensitive body part that can detect subtle vibrations and perform a variety of tasks ranging from the most delicate (e.g., picking up a grape) to those requiring brute strength (Rasmussen & Munger, 1996).

Elephants use tactile behaviors in a variety of contexts, ranging from affiliative and/or playful interactions to aggressive interactions. For example, mothers and calves engage in a high rate of contact behaviors (Berg, 1983; Garai, 1992; Lee, 1986). Significantly, elephant calves may develop at a faster rate when they are exposed to greater amounts of contact (Moss, 1975), as is the case for human infants (Hertenstein, 2002; Weiss, Wilson, Seed, & Paul, 2001). The use of touch during play, especially between calves, may help calves develop normal behavioral patterns as well as test their strength and capabilities (Adams & Berg, 1980; Lee, 1987; Vidya & Sukumar, 2005). Finally, higher-ranking group members use touch to discipline lower-ranking group members and younger animals (Archie, Morrison, Foley, Moss, & Alberts, 2006; Freeman, Weiss, & Brown, 2004; Langbauer, 2000).

Although contact behaviors in elephant social interactions have been described in some detail, there has been little systematic investigation of the factors that influence the use of touch during social exchanges and the body parts that play a central role during these interactions. In order to better understand the factors that influence the use of tactile behaviors in elephant social interactions, the present study investigated the use of these behaviors in a group of captive Asian elephants housed at Busch Gardens in Tampa, Florida. General patterns of tactile behaviors across elephants were examined, as were individual patterns of aggressive and nonaggressive tactile behaviors. Additionally, the body parts that were involved in these tactile interactions were also investigated.

Method

Subjects and Habitat

The study group consisted of six female Asian elephants housed in an approximately one acre grassland/dirt habitat at Busch Gardens in Tampa Florida. The habitat consists of an oval tract of land surrounding a flat hill, with a pond at one end of the tract. The hill is not accessible to the elephants and visually impedes one side of the oval tract from the other, so that the entire habitat is not visible from any one vantage point. The elephants, therefore, were not visible to each other at all times, depending on their position in the habitat. However, the elephants chose to remain mainly on the side that was more accessible to the public and where the majority of the training (and thus reinforcement) and enrichment took place.

A social dominance hierarchy was evident in the study group and is depicted in Figure 1, along with each elephant's age at the time of the study. All of the animals, with the exception of KA, were wild born, and therefore, their included ages are approximations. ME was the oldest animal and the matriarch of the group. At the time of the study, contact between TI and SI was restricted, due to the high level of aggression that TI directed towards SI. As a result, both TI and SI alternated going out on the habitat every day (one of them stayed in the barn, while the other was out on the habitat with the other five elephants), where both were second in dominance to ME. When TI and SI were placed in close proximity (in the elephant barn), TI was the more dominant animal. KA was the youngest animal in the group. At the time of the study, RO and KA's behavioral patterns suggested that both were competing to move ahead of the other in the dominance hierarchy, and it was not clear whether one ranked above the other. CA, who is KA's mother, was the lowest in the hierarchy. None of the elephants, with the exception of CA and KA, were related to each other.

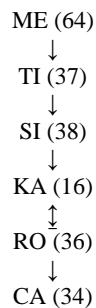


Figure 1. The dominance hierarchy and ages of the six female Asian elephants housed at Busch Gardens. The ages are included in parentheses, while the arrows indicate direction of dominance, with ME being the most dominant animal and CA being the least dominant animal. The two-way arrow between KA and RO indicates a roughly equal position in the dominance hierarchy.

Procedure

Data collection took place during a five-week period from December 11th, 2006 through January 13th, 2007 and focused on the tactile behaviors present in the social interactions of the six elephants. All of the observations were collected, coded, and analyzed (see below) by one primary observer. Observations were non-invasive and were collected using a Sony DCR-VX1000 digital camera. Observations began as soon as two elephants were placed on the habitat -- elephants were shifted onto the habitat individually immediately after husbandry procedures (e.g., blood-draws, scale-weights, eye- or oral-exams, foot-trims, ultrasound examinations, etc.) or relationship-building sessions with trainers. This typically occurred between 9:30am and 10:00am each day. [NOTE: At Busch Gardens Tampa, the elephants spend the night on the habitat and shift into the barn area in the morning so that the habitat can be cleaned. Individual shifting is conditioned and maintained as a husbandry tool, but the "default" is that the elephants are together, outside as much as possible.] Observations continued throughout the rest of the morning, lasting approximately two hours and

commenced again in the afternoon, lasting approximately four hours. All instances of tactile behaviors were recorded during the observations.

A total of 152 hours of observation were collected. However, due to the individual shifting of elephants onto to the habitat following husbandry procedures (the order for each elephant varying on a daily basis) each elephant was on the habitat for different amounts of time, resulting in varying observation times for each individual. The total number of hours each individual was observed is shown in Table 1. All video recordings were coded for the presence of tactile behaviors. Aggressive tactile contact was defined as any part of an elephant's body engaging in contact that involved hitting, pushing, or grabbing, with any part of another elephant's body. Nonaggressive contact was defined as any part of an elephant's body engaging in contact with any part of another elephant's body that did not involve hitting, pushing, or grabbing. Although many of the behaviors were defined as nonaggressive in our study, we do acknowledge that these behaviors may have been precursors to aggressive behaviors/used to signal dominance.

Table 1
Number of hours of observation for each elephant.

Elephant	Number of Hours Observed
ME	117.2
TI	74.3
SI	73.9
KA	136.2
RO	138.2
CA	127.3

Reliability

Inter-observer reliability using the Cohen's Kappa coefficient (Cohen, 1960) was determined for the categories of behaviors coded (e.g. trunk placement behaviors, tail placement behaviors, etc.), as well as the nature of these behaviors (aggressive versus nonaggressive). Ten percent of the behaviors coded by the primary observer were selected randomly for a second observer to code. The second observer was asked to indicate both the category of behavior as well as the type of behavior being observed. The Cohen's Kappa coefficient for category of behavior was 0.81, while the Cohen's Kappa coefficient for the nature of the behaviors was 0.85, indicating strong agreement between observers (Landis & Koch, 1977).

Results

Rates (defined as frequency per hour), the chi-square goodness-of-fit test, and the binomial test, were all used to analyze tactile behaviors. Rates were used to account for the unequal observation times collected for each elephant. Therefore, the results will be discussed in terms of rates as well as frequencies (chi-square goodness-of-fit test/binomial test). The total tactile behaviors initiated and received by each elephant as well as the aggressive and nonaggressive tactile behaviors initiated and received by each elephant were examined. The recipients of each elephant's tactile behaviors (including aggressive and nonaggressive tactile behaviors) were also examined. Additionally, the body parts involved in initiating tactile behaviors were investigated. The trunk played an especially salient role in the initiation of tactile behaviors and was therefore examined in further detail, including the body parts these behaviors were directed towards, and how many of these behaviors included aggression.

General Tactile Behaviors

There was a significant difference in the frequency of tactile behaviors that each elephant initiated, $\chi^2(5, N=2649) = 1239.43, p < 0.001$. ME and KA initiated the highest rates of tactile behaviors, while CA initiated the lowest rate of tactile behaviors (see Figure 2). There was also a significant difference in the frequency of tactile behaviors that each elephant received, $\chi^2(5, N=2649) = 319.085, p < 0.001$. RO and ME received the highest rates of tactile behaviors while CA received the lowest rate (see Figure 3).

