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Consolation and cooperation: A proximate analysis of social behavior in Asian elephants (*Elephas maximus*)

By

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Doctor of Philosophy

Psychology

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Joshua M. Plotnik
M.A., Emory University, 2006
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An abstract of
A dissertation submitted to the Faculty of the
James T. Laney School of Graduate Studies of Emory University
In partial fulfillment of the requirements for the degree of
Doctor of Philosophy
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Abstract

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Did seemingly rare cognitive capacities in humans and non-human primates evolve convergently in other, more distantly related species? Did this perhaps happen in the elephant, an animal widely known for its social complexity despite the lack of systematic evidence? Following our recent demonstration of mirror self-recognition (considered a hallmark of self-awareness correlated with advanced empathy) in Asian elephants (Plotnik et al. 2006), we conducted this dissertation research to further assess this species' cognitive complexity adapting techniques designed originally for use in the study of primate social cognition. First, we studied the elephant's capacity for consolation (i.e. reassurance of distressed individuals) in a semi-free sanctuary in Thailand. We found that elephants not only consoled each other following displays of distress, but bystander elephants also seemed to adopt the emotional state of the focal individual, suggesting emotional contagion. Second, we conducted an experimental study to investigate whether or not elephants could learn how to cooperate when both a partner's presence and actions were needed for success. In a task that required two elephants to each pull one of two rope ends to retrieve a food reward, elephants learned not only to wait for their partner's arrival before pulling, but also to inhibit pulling if their partner could not help. These studies suggest that elephants rely on complex cognitive evaluations in their social interactions, not unlike what we know for nonhuman primates, and that further attention to intelligent non-primates may provide important insight into the convergent evolution of social behavior.

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Acknowledgements

General: Thank you to my advisor, Frans de Waal, for his support and guidance throughout my tenure as a graduate student. Thank you also to my dissertation committee members – Harold Gouzoules, Robert Hampton, Donald Moore III, Michael Owren, and Philippe Rochat – for their advice during this process. I would also like to thank David Edwards, Scott Lilienfeld, and Lynne Nygaard for their personal and professional advice both while I was in residence at Emory and abroad. This research was supported by a U.S. Department of Education Fulbright-Hays DDRA, the Living Links Center of the Yerkes Primate Center, the Laney Graduate School and the Dept. of Psychology at Emory University. This project was approved by the National Research Council of Thailand, and Emory University's Institutional Animal Care and Use Committee (ID 219-2007Y). None of this work could have been done without the support of the Thai, Burmese, Shan and Karen mahouts, who helped me with my research while performing one of the most dangerous jobs on the planet. Thank you.

Consolation: The work at the Elephant Nature Park was conducted with the permission and support of Sangduen "Lek" Chailert, the founder and director of the Park. Thank you to Jeff Smith, the Park's project manager, for introducing us and providing advice along the way. I thank Lek and all of her staff for their assistance, including Karl Cullen, Michelle Kobylka, Jodi Thomas, Janna Schurer, Georgina Hayworth, James Hilton, and Kirsten Highet.

Cooperation: I am grateful to Richard Lair for his wealth of elephant knowledge, his friendship and his connections in Thailand. Thank you to Wirot Suphachoksakun, Prasob Tipprasert, Worrawit Rothjanaphaithoon, and Manoonsak Tantiwiwat of Thailand's

Forest Industry Organization for their support. Thank you to Aumnuaychai Kingkaew, Chaiya Hnangwong, Jen Pokorny, Jenn Hua, Gretchen Ramsey and Monte Richardson for their assistance with the study design, and Nancy Bliwise for statistical advice. This paper follows the style of The Quarterly Review of Biology (University of Chicago Press).

Permissions:

1) Sections of the Introduction in this dissertation were taken from:

Plotnik J. M., de Waal F. B. M., Moore D., Reiss D. 2009. Self-recognition in the Asian elephant and future directions for cognitive research with elephants in zoological settings. *Zoo Biology* DOI 10.1002/zoo.20257. Permissions number 2372020701380, John Wiley and Sons License (and as permitted by the copyright transfer agreement, signed May 15, 2009).

2) The data and portions of text presented in Investigation II are currently in revision as of April 16, 2010:

Plotnik J. M., Lair R., Suphachoksakun W., de Waal F. B. M. in revision. Elephants know when they need a helping trunk in a cooperative task.

3) Figure 5, panel A was re-printed with permission, as noted in the figure legend.

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In *Mental Evolution*, George Romanes wrote: “The question, then, as to whether or not human intelligence has been evolved from animal intelligence can only be dealt with scientifically by comparing the one with the other, in order to ascertain the points wherein they agree and the points wherein they differ” (1881, p. 9). While attempting to organize the potential manifestations of human-like capacities in animals, Romanes began to lay the first framework for today’s growing psychological field of animal comparative cognition. Comparative cognition attempts, in part, to investigate the underlying psychological capabilities of non-human animals, or, more broadly, “how animals think” when performing complex individual or social behaviors in the laboratory (e.g., Skinner 1965; Griffin 1976; Shettleworth 1998). Ethology and sociobiology, on the other hand, center more on the functionality of behavior, and primarily focus on animals in nature (Tinbergen 1963; Wilson 1975). The fields often overlap because both focus on the behavior of non-human animals as a window into understanding evolutionary processes and as a mechanism for assessing cross-species behavioral similarities and differences (Griffin 1976).

The study of intelligence in evolutionarily distant species is a burgeoning field with a focus primarily on non-human primates (e.g., de Waal 1982; Tomasello and Call 1997), birds (e.g., Shettleworth 1998; Emery and Clayton 2004), cetaceans (e.g., Marino 2002; Marino et al. 2007), and elephants (e.g., Poole 1996; Byrne et al. 2009). Remarkably, the latter species have received almost no attention in terms of systematic investigation of cognitive complexity, most likely because of the relative inaccessibility to viable subjects. This dissertation attempts to further investigate, using both ethological and experimental techniques, the potential for convergent cognitive evolution of complex sociality in Asian elephants and other large-brained animals.

Elephants, as a family of two genera (*Elephas* and *Loxodonta*), are a majestic species well known, at least in fiction, to most people on earth. In science, however, elephants have been remarkably understudied, although it is surprisingly well accepted, due almost entirely to anecdotal evidence and longitudinal field observations (e.g., Douglas-Hamilton and Douglas-Hamilton 1975; Poole 1996), that elephants are intelligent and socially complex (Byrne et al. 2009; Plotnik et al. 2009). Interestingly, elephants are the only animals to have been employed by man for centuries without any formal history of domestication or artificial selection and have been noted for their supposed intelligence for equally as long without much formal investigation (Lair 1997).

African elephants (primarily *L. africana* or the savannah elephant; Poole 1996, but see also *L. cyclotis*; Roca et al. 2001) have been studied continuously for more than 30 years (Douglas-Hamilton and Douglas-Hamilton 1975; Moss 1988; Poole 1996), almost wholly within the fields of elephant population dynamics (e.g., Douglas-Hamilton and Douglas-Hamilton 1992) and vocal communication (e.g., Payne et al. 1986; Poole 1996; Payne 2003; Moss et al. in press), with as-of-yet very little attention to social behavior outside these areas (Payne 2003; Moss et al. in press). The Asian elephant (*E. maximus*) has received even less attention, with very little evidence of their behavioral repertoire available in peer-reviewed scientific journals (but see Sukumar 1989; Seidensticker and Lumpkin 1990; Nair et al. 2009).

This dissertation investigates the social complexity of elephants in two parts: the first assesses one aspect of natural social behavior, the response of bystander individuals to others in distress, through a systematic ethological study of consolatory behavior. The second investigates cooperative behavior using an experimental paradigm that has, in the past, been used to assess the cognition underlying cooperation in non-human primates and some other animals, such as birds and hyenas. As a whole, this dissertation is an analysis of the proximate mechanisms underlying sociality in a large mammal, the Asian elephant, and clarifies the need for further attention to elephant behavior in the study of convergent evolution. Such an exploration makes sense in light of recent research on elephants and theoretical frameworks that highlight elephants as a potential candidate for complex cognition and sociality (e.g., Gallup 1983; de Waal 1996).

A General Perspective on Social and Cognitive Complexity in Elephants

Wild and Captive Experimental Evidence

The idea of the elephant as a highly cognitive animal is by no means a new topic of study (Romanes 1881; Williams 1950; Rensch 1957; Schulte 2000; Nissani 2004). Multiple anecdotes discuss the elephant's remarkable memory (e.g., Rensch 1957; Markowitz 1982), problem-solving skills (an African elephant using a self-made tool to plug and cover a water source - Gordon 1966), attention to dead conspecifics and the covering-up of carcasses with debris (e.g., Douglas-Hamilton and Douglas-Hamilton 1975; Moss 1988; McComb et al. 2006), and potential deception (reports of Asian elephants stuffing the bells around their necks with dirt to silence the bells and perhaps avoid being heard - Williams 1950). Perhaps one of the most recognized and well-documented examples of advanced cognitive capacity in elephants stems from observations of elephants' attention to others in need (Bates et al. 2008). De Waal (1996;

2008) terms the sort of helping behavior observed as “targeted helping,” or help fine-tuned to another’s specific situation and goals. Douglas-Hamilton et al. (2006) described a family’s attempts to assist and lift a fallen matriarch, while Moss (1988) related an elephant family’s response to the mortal wounding (by gunshot) of a family member:

“Teresia and Trista became frantic and knelt down and tried to lift her up. They worked their tusks under her back and under her head. At one point they succeeded in lifting her into a sitting position but her body flopped back down. Her family tried everything to rouse her, kicking and tusking her…(pg. 73).”

Targeted helping may be linked to empathic perspective-taking, or the capacity to take another’s perspective (de Waal 2008). Such a capacity for “cognitive empathy” (defined as: “empathy combined with contextual appraisal and an understanding of what caused [an individual’s] emotional state” – de Waal 2008, p. 4.5) is extremely rare in the animal kingdom, seemingly limited to the great apes (chimpanzees – *Pan troglodytes*, bonobos – *P. paniscus*, orangutans – *Pongo pygmaeus*, and gorillas – *Gorilla gorilla*, see de Waal 1996 for a review), bottlenose dolphins (*Tursiops truncatus*, Siebenaler and Caldwell 1956; Caldwell and Caldwell 1966), and elephants (e.g., Moss 1988; Poole 1996; Bates et al. 2008). Suggestions of advanced elephant empathy led Gallup (1983) to predict that these animals would make good candidates for mirror self-recognition and complex self-awareness, a prediction verified by Plotnik et al. (2006).

The first systematic investigation of elephant cognition was undertaken by Rensch (1957) on one five-year-old Asian elephant housed at the Münster Zoo in Germany, and remarkably, no other comprehensive study of elephant cognition via controlled experiments was conducted in the more than 40 years following its publication. Although it took the elephant more than 300 trials to reach criterion on a single-pair discrimination task (i.e., it was trained to choose one of two shapes – a circle and a half-circle, for example - to obtain food), it eventually learned to discriminate consistently between more than 20 pairs of different shaped stimuli (Rensch 1957). Visual discrimination tasks are among the most common types of laboratory cognition studies conducted on a wide variety of species, including primates and birds (cf. Vallortigara 2004), but many of the species tested use vision as a primary or secondary sensory modality; elephants, on the other hand, seem to primarily use their auditory, olfactory and seismic senses when interacting with their environment and when communicating with conspecifics (Moss 1988; Poole 1996). Many have hypothesized however, that the vision of the elephant may be highly underestimated (e.g., Lair 1997), and although there have been a few studies on the physiology and anatomy of the elephant eye (e.g., Stone and Halasz 1989; Murphy et al. 1992; Yokoyama et al. 2005), we know of only one other cognition study on elephant vision, and it too was a basic assessment of shape and color discrimination (Nissani et al. 2005).

One additional area of research focuses on tool-use, often mentioned as one of the first markers of complex cognition (McGrew 1992; Shettleworth 1998; van Schaik et al. 1999; de Waal 2001) that is exhibited across animal taxa. Corvidae – the family of birds that includes crows, ravens, rooks and magpies – manipulate tools in various ways to obtain food (see Emery and Clayton 2004 for a review). Tool-use is extensive and well documented in chimpanzees, orangutans, and a few other primates (see van Schaik et al. 1999 for a review). Bottlenose dolphins have been observed to carry sponges when foraging on the sea floor for fish and it has been suggested that they use the sponges to protect their sensitive beaks when they probe for prey in the sandy substrate (Smolker et al. 1997; Krützen et al. 2005). Tool-use and tool manufacture has also been documented in the Asian elephant, where branches are used, stripped and further manipulated to swat insects (Chevalier-Skolnikoff and Liska 1993). In addition, it has been postulated that the prehensile trunk enables elephants to engage in complex manipulative behaviors quite similar to those of primates (Hart et al. 2001). These authors explain that such evidence "would appear to place [elephants] in the category of great apes in terms of cognitive abilities..." (p. 839).

In fact, some researchers have already begun to synthesize the literature on elephant social complexity to assess the basis for these claims of advanced cognition (using neuroscience, anatomy and neuroethology as a starting point - Bradshaw and Schore 2007; Hart et al. 2008, or using anecdotal evidence from long-term social behavior research – Bates and Byrne 2007), but cite little experimentally-based literature because of its relative scarcity. However, a select few studies have attempted to reinvigorate the field of elephant cognition within the past three years. Bates et al. (2007) demonstrated that wild African elephants are capable of classifying potential predators (in this case, the Maasai of Kenya, who hunt them, and the Kamba, who do not) by both visual (shirt color discrimination) and olfactory cues (smells associated with each of the two ethnic groups). The authors hypothesize that such an ability to classify a same-species predator into subcategories based on their relative threat is likely related to their cognitive capacities. Bates et al. (2008) subsequently looked at the ability of elephants to recognize the locations of family members through olfactory cues. Not only did the authors demonstrate that elephants are capable of recognizing up to 30 family members from cues available to them in a mix of urine and earth, but when experimentally presented with these urine-earth mixes of specific, out-of-sight family members, the elephants displayed differential behavior depending on the location of these particular individuals. In particular, elephants spent more time investigating urine when the individual was either absent or behind them – thus making it impossible for the sample to have been deposited there - than when they were present or in front of them. The authors suggest that the known social complexity of elephants and the need to keep track of large numbers of individuals may require complex cognition.

Three recent studies investigated elephant cognitive capacity in a captive setting. Nissani (2006) reported that elephants were unable to successfully accomplish what he termed "a causal reasoning" task by transferring knowledge of a lid/bucket paradigm across experimental conditions. When presented with a bucket of food with a lid, the elephants would remove the lid and obtain the food, but continued to remove, or flip the lid even if it was placed beside the bucket and thus was irrelevant to obtaining food. Although the author argued this suggests an inability to reason causally, the strong indication that the elephants were heavily trained by their handlers and that this training may have unduly affected their performance suggests further investigation is necessary before any conclusion on elephants' causal reasoning abilities can be reached. In this particular experiment, the elephants were first trained to "flip" or remove the lid and then expected to forget this training when subsequently presented with a paradigm with the lid beside the bucket, and as far as we can tell, the elephants were handled throughout the experiment without controls in place to prevent the caretakers from influencing the elephants' responses. Because Asian elephants in Southeast Asian countries are often handled daily either for work - in Nissani (2006)'s case, logging in Myanmar - or for tourism (as in Thailand and Cambodia), controls must be implemented in cognition experiments conducted in these countries to ensure the results are not influenced by the behavior of the elephants' handlers.