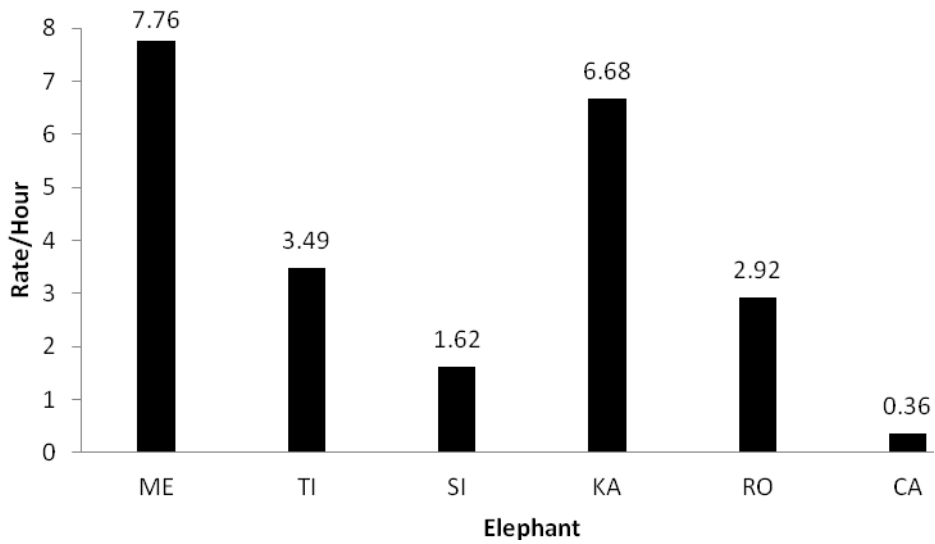


Figure 2. Rates (frequency/hour) of tactile behaviors initiated by each elephant.

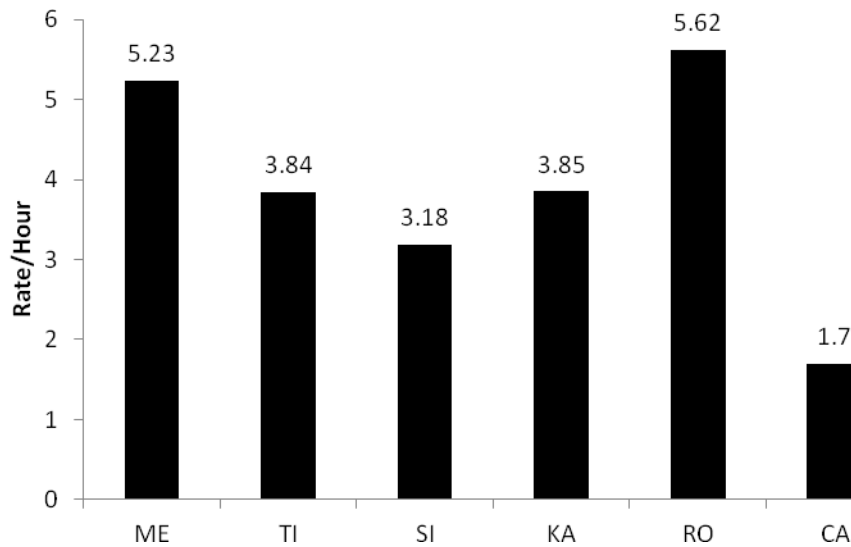


Figure 3. Rates (frequency/hour) of tactile behaviors received by each elephant.

The recipients of each elephant's rate of tactile behaviors are summarized in Table 2. ME directed the highest rate of tactile behaviors towards RO and the second highest rate towards KA. Of the tactile behaviors that KA initiated, the highest rate was directed towards ME and the second highest rate towards TI. RO directed the highest rate of her tactile behaviors towards ME and the second highest rate towards KA. CA, in comparison to the other group members, directed low rates of tactile behaviors to each of her conspecifics. However, when she did direct tactile behaviors towards other group members, her highest rates were directed towards KA and RO. Also important to note is that KA and RO often received the highest rates of tactile behaviors from other group members.

Table 2
Tactile behavior initiation rates (frequency/hour) directed towards other elephants (ordered from highest to lowest initiation rate).

Elephant	Rate				
	1	2	3	4	5
ME	RO (4.12)	KA (1.73)	SI (1.53)	TI (0.31)	CA (0.17)
TI	KA (1.94)	RO (1.20)	ME (0.27)	CA (0.08)	
SI	RO (0.64)	KA (0.37)	ME (0.35)	CA (0.27)	
KA	ME (2.58)	TI (1.73)	RO (1.11)	CA (0.92)	SI (0.35)
RO	ME (1.53)	KA (0.84)	CA (0.33)	TI (0.17)	SI (0.06)
CA	KA (0.27)	RO (0.05)	ME (0.03)	TI (0.01)	SI (0.01)

Aggressive Tactile Behaviors

After examining the initiation rates of total tactile behaviors across elephants, the tactile behaviors were broken down into aggressive and nonaggressive tactile behaviors and examined for differences. CA was not observed initiating any aggressive tactile behaviors, and was therefore excluded from the chi-square analysis. The frequency of aggressive tactile behaviors initiated for the remaining five elephants significantly differed, $\chi^2(4, N=507) = 724.75, p < 0.001$. ME initiated the highest rate of aggressive tactile behaviors, followed by RO (see Figure 4). Apart from CA, KA initiated the next lowest rate of aggressive tactile behaviors.

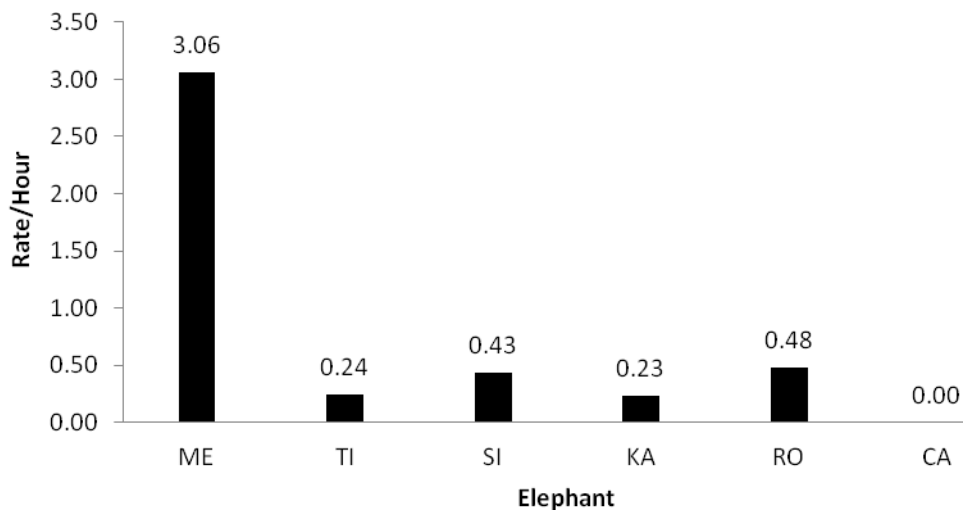


Figure 4. Rates (frequency/hour) of aggressive tactile behaviors initiated by each elephant.

When examining the frequency of aggressive tactile behaviors received by each elephant, a significant difference was also found, $\chi^2(4, N=506) = 313.231, p < 0.001$. However, TI was excluded from the chi-square analysis because she was the recipient of only one aggressive tactile behavior. RO received the highest rate of aggressive tactile behaviors from other elephants, while, apart from TI, ME received the lowest rate of aggressive tactile behaviors (see Figure 5).

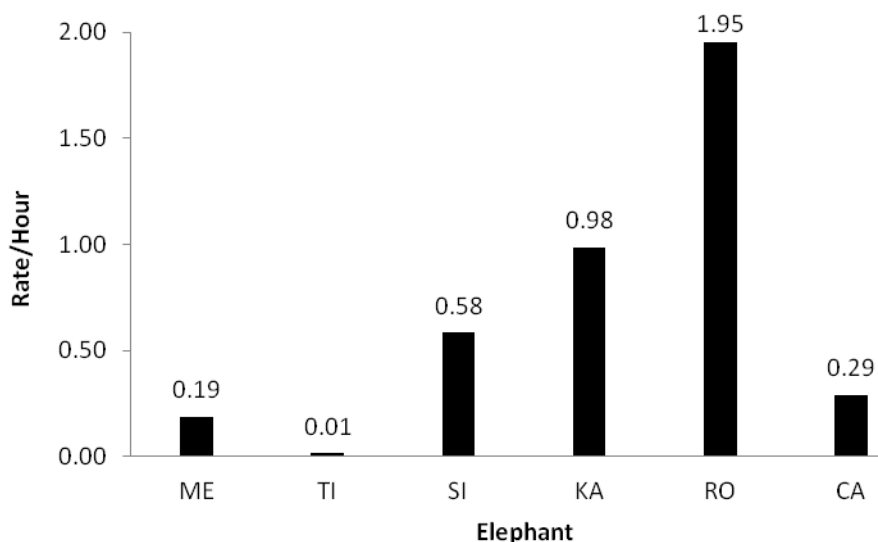


Figure 5. Rates (frequency/hour) of aggressive tactile behaviors received by each elephant.