In a recent study by Irie-Sugimoto et al. (2008), Asian elephants demonstrated both an ability to differentiate between two different food quantities when the food was presented to them in two buckets (experiment 1), and an ability to successfully differentiate between two different quantities when the visual component of food placement was removed (i.e., when only the sound of the food being placed in the bucket or the actions of the experimenters were visible – experiment 2). The ability to make such a differentiation between quantities is generally referred to as "relative quantity judgment" (or RQJ) and usually relates to two general trends found in animals (e.g., Call and Tomasello 1997). The first is known as the disparity effect, which suggests that the animal's success rate on the task should decrease with the relative difference between the two food quantities; the second is known as the magnitude effect and suggests that an increase in overall magnitude should be paired with a decrease in RQJ ability (Irie-Sugimoto et al. 2008, p. 194). Although the elephants were successful in differentiating between the quantities in both experiments, eight of nine subjects tested did not show either the disparity or magnitude effects common in primate species. The authors suggest this may have something to do with the relatively low quantities of food presented, but also that this dichotomy between elephants and other animals may be related to species differences in mechanisms for detecting differences in food (and object) amounts.

In another study, Irie-Sugimoto et al. (2007) used a simple yet compelling tray-pull task to investigate elephants' ability for understanding means-end relationships. When presented with two trays so that only one of the two, when pulled, would result in success and thus yield a food reward, one elephant performed significantly above chance, suggesting goal-directed behavior driven by an "understanding that pulling the tray was the 'means' for achieving the 'end' of obtaining the bait" (p. 1). Such performance is similar to that demonstrated in non-human primates (e.g., Hauser et al. 2002), and suggests that some experimental designs detailed in the extensive cognition literature on non-human primates may be adaptable to studies on elephants.

Non-human primates in particular are being tested across cognitive facilities: for instance, they have been tested for individual and kin recognition with computerized tasks (Parr and de Waal 1999), between and within species differences in cooperative tendencies (Melis et al. 2006), imitation and cultural transmission (e.g., Whiten et al. 2005; Horner et al. 2006), planning for the future (Mulcahy and Call 2006; Osvath 2009), and their tendencies to be altruistic (Warneken et al. 2007) or sensitive to inequity (Brosnan and de Waal 2003). This literature is growing rapidly and beginning to inspire work on large-brained birds, canids, dolphins, and so on. The practicality of conducting similar tests with elephants may be limited, especially since these animals cannot be brought into a laboratory situation, but many of the test paradigms can be adapted for outdoor use, and are actually extremely simple and straightforward.

The most promising areas of research on primates try to address cognitive questions related to behavior observed under naturalistic conditions, such as the testing of imitation skills related to the evidence for cultural traditions in wild chimpanzees -

traditions thought to be socially learned (Whiten et al. 1999) - or the testing for reciprocity related to the evidence for cooperation among unrelated chimpanzees (de Waal 1997). Similarly, cognition research on elephants should receive its main inspiration from natural elephant behavior, and thus aim to elucidate suspected but as yet unproven cognitive capacities.

Ethological Evidence from the Wild

Relative to primates – e.g., Goodall 1968; 1986; de Waal 1982; Kappeler et al. 2006 – there is little known about elephant social complexity (e.g., Sukumar 1989 for Asian elephants). In fact, the only long-term study of Asian elephants in the wild focuses specifically on ecology and population dynamics rather social behavior (Sukumar 1989: Mudumalai Wildlife Sanctuary, Tamil Nadu, India). This research has however been used to justify the use of cross-species information when describing "elephant" behavior (Payne 2003). Elephants live in matriarchic-centered groups, where the males leave the family unit at an early age and roam alone, or form their own male-dominated bachelor groups. Unlike many mammalian species, adult males play no part in offspring care. Asian elephant family groups typically consist of a relatively small number of individuals (5-10 individuals), with most (if not all) being closely related (Sukumar 1989). Family group members often engage in allomothering (behavior that often includes protecting, playing with, and instructing calves and juveniles), allowing the mother to forage away from the family. Adult relatives of the mother may suckle the infant, and adoption of orphans of close relatives can occur (Lee 1987; Moss 1988). Importantly, in the first 2-4 years of life, calves spend a great deal of their time (usually as much if not more than they spend nursing) with allomothers, also known as “aunties,” and much less time with other elephants (Lee 1989; Payne 2003). According to Payne (2003), there is an indirect correlation between calf mortality and allomother frequency, indicating that allomothers play an important role in calf and general family survival.

For African elephants specifically, multiple family groups – usually consisting of closely related family unit matriarchs (Moss and Poole 1983), but sometimes of maternally unrelated elephants (Moss 1988) – often form a single “bond group.” Interestingly, these groups greet each other as a single family (often displaying behaviors indicative of excitement or agitation, such as screaming, trumpeting, ear flapping, touching, etc. – see later procedures for details on these behaviors), but move off as separate family units. Payne (2003) hypothesizes that such “bond groups” between unrelated families probably provide unique cooperative advantages in the form of complex allomothering relationships and calf predator protection. In any type of threatening situation, family units – and bond groups when formed – quickly unify around an infant, with the adults facing outward in a circular formation with the infants in the middle (Moss 1988; Poole 1996; Payne 2003). Such behavior clearly indicates a protective strategy from an ultimate perspective – increased predator protection and allomothering capacity leads to increased fitness benefits for the calves and their relatives - but the proximate mechanisms underlying such cooperative behavior are still unknown.

Cooperation in Non-Human Animals and Attention to Levels of Analysis

What is the benefit of a seemingly costly act? This basic question has been a fundamental concern for evolutionary biologists for 150 years in studies of humans and other animals, and has spawned a vast body of literature on the study of altruism. One particular focus of this literature has been the evolution of altruism through ‘cooperation’ (Trivers 1971), which extends from the simplest of life’s building blocks (cells: Axelrod et al. 2006) to complex organisms (humans: Hammerstein 2003 for a review). Cooperation – “the voluntary acting together of two or more individuals that brings about, or could potentially bring about, an end situation that benefits one, both, or all of them in a way that could not have been brought about individually” (Brosnan and de Waal 2002) - represents one of evolutionary biology’s most debated topics, and is well-represented across the phylogenetic spectrum of species. Within the literature on cooperation, there are two primary schools of thought: the first follows an evolutionary perspective (Trivers 1971, 2004, 2006; Wilson 1975; Mesterton-Gibbons and Dugatkin 1992; Dugatkin 1997; Gadagkar 1997), postulating continuity between the selective pressures that have produced cooperation across species. In this sense, although cooperation may explain similar behaviors across species with varying levels of cognitive complexity, some of the basic cognitive processes underlying these behaviors should be evolutionarily continuous. The second, more recently emerging school, suggests instead that there are higher, more cognitively demanding categories of cooperation unique to humans (e.g., Fehr and Fischbacher 2003; Stevens and Hauser 2004). In this view, there should be marked differences in the cognitive processes underlying cooperative behaviors between humans and other animals, the latter lacking in many of those processes necessary for complex cooperation. Others have argued that reciprocal altruism and cooperation may be constructed upon simpler processes, which don’t necessarily require human-like capacities for scorekeeping (Brosnan and de Waal 2002), and may in fact have evolved in a wide range of species (Akçay et al. 2009).

Although this dissertation does not take up the debate between these two schools directly, the studies outlined herein aim to further investigate the cognitive processes underlying social behavior in a socially complex animal, and, by default, provide further evidence for consideration on the continuity (and thus convergence) of cognitive evolution in distant species.

Investigation I: Bystander Post-Distress Affiliations and Consolation in Elephants

An Ethological Study of Social Complexity: Reconciliation and Consolation in Animals

Socially complex animals rely on group living for various adaptive reasons, including predator protection, resource defense and offspring care (van Schaik and van Hooff 1983; Harcourt and de Waal 1992; Aureli 1997; Palagi et al. 2006). Such group living promotes active cooperation – the acting together of two or more individuals to gain a benefit otherwise inaccessible to a single individual acting alone (especially in the form of mutualism: Brown 1983; e.g., cooperative breeding and hunting in lions: Packer et al. 1991). However, group living causes intra-group strife as well, especially in species where mate access and resource limitations often lead to complex conflict (e.g., primates: de Waal 1982; Aureli et al. 2002). Coping mechanisms have evolved for such conflict, specifically in various forms of peacekeeping (de Waal 1989; de Waal and Aureli 1996 for a review). Reconciliation – the tendency of individuals to perform reassuring and appeasing behavior usually in the form of physical contact towards former opponents relatively soon after a conflict – was first described by de Waal and van Roosmalen

(1979) in chimpanzees (*Pan troglodytes*). To date, reconciliation has been demonstrated in various species across animal taxa (e.g., for primates, including various monkey species see Aureli et al. 2002; for goats, *Capra hircus*, Schino 1998; for spotted hyenas, *Crocuta crocuta*, Wahaj et. 2002; for dolphins, *T. truncatus*, Weaver 2003; for rooks, *Corvus frugilegus*, Seed et al. 2007; for domestic dogs, *Canis lupis familiaris,* Cools et al. 2008; for wolves, *C. lupis*, Cordoni and Palagi 2008).

Reconciliation is much more common in the animal kingdom than another form of peacekeeping, consolation (de Waal and van Roosmalen 1979; de Waal 2003). Although reconciliation appears to have selfish motivations for both/all individuals involved (i.e., the need to maintain the cooperative relationship), the significance of consolation – "reassurance and friendly contact directed by an uninvolved bystander to one of the combatants in a preceding aggressive act" – for the bystander is unclear (de Waal 2003). Consolation is rare in the animal kingdom (thus far, only demonstrated in the great apes, *P. troglodytes* – de Waal and van Roosmalen 1979; de Waal and Aureli 1996, *P. paniscus* – Palagi et al. 2004, and *G. gorilla gorilla* – Cordoni et al. 2004, recently in rooks, *C. frugilegus* – Seed et al. 2007, dogs, *C. lupis familiaris* – Cools et al. 2008, and wolves – Palagi and Cordoni 2009, but not in most monkey species – de Waal and Aureli 1996; Watts et al. 2000, but see Call et al. 2002).

When de Waal and van Roosmalen (1979) originally proposed the terms "reconciliation" and "consolation" in non-human primates, they assumed that these behavioral acts had specific functions, specifically, the alleviation of distress (i.e., the lowering of stress) in the victim of an aggressive act. But this term has most recently been loosely applied to any third-party (bystander) contact towards the victim regardless of the specific functional implications of the act (Aureli 1997; Romero and de Waal in press). In fact, Seed et al. (2007) and Call et al. (2002), for example, have avoided use of the term "consolation" in favor of "postconflict third-party affiliation," which allows for analysis of the contact between bystanders and both victims and aggressors in conflict without any functional implications. But Romero and de Waal (in press) argue that consolation is a specific enough category (i.e., behavior initiated by the bystander and directed at a distressed party) with enough support for the calming function suggested by the word "consolation" that the original terminology remains justified.

To date, only three studies on chimpanzees have attempted to assess the direct functional implications of consolatory behavior on a target individual (Koski and Sterck 2007; Fraser et al. 2008; Romero and de Waal in press). In general, there are two primary hypotheses for the functionality of consolation behavior in animals. The first, from de Waal and Roosmalen (1979), suggests that the bystander acts empathically by reacting to the distress of another individual, and their subsequent actions alleviate distress (Aureli 1997; Aureli and de Waal 2000). This hypothesis has been supported by evidence that chimpanzees reduce self-directed behavior, a likely indicator of stress (self-scratching and self-grooming, for instance), following consolatory interactions (Fraser et al. 2008, but see also Koski and Sterck 2007). A second hypothesis suggests that consolation may take the place of reconciliation in alleviating distress by both lowering stress levels and positively affecting the relationship between the victim and aggressor (via contact between an aggressor-allied bystander and the victim), but Romero and de Waal (in press)'s data fail to support this. In fact, the data in that study show that consolations were more likely to occur between victims and their friends (closely-bonded bystanders) than between victims and the friends of aggressors, perhaps lending further support to the original hypothesis and further implying that the relationships between individuals is an important predictor of consolatory behavior in consolation-capable species.

Studying Consolation and Cooperation in Tandem

In addition to the recent focus on ultimate questions regarding the "functionality" of consolation in the few species that have demonstrated it, there also exist important evolutionary questions pertaining to its overall rarity in the animal kingdom. Two hypotheses have been proposed to explain why consolation may be so rare in the animal kingdom, with specific attention to the gap between apes and monkeys. The "social constraints" hypothesis argues that postconflict behavior may be less advantageous and more of a risk in monkey social groups than in chimpanzee social groups. De Waal and Aureli (1996) suggest that such behavior – reconciliation and consolation – should be expected only in species with high levels of cooperation and attachment. Although many monkey species and apes fit this description, the latter have a) a more flexible hierarchical structure and greater social tolerance and b) social relationships that allow for lower ranking individuals to influence higher ranking individuals (i.e., the despotic nature of many monkey species' hierarchies prevents consolatory behavior between different ranked individuals). Such differences in social structure and individual relationships, the authors suggest, may explain the absence of consolation in monkeys since in a strictly hierarchical society it may be risky to approach a recent recipient of aggression. In fact, it may cause aggression to be generalized against the third party rather than be relieved by it, as is often the case in reconciliations (Cheney and Seyfarth

1989; Watts et al. 2000). The second hypothesis, the "social cognition" hypothesis, relates to the greater demonstrated cognitive ability of chimpanzees compared to monkeys (in terms of tool-use, mirror self-recognition, and examples of targeted helping – de Waal 1996; Tomasello and Call 1997), suggesting that such advanced social cognition, or perhaps even cognitive empathy (de Waal 2008) is required for consolation behavior. The proposed relationship between consolation and advanced forms of empathy (de Waal and Aureli 1996; Preston and de Waal 2002; de Waal 2008) is grounded in studies of chimpanzee behavior (de Waal 1996), but it has been hypothesized that such a relationship may extend to a select few other species.