The recipients of each elephant's aggressive tactile behaviors were also examined (see Table 3). ME and TI both directed their highest rates of aggressive tactile behaviors towards RO and their second highest rates towards KA. SI directed her highest rate of aggressive tactile behaviors towards RO, and her second highest rate towards CA. KA and RO both directed their highest rates of aggressive tactile behaviors towards each other. While RO directed her second highest rate of aggressive tactile behaviors towards ME, KA, apart from the aggressive tactile behaviors she directed towards RO, rarely directed aggressive tactile behaviors towards other group members. In fact, she only directed a total of four aggressive tactile behaviors towards other group members (reflected in the rates of 0.01 for TI, SI, and CA), none of which were directed towards ME. CA was not observed directing any aggressive tactile behaviors towards the other group members. It is important at this point to note that *all* of the elephants that engaged in aggressive tactile behaviors (with the exception of CA) directed their highest rates of aggressive tactile behaviors towards RO.

Several elephants received a low rate of aggressive tactile behaviors from other elephants, and in some cases, did not receive any aggressive tactile behaviors at all. ME only received aggressive tactile behaviors from RO and SI (the majority from RO, who seemed to be retaliating to ME's aggressive tactile behaviors directed towards her). TI did not receive any aggressive tactile behaviors from other group members, with the exception of KA, who directed only one aggressive tactile behavior towards her (see above). Two pairs of elephants, ME and TI, and TI and CA, did not direct any aggressive tactile behaviors towards each other. Also, SI did not direct any aggressive tactile behaviors towards KA, and KA only directed one aggressive tactile behavior towards SI (again, reflected in the rate of 0.01). However, this behavior may have been coincidental instead of being intentionally directed towards SI (both elephants were trying to pull at a tire toy and KA's head jerked up while pulling at the tire, pushing SI's head).

Table 3
Aggressive tactile behavior initiation rates (frequency/hour) directed towards other elephants (ordered from highest to lowest initiation rate).

Elephant	Rate				
	1	2	3	4	5
ME	RO (1.76)	KA (0.89)	SI (0.35)	CA (0.07)	TI (--)
TI	RO (0.20)	KA (0.04)	ME (--)	CA (--)	
SI	RO (0.28)	CA (0.14)	ME (0.01)	KA (--)	
KA	RO (0.21)	TI (0.01)	SI (0.01)	CA (0.01)	ME (--)
RO	KA (0.20)	ME (0.15)	CA (0.12)	SI (0.01)	TI (--)
CA	ME (--)	TI (--)	SI (--)	KA (--)	RO (--)

Nonaggressive Tactile Behaviors

There was also a significant difference in the frequency of nonaggressive tactile behaviors each elephant initiated, $\chi^2 (5, N= 2142) = 966.07, p < 0.001$, with KA initiating the highest rate of nonaggressive tactile behaviors, and CA initiating the lowest rate of nonaggressive tactile behaviors (see Figure 6). Additionally, there was a significant difference in the frequency of nonaggressive tactile behaviors each elephant received, $\chi^2 (5, N= 2142) = 282.68, p < 0.001$. ME received the highest rate of nonaggressive tactile behaviors, while CA received the lowest rate of nonaggressive tactile behaviors (see Figure 7).

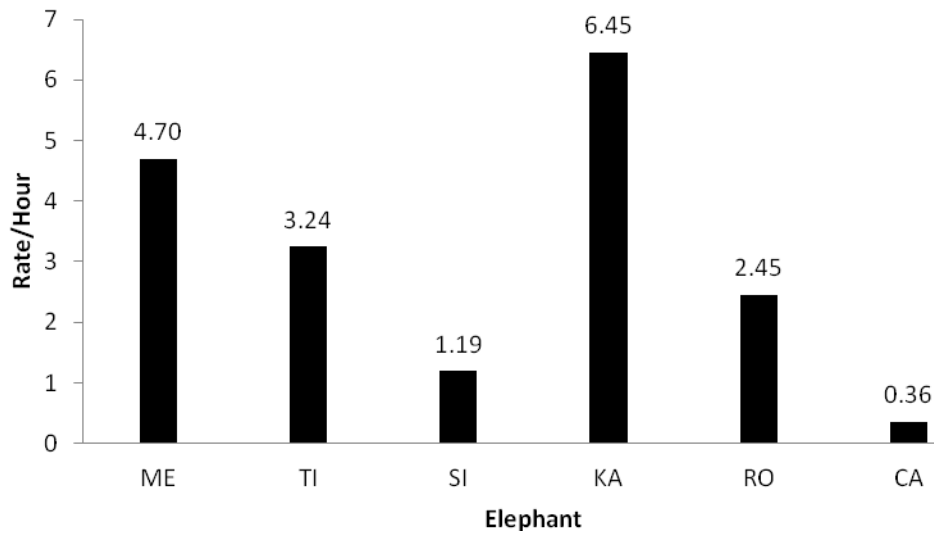


Figure 6. Rates (frequency/hour) of nonaggressive tactile behaviors initiated by each elephant.

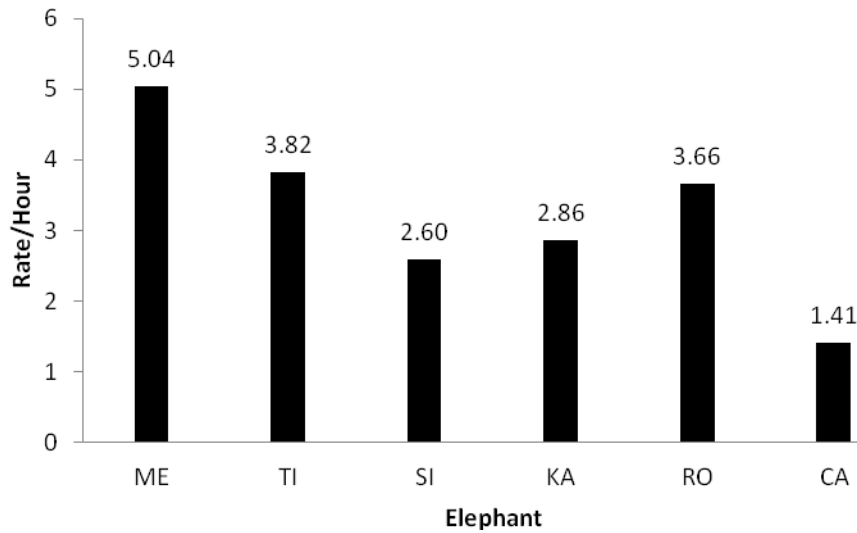


Figure 7. Rates (frequency/hour) of nonaggressive tactile behaviors received by each elephant.

Examination of the recipients of each elephant's nonaggressive tactile behaviors revealed that TI, SI, and CA all directed their highest rates of nonaggressive tactile behaviors towards KA and their second highest rates towards RO. RO and ME both directed their highest rates of nonaggressive tactile behaviors towards each other. Also, KA directed her highest rate of nonaggressive tactile behaviors towards ME and her second highest rate towards TI. Additionally, the two pairs of elephants that did not direct any aggressive behaviors towards each other, ME and TI, and TI and CA, also directed low rates of nonaggressive tactile behaviors towards each other.

Table 4

Nonaggressive tactile behavior initiation rates (frequency/hour) directed towards other elephants (ordered from highest to lowest initiation rate).