Empathy, in a broad sense, is probably not unique to just a few species in the animal kingdom. Emotional contagion, where one individual is affected by another individual's emotional state, such as pain or distress, is found in many mammals (see de Waal 2003 for a review). Sympathetic concern (often the preferred term for human consolation), involves concern for another's (emotional or behavioral) state and an attempt to "alleviate" this state (de Waal 2008), and has been thoroughly studied in human children (e.g., Eisenberg and Mussen 1989; Zahn-Waxler et al. 1992). The behavioral manifestations of sympathetic concern are very similar in children and chimpanzees, and Zahn-Waxler et al. (1984) have noted that they are similar in household pets as well. Although expressions of empathy in general have been suggested for multiple species, including monkeys, birds, and rodents (see de Waal 2003 for a review; Langford et al. 2006), consolation, again, may have a much more limited distribution as it may rest on so-called cognitive empathy (i.e., "empathy combined with contextual appraisal and an understanding of what caused [an individual's] emotional state" – de Waal 2008, p. 4.5).

"Targeted helping" (de Waal 1996) - help aimed at another individual and fine-tuned for that individual's specific needs and goals (discussed previously) – is another possible example of cognitive empathy. This behavior often comes at great cost to an individual, with seemingly little expectation of reciprocation or return benefits. Table 1 provides detailed, anecdotal examples of targeted helping in chimpanzees (*P. troglodytes*), dolphins (*T. truncatus*), and elephants (*E. maximus; L. africana*), including costly acts towards needy, injured, or dying conspecifics and humans.

The aforementioned relationship between consolation and empathy has been studied developmentally in human children for three decades. The development of prosocial behavior, for instance, seems to occur between 1 and 2 years of age. 18-30 month olds clearly assist "needy" relatives and strangers (e.g., Rheingold 1982), while infants between the ages of 6-12 months show little or no reaction to others in need (Zahn-Waxler and Radke-Yarrow 1982). By 18-24 months, children show consolation and actively respond to "distressed" individuals (Bischof-Köhler 1991; Zahn-Waxler et al. 1992).

Interestingly, the developmental emergence of MSR in humans, or mirror self-recognition seems to coincide with the emergence of empathy as well (e.g., Zahn-Waxler et al. 1992, Rochat 2003 for a review). Bischof-Köhler (1991) conducted a study of 16-24 month old children, separately testing two abilities: 1) to pass the "rouge-test" in front of a mirror, and 2) to show targeted helping, such as the reaction to a playmate who had broken his/her teddy bear. When comparing MSR with empathic behavior, all those who demonstrated targeted helping passed the mark test.

The same parallels in ontogeny between empathy and MSR seem to exist in phylogeny as well (e.g., Gallup 1982; de Waal 2008). Some of the only animals to have demonstrated mirror self-recognition (MSR), an indicator of self-awareness thought to correlate with empathy, are the same aforementioned species that clearly demonstrate targeted helping (e.g., chimpanzees: Gallup 1970; elephants: Plotnik et al. 2006; dolphins: Reiss and Marino 2001). Because many anecdotal examples of empathic perspective-taking in the literature (Table 1 and de Waal 2008) exist for elephants, it seems logical to follow these examples with a systematic assessment of consolation behavior.

Both the social cognition and the social constraints hypotheses proposed by de Waal and Aureli (1996) can be tested using the Asian elephant as a subject model. Elephants' flexible dominance hierarchy, displays of targeted helping and MSR, low levels of intra-group conflict and complex sociality in nature make it an ideal species for investigation of both consolatory and cooperative behavior (Poole 1996; Payne 2003; Plotnik et al. 2006).

Species	**Description**
Chimpanzees 1. Goodall (1990, p. 213) 2. Yerkes and Yerkes (1929, p. 297)	1. Chimpanzees, unable to swim, "sometimes made heroic efforts to save companions from drowning – and were sometimes successful. One adult male lost his life as he tried to rescue a small infant whose incompetent mother had allowed it to fall into the water." 2. Juvenile chimpanzees in "all their boisterous play…scrupulously avoided disturbing [a dying companion]…a certain solitude, sympathy, and pity, as well as almost human expression of consideration were thus manifested by these little creatures."
Gorilla	Binti-Jua, a female gorilla at the Brookfield Zoo in Chicago, reacted to a three-year-old boy who had fallen into the gorilla enclosure – she cradled the child and then carefully laid him in front of an access door, where the keepers could easily retrieve him.
Dolphins 1. Siebenaler and Caldwell (1956) 2. Caldwell and Caldwell (1966, p. 766)	1. After an explosion, an injured dolphin was immediately assisted by two companions that came up to support it on either side, buoying it to the water surface to help it breathe. 2. "…when a group of neurophysiologists were attempting brain-mapping studies on dolphins one of the young male experimental animals received an overdose…and developed difficulty in swimming. [Two females] came under and supported him at the surface…until the distressed individual was able to swim…it was possible, though highly unlikely, that the [individuals were related]."
Elephants 1. Moss (1988, p. 73) 2. Poole (1996, p. 165)	1. Moss relates an elephant family's response to the mortal wounding (by gunshot) of one among them: "Teresia and Trista became frantic and knelt down and tried to lift her up. They worked their tusks under her back and under her head. At one point they succeeded in lifting her into a sitting position but her body flopped back down. Her family tried everything to rouse her, kicking and tusking her…Tallulah went off and collected a trunkful of grass and tried to stuff it into her mouth." 2. Poole has relayed numerous accounts where elephants have protected injured men from other animals and other humans, often at the expense of staying behind while the herd moved on.

Table 1. Examples of targeted helping and cognitive empathy in MSR species.

In this study, we performed a systematic investigation of consolatory behavior in Asian elephants, and focus specifically on the question of whether or not the reaction of elephants to distressed individuals can be defined as consolation. In addition, because 1) consolation may depend on empathy (the human literature clearly relies on this assumption – e.g., Eisenberg and Mussen 1989; Eisenberg 2000), and 2) Moss (1988), Poole (1996), Douglas-Hamilton et al. (2006) and Bates et al. (2008), among others, describe elephant social interactions that fit the criteria for empathic perspective taking, the overall potential connection between distress-related behaviors, consolation and empathic responses is relevant. Clearly, whether or not ape or elephant consolation reflects a higher form of empathy is yet to be determined, and this study will only help to support the notion that the latter species deserves further attention in social complexity studies.

Distress as a Focal Behavior

The literature on consolation in animals focuses almost entirely on post-conflict interactions (Aureli and de Waal 2000). However, because conflict is relatively rare in elephant groups and because my specific study site did not permit analysis of conflict behavior on a regular basis, this study will focus on the reaction of bystanders to distressed individuals in primarily non-conflict situations rather than their reaction to victims of aggression. We will still use the word consolation here because we continue to focus on the bystander's responses to distress in others. Because consolation centers on distressed individuals, I first define distress as it is used in this study.

Unfortunately, there is very little literature on Asian elephant behavior in general, and so the vast literature on African elephant behavior (Douglas-Hamilton and Douglas-Hamilton 1975; Moss 1988; Poole 1996) is often applied to Asian elephants as well because of their phylogenetic closeness (Payne 2003). Douglas-Hamilton and Douglas-Hamilton (1975) and Lee (1987), for example, describe distress in individual elephants, specifically infants, based on specific vocalizations and stimuli. Infants give a specific call – either an infant roar or squeal – and assume an alert posture where the head is raised, the ears are extended, the tail is raised and the trunk is either raised or stiffened outward (Olson 2004). Deep rumbles or "roars" (similar to a "scream" in African elephants but potentially unique to Asians) are often given in response to infant distress calls, or as a signal of an adult's own distress. Using 1) Lee (1987)'s definition of distress events in calves as those that result in "a dramatic response on the part of other animals … rushing to assist the calf" (p. 287), 2) Bates et al. (2008)'s definition of empathic responses to distress as: "A voluntary, active response to another individual's current or imminent distress or danger, that actually or potentially reduces that distress or danger" (p. 208), and 3) Olson (2004)'s comprehensive ethogram of elephant behavior with specific attention to those behaviors occurring when an infant or adult is distressed or agitated, I define a distress event in elephants as follows:

A distress event is one resulting from an obvious negative stimulus (e.g., negative mahout intervention, conspecific intimidation or aggression, family separation, environmental threat or accident) or an unknown stimulus that causes the actor, or victim, to become agitated and to signal such agitation to others (which can be visually identified with specific changes in body state – ears forward, tail erect - and movement, *and acoustically identified by various vocalizations, specifically trumpets, roars and deep rumbles).*

It is important to note that in a species with complex mechanisms for communication, the context in which a distress event occurs may be difficult to identify. Often, the context may be masked by the reaction of the elephants or the cause of the distress may be an inaudible distress call from an out-of-sight elephant. We will pay particular attention then to the reaction of the bystanders to the distressed individual to ensure that we differentiate between contexts that may cause distress in all the individuals and contexts that cause one individual to be contacted as a result of his/her distress.

This study attempts to investigate the reaction of conspecifics or bystanders to such behavior, specifically in terms of the bystander's post-distress affiliative contact with the victim (i.e., their tendency to approach the victim). This procedure of prioritizing affiliative tendencies based on physical contact is consistent with the literature on conflict resolution in animals (Aureli and de Waal 2000). Elephants, in particular, are extremely sensitive to vocal communication, and although it may not be possible to effectively determine whether vocalizations constitute affiliative contact in elephants, we also attempted to investigate whether or not post-distress activity triggers specific vocal responses in elephants.

General Methods

Subjects

This study involved the ethological observation of ~ 30 elephants at the Elephant Nature Park (henceforth referred to as "the Park") in Chiang Mai, Thailand. The Park is a sanctuary for elephants, and thus the number of elephants changed relatively often over the course of the study as individuals were donated or removed from the group. Although genetic tests on the relatedness of the elephants were never done, it is reasonable to conclude based on the life histories of the individual elephants that all individuals, except for mother-juvenile pairs brought to the Park together, were unrelated. Each elephant was taken care of by one or two *mahouts* – elephant caretakers – every day. Adult male elephants (n = 4) were completely excluded from the study as they were unable to participate in most of the natural, social interactions within the group. When a female elephant was brought to the Park, they were generally allowed to integrate with a smaller group of their choosing. In this study, these smaller social groups (generally of n = 5 – 7 individuals) will be called "pseudo-families" when they refer specifically to closely bonded individuals regardless of genetic relatedness; such bond groups may form between wild elephant family groups as well (Payne 2003). There was no single herd at the Park, but six individual family groups that interacted at specific times during the day. Based on interviews with the Park mahouts during data collection but prior to data analysis, Figure 1 was drawn to illustrate pseudo-family group dynamics.

Each day, elephants followed a specific routine relevant to the Park's mission as a center for ecotourism. Mahouts moved their elephants to a specific location on the property, as a pseudo-family group, beginning at 0700 hours. They ate at a central location at 1130 hours – fed either by their mahouts or visiting tourists – bathed communally at 1300 hours and 1630 hours, and returned to their night shelters, in which they were tethered for the night, at 1700 hours. Mahouts moved elephants with vocal commands or by grasping ears or legs and walking them to different locations on the property. Throughout the day, elephants were left to graze or play in various parts of the property.

General Data Collection

Locations on the property for data collection were chosen so that they ensured both a full view of particular pseudo-family groups and my safety at all times. These locations included viewing platforms constructed specifically for observations, locations in the trees and fields in close proximity to mahouts, or from platforms constructed for tourist interaction with the elephants. Observation locations were chosen based on three factors in decreasing priority: 1) safety of observation vantage point at any given time, 2) view of a maximum number of pseudo-family groups at the beginning of the observation period, and 3) view of the pseudo-family groups from which there were the least amount of data. The property was divided into four grids for observation purposes, and an observation location was chosen within a grid based on these three factors. The property is ~ 55 acres in total size, but only ~ 30 acres were observable for this study. Thus, each of the four grids was approximately eight acres in area (Figure 2).

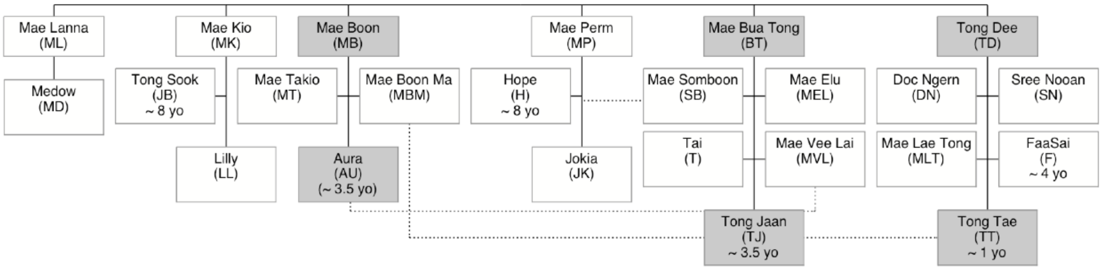

Figure 1. Elephant pseudo-family groups. This diagram shows the general group structure of the six elephant pseudo-family groups based on initial mahout observations and corroboration by three other Elephant Nature Park long-term staff members. Gray boxes indicate mother / infant pairings. The TD/TT pairing replaced another mother/infant pair (MTK / PP) early in data collection. Dotted lines represent elephants that spend time with two groups.

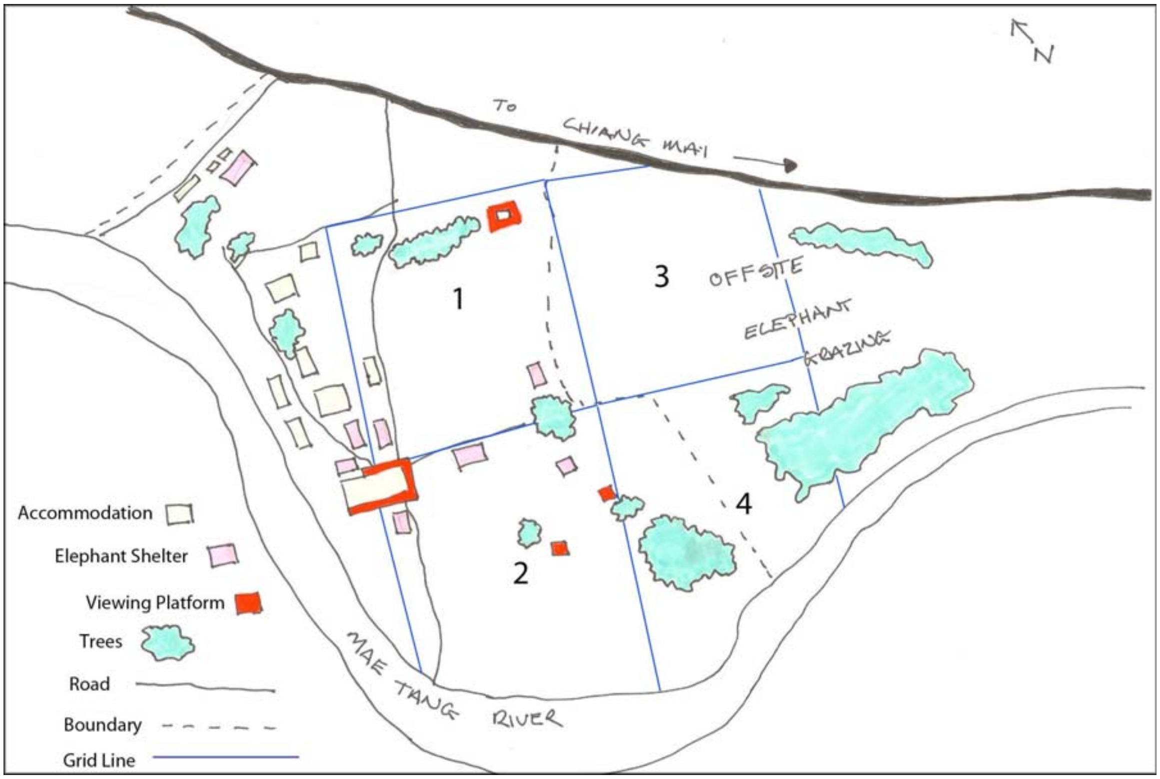

Figure 2. Elephant Nature Park (ENP), bird's-eye view. The four observation grids are clearly marked. Observations were done from both the viewing platforms and from other positions, either in the trees or in the field, but always close to mahouts. Diagram by K. Cullen (ENP mahout).

On average, data were collected during 1-2 week periods each month from April, 2008 – February, 2009. Data were collected using two systematic sampling techniques (Altmann 1974). We collected scan sampling data on relationship quality to systematically identify pseudo-family groups for comparison with Figure 1. General observation periods ran for no less than 30 minutes and no more than 180 minutes from 0730 – 1030 and from 1400 – 1630, with scan samples taken every 10 minutes. Data on proximity distance only (due to the lack of grooming in elephants) were collected for relationship quality designations within elephant groups (e.g., Olson 2004; Appendix I for details). All observation periods began after 10 minutes of no mahout interference on elephant behavior. Individual scan samples were cancelled if such interference occurred within one. The scan sampling / relationship quality data were meant to provide a) confirmation of the pseudo-family group structures (both within and across groups, and between kin and nonkin), and b) information on the influence of relationship on consolation behavior. Unfortunately, due to the overwhelming influence of the mahouts on the proximity of the elephant pseudo-family groups to one another, the scan sampling data were not included in the final analysis (see discussion). Instead, we relied on the Figure 1 designations as a measure of the elephants' relationships; members within a pseudo-family were labeled "friends" of one another, while all others were labeled "non-friends" for later analysis.

During these observation periods, all-occurrence sampling was used for distress behaviors and the reactions of others to these behaviors (i.e., post-distress observations). In addition, if an interaction was clearly observed outside these specific observation periods, the same quality of data was collected ad-libitum.

Consolation Data Collection

Post-distress behavior data collection was done following the PC/MC methodology for reconciliation and consolation behavior in primates (de Waal and Yoshihara 1983). The PC (or "post-conflict") period is an observation period in which all approach and affiliative behavior is recorded for a set period of time following the target behavior (in a conflict situation, this is usually an aggressive interaction). In this study, the "PC" was a period of observation following the targeted distress behavior, and was relabeled as a "PD." The term PD ("post-distress") was used for this study in lieu of PC, or "post-conflict" due to the nature of the focal behavior and the lack of conflict interactions. The MC, or matched control, was a period of time during which no distress behavior occurred immediately preceding it. By comparing the data within the PD period and a control period (the MC), we are able to assess whether or not the behavior seen in the PD is the result of the distress behavior immediately preceding it. The PD/MC methodology has been employed for both reconciliation and consolation, however the latter, again, involves comparisons of post-affiliative interactions between bystanders and victims rather than conflict opponents (de Waal and Yoshihara 1983; Aureli and de Waal 2000). Thus, this study focuses solely on consolation.

The PD for this study was a 10-minute observation period following the initial distress behavior (this period was initially defined by de Waal and van Roosmalen 1979, and is further discussed in Aureli and de Waal 2000) and involved the collection of the following data:

1) Initial data collected on distress behavior:

a) The identity of the first distressed individual or “victim” (because elephant interactions may involve multiple distressed individuals – Lee 1987 – the first individual to vocalize, or display a distress behavior was labeled the victim and thus the focal individual. If more than one individual responded simultaneously, the rarest case (if known, the least-often distressed individual) was chosen.

b) Information on the date and time of the event, as well as the weather condition

c) The cause of the distress, if known

d) Initial distress behaviors of the victim

e) All individuals present (within 50 m of the victim, regardless of their reactions)

f) Mahout reactions or causation

2) Data collected during the PD period:

a) Behaviors were taken on each bystander, recorded by minute for 10 min. Thus, multiple behaviors in the same minute were recorded with the same time stamp. “Directed behavior” was recorded for each bystander relative to the victim, and bystanders to each other. All behavior was recorded per minute in chronological order. Directed behavior fell into two categories: trunk to body contact and vocalizations. All vocalizations, when the individual vocalizing could clearly be identified by visual cue, were recorded. Proximity changes were also noted, mainly to ensure that similar proximity was observed when choosing a corresponding MC period. The ethogram for systematically coding these behaviors is listed in Appendix I. Elephant body state information was also taken as vocalizations and body touches were recorded, specifically noting the state of bystanders after the victim’s distress behavior.

An MC (or "matched control"), as in the PD, was taken for a period of 10 minutes, with all directed behaviors towards the victim and body state changes recorded. To ensure certain properties of the PD were maintained in the MC as well, the MC was treated as a "smart" control period (Aureli and de Waal 2000). This "smart MC" was an observation of the victim and bystanders, with priority given to a time period on the next possible day where no significant social interaction (and certainly no interaction that could be classified as agonistic conflict or distress) between individuals had taken place in the period at least 30 min. prior to the MC. Such a conservative "no-interaction period" was observed prior to collecting MC data to ensure, to the best of our ability, that the behavior of the elephants was not influenced by any immediately preceding interactions. In addition, an MC period began after a period of at least 15 min. with no mahout/elephant interactions. The following criteria were also met before an MC period began, in decreasing prioritized order: a) individuals present: 75% or more of the original PD elephants had to be within 25 m of the victim and in view when the MC period began, b) field location: the elephants had to be within the same grid as in the PD, c) time of day: designated as being in the same time period as the PD, divided into specific time blocks: 0730 – 1000, 1000 – 1300, 1300 – 1600, and 1600 - 1700, and d) weather condition. All MCs were collected within seven days of its corresponding PD (in 80% of PD/MC cases, the MC was collected within 48 hours). If an MC was conducted when an elephant that had made contact with the distressed individual in the corresponding PD was absent or more than 25 m away, that PD/MC pairing was excluded from the analysis to avoid biasing the data in favor of our predictions.

Data Entry and Analysis

The timing of the first affiliative interaction after the distress in the PD was compared to the timing of the first affiliative interaction between the bystander(s) and the victim in the corresponding MC. The first step was to determine whether or not these "distress" interactions resulted in a higher affiliative contact level when compared with controls. PD/MC pairs were split into three distinct categories: attracted, dispersed and neutral. Attracted pairs were those in which the first affiliative contact occurred earlier in the PD than in the MC (or where there was no affiliative contact in the MC), dispersed pairs were those in which the first affiliative contact occurred earlier in the MC than in the PD (or not at all in the PD), and neutral pairs were those in which affiliative contact times did not differ in the PD and its corresponding MC (de Waal and Yoshihara 1983; Veenema et al. 1994; Palagi et al. 2006).

To analyze the affiliation levels post-distress across individuals, a calculation of group conciliatory tendency (i.e., a percent tendency of the group or individual dyads to console each other following a distress event) was also calculated. This calculation, "attracted minus dispersed pairs divided by the total number of PC-MC pairs" gives a CCT (conciliatory tendency) measure for each individual (when only PC/MC pairs per focal individual were included in the numerator) that can be combined to find a group mean CCT (Veenema et al. 1994). This calculation is independent of the duration of observations, and accounts for the influences of baseline levels of affiliative interactions (Veenema et al. 1994). In the case of third-party affiliation, the "CCT" is relabeled "TCT," or triadic contact tendencies, and pays special attention to the difference between "solicited" (victim approaches bystander before contact) and "unsolicited" (bystander approaches first) interactions (Call et al. 2002). In this study, we re-label this measurement "BCT", or bystander contact tendencies to reflect the fact that the bystander's reaction is to a single distressed individual and not the reaction of a victim to a dyadic conflict.

PD and MC periods were limited to 10 minutes for two reasons: 1) the chimpanzee literature overwhelmingly indicates that differences between PC and MC affiliative contact occur within the first 10 minutes following conflicts (Arnold and Whiten 2001; Palagi et al. 2006; Romero and de Waal in press), and 2) longer periods of observation time were impractical given the regular human / elephant interactions at the Park.

Statistical analyses: We used Wilcoxon matched-pair signed-ranks tests (all tests were two-tailed) to analyze the differences between PD and MC pairs because of the relatively small sample size and the violation of the rules for normality. These tests used the differences between the attracted and dispersed pairs of each focal individual in the analyses to avoid biasing the data towards any particularly well-represented focal elephant. In addition, the McNemar test was used to assess the differences in elephant clustering (i.e., differences in multiple-individual groupings) across PD and MC periods.

Primary Predictions:

Prediction I: Based on the overall social complexity of elephants (e.g., Poole 1996; Payne 2003), as well as documented cases of targeted helping (Moss 1988; Poole 1996; Payne 2003; Douglas-Hamilton et al. 2006), we will look for consolation behavior in elephants through an assessment of bystander affiliative contact towards distressed individuals.

Prediction II: If consolation is an affiliative reaction to distress based on empathy with the victim, emotional contagion is expected to underlie such a reaction. Thus, we should expect that bystanders adopt the emotional state of the distressed individual more often following distress events than in control periods. We might also expect in larger groups that the distress of one individual spreads to others leading to empathic reactions between bystanders as well, visible in increased affiliative contact.

Results

Prediction I: There were 84 PD/MC pairs (and thus 84 distinct initial signals of distress) across 18 different focal individuals (mean number of PD/MC pairs per individual = 9.5, range = 1- 38). Within these 84 PD/MC pairs, there were a total of 183 focal-bystander dyads, 171 of which involved at least one affiliative physical contact in the PD period (93.4%). 53 of the 84 PD/MC pairs included affiliative contact by multiple individuals directed towards a single focal individual. All 183 dyads were “friends;” “non-friends” were never present during PD periods (based on Figure 1 designations).

Focal	**A (S)**	**D (S)**	**N (S)**	**A (US)**	**D (US)**	**N (US)**	**BCT (S)**	**BCT (US)**
AU	3	0	0	11	1	1	100.0%	76.9%
BT	3	0	0	7	0	1	100.0%	87.5%
F	2	0	0	12	0	1	100.0%	92.3%
JB	0	0	0	2	0	0	-	100.0%
JK	0	0	0	26	0	2	-	92.9%
MB	2	0	0	11	0	0	100.0%	100.0%
MD	0	0	0	3	0	0	-	100.0%
MEL	3	0	0	0	0	0	100.0%	-
MK	0	0	0	2	0	0	-	100.0%
ML	1	0	0	0	0	1	100.0%	0.0%
MLT	0	0	0	2	0	0	-	100.0%
MP	6	0	0	1	0	0	100.0%	100.0%
MTK	3	0	0	0	0	0	100.0%	-
MVL	0	0	0	3	1	0	-	50.0%
SB	0	0	0	0	0	1	-	0.0%
TD	0	0	0	2	0	0	-	100.0%
TJ	1	0	0	33	1	9	100.0%	74.4%
TT	0	0	0	19	4	2	-	60.0%
Total	*24*	*0*	*0*	*134*	*7*	*18*	*100%*	*79.9%*
Mean TCT ± SEM							100.0%	77.1% ± 8.5%

Table 2. Solicited and unsolicited affiliative contacts for each focal individual. Columns indicate numbers of attracted (A), dispersed (D) and neutral (N) pairs per individual in both solicited (S) and unsolicited (US) contacts, as well as the calculated bystander conciliatory tendency (BCT). The pooled data are provided in italics.

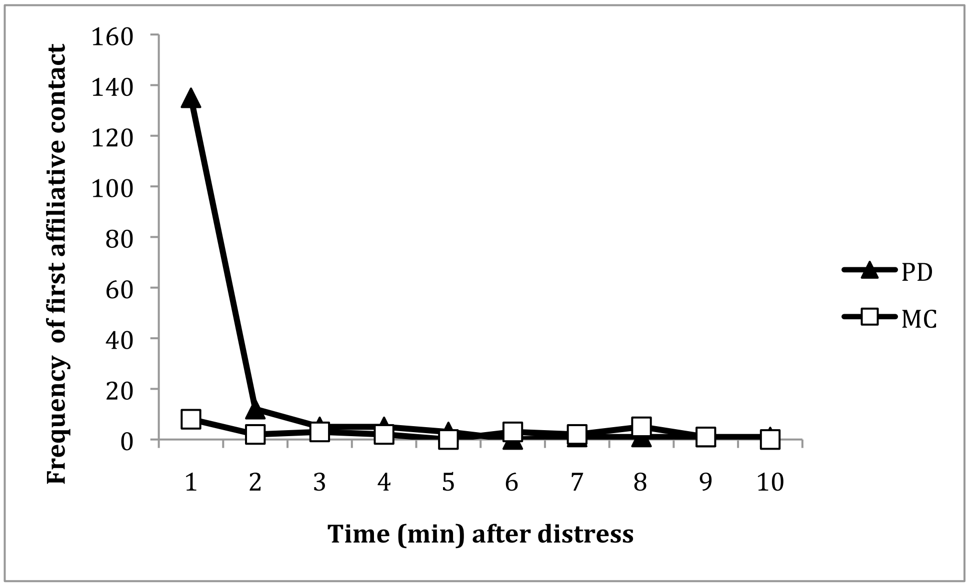

Figure 3. Temporal distribution of the first affiliative, physical contacts in PC (closed triangles) and MC (open squares) periods across all dyads.

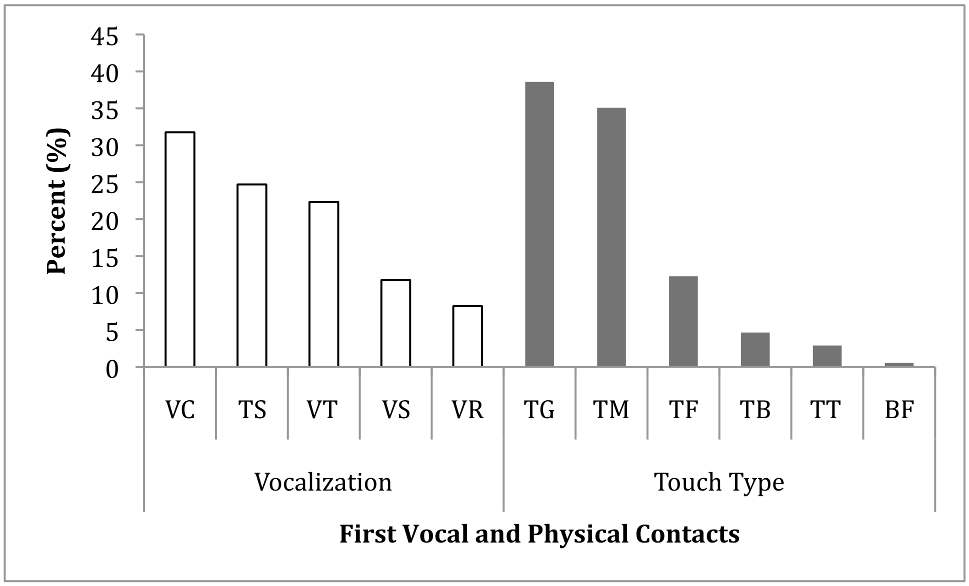

Figure 4. Distribution of first contacts (Vocalizations: VC – chirp, TS – trunk smack, VT – trumpet, VS – roar, VR – rumble. Touches: TG – genitals, TM – mouth, TF – rest of face / head, TB – rest of body, TT – trunk/trunk, BF – breast-feeding). The y-axis indicates the percent (%) occurrence of each type of vocalization or trunk touch as the first affiliative contact across all dyads.