Elephant	Rate				
	1	2	3	4	5
ME	RO (2.36)	SI (1.18)	KA (0.84)	TI (0.21)	CA (0.10)
TI	KA (1.90)	RO (1.00)	ME (0.27)	CA (0.08)	
SI	KA (0.37)	RO (0.35)	ME (0.34)	CA (0.14)	
KA	ME (2.58)	TI (1.72)	RO (0.90)	CA (0.90)	SI (0.34)
RO	ME (1.37)	KA (0.64)	CA (0.20)	TI (0.17)	SI (0.05)
CA	KA (0.27)	RO (0.05)	ME (0.03)	TI (0.01)	SI (0.01)

Body Part Use During Tactile Behavior Initiation

The frequencies at which the trunk, head, tail, legs, and rear (collapsed across elephants) were used to initiate tactile behaviors significantly differed,

$\chi^2(4, N = 2649) = 4195.404, p < 0.001$. The trunk was used at the highest rate to initiate tactile behaviors (see Figure 8). This was true even when examining body part use for each elephant individually (see Figure 9). The tail was used at the next highest rate, while the legs were used at the lowest rate.

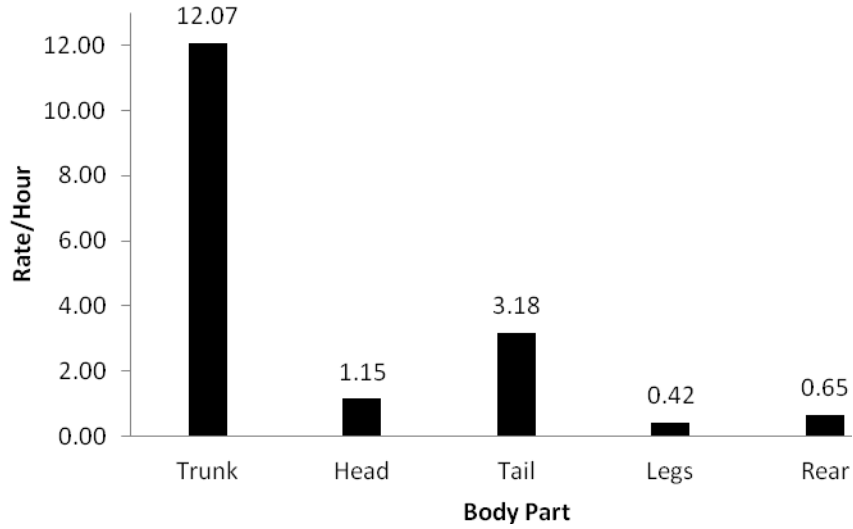


Figure 8. Initiation rates (frequency/hour) of tactile behaviors using various body parts.

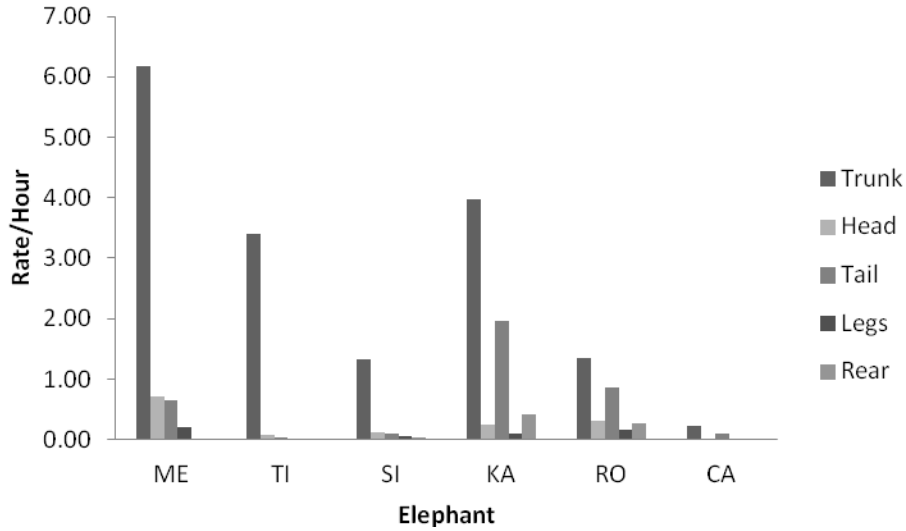


Figure 9. Initiation rates (frequency/hour) of tactile behaviors using various body parts for each elephant.

Trunk Tactile Behaviors

Given that the trunk was used at the highest rate to initiate tactile behaviors and is the most versatile out of the body parts examined, trunk use during tactile interactions was examined in greater detail. More specifically, the body parts that were the targets of trunk tactile behaviors were examined. Body parts that trunk tactile behaviors were directed towards included the head (excluding the mouth), trunk, legs, side, back, tail, rear, mouth, belly, and genitals. Trunk tactile behaviors directed towards the head and mouth were considered separately, due to the number of behaviors that specifically targeted the mouth, rather than the head in general. A significant difference in the frequency at which each body part was targeted by the trunk during tactile interactions was revealed, $\chi^2(9, N = 1810) = 1212.21, p < 0.001$. Trunk tactile behaviors directed toward another elephant's trunk occurred at the highest rate, followed by trunk tactile behaviors directed towards the head and mouth (see Figure 10).

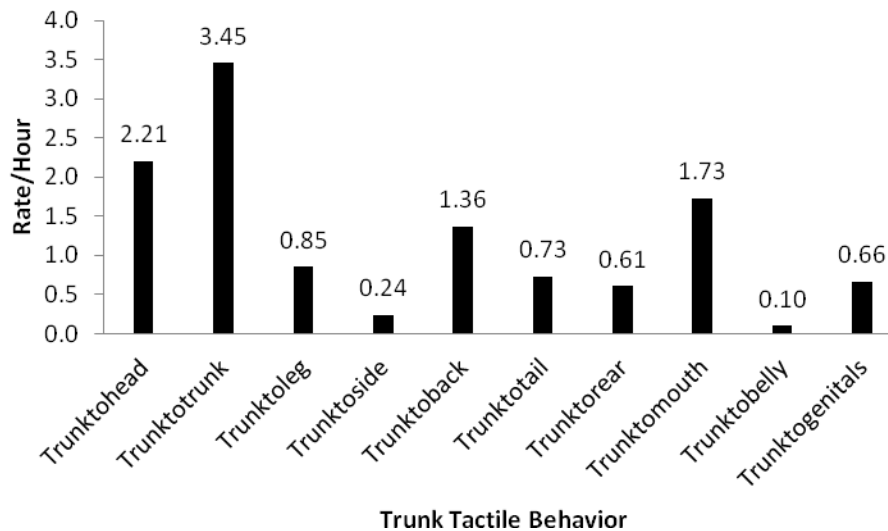


Figure 10. Initiation rates (frequency/hour) of trunk tactile behaviors directed towards various body parts.

Significant differences in the frequency at which each body part received aggressive trunk tactile behaviors, $\chi^2(5, N = 294) = 254.90, p < 0.001$, and nonaggressive trunk tactile behaviors, $\chi^2(9, N = 1507) = 936.192, p < 0.001$, were also revealed. However, aggressive tactile behaviors involving the trunk targeting the back, mouth, belly, and genitals were removed from the chi-square analysis due to a low number of occurrences (less than five). Aggressive trunk tactile behaviors directed towards the trunk occurred at the highest rate, followed by the head and tail. Although aggressive tactile behaviors directed from the trunk to the mouth had a low rate of occurrence, nonaggressive tactile behaviors directed from the trunk to the mouth occurred at the third highest rate, preceded by the trunk (highest rate) and head [(second highest rate) (see Figures 11 and 12)].