To assess consolation, we categorized attracted and dispersed pairs based on whether or not each interaction was "solicited" (the focal individual approached the bystander to "seek reassurance") or "unsolicited" (the bystander was the first to approach the focal, i.e., true "consolation" – e.g., Call et al. 2002; Palagi et al. 2006; Romero and de Waal in press). A significant difference was found between attracted and dispersed pairs in both "solicited" contacts ($Z = 2.694$, $n = 18$, $P = 0.007$), and "unsolicited" contacts ($Z = 3.312$, $n = 18$, $P = 0.001$; Figure 3). The mean BCT ± SEM for all focal individuals in unsolicited contacts was 77.1% ± 8.5%, while the mean BCT in solicited contacts was 100%. Bystander conciliatory tendencies (BCT) were higher for solicited contacts than for unsolicited contacts ($Z = 2.201$, $n = 8$, $P = 0.028$).

Because elephants primarily use acoustic modalities for communication, we also looked at bystander's vocalizations in response to distress events. In a comparison of first bystander vocalizations in the PD and MC periods, we found a significant difference between attracted and dispersed pairs across 15 focal individuals (only three focal individuals never had a bystander vocalize in a PD: $Z = 3.420$, $n = 15$, $P < 0.001$, BCT = 94.9% ± 4.4%; Figure 4).

<u>Prediction II:</u> We first assessed differences in the body state of bystanders - in relation to the body state of distressed individuals - between PD and MC periods. Vocalizations often signal agitation or excitement in elephants and are usually paired with similarly "agitated" body states (cf. Olson 2004). Within the 183 total dyads, bystanders adopted the agitated body state of the distressed, focal individual in the PD and showed no sign of agitation or distress themselves in the MC in 94.0% of cases, or 172 times (analyzed by

focal individual: Z = 3.738, n = 18, P < 0.001). Trunk contact between two bystanders (n = 19) occurred in 37 of the 84 PD interactions in which there were focal-bystander contacts. We found a significant difference between attracted and dispersed pairs when looking at the first affiliative contact between bystanders in the PD and MC periods (Z = 3.854, n = 19, P < 0.001; BCT = 94.7% ± 3.8%).

Elephants often form a close proximity circle around an infant following a distress call (e.g., Moss 1988; Poole 1996). To systematically assess whether this occurs as a result of distress, we looked at the occurrence/non-occurrence of "clustering" in PD and MC periods (re-named from "bunching," Nair et al. 2009). Clustering, as defined here, involves the coming together of three or more individuals around the distressed individual so that all individuals are within trunk's reach of one another. Thus, we excluded all events in which less than four individuals were present (this excluded n = 7 focal individuals all together). Clustering occurred only in the PD and not the MC in 30 of the 42 remaining PD/MC pairs (McNemar test, n = 42, $\chi^2 = 28.033$, P < 0.001).

Discussion

This study investigated the capacity for consolation in Asian elephants assuming distress as the cause of such behavior. In frequency, elephants overwhelmingly engaged in unsolicited contacts (bystanders approach and affiliate with the distressed/focal individual first) more than solicited contacts (the victim is the initiator of the contact) following signs of distress from the focal animals, and did so significantly more often than in control periods.

One unexpected result was that the bystander conciliatory tendency (BCT) was significantly higher for solicited contacts than for unsolicited contacts. Non-human primate studies show variability in both a bystander's acceptance of solicited contact and the willingness of victims to seek contact from bystanders (de Waal and van Roosmalen 1979; Aureli and de Waal 2000; Palagi et al. 2006), as well as demonstrations of complex, volatile coalitions and alliances that dictate group relationship dynamics (de Waal 1982; Harcourt and de Waal 1992). Elephants, on the other hand, form cohesive, largely female family groups where the hierarchy is highly egalitarian (even more so than in chimpanzees – de Waal 1982; Boesch and Boesch-Achermann 2000) and, relative to non-human primates, lacking in regular conflict (Poole 1996; Payne 2003). It seems unlikely then, that elephants within a family group would often reject the solicitation of contact from another. In fact, in this study, elephants never rejected solicited contacts. Thus, the difference in BCT levels between solicited and unsolicited contacts is most likely due to the infrequency of solicited contacts (i.e., the low relative frequency of solicited contacts compared to unsolicited contacts may have influenced the BCT values) as well as the relative lack of influence by a third party in elephants' responses to distress (see below), and not to differences in the overall tendency towards consolation.

We also found unusually high BCT values, especially when compared to TCT values (conciliatory tendencies calculated in triadic interactions) found in chimpanzee studies. Often, consolation is in the context of post-conflict reaction to distress and is focused on triadic relationships (Call et al. 2002). BCT levels are related to the interactions between the focal and a bystander without the additional effect of a third-party on the bystander's behavior (in conflict this third-party is usually the aggressor, who may influence the consolatory tendency of the bystander). In post-conflict interactions from which a TCT is usually calculated, a bystander's tendency to console a victim may be heavily influenced by the identity of the aggressor and the risk of helping the victim of conflict, influences that are most likely not applicable in our study. Thus, we should expect that overall BCT levels would be higher than TCT levels. In fact, our BCT level for unsolicited contacts (77.1%) is 57.1 percentage points higher than for rooks (20%), and 53.5 points higher than for chimpanzees (23.6% - the average TCT across four different chimpanzee groups: Palagi et al. 2006 – 49.5%; Koski and Sterck 2007 - 12.7%; Romero and de Waal in press – 16.5% and 15.6% for two groups). As all of these authors note, TCT levels are highly influenced by the variability in partner relationships, variability we did not have in our elephant study group.

There were substantial confounds on the elephants overall ability to form natural groups at the Park, and on their ability to freely interact with one another. As previously described, mahouts regularly moved their elephants and separated pseudo-family group members for tourism-related activities. In most non-human primate studies of reconciliation and consolation, behavior is rarely actively interrupted or influenced by handlers or experimenters, and thus, interactions between "friends" and "non-friends" are both definable and quantifiable. Since "non-friends" had less opportunity to interact with distressed individuals than did "friends" simply due to the husbandry dynamics at the Park, there was no opportunity for the overall conciliatory tendency data to be influenced by relationship quality. In recent studies on consolation in chimpanzees, the species with which the majority of consolation studies have been conducted, relationship quality has been an important factor for determining both the likelihood and function of consolation (e.g., Call et al. 2002; Palagi et al. 2006; Fraser et al. 2008; Romero and de Waal in press). These studies support the fact that the greater the relationship quality (based on kinship, proximity and affiliative behaviors) the higher the incidence of consolation. In addition, as Romero and de Waal (in press) argue, if consolation is an empathic response primarily used as a mechanism for lowering distress in others, it should be found most often in closely bonded individuals. In fact, empathy is a capacity linked most often to individuals that are alike, familiar, and socially bonded (for a review, see Preston and de Waal 2002). In the Park elephants, individuals within a single, pseudo-family group were closely bonded with one another (although not necessarily related), and rarely interacted with individuals with whom they had poor relationships (again, the dynamics at the Park often precluded interactions or close proximity between groups). Thus, it was impossible to compare the presence or absence of consolation between "friends" and "non-friends." Nonetheless, we have demonstrated here the capacity for consolation in closely-bonded elephants, where the unsolicited affiliation of bystanders towards a distressed individual mirrors the results found in studies of consolation in some other non-human animals.

The term "consolation" itself implies distress alleviation as a function (de Waal and van Roosmalen 1979; de Waal and Aureli 1996), and many authors have instead used the term "postconflict third-party affiliation" to describe the behavioral interaction between partners without implying the behavior's specific function (e.g., macaques: Call et al. 2002; rooks: Seed et al. 2007; dogs: Cools et al. 2008; wolves: Palagi and Cordoni 2009). This latter group of authors avoid the use of the term consolation either because of an inability to demonstrate its implied function, or because the term refers specifically to unsolicited contacts between bystanders and victims. Fraser et al. (2008) and Romero and de Waal (in press), on the other hand, used the term consolation because they were able to satisfy both conditions.

We too label what we have found in elephants as consolation for the following reasons: First, we were able to demonstrate that unsolicited contacts may lead to affiliation within elephant dyads after distressful or alarming events. Second, Romero and de Waal (in press) note that consolation's alleviation of a focal individual's distress likely relies on the adoption of that individual's emotional state (i.e., "emotional contagion" – Hatfield et al. 1994; de Waal 2003). Here, we demonstrated emotional contagion in the form of bystander expressions of distress following the focal individual's distress compared to its relative absence in control periods. We do recognize, however, that this argument would be stronger with two additional pieces of information: the first is a significant number of interactions between *both* "friends" and "non-friends" – to have a comparison group in which to assess consolation levels - and the second is an additional, quantifiable signal of distress in elephants. For the former piece of information, only a wild population would suffice, and such populations are extremely difficult and dangerous to follow, especially for forest-dwelling Asian elephants under stress (Sukumar 1989; Lair 1997). For signals of distress in elephants, we used body state changes paired with vocalizations, but perhaps attention to other elephant-specific behaviors would be a better indicator of distress. Fraser et al. (2008) argued that the change in the quantity of specific, stress-indicating behaviors (self-directed scratching and grooming in chimpanzees) within the PD period was related to the occurrence of consolation. In our study, we could only compare the occurrence of distress behavior across the PD and MC periods. The reason for this is that the primary measures of distress in elephants – ear, trunk and vocal displays – do not individually have one clear function. Rapid ear flapping, for instance, might indicate agitation, active vocal communication or over-heating, while trumpeting might indicate anger or excitement (Olson 2004; Nair et al. 2009). Although I could identify the occurrence of distress by identifying paired behaviors, I could not quantify its occurrence within a single PD. Unfortunately, the identification of a single quantifiable behavior signaling distress, which is relatively easier in a heavy visual signaler like primates, may be much more difficult in elephants due to the overwhelming dominance of their acoustic repertoire over their visual one (e.g., Poole 1999; Olson 2004). This particular population of elephants, however, still provided one of the best elephant study groups available for systematically collecting data on distress interactions (see the general discussion at the end of this dissertation for further details on project limitations). In the future, measuring physiological (i.e., monitoring adrenal hormone levels through stressful periods – Brown et al. 1995; Brown 2000) and behavioral responses to distress in tandem may provide a more complete picture of consolation in elephants.

Even though we found that elephants used physical trunk contact in post-distress affiliation, we also found that bystanders used vocalizations signaling distress in response to the activity of distressed individuals. Because of the elephant's overwhelming use of vocal communication within family groups (e.g., Langbauer Jr. 2000; McComb et al. 2000) and based on the detailed repertoire of calls they use in a variety of stressful situations (Nair et al. 2009), we analyzed the vocalizations as if they were an alternative method to physical contact for assessing affiliation. This makes sense in light of the fact that elephants vocalize in a wide range of contexts, including reunions, play, aggression, fear and other stressful situations (Poole et al. 1988; Poole 1999; Nair et al. 2009). In this study, the vocalizations most often used by the elephants following distress calls were the chirp, the trunk smack (or trunk bounce), and the trumpet, all vocalizations in Asian elephants most often associated with distress in the individual vocalizing (Olson 2004; Nair et al. 2009; Figure 4; also see Figure 5 at the end of the dissertation in Appendix C).

In addition, distress behaviors in the focal individual seemed to draw physical contact to the focal, but also between the bystanders themselves. This is an interesting category of contact until now never demonstrated, or even mentioned in primate studies. Quadratic reconciliation – whereby two, usually related individuals reconcile following a conflict between two of their kin (Aureli and de Waal 2000) – is similar in behavior but not in function. Bystander-bystander consolation, on the other hand, indicates perhaps a higher degree of emotional contagion in elephants so that not only the focal individual but also everyone around it requires reassurance, which the bystanders provide to each other. We call these contacts "extra-consolatory" because they seem to be related to the distress of the focal individual but may also act as an alternative method for alleviating stress within a closely bonded group. Again, further analysis, if possible, with a population that allows for differentiating between contacts within and between bonded individuals and groups of varying relationship quality would provide further support for the existence of consolation; such a population would allow for differentiating between bystander-bystander contacts in closely bonded and lesser bonded individuals.

Overall, these vocalizations and bystander-bystander affiliations complement the data on the distress response between the PD and MC periods in suggesting that emotional contagion (the most basic form of empathy – de Waal 2003) may play an important role in the expression of consolation (a potentially more complex form of empathy – Preston and de Waal 2002) in elephants.

It is important to emphasize the high number of unsolicited contacts in this study, as emotional contagion may be difficult to isolate when the context of the distress events is unclear. If the display of agitation by multiple elephants is due to the reaction of all the individuals to the context causing distress and not to a focal, distressed individual, we are simply identifying a group of individuals distressed by the same "stressful event" rather than the potentially more complex, emotional contagion of multiple bystanders to a focal elephant. In cases where the focal individual is the victim of some identifiable, stressful event (i.e., the context of the distress is clear), the reaction of others may be a clear indication of emotional contagion when the bystanders adopt the focal's emotional state, and of consolation when they make unsolicited contact with the focal. In most of our PD cases, the context was not clear. If most of our PD cases, even those in which the context was unclear, involved solicited contacts, it would be difficult to differentiate between consolation and generalized distress (i.e., the entire group becoming distressed by the same stimulus). However, because most of the contacts to the focal were unsolicited – i.e., contacts where the focal made no attempt to approach or touch the bystanders prior to the bystanders' contact – and because the difference between attracted and dispersed pairs in these unsolicited contacts was highly statistically significant, it seems that our classification of these reactions as responses to distress in others is justified.

Here, we have demonstrated consolation in elephants, which fits well with what we already know about their social complexity and empathetic capacity (Bates et al. 2008). But further research is certainly needed with larger, more naturalistic populations to better understand the expression of consolation in elephants, specifically in terms of a) its prevalence and relevance to relationship dynamics within and between groups, and b) its positive (functional) effects on an elephant's emotional state.

Investigation II: An Experimental Study of Elephant Cooperative Behavior

Although the evolution of cooperative behavior is fairly well understood (e.g., Trivers 1971; Axelrod and Hamilton 1981; Dugatkin 1997), the cognition underlying it is not. The last decade has seen increased attention to the "understanding" animals possess of cooperation, tested experimentally by gauging their reactions to their partner's presence or absence, specific behavior, and motivation (or lack thereof) (Dugatkin 1997; Noë 2006). We use the word "understand" here to imply that the animals have learned the relevant contingencies of the task, not necessarily that they are fully cognitive of the effect of their behavior, or its relationship to another's.

Crawford (1937) conducted one of the first cooperative tasks in chimpanzees in a lab, and this original design will serve as the fundamental basis for our elephant apparatus. One chimpanzee was presented with rope that was attached to an out-of-reach box, however, the box was too heavy to be pulled in by one individual. Although two chimpanzees, when presented with the box and two ropes together, did not spontaneously cooperate by pulling the ropes in tandem, teaching the chimpanzees to do so eventually led to cooperation without any experimenter-generated verbal cues. This study proves interesting because even with teaching, the chimpanzees had to learn to continue to "coordinate" their pulling to ensure success in the task. The differences between coordinated cooperative behavior and haphazard mutualistic cooperation are a matter for debate – see Boesch 1994 and Stanford et al. 1994 for a discussion of chimpanzee hunting behavior in the wild – but most cooperation studies do not focus on the need to teach animals the task, only the ability for the animals to maintain it without further cuing (Melis et al. 2006; Hirata and Fuwa 2007). By introducing specific controls and experimental variables, one can test whether or not the ability of two animals to cooperate in a task is due to "random pulling of the rope" or to a recognition of partner roles and coordination (e.g., Mendres and de Waal 2000).

Chalmeau (1994) and Chalmeau and Gallo (1996) tested chimpanzees with a fruit task that required two individuals to pull a handle simultaneously to obtain a food reward. Although the dominant male (one of the partners) obtained most of the food, he glanced increasingly more often towards the partner as the experiment progressed, suggesting a possible recognition of the need to cooperate to complete the task (Hirata et al. 2007). Although Chalmeau et al. (1997) and Visalberghi et al. (2000) suggest that capuchin monkeys (*Cebus apella*) only succeeded in a cooperative-pulling task by random pulling, Mendres and de Waal (2000) used a bar-pull similar to the Crawford apparatus to demonstrate the monkeys' ability to learn about the need for partner cooperation to achieve success in the task. Melis et al. (2006) used a procedure designed by Hirata et al. (2007 – described in detail below) and demonstrated that chimpanzees not only recruited partners to cooperate in pulling tasks, but selectively chose partners that had been more effective in previous interactions.

Hirata et al. (2007) suggest that the Crawford task, although a clear demonstration of cooperative tendencies, may not require a complete understanding of partner-partner cooperation because of the ability of the animals to solve the task through random rope pulling. If the task requires true coordination (i.e., random pulling rarely if ever results in success), there may be a greater need for communication between partners (Povinelli and O'Neill 2000; Hirata et al. 2007).

In the Crawford task and in the similar bar-pull tray outlined in Mendres and de Waal (2000), the weight of the object requires the cooperation of two individuals to pull it in. Hirata et al. (2007) designed a similar apparatus, but it was not the weight of the object that determined the cooperation parameters.

In the Hirata et al. (2007) apparatus, two styrene blocks – on the top of which food could be placed – were separated with a pipe and through each block a long rope was fed so that each of two ends could be placed inside the test chamber (one rope end for each chimpanzee partner). Thus, in this task, if one partner pulls the rope too quickly or before the other is able to similarly begin pulling the other end, the other end is lost from the test chamber and that particular test is a failure. This modification of the Crawford task permits the experimenter to a) assess coordination tendencies, and b) require cooperation between two individuals without the need for an excessively heavy object. Hirata et al. (2007) first trained the chimpanzee subjects to pull both ends of the rope together, by themselves. When the subjects were then given the opportunity to cooperate by pulling each end of rope, they were unable to successfully due so at all (i.e., within 3 sessions of 10 trials each). After an additional variable was introduced – varying the rope end lengths inside the chamber from 10 cm – 130 cm – the chimpanzees gradually improved their performance until they were highly successful in all rope-length conditions. In the longer rope condition a chimpanzee could succeed on its own by joining the two ropes together and pulling (thus repeating its performance in the initial training phase), but in the short rope condition, cooperation between two partners was necessary for trial success. Although there was never any solicitation behavior observed between conspecifics (chimpanzees did solicit cooperation from human experimenters in a separate experiment), the chimpanzees did glance at the other partner more often in the short-rope condition, and glanced before pulling more often in the short-rope than in the longer-rope conditions. Glancing coupled with the high level of cooperative success in the short-rope condition (even in the 89% of trials when one chimpanzee reached the rope first and thus was required to wait for the partner before pulling) suggests an ability of chimpanzees to learn how to cooperate and to coordinate such cooperation to successfully obtain food. In fact, Hirata et al. (2007) suggest that this need to coordinate cooperation, specifically in the short-rope conditions, is the more difficult task requiring a greater understanding of the need for a partner.

Here, I conducted a variation of the Hirata task on Asian elephants to investigate the cognitive underpinnings of cooperative behavior in this socially complex species. I constructed a pulling apparatus similar to that used by Hirata et al. (2007) and Melis et al. (2006), but adapted it for the largest land mammal and developed an experimental protocol that would best suit the use of an intelligent but potentially volatile test subject.

General Methods

Subjects

This study enlisted 12 elephants at the Thai Elephant Conservation Center in Lampang, Thailand, and each of the elephant's main human caretakers, or *mahouts*. Basic information on elephant demography is available in Table 3. These are tame elephants that in most novel situations respond to mahout commands only, whereas this study required spontaneous problem solving. The Thai Elephant Conservation Center is a government-run facility, housing more than 50 elephants and a national elephant hospital. Elephants participate in daily shows for tourists, and have some time to socialize with one another under mahout supervision.

Six elephant-pairs were selected based on their overall docility and relationship with each other (the selection was based on careful consultation with the mahout staff). These six elephant-pairs consisted of four female-female pairs, one male-male pair, and one male-female pair – Table 3).

Experimental Setup

The pulling apparatus (henceforth referred to as the table) was comprised of two pieces of plywood painted and bolted to a rectangular PVC pipe frame 3.3 m wide and 1.2 m deep. The table was placed 4 m beyond two trees, and three wooden planks set in the ground ensured smooth movement of the table (see Figure 6 for a diagram of the experimental arena). A 7 m wide volleyball net was strung between the two trees, anchored by two strong, taut wire ropes, forming a transparent but impassable barrier between the elephants and the table. In training trials, a single piece of rope, ~ 6m in length, was clipped to the front of the table and fed through a metal ring set in the ground beneath the net. Elephants could approach this rope and pull, drawing the table towards them. A wooden post embedded in the ground (replete with rubber shock absorber made from old tires) served as a stopper that prevented the table from advancing past the net. To keep the table centered as it was pulled in, a ~ 2.5 cm thick wire rope – running perpendicular to the volleyball net – was strung from the buried table stopper, through the central PVC pipe of the table's frame, and then fixed to a tree on the central axis beyond the table. This rigid guide cable prevented any skewing of the table and thus eliminated incongruities in food availability. Two red food bowls were attached to wooden boards, 50 cm in length, on each side of the table; as the table reached the stop point, the two bowls became available to the elephant just under the net. In test trials, a single piece of 16.5 m long, 1 cm thick hemp rope was threaded through guides and around the back and two sides of the PVC frame so that the loose ends appeared out of two openings on either side of the front of the table. Each rope end was threaded through a metal ring set in the ground under the net, leaving 1.6 m of rope available to each elephant upon approach.

To demarcate the test area, from each of the two central trees was strung a single, flagged green rope about 1.5 m above the ground and reaching back 10 m behind the net to the release point. During testing and control trials, a third flagged rope was strung down the center of the test area, dividing it into two equally wide lanes (3.5 m); thus, each elephant was released into a single lane and had access only to a single rope end.

All data were coded from two video cameras. A Panasonic PV-GS500 miniDV camera was fixed to a metal mount on a 7 m long bamboo ladder, which was hoisted on pulleys between the two trees to a height approximately 8 m above the ground. This camera’s view was monitored on the ground via closed-circuit television, and provided a bird’s-eye view of the testing arena. A second camera, a Canon HV20, was placed on a tripod beyond the table, providing a heads-on view of the elephants.

General Procedure

Training: Elephants were first given two trials in which they could freely approach the table (it was already positioned at the final stop point) so that they would have experience eating out of the two bowls on it. In subsequent training trials, the table was reset to its starting position, and a single piece of rope was clipped to the center of the table and fed through a center ring underneath the net. The mahout would then walk with his elephant to the single available rope end and train his animal to pick up and pull the rope using vocal commands. Rope pulling strategies were ultimately at the discretion of the elephant, but all elephants had earlier, as part of the facility’s routine, been trained to pull chains alone. Elephants needed to successfully pull in the table, without mahout prompting, in three consecutive trials before moving on to simultaneous release trials (Table 3).

Testing and control phases: The two mahouts stood at the release point with their elephants and restrained them by grasping the ear or front leg. When signaled by the experimenters – who were positioned 10 m to the side and back from the setup – elephants were released down their respective lanes. Upon release, mahouts turned away from the elephants and remained silent to minimize chances for cuing, and in position behind the elephants for safety. Trials began when the mahouts gave release commands – they released their hold on the elephant and gave a single word, “go” command once so that it was up to the elephant whether to proceed or not – and ended when the rope became unthreaded from the table, or when all the food had been eaten (at which point a simple “stop” command was given and the elephants were recalled). During simultaneous release and the subsequent delayed release and control phases, each of the two food bowls on the table contained two halves of a full ear of corn, a highly desirable but rarely used food reward at the elephant facility. In between all trials, mahouts gave elephants pieces of banana and sugarcane to ensure they remained relaxed. Commands were never given during trials, and mahouts were cued to release their elephants with a hand signal that was not visible to the subjects. Elephant pairs never received more than 30 trials a day, nor were they tested for more than 1.5 hours a day. Testing occurred between January and May, 2009. Depending on prior obligations at the facility, elephants were tested in the early morning or early afternoon, and were often hosed down with water on exceptionally hot days.

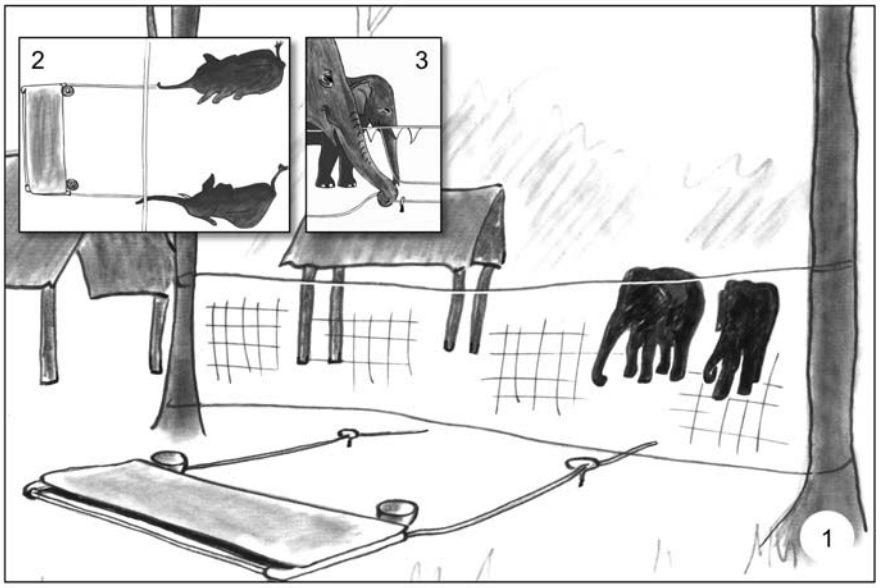

Figure 6. A multi-view diagram of the elephant cooperation apparatus. View 1 pictures a ground view from beyond the table. In test and control trials, the two elephants, lined up at the release point, walked down two separate, roped-off lanes (not presented in this diagram for ease of viewing) from a point 10 m behind the apparatus. View 2 mirrors that of the bird's-eye video, and View 3 shows a side view from the base of the barrier. Drawing by F. de Waal.

Condition I: Simultaneous Release

<u>Prediction</u>: Given the elephants' known social complexity and examples of coordinated targeted helping in wild populations (e.g. Payne 2003; Douglas-Hamilton et al. 2006), we expect that elephants will successfully coordinate their behavior in this cooperative pulling paradigm without additional training, and will thus be successful in pulling in the table when both elephants are needed to do so.

Procedure and Results

Both elephants were released together (simultaneously) down their respective lanes from 10 m back by their respective mahouts. The elephants received no training or guidance on this particular condition, which was tested in 20 trials per day for two days. To move on to the delayed release trials, elephants had to successfully pull in the table in eight of the final 10 trials. All pairs reached the criterion of at least eight successful pulls in the final 10 trials (see Table 3 for raw data). Although this phase tells us little about coordination as the elephants could, after having reached the rope ends at the same time, simply have employed a "see the rope, pull the rope" strategy based on previous training, the simultaneous release phase was necessary before progressing to the next condition.

Condition II: Delayed Release

Prediction: If one elephant is released before the other and learns, without explicit training, to pair their partners' presence with success or that success requires both rope ends to be pulled simultaneously, then they will wait for their partner's arrival before pulling the rope.

Procedure

Using the same apparatus, the elephants' release times were staggered. Now, for the elephants to retrieve the table, the first released individual must learn, without explicit training, to wait for its partner before pulling its own rope end. One elephant in each pair was selected to be the first released, and the release order was not switched until the completion of the entire testing protocol. Each lead elephant was initially released 5 seconds (s) before its partner until the pair successfully pulled in the table for three consecutive trials, upon which the interval was increased to 10 s until the same criterion was reached. This procedure was followed in added 5 s increments through 25 s (a similar procedure was used by Melis et al. 2006). The same subjects were then tested for three days with 20 randomized trials per day including 10 trials of release intervals between 1 s – 25 s and 10 trials of longer release intervals, not previously experienced, between 26 s – 45 s.

Results

The first elephants tested in each of the six pairs all reached this criterion in 30 trials or less (in theory, the fastest way to accomplish all criteria is in 15 trials – see Table 3), and each elephant made fewer than a total of 12 errors (if an elephant made three consecutive errors in the same time interval, they reverted back to the previous interval).

All six elephants were highly successful in waiting for their partners across the 60 trials (i.e., 20 trials over three days), which they did between 88% and 97% of the time (mean ± SD = 93.33 ± 3.72%). While on the final test day their combined success rate per delay interval correlated negatively with delay length in seconds (Spearman's $r = -0.72$, $n = 20$, $P < 0.001$), by the second and third day this correlation dropped to a nonsignificant level ($r = -0.28$, $n = 20$, NS with data combined for days two and three, Figure 7).