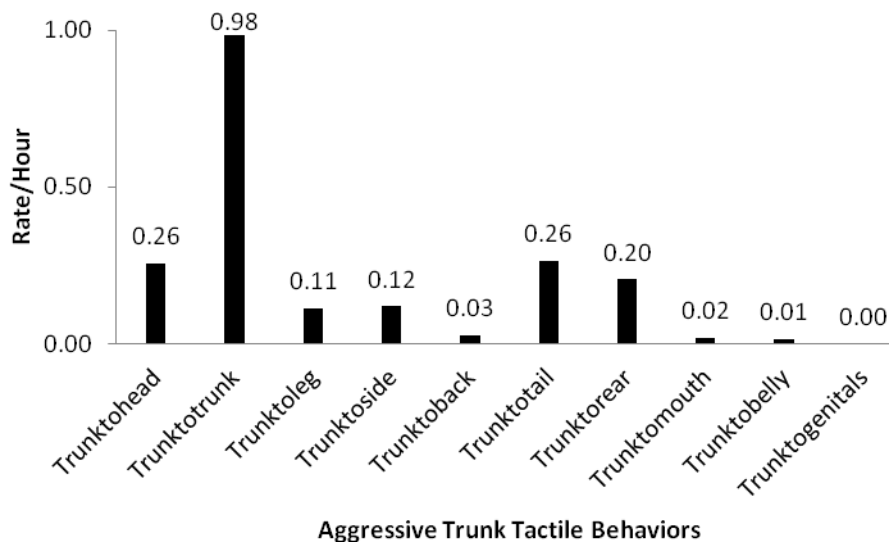


Figure 11. Initiation rates (frequency/hour) of aggressive trunk tactile behaviors directed towards various body parts.

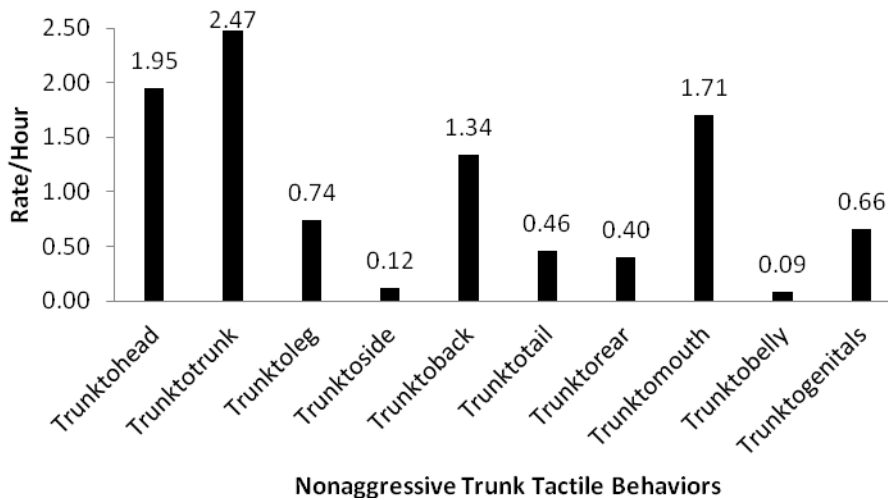


Figure 12. Initiation rates (frequency/hour) of nonaggressive trunk tactile behaviors directed towards various body parts.

Also, when engaging in aggressive tactile interactions towards lower-ranking animals, higher-ranking animals tended to use the trunk more so than other body parts to initiate aggressive tactile behaviors, $z = 6.53$, $p < 0.001$. Lower-ranking animals rarely directed aggressive tactile behaviors towards higher-ranking animals. Only 25 aggressive tactile behaviors were directed from lower-ranking animals towards higher-ranking animals (as opposed to the 427 aggressive tactile behaviors that were directed from higher-ranking to lower-ranking animals), none

of which involved the use of the trunk. The aggressive tactile behaviors exchanged between KA and RO were excluded from the analysis due to the uncertainty in who ranked above the other.

Discussion

The use of touch is a salient component of Asian elephant social interactions. The present study found significant differences in the frequency of tactile behaviors initiated and received by each elephant in the group as well as in the frequency of aggressive and nonaggressive tactile behaviors each elephant initiated and received. Additionally, individual differences were seen amongst the elephants in regards to the animal with which they preferred to initiate contact. Finally, there were significant differences in the frequencies at which each body part was used to initiate tactile behaviors, with the trunk being used the most.

General Tactile Behaviors

Several studies support our findings that individual differences exist in the amount of tactile behaviors elephants engage in as well as the conspecifics they prefer to direct these behaviors towards (Adams & Berg, 1980; Gadgil & Nair, 1984; Garaï, 1992). For example, in their study of Asian elephants living in three different sanctuaries in India, Gadgil and Nair (1984) found that certain pairs of females preferred to remain in close proximity with each other, providing an impetus for a greater number of tactile interactions to occur. Similarly, Garaï (1992) reported the presence of special relationships in three groups of captive unrelated Asian elephants, the defining factors being the lack of agonistic behavior between the elephants involved, the degree of spatial proximity, and the involved elephants' reactions to their partner's vocalizations and arousals. Adams and Berg (1980) also found that preferential relationships existed in the group of captive African elephants (*Loxodonta africana*) they studied, with the presence of touch being one of the defining factors.

It is clear that tactile behaviors do play an important role in elephant social interactions and that individual differences in the use of tactile behaviors are evident across both Asian and African elephants. Therefore, personality likely plays a critical role in the frequency and types of social interactions in which individual elephants engage. For example, Freeman et al. (2004) found that dominance status and temperament (judged by how aggressive or submissive an elephant was relative to the rest of the group) were positively correlated.

As mentioned above, dominance status ties into the differences seen in the rates of tactile behaviors elephants exchange. For example, ME, the highest ranking animal, initiated the highest rate of tactile behaviors and, ME, as well as RO and KA, the two animals that seemed to be competing for dominance status at the time of the study, were often the recipients of the highest rates of tactile behaviors from other elephants. Perhaps ME's importance as the matriarch played a role in the high rates of tactile behaviors she initiated and received, while RO and KA's shifting dominance statuses required more interaction with other elephants (including each other), and therefore more tactile interactions, accounting for the

high rates of tactile behaviors they received. CA, whose low dominance rank seemed to be well established, initiated and received the lowest rates of tactile behaviors. Therefore, tactile interactions may play a greater role for those group members whose statuses are still dynamic and not well-established, as well as those group members responsible for maintaining the social hierarchy of a group, such as the matriarch (Freeman et al., 2004; Langbauer, 2000).

Aggressive Tactile Behavior Patterns

In addition to each elephant initiating significantly different amounts of tactile behavior, significant differences were seen in the amount of aggressive tactile behaviors each elephant initiated and received. There were also differences in who each elephant directed these behaviors towards. Dominance status, again, plays an especially salient role in aggressive tactile interactions. Higher-ranking animals initiate more aggressive tactile behaviors than do lower-ranking animals, such interactions providing a means to discipline members of the group, especially young animals (Freeman et al., 2004). Aggressive tactile behaviors include trunk slapping, kicking, poking, and shoving (Langbauer, 2000). It is not surprising, then, that ME, the matriarch of our study group, initiated the highest rate of aggressive tactile behaviors and that both ME's and TI's (the second highest-ranking animal) highest and second-highest rates of aggressive tactile behaviors were directed towards the two lower-ranking animals that were competing for dominance status, RO (received ME's and TI's highest rates) and KA (received ME's and TI's second highest rates).

RO, who received the highest rate of aggressive tactile behaviors from ME, was often observed standing in close proximity to ME (less than two body lengths), even immediately after receiving aggression from her. Perhaps the attention RO received from ME was reinforcing to RO, and so, rather than cause RO to turn away or leave ME's space, ME's aggressive tactile behaviors may have instead increased RO's proximity seeking behavior. In children, negative attention can oftentimes be reinforcing and serve to strengthen whatever undesirable behavior in which they are engaged (Gallimore, Tharp, & Kemp, 1969), and the same thing could have been happening in ME's and RO's interactions. Although other group members were seen standing in close proximity to ME, especially TI, aggressive tactile behaviors occurred at a lower rate, and did not occur at all between ME and TI.

KA's behavior also likely influenced the rate of aggressive tactile behaviors ME directed towards her. KA sometimes approached ME while they were feeding and placed her tail in ME's mouth while ME was chewing on hay. Although ME often responded with aggressive tactile behaviors when KA did this, KA did not terminate her behavior immediately afterwards and so often received additional tactile aggression from ME. However, given that the tail is often the target of aggressive behaviors, it is possible that KA was placing her tail in ME's mouth as a sign of submission by placing an often targeted body part within ME's reach. Similarly, Garai (1992) found that, in her study group, the posterior end was often directed towards group members that were the most aggressive, and also speculated that presentation of the posterior plays a role in demonstrating

submission. These findings are consistent with reports that submissive elephants will often back into the sides and heads of dominant animals (Kahl & Armstrong, 2000; Langbauer, 2000).