Pairs	**Elephant**	**Age (y)**	**Sex**	**Pull-Train**	**Sim. Release**	**Delay (Error)**
1	SS	6	M	3	40 / 10	19 / 3
	KW	10	M	5		
2	PT	16	F	7	36 / 10	30 / 9
	LK	16	F	7		
3	WL	12	F	6	38 / 10	28 / 8
	JO	18	M	5		29 / 12
4	UP	10	F	6	39 / 10	20 / 3
	KD	26	F	6		
5	PP	30	F	7	37 / 9	30 / 12
	PJ	28	F	5		
6	NU	5	F	8	34 / 9	27 / 9
	AL	5	F	8		

Table 3. Elephant demography and trial counts. *Pairs*: 1 (SS = Sri Sayam, KW = Kaew), 2 (PT = Phrathida, LK = Luuk Khang), 3 (WL = Wanalee, JO = JoJo), 4 (UP = Umpang, KD = Khaw), 5 (PP = Phumphuang, PJ = Prajuab), 6 (NU = Neua Un, AL = Alina). *Pull-Train* indicates the number of trials needed for each elephant to pull in the table on their own in three consecutive trials. *Sim. Release* shows two numbers (/) per pair: the first number represents total successful trials out of the 40 total, while the second number represents successful trials in the final 10 (criterion). *Delay (Error)* shows two numbers (/) per individual: The first tells the number of trials needed for each elephant to successfully pull in the drawer in three consecutive trials of 25 s (criterion) before moving on to test trials, while the second number refers to the total number of errors made by each elephant before they reached this criterion.

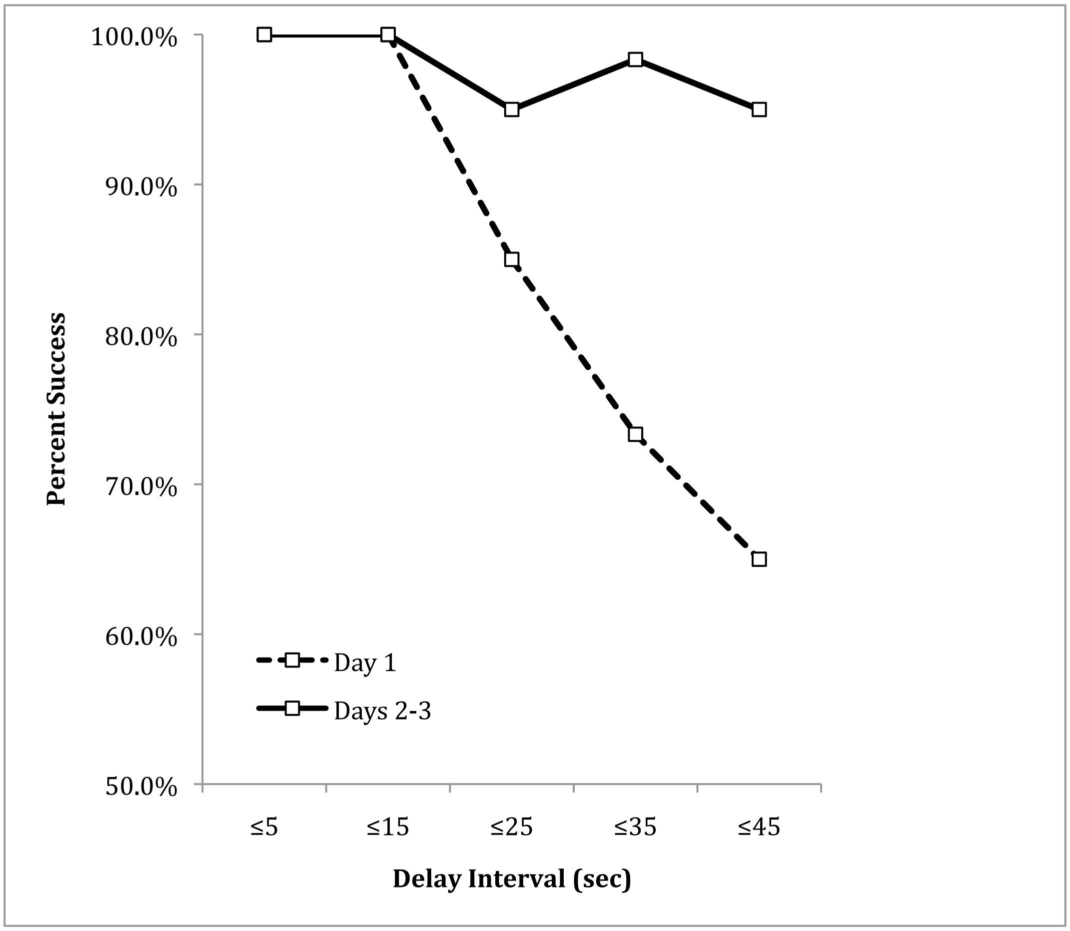

Figure 7. Combined success rate of all elephants across three days of delayed release trials. The dotted line indicates trial success rate during the first day of testing, while the solid line indicates trial success rate for days two and three combined. Each daily session consisted of a randomized set of 20 trials: 10 trials contained delay intervals from 1 – 25 s, and 10 trials contained delay intervals from 26 s – 45 s (each bin along the X-axis corresponds to a range of delay intervals). The first testing day was the elephants' first experience with any interval longer than 25 s.

In order to assess not only whether or not a pair succeeded in pulling in the table but whether or not the first-released elephant waited for the partner before pulling, pulling frequency over time (pulling rate) for each trial was determined. Each trial was divided into two time intervals. Interval 1 began when the first elephant arrived at one rope end and ended with the arrival of the second elephant to within reach of the other rope end. Interval 2 began with the arrival of the second elephant and ended when either the table was retrieved or the rope became unthreaded. The first-released elephant's rope pulling rate in each time interval was calculated to determine whether or not there was a significant difference in pulling rates depending on whether or not the partner was present. Inter-rater reliability of pulling rates was assessed through a Pearson's correlation between two raters' reported frequency per trial, which was highly significant (Interval 1: $r = 0.96$, $n = 67$, $P < 0.001$; Interval 2: $r = 0.87$, $n = 67$, $P < 0.001$). The data from five elephants were analyzed (i.e., the first elephant released in each of the pairs, except for one elephant (NU), which was excluded from these analyses for reasons explored in the discussion).

All five elephants pulled significantly more during interval 2, following the arrival of their partner, than during interval 1 as shown by analyzing each subject with one-tailed, Wilcoxon signed-ranks tests (each elephant is denoted by an italicized two-letter abbreviation, see Table 3 for full names): *SS*: $Z = -4.97$, $n = 51$, $P < 0.001$; *PT*: $Z = -5.03$, $n = 56$, $P < 0.001$; *WL*: $Z = -6.65$, $n = 60$, $P < 0.001$; *UP*: $Z = -5.20$, $n = 59$, $P < 0.001$; *PP*: $Z = -4.70$, $n = 53$, $P < 0.001$ (Figure 8). Each elephant was tested for 60 trials, but only trials with both an interval 1 and an interval 2 were included in the analysis (i.e., trials in which both elephants arrived at their respective rope ends at the same time did not have an interval 1 and thus were not included). The Wilcoxon signed-ranks test takes into account both the direction and the magnitude of the difference in pulling rates between the two intervals (Siegel and Castellan 1988). Because I was unable to differentiate between or interpret the quality of pulls when coding the videotapes, I conducted an additional analysis to investigate whether or not the significant difference between the two interval pulling rates remained when I ignored the number of pulls in each interval and just focused on whether or not an elephant pulled at all. This additional analysis by sign test thus conservatively rejects trials in which an elephant pulled (at least once) in both intervals, regardless of how often.

This additional analysis found that four of the five elephants, in a significant number of trials, *never* pulled until their partner had arrived (sign test for pulls vs. no pulls: *SS:* P = NS, *PT:* Z = -5.40, n = 56, P < 0.001; WL Z = -6.29, n = 60, P < 0.001; *UP*: Z = -4.58, n = 59, P < 0.001; *PP*: Z = -3.01, n = 53, P = 0.002).

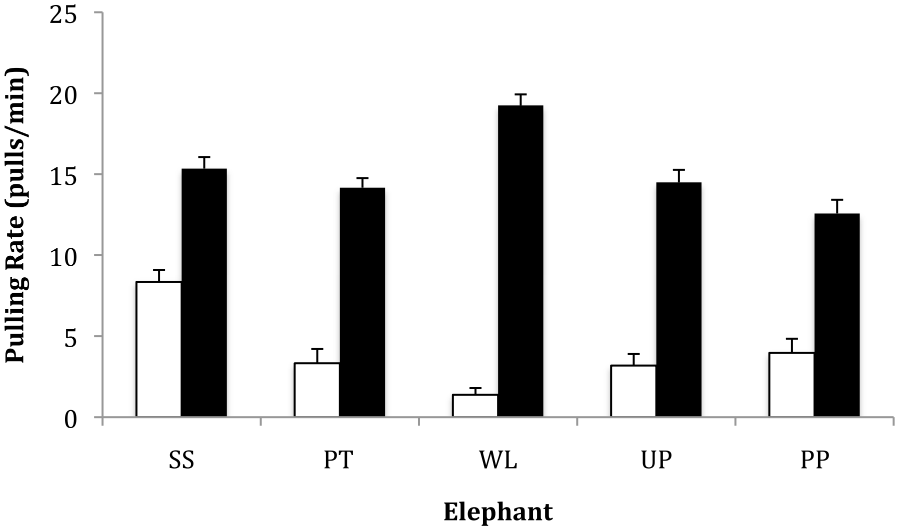

Figure 8. Pulling rate per minute of each individual elephant across all delayed release trials. White bars represent the pulling rates in interval 1, before arrival of the second elephant at the rope ends, while black bars represent the pulling rates in interval 2, when both elephants had reached the rope ends. Error bars represent + SEM.

<u>Prediction Evaluated</u>*:* Although the prediction for the delayed release condition was verified, and the elephants clearly waited for their partners before pulling, one possible explanation for their behavior (i.e., *why* they waited) is that they simply learned to coordinate their pulling with the arrival of their partner, rather than that they

understood how their partner's actions contributed to success. Thus, to further assess what they might have actually known about their partner's role in the task, we instituted a third condition.

Condition III: No-Rope Control

Prediction: If the elephants have learned only the contingency between their partners' presence and success, the first-released elephant should pull immediately after their partner arrives regardless of their partner's eventual action. If the elephants have learned both that their partners presence *and* actions (rope pulling) are necessary to successfully pull in the table, then the first-released elephant should only pull if the partner pulls as well.

Procedure and Results

In a subsequent control phase, only the rope end of the first-released elephant was available; the partner's rope was coiled at the base of the table but out of reach, thus making retrieval of the table impossible. Elephants were released simultaneously, and control trials alternated in a random order with an equal number of simultaneous release trials. All five elephants pulled significantly more often in trials when their partner had access to and pulled at the rope than when the partner lacked access to the rope and stood idle (Two-sample Kolmogorov-Smirnov (K-S) Test per subject, with a K-S Z-value reported: *SS*: $Z = 1.27$, $n = 10$, $P = 0.041$, one-tailed; *PT*: $Z = 2.24$, $n = 20$, $P < 0.001$; *WL:* $Z = 2.24$, $n = 20$, $P < 0.001$; *UP:* $Z = 2.24$, $n = 20$, $P < 0.001$; *PP*: $Z = 1.80$; $n = 20$, $P = 0.003$; Figure 9). In this analysis, there was no interval 1, so pulling rates were determined using interval 2 only (i.e., elephants were released simultaneously, so the analysis was based on the *focal* elephant's pulling rate after both elephants had arrived at the rope ends). Unlike in the previous condition, which used a paired-replicates design to assess pulling rate differences within trials (Siegel and Castellan 1988), this condition used a two-sample design comparing pulling rates across two different types of trials. A K-S test was chosen over a rank-order nonparametric statistic due to the uniformity of each sample and thus the large number of tied scores. These data indicate pulling rates close to or at zero when a partner's rope was unavailable, but normal pulling rates until success when the partner had access to the rope.

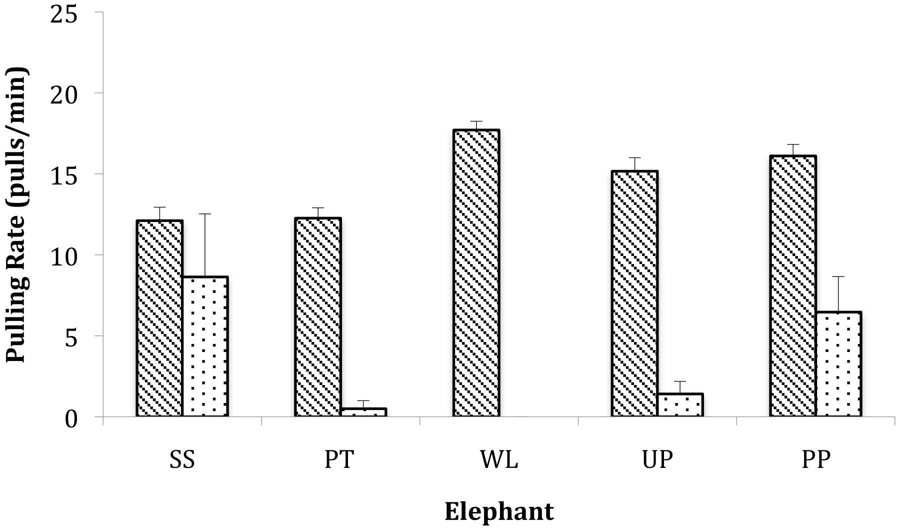

Figure 9. Pulling rate per minute of each individual elephant across the control condition. Dotted bars represent the pulling rates in control trials where the lead elephant had access to the rope but the partner's rope was placed out of reach. Diagonally hatched bars represent the simultaneous release trials (in which both individuals had access to the rope) that were randomized with control trials. Error bars represent + SEM.

Prediction Evaluated: It seems that the elephants demonstrated both a propensity to wait for partners before pulling in the task and recognition that success, or a need to pull, requires not only the partner's presence, but also its access to and handling of the rope. Yet, their behavior could still be explained in terms of a learned contingency related to the rope, specifically as it relates to feeling the rope tense when their partner grabs or pulls it. We discuss this further below.

Discussion

In this study, we instituted various experimental conditions to systematically investigate the potential cognitive underpinnings of elephant cooperative behavior. I noted above that each, subsequent condition was instituted to further test the elephants' potential understanding of their cooperative behavior, and that the results of each condition could not be too broadly interpreted. This was true primarily because the elephants' behavior, although remarkable, could have been explained at each individual level with learned contingencies.

The elephants were first trained to pull a single rope (*training)*, and then, in the first testing condition, were released together and simultaneously (*simultaneous release*). The elephants successfully pulled the two rope ends in a coordinated fashion in this first condition, but because the elephants arrived at the ropes at the same time, this "coordination" could be explained based on their previous training. In other words, the elephants could have simply learned that pulling the rope in front of them resulted in the arrival of a food reward. If they were merely employing this "see the rope, pull the rope" strategy based on their previous, explicit training, the presence or absence of their partner should be irrelevant. However, we felt that exposure to simultaneous release trials was necessary, even though not directly interpretable, because it gave substantial exposure to the elephants of a) the test apparatus with two rope ends, and b) trials with a simultaneously released partner. Thus, we instituted the *delayed release* condition to further assess the elephants' understanding of the task. I want to emphasize here that my use of the word "understanding" relates to the elephants' ability to succeed in conditions that were designed to be accomplishable only if the subjects recognized specific aspects of the task. In other words, we were primarily interested in whether or not the elephants could learn that both a partner's presence and actions were needed to complete the task. Although such learning may imply relatively complex cognition underlying the behavior, we may not be able to draw that conclusion definitively from this experiment.

In the *delayed release* condition, the elephants were not only successful in waiting for their partners' arrival before pulling, but four out of five of them *never* pulled (in a significant number of trials) until their partner arrived. This condition demonstrated the elephants' ability to wait for their partner (the fact that four out of five of them never pulled until the partner arrived suggests, at least, that the elephants recognized that pulling was not going to result in a food reward until the partner was present), but it did not demonstrate what the elephants had learned about their partners' role in the task. Perhaps the elephants were simply learning to pull as soon as their partner arrived (i.e., their partner's presence was needed to get the food).

Thus, we introduced a *no-rope control* condition, in which only the first-released elephant (in this condition, elephants were released simultaneously, but we focused on the individual who had, in previous conditions, been released first) had access to his/her rope end. All five elephants pulled significantly more often when their partner could help (i.e., in *simultaneous release* trials randomized with *no-rope control* trials) than when their partner was present but could not help (i.e., their rope end was unavailable). In conjunction with the previous condition, the elephants seemed to have learned about the <u>need for</u> and <u>actions of</u> their partners. But this condition too was unable to completely rule out a possible learned, task contingency – perhaps the elephants had learned to pull their rope only after they felt tension. This could potentially explain why the elephants waited without pulling when their partner was next to them (see Appendix B for further conditions).

Although Phrathida (PT) regularly picked up the rope only after her partner was released (demonstrating that she may have known, at least, that it was her partner that caused the rope to tense), all the other elephants regularly held the rope – without pulling – until the partner arrived. Even so, in *no-rope control* trials, four elephants retreated (i.e., returned to the starting point without prompting by their mahouts) either before or soon after their partners did in more trials – PT: 100%, WL: 50%, UP: 50%, PP: 60% of trials – than would be expected if these elephants were only waiting for tension in the rope. Thus, if these elephants had simply learned to pull the rope when it tensed, regardless of the partners' contribution, they should not have responded to their partner's retreat by retreating themselves, and should have waited instead for their mahout's end-of-trial command.

The most conservative interpretation of these results, then, is that the elephants may have learned to pull only when both a) the partner was present, and b) the rope tensed. In other words, the elephants may have paired the partner's presence with the rope tension but not necessarily learned that the relationship between the two was causal. This would explain both the elephants' waiting in *delayed release* trials, and their retreat without pulling in the *no-rope control* trials. This study, then, seems to have demonstrated that the elephants, at the very least, learned that a partner was needed to complete the task. Although these results do not allow me to directly interpret the elephants' understanding of cooperative partnership, they suggest that elephants are able to learn how a partner's role influences success. Thus, further testing is necessary to assess the cooperative behavior of elephants and whether or not they are able to differentiate between their partner's presence and their partner's specific actions.

It is important to note, however, that in a natural context, waiting behavior is quite common in elephants (Poole 1996; Moss et al. in press). Elephants often will wait for other family members before moving on from a watering hole or other location. Their waiting posture is alert but quiet, and is always in the context of one individual waiting the arrival or approach of others (e.g., Poole and Granli 2010). This is more a general social behavior than one naturally related to cooperation, but it is evidence that the waiting behavior of the elephants in an experimental context may not be related simply to a learned contingency of rope tension but instead to a natural behavior of waiting for other elephants before moving on (i.e., proceeding with the rope pull).

The aforementioned results only concern six of the 12 elephants, and only the first elephant in each pair. Due to constraints at the elephant facility, we could only work with one pair at a time for three weeks. To ensure that at least one individual per pair had sufficient time to learn the task, the second individual was not tested (i.e., released first in a trial) until the first elephant's testing was completed. This may have compromised the second elephant's ability to succeed for two reasons. First, this elephant may have been over-exposed to trials in which it was successful by pulling immediately upon arrival at the rope, which may have prevented it from learning patience. Second, the first elephant had usually not finished testing until the third week, leaving insufficient time for the second elephant to learn the task. Thus, none of the partner elephants except for one (JO discussed below) reached the 25 s waiting time criterion when subjected to delayed release as the first elephant.

<u>Alternative strategies</u>: We discussed previously that five of the six elephants released first were analyzed by pulling rates within trials. It speaks to the flexibility of elephant behavior that two highly successful individuals (the sixth elephant released first, and a second-released elephant, WL's partner, JO) could not be included in the pulling rate analysis due to their unconventional solutions to the task. The sixth elephant, NU, reached 97% success in *delayed release* trials by approaching her rope end and firmly placing one foot on it, thus preventing the rope from being pulled away when her partner arrived and pulled. She had been trained, as had all the other subjects, to first pull a single rope. She then completed the *simultaneous release* trials by pulling the rope with her partner, AL, not by standing on it. This technique was learned independently by NU in *delayed release* (she used trunk pulls consistently until the tenth trial of the first day when she used both her feet and her trunk; by the second day, she used her "standing on the rope" technique almost exclusively). This technique had the advantage of forcing her partner to do all the work to retrieve the table. A seventh elephant, Jojo (JO) reached 83% success on test trials, but did so by waiting for his partner's (WL) release at the release point rather than close to the table. This means that there was never an interval 1 for JO,

precluding his inclusion in our pulling rate analysis. The fact that three distinct strategies – 1) approach, wait, then pull (n = 5), 2) stand on rope and wait (n = 1), and 3) wait, approach and then pull (n = 1) – were employed by seven different subjects suggests a greater potential understanding of the partner's role in the task than might be suggested by a uniform learned task performance.

Because chimpanzees perform better in cooperation tasks when paired with tolerant partners (Melis et al. 2006), and bonobos (*P. paniscus*) perform better than chimpanzees overall because of greater food-related tolerance (Hare et al. 2007), we attempted in a final set of "tolerance trials" to further assess cooperative tendencies by determining if the degree of elephant cooperation varied with available food. During this final tolerance condition, two trials each of the following were randomized over six trials: 1) each bowl was baited as in test trials, with two half-ears of corn, or 2) one (or the other) bowl was baited with six half-ears of corn. In all trials across all elephants, however, there was never a failed cooperation attempt or an incidence of aggression between both individuals. We never could be sure whether or not elephants could tell before a trial began if food was available or not due to their general reliance on scent and sound over sight (Fowler and Mikota 2006). We were also unable to pair potentially intolerant partners due to safety and husbandry concerns, but the absence of aggression suggests high tolerance between the selected individuals. Although open conflict is relatively common in chimpanzee groups (de Waal 1982), it is relatively rare among elephants (Poole 1996), suggesting a greater tolerance within the latter's social relationships. It is important to note that elephants never conspicuously vocalized or glanced at their partners during trials; elephants are considered sophisticated vocal communicators (Poole and Moss 2008), but in this task, it is more likely elephants used other auditory and olfactory cues – especially the sound and smell of the partner's approach – to successfully coordinate their behavior. Elephants also communicate infrasonically (Payne et al. 1986), but such communication would not be expected over such short distances. We did not record infrasonic communication for this reason, as well as for the fact that we would not have been able to easily localize the signal from two elephants at a facility where 50 elephants were located within a short distance from the experiment site.

In similar cooperation studies conducted on both non-primates and primates, the animals' cooperative behavior varied markedly. In fact, only two studies have been conducted to look specifically at the potential cognition underlying cooperation in non-primates. In a task similar to ours and also based on Hirata and Fuwa (2007), rooks (*Corvus frugilegus*) pulled the two rope ends as a pair but failed to wait for each other in the *delayed release* condition, suggesting a lack of task contingency learning and recognition of the need for a partner (Seed et al. 2008). Recent experiments with hyenas (*Crucuta crocuta*: Drea and Carter 2009) and capuchin monkeys (*Cebus apella*: Mendres and de Waal 2000) used variations of the single rope task and found that both species recognized the need for a partner, but it was unclear whether or not they also recognized their partners' behavioral contribution. Chimpanzees, on the other hand, have demonstrated clear knowledge of both a partner's role and contribution (Melis et al. 2006; Hare et al. 2007; Hirata and Fuwa 2007). Our own study shows that elephants not only a) cooperate successfully in a coordinated pulling task but also b) recognize the need for a partner by waiting if the partner is delayed. Elephants perhaps also c) understand the necessity of their partner's actions, given that they discriminate between a partner with or without rope access. Particularly striking was the speed with which elephants mastered the task contingencies, and the fact that some developed unanticipated alternative strategies. Although various aspects of proximate-level cooperation remain to be tested, the present study suggests that the elephant's abilities may be close to or on a par with that of the apes. Greater empirical attention to elephants may thus provide important insight into the evolution of complex cooperation skills.

General Discussion

Consolation and Cooperation Revisited

In this dissertation, I conducted two studies at two separate field sites in the Kingdom of Thailand to investigate the cognition underlying elephant social behavior. The first study focused on an investigation of consolation behavior in a population of semi-free elephants at a sanctuary. This study used ethological techniques, originally designed for conflict resolution research in primates (de Waal and van Roosmalen 1979; de Waal and Yoshihara 1983), to investigate the reactions of bystanders to distress in nearby conspecifics. We demonstrated that bystanders affiliated with these conspecifics, and each other, more often than not following a sign of distress. In addition, elephants seemed to show a level of emotional contagion both in their vocal reaction and their physical displays in response to distress. These results, obtained by following thirty years of accepted observational protocol (for a review, see Aureli and de Waal 2000), suggest that elephants are indeed good candidates for further research on empathy in socially complex animals. These results fit well with the "social constraints" hypothesis outlined by de Waal and Aureli (1996), which suggests that consolation, a relatively rare capacity in the animal kingdom, should be unique to egalitarian species with flexible hierarchies and cooperative tendencies. In addition, the "social cognition" hypothesis indicates that the demonstration of consolation may be predicated on the prevalence of other cognitively complex behaviors or capacities in a given species, including mirror self-recognition and targeted helping behavior. The elephant is a large-brained, socially complex mammal that forms large social groups (e.g., Payne 2003), follows often life-long matriarchic leaders (e.g., Moss 1988), has demonstrated mirror self-recognition (Plotnik et al. 2006), and displays targeted helping and other-regarding behavior (e.g., Poole 1996; Douglas-Hamilton et al. 2006; Bates et al. 2008). Thus, our demonstration of consolation in elephants makes sense in light of both of these hypotheses.

Our second study investigated the potential cognitive mechanisms underlying cooperative behavior in elephants. This research was conducted at a second site where elephants could be easily paired and given a cooperative-pulling task. Elephants demonstrated a propensity to cooperate by pulling two rope ends - an elephant was needed at each end - in tandem to retrieve a food reward. In addition, elephants both waited for partners when their arrival at the rope was delayed, and chose not to pull if their partners were unable to do so. These results seem to demonstrate, at least, an ability to learn about the contingencies involved in partner-driven cooperative tasks, and possibly an understanding of partner roles in coordinated behavior. The elephant's performance seems to be on a level similar to that of chimpanzees, and above that of other non-primates. These results, too, make sense in light of the aforementioned hypotheses.

The link between consolation and cooperation may also relate to the self-other distinction and empathy. Gallup (1982; 1983) hypothesized that mirror self-recognition, as an indicator of self-awareness, may be a demonstration of the self-other distinction (i.e., an animal's cognitive ability to distinguish itself from conspecifics) needed to respond empathically to others and evident in empathic perspective taking (i.e., targeted helping - see Bischof-Köhler 1991). But whether or not this higher level self-other distinction demonstrated through MSR is tied through perspective taking specifically with an empathic component or not is still unknown; in fact, this self-other distinction may be tied instead to perspective taking independent of empathy (i.e., knowledge about what other's see or know), which has been demonstrated in a range of species (e.g., chimpanzees: Hare et al. 2001; Call and Tomasello 2008; corvids: Emery and Clayton 2004; dogs: Hare and Tomasello 2005). The first, recent demonstration of MSR in a corvid species, the magpie (*Pica pica* – Prior et al. 2008) supports this possibility; perhaps, the self-other distinction in mirror-understanding species relates instead to the evolution of general perspective taking independent of empathy. In this way, it is possible that MSR would be evident in a range of perspective-taking species, and thus should be expanded, systematically, to include a wider range of these species.

Empathic perspective taking has already been discussed here in relation to targeted helping and our demonstration of mirror self-recognition in elephants, but the form lacking an empathic component has not. Although our cooperation study did not test directly for general perspective taking abilities in elephants, our findings suggest that elephants may have knowledge of their partner's role in cooperative tasks and that elephants act patiently and deliberately when not trained to do so. Their behavior in this task suggests that studies on perspective taking in elephants would be a logical progression for future research. In addition, the elephants' demonstration of mirror self-recognition, consolation and cooperation seems to relate to their complex natural social behavior and attention to others in empathetic contexts.

Limitations

Most of the recent interest in elephant cognition research has focused on experiments with truly wild elephants (e.g., Bates et al. 2007; 2008), or on small groups in zoological settings (e.g., Plotnik et al. 2006; Irie-Sugimoto et al. 2007; 2008; 2009). Earlier attempts at controlled experiments with larger populations of tame elephants in range countries faced limitations on controls (e.g., Nissani et al. 2005; Nissani 2006). For our consolation study, we chose a site that would allow us to work with a relatively large group of elephants in a safe environment and, at least in part, to observe relatively natural elephant behavior. The Elephant Nature Park is a sanctuary in which elephants were relatively free to form groups, and to actively socialize with one another. This coupled with the fact that the elephants were on a small piece of land on which we could freely observe their behavior made the Park an ideal location to conduct this project. We recognize that these pseudo-family groups were made up of primarily unrelated individuals, many of whom had spent relatively little time with one another in the course of their lifetimes, and that the groups were actively separated from one another to prevent conflict. This is, of course, then not a true representation of natural elephant behavior or social dynamics. Nonetheless, the fact that the elephants still demonstrated consolatory behavior in such a setting suggests both substantial flexibility in elephant social behavior, and a strong capacity for consolation in natural elephant behavior. After all, if there were any situation where consolation or empathy would be least likely to occur, it would be in a group of unrelated individuals that had only recently become socially bonded to one another.

In our cooperation study, we were able to work with tame elephants that were motivated to perform in our experiments, but we paired our elephants for the task based on their previous relationships and their overall docility. This, for the safety of all involved in the project on-site, was required. However