Also observed was that RO and KA directed their highest rates of aggressive tactile behaviors towards each other. Archie et al. (2006) reported that aggressive tactile behaviors were used to assess and maintain dominance rank status in wild female African elephants. These findings fit well with our speculation that RO and KA directed high rates of aggressive tactile behaviors towards each other as a means to compete and establish their relative dominance ranks.

CA, the lowest ranking elephant, was rarely the target of ME's aggressive tactile behaviors. This is most likely because she was quite submissive and so rarely placed herself in a position that annoyed ME. Additionally, CA was never observed directing any aggressive tactile behaviors towards other group members, which may have also been another reason she was rarely targeted by not only ME, but most of the other group members as well. Also, CA was blind in one eye, which may have also influenced the rate at which she interacted with the other elephants in the group.

Another factor that may have influenced the patterns of aggressive tactile behaviors observed in the group is redirected aggression. All of the elephants, except for CA, directed their highest rate of aggressive tactile behaviors towards RO. Also, ME directed her third highest rate of aggressive tactile behaviors towards SI, who, when within TI's reach during morning barn feeds, also received aggressive tactile behaviors from TI. Consequently, SI was observed directing her highest rates of tactile behaviors towards RO, followed by CA, while RO was sometimes observed directing aggressive tactile behaviors towards CA. It is possible that the aggressive tactile behaviors that RO and SI directed towards other elephants were a form of redirected aggression, resulting from the aggression they received from more dominant group members. For example, on several occasions, RO was witnessed directing aggressive tactile behaviors towards CA, right after being the recipient of aggressive tactile behaviors from SI.

Redirection of aggression towards other group members has been observed in several species of primates and is speculated to reduce post-conflict anxiety and tension in the original recipients of aggression (Aureli, 1992; Cheney & Seyfarth, 1989; Koski, de Vries, van den Tweel, & Sterck, 2007). For example, long-tailed macaques (*Macaca fascicularis*) will often redirect aggression towards other group members after an aggressive interaction, irrespective of whether the third party is related to the aggressor (Aureli, 1992). Vervet monkeys (*Cercopithecus aethiops*) were also observed engaging in redirected aggression, but were more likely to redirect aggression towards their opponents' relatives after an aggressive conflict. In addition, the relatives of opponents were more likely to direct aggression towards each other after an aggressive conflict, much like the family feuds of humans (Cheney & Seyfarth, 1989). RO and SI's possible redirected aggression, then, may have helped to reduce any anxiety or tension they may have been experiencing after receiving aggression from other group members.

Finally, three pairs of individuals engaged in little to no aggressive tactile behaviors with each other, ME and TI, SI and KA, and TI and CA. ME and TI,

who were often seen together, never directed aggressive tactile behaviors towards each other. Also, ME sided with TI when conflicts arose between TI and SI in the barn during morning feeds. ME and TI were the highest and second highest-ranking individuals in the group, which may have contributed to the lack of tactile aggression between the two animals. Scott and Lockard (2006) found that higher-ranking captive western lowland gorilla females (*Gorilla gorilla gorilla*) were more likely to direct agonistic behaviors, including aggressive contact behaviors, towards lower-ranking females than to each other.

SI did not direct any aggressive tactile behaviors towards KA, while KA was only seen engaging in aggressive contact with SI on one occasion, which seemed more coincidental than intentional, where KA's head pushed SI's head when they were both trying to play with a tire. Also, SI occasionally exhibited behaviors that seemed to be indicative of anxiety or uneasiness, such as tapping on the bars in the barn with her trunk and vocalizing. On many of these occasions, KA would approach SI and point her trunk towards SI's trunk or place her trunk somewhere on SI's body, perhaps as a sign of reassurance (Garai, 1992, Lee, 1986).

Finally, TI and CA were rarely seen associating, which may have contributed to the lack of aggressive tactile behaviors between them. Additionally, as mentioned earlier, CA may have been displaying the appropriate submissive behaviors. Therefore, TI may not have needed to use outright aggression to express her dominance towards CA.

One possible explanation for the dearth of aggressive tactile behaviors between these three dyads is that they shared a special relationship, similar to the elephants in Garai's (1992) study, where omission of agonistic behavior was one of the defining factors of these relationships. However, although TI and CA's relationship lacked aggressive tactile behaviors, it is not likely that their relationship could be defined as special, due to their lack of association.

Nonaggressive Tactile Behavior Patterns

Significant differences were seen in the number of nonaggressive tactile behaviors each elephant initiated and received. Once again, differences did exist in who each elephant preferred to direct these behaviors towards. ME received the highest rate of nonaggressive tactile behaviors, one possible explanation being that, through the use of nonaggressive tactile behaviors, other group members were expressing their submission towards the matriarch.

Also, RO and ME directed their highest rates of nonaggressive tactile behaviors towards each other. Perhaps this was a function of the close proximity RO maintained with ME, and perhaps RO was using some of these nonaggressive tactile behaviors to express submission to ME. Furthermore, ME, may have directed a high rate of nonaggressive tactile behaviors towards RO as a means to express her dominance, along with the aggressive tactile behaviors she directed towards RO. As mentioned earlier, certain nonaggressive tactile behaviors may actually contain dominant behaviors as well as precede certain aggressive behaviors. Therefore nonaggressive tactile behaviors may serve to express both dominance and submission (e.g., in the case of RO), depending on the type of

behaviors involved. For example, Burks et al. (2004) described trunk to back placement behaviors, where at least 2/3rds of the length of the trunk is placed on another elephant's back, as a passive aggressive behavior, while in our study, this behavior was categorized as a nonaggressive tactile behavior. If aggression is considered to play a role in maintaining the dominance hierarchy, passive aggressive behaviors may also play a role in signaling dominance.

Another interpretation of RO's behavior is provided by the literature on human grooming. Nelson and Geher (2007) reported that humans who exhibited more anxiety were more likely to exhibit grooming behaviors towards their partners in romantic relationships. RO occasionally pulled/twisted her own right nipple (which was already elongated) with her trunk. Although it is not clear why RO engaged in this behavior, one possible interpretation is that this behavior may have been a self-comforting technique to cope with minor anxiety. If so, then RO may have directed a high rate of nonaggressive tactile behaviors, some of which may have served affiliative functions, towards ME in order to strengthen the bond between them (although their relationship cannot be considered romantic), similar to the anxious individuals reported in Nelson and Geher's (2007) study.

KA, unlike RO, never initiated aggressive tactile behaviors towards ME. Additionally, KA initiated the highest rate of nonaggressive tactile behaviors, the majority of which were directed towards ME and TI, the two highest-ranking animals. It could be that KA was communicating appropriate submissive behaviors towards higher-ranking animals through the use of nonaggressive tactile behaviors, which therefore, may explain the lower rate of aggressive tactile behaviors she received from these animals. It is also possible that KA used nonaggressive tactile behaviors to curry favor from ME and TI, perhaps in an attempt to gain their support as she tried to move past RO in the social hierarchy.

Also, TI, SI, and CA directed their highest rates of nonaggressive tactile behaviors towards KA. TI may have been reciprocating the high rate of nonaggressive tactile behaviors she received from KA. Perhaps the nonaggressive tactile behaviors that KA directed towards TI were submissive in nature, while the nonaggressive tactile behaviors TI directed towards KA contained dominance signals. On the other hand, the nonaggressive tactile behaviors SI directed towards KA may have been a function of their "special" relationship (see above). However, due to SI's higher position in the dominance hierarchy, some of the nonaggressive tactile behaviors she directed towards KA may have also contained dominance signals. Finally, CA may have directed her highest rate of nonaggressive tactile behaviors towards KA because KA was her daughter.

Additionally, the two pairs of elephants that did not direct any aggressive tactile behaviors towards each other, ME and TI, and TI and CA, also directed low rates of nonaggressive tactile behaviors towards each other. ME and TI were often seen standing close together, while TI and CA were rarely seen together. Perhaps ME and TI directed a low rate of nonaggressive tactile behaviors towards each other due to the lack of the need to express dominance and submission to each other. What little nonaggressive tactile behaviors that passed between them may have been affiliative in nature, although the expression of dominance and submission between the two cannot be completely ruled out. Conversely, the low rate of nonaggressive tactile behaviors exchanged between TI and CA may have

again been due to the lack of interaction in general between the two elephants, and what little exchange that did occur between them may have again served to express their respective positions in the dominance hierarchy.

Body Part Use During Tactile Interactions

The trunk may be the most important adaptation in elephant evolution. It is extremely versatile and sensitive (Rasmussen & Munger, 1996), and is used for a variety of behavioral activities, such as feeding, drinking, maintaining bodily hygiene, and obtaining chemical information. It was also the body part that was used the most often by each of the elephants to initiate tactile behaviors. Although important during tactile social interactions, little is known about the specific functions of trunk tactile behaviors. One possible use of trunk tactile behaviors may be to display dominance (Burks et al., 2004; Douglas-Hamilton & Douglas-Hamilton, 1975; Garai, 1992; Langbauer, 2000). For example, the trunk was never used by lower-ranking animals to initiate aggressive tactile behaviors towards higher-ranking animals, while higher-ranking animals frequently used the trunk during aggressive tactile interactions directed towards lower-ranking animals, suggesting that aggressive trunk tactile behaviors are used by higher-ranking animals to discipline lower-ranking animals.

In addition to being the body part that was used the most to initiate tactile behaviors, the trunk was also the body part that received the highest rate of trunk tactile behaviors, including aggressive and nonaggressive trunk tactile behaviors. Although these findings highlight the importance of the trunk during tactile interactions, even less is known on the functions of trunk to trunk tactile behaviors. Garai (1992) observed that the placement of the trunk tip against another elephant's trunk tip (a behavior that was categorized as nonaggressive in our study) was especially prominent between the "special" dyads of Asian elephants that she observed. From her observations, she speculated that these nonaggressive trunk to trunk placement behaviors were affiliative in nature. Other studies describe behaviors involving the intertwining of two elephants' trunks. They speculate that trunk intertwining occurs during play sequences (Adams & Berg, 1980; Burks et al., 2004; Langbauer, 2000; Lee, 1987) as well as during sequences involving aggression/competition for dominance (Burks et al., 2004; Douglas-Hamilton & Douglas-Hamilton, 1975).

Following the trunk, the head and mouth received the next highest rates of trunk tactile behaviors. Also, the mouth received the third highest rate of nonaggressive trunk tactile behaviors, while rarely receiving any aggressive trunk tactile behaviors. Trunk to mouth behaviors have been observed in several other studies of elephant social behavior, especially between mothers and calves (Adams & Berg, 1980; Berg, 1983, 1987). However, the social function of these behaviors is not clear. One possibility is that trunk to mouth tactile behaviors are used by elephants to learn what other group members are ingesting (Garai, 1992; Langbauer, 2000; Lee, 1986). This behavior may be especially important for calves, who may learn what to eat by tasting what is in their mothers' mouths (Berg, 1983, 1987). Other hypothesized functions of trunk to mouth placement behaviors include providing another elephant with physiological, reproductive, and

emotional information (Langbauer, 2000), serving as a form of greeting between elephants as they get older, serving as a gesture of recognition and friendship (Adams & Berg, 1980; Berg, 1983, 1987; Garaï, 1992; Lee, 1986), and serving as a form of reassurance or appeasement (Adams & Berg, 1980; Berg, 1983, 1987; Garaï, 1992). For example, Adams and Bergs (1980) observed that placing the trunk in another's mouth occurred when the receiving elephant had experienced fright. All of these functions support the notion that trunk to mouth behaviors are largely nonaggressive in nature, an interpretation that our findings lend support to.

Following the trunk, the tail was the body part that was most likely to be used to initiate tactile behaviors. Like the trunk, the tail was used in a variety of ways. For example, ME was the main initiator of tactile behaviors that involved hitting another elephant with the tail, most likely as a disciplinary measure. KA and RO were often seen placing their tails in ME's mouth and KA, RO, and CA were seen placing their tails on another elephant's trunk. These latter behaviors were typically directed towards higher-ranking animals, and involved orienting the rear towards another animal's side or head, which, as mentioned earlier, is considered to be a sign of submission (Garaï, 1992; Kahl & Armstrong, 2000; Langbauer, 2000). Tail to mouth and tail to trunk tactile behaviors may also be considered submissive behaviors given that the tail is a vulnerable body part that is being placed in a compromising position once it is placed near the mouth or trunk. This may also explain why the tail received a high rate of aggressive trunk tactile behaviors (although it equaled the rate at which aggressive trunk to head tactile behaviors occurred, which was the second highest). However, the use of the tail to contact another elephant's body part may also be a way to monitor the presence of other group members that are standing in close proximity (Langbauer, 2000).

Conclusions

The results presented in this paper are consistent with other descriptions of elephant tactile behaviors (Adams & Berg, 1980; Berg, 1987; Gadgil & Nair, 1984; Langbauer, 2000; Vidya & Sukumar, 2005) and demonstrate the saliency of tactile behaviors in elephant social interactions. The overlap between our results and those from wild populations also suggests that the study of elephant social interactions in captivity can provide insights into elephant behavior in the wild. More importantly, comparing social behavior in enclosed settings with social behavior in the wild may provide an important diagnostic tool concerning the well-being of elephants in human care. If the social behavior of captive elephants differs dramatically from that of their wild counterparts, it seems likely that the elephants' environment is lacking in some way. We believe that it is important for elephants to be afforded opportunities to interact with other elephants, and that the social interactions we have reported here reflect the opportunities provided for the six elephants we studied. Of course, we do not know the optimal size of an elephant group kept under human care nor the minimum number of elephants necessary for normal social interactions to occur. However, Sukumar (1989) reported that in India, the average family size for Asian elephants ranges from 5.8 to 8.8 individuals. Additional studies of the social interactions of elephants housed throughout the world would contribute greatly to examining these areas.

We should also note that little is known about the communicative function of elephant tactile behaviors. It is clear that a more detailed analysis of the nature of tactile behaviors is warranted, especially the nonaggressive tactile behaviors reported in this study. Furthermore, examining the sequence of behaviors that surround certain tactile behaviors would benefit our understanding of their use during social interactions. Also, additional information concerning the effects of age, personality and social dominance rank would aid in our understanding of how elephants integrate different sensory modalities to communicate, and therefore provide a more complete picture of elephant communication.

References

- Adams, J., & Berg, J. K. (1980). Behavior of female African elephants (*Loxodonta africana*) in captivity. *Applied Animal Ethology*, *6*, 257-276.
- Archie, E. A., Morrison, T. A., Foley, C. A. H., Moss, C. J., & Alberts, S. C. (2006). Dominance rank relationships among wild female African elephants, *Loxodonta africana*. *Animal Behaviour*, *71*, 117-127.
- Aureli, F. (1992). Post-conflict behavior among wild long-tailed macaques (*Macaca fascicularis*). *Behavioral Ecology and Sociobiology*, *31*, 329-337.
- Berg, J. K. (1983). Vocalizations and associated behaviors of the African elephant (*Loxodonta africana*) in captivity. *Zeitschrift für Tierpsychologie*, *63*, 63-79.
- Berg, J. K. (1987). Developmental behavior of three African elephant calves (*Loxodonta africana*) in captivity. *Zoologische Garten*, *57*, 191-196.
- Burks, K. D., Mellen, J. D., Miller, G. W., Lehnhardt, A. W., Figueredo, A. J., & Maple, T. L. (2004). Comparison of two introduction methods for African elephants (*Loxodonta africana*). *Zoo Biology*, *23*, 109-126.
- Cheney, D. L., & Seyfarth, R. M. (1989). Redirected aggression and reconciliation among vervet monkeys, *Cercopithecus aethiops*. *Behaviour*, *110*, 258-275.
- Chevalier-Skolnikoff, S. (1973). Visual and tactile communication in *Macaca arctoides* and its ontogenetic development. *American Journal of Physical Anthropology*, *38*, 515-518.
- Cohen, J. A. (1960). Coefficient of agreement for nominal scales. *Educational and Psychological Measurement*, *20*, 37-46.
- Connor, R. C., Mann, J., & Watson-Capps, J. (2006). A sex-specific affiliative contact behavior in Indian Ocean bottlenose dolphins, *Tursiops* sp. *Ethology*, *112*, 631-638.
- Cooper, M. A., & Bernstein, I. S. (2000). Social grooming in assamese macaques (*Macaca assamensis*). *American Journal of Primatology*, *50*, 77-85.
- Croney, C. C., & Newberry, R. C. (2007). Group size and cognitive processes. *Applied Animal Behaviour Science*, *103*, 215-228.
- de Waal, F. B. M., & van Roosmalen, A. (1979). Reconciliation and consolation among chimpanzees. *Behavioral Ecology and Socioecology*, *5*, 55-56.
- Douglas-Hamilton, I., & Douglas-Hamilton, O. (1975). *Among the elephants*. New York: Viking Press.
- Dudzinski, K. M. (1998). Contact behavior and signal exchange among Atlantic spotted dolphins (*Stenella frontalis*). *Aquatic Mammals*, *24*, 129-142.
- Dudzinski, K. M., Gregg, J. D., Ribic, C. A., & Kuczaj, S. A. (2009). A comparison of pectoral fin contact between two different wild dolphin populations. *Behavioural Processes*, *80*, 182-190.

- Franz, C. (1999). Allogrooming behavior and grooming site preferences in captive bonobos (*Pan paniscus*): Association with female dominance. *International Journal of Primatology*, 20, 525-546.
- 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*, 23, 431-448.
- Gadgil, M., & Nair, P. V. (1984). Observations on the social behavior of free ranging groups of tame Asiatic elephant (*Elephas maximus* Linn). *Proceeding of the Indian Academy of Sciences (Animal Science)*, 93, 225-233.
- Gallimore, R., Tharp, R. G., & Kemp, B. (1969). Positive reinforcing function of "negative attention." *Journal of Experimental Child Psychology*, 8, 140-146.
- Garaï, M. E. (1992). Special relationships between female Asian elephants (*Elephas maximus*) in zoological gardens. *Ethology*, 90, 187-205.
- Goosen, C., & Ribbens, L. G. (1980). Autoaggression and tactile communication in pairs of adult stumptailed macaques. *Behaviour*, 73, 155-174.
- Hertenstein, M. J. (2002). Touch: Its communicative functions in infancy. *Journal of Human Development*, 45, 70-94.
- Kahl, M. P., & Armstrong, B. D. (2000). Visual and tactile displays in African elephants, *Loxodonta africana*: A progress report (1991 – 1997). *Elephant*, 2, 19-21.
- Kaplan, J. D., & Connor, R. C. (2007). A preliminary examination of sex differences in tactile interactions among juvenile Atlantic spotted dolphins (*Stenella frontalis*). *Marine Mammal Science*, 23, 943-953.
- Koski, S. E., de Vries, H., van den Tweel, S. W., & Sterck, E. H. M. (2007). What to do after a fight? The determinants and inter-dependency of post-conflict interactions in chimpanzees. *Behaviour*, 144, 529-555.
- Landis, J. R., & Koch, G. G. (1977). The measurement of observer agreement for categorical data. *Biometrics*, 33, 159-174.
- Langbauer, W. R. (2000). Elephant communication. *Zoo Biology*, 19, 425-445.
- Lazaro-Perea, C., Arruda, M., & Snowdon, C. T. (2004). Grooming as a reward? Social function of grooming between females in cooperatively breeding marmosets. *Animal Behaviour*, 67, 627-636.
- Lee, P. C. (1986). Early social development in African elephants. *National Geographic Research*, 2, 388-401.
- Lee, P. C. (1987). Allomothering among African elephants. *Animal Behavior*, 35, 278-291.
- Leinfelder, I., de Vries, H., Deleu, R., & Nelissen, M. (2001). Rank and grooming reciprocity among females in a mixed-sex group of captive hamdryas baboons. *American Journal of Primatology*, 55, 25-42.
- Matheson, M. D., & Bernstein, I. S. (2000). Grooming, social bonding, and agonistic aiding in rhesus monkeys. *American Journal of Primatology*, 51, 177-186.
- Matsumura, S. (1996). Postconflict affiliative contacts between former opponents among wild moor macaques (*Macaca maurus*). *American Journal of Primatology*, 38, 211-219.
- Moss, C. J. (1975). *Portraits in the wild: Behavior studies of east African mammals*. Boston: Houghton Mifflin.
- Nakamura, M. (2003). 'Gatherings' of social grooming among wild chimpanzees: Implications for evolution of sociality. *Journal of Human Evolution*, 44, 59-71.
- Nelson, H., & Geher, G. (2007). Mutual grooming in human dyadic relationships: An ethological perspective. *Current Psychology*, 26, 121-140.
- O'Brien, T. G. (1993). Allogrooming behavior among adult female wedge-capped capuchin monkeys. *Animal Behaviour*, 46, 499-510.

- Paulos, R. D., Dudzinski, K. M., & Kuczaj, S. A., II (2008). The role of touch in select social interactions of Atlantic spotted dolphin (*Stenella frontalis*) and Indo-Pacific bottlenose dolphin (*Tursiops aduncus*). *Journal of Ethology*, 26, 153-164.
- Payne, K. (2003). Sources of social complexity in the three elephant species. In F. B. M. de Waal & P. J. Tyack (Eds.), *Animal social complexity: Intelligence, culture, and individualized societies* (pp. 261-287). Cambridge, MA: Harvard University Press.
- Poole J. H. (1994). Sex differences in the behaviour of African elephants. In R. V. Short & E. Balaban (Eds.), *The differences between the sexes* (pp. 331-362). Cambridge, UK: Cambridge University Press.
- Rasmussen, L. E. L., & Munger, B. (1996). The sensorimotor specializations of the trunk tip of the Asian elephant, *Elephas maximus*. *Anatomical Record*, 246, 127-134.
- Sakai, M., Hishii, T., Takeda, S., & Kohshima, S. (2006). Flipper rubbing behaviors in wild bottlenose dolphins (*Tursiops aduncus*). *Marine Mammal Science*, 22, 966-978.
- Schaffner, C. M., & Aureli, F. (2005). Embraces and grooming in captive spider monkeys. *International Journal of Primatology*, 26, 1093-1106.
- Schino, G. (2001). Grooming, competition, and social rank among female primates: A meta-analysis. *Animal Behaviour*, 62, 265-271.
- Scott, J., & Lockard, J. S. (2006). Captive female gorilla agonistic relationships with clumped defendable food resources. *Primates*, 47, 199-209.
- Seyfarth, R. M. (1977). A model of social grooming among adult female monkeys. *Journal of Theoretical Biology*, 65, 671-698.
- Spinate, C.A. (1994). *Elephants*. Cambridge, UK: Cambridge University Press.
- Sukumar, R. (1989). *The Asian elephant: Ecology and management*. Cambridge, UK: Cambridge University Press.
- Tamaki, N., Tadachi, M., & Michihiro, T. (2006). Does body contact contribute towards repairing relationships? The association between flipper-rubbing and aggressive behavior in captive bottlenose dolphins. *Behavioral Processes*, 73, 209-215.
- Vidya, T. N., & Sukumar, R. (2005). Social organization of the Asian elephant (*Elephas maximus*) in southern India inferred from microsatellite DNA. *Journal of Ethology*, 23, 205-210.
- Weber, I. (1973). Tactile communication among free-ranging langurs. *American Journal of Physical Anthropology*, 38, 481-486.
- Weiss, S. J. Wilson, P. Seed, J., & Paul, S. M. (2001). Early tactile experiences of low birth weight children: Links to later mental health and social adaptation. *Infant and Child Development*, 10, 93-115.
- Whitehead, H. (1997). Analyzing animal social structure. *Animal Behaviour*, 53, 1053-1067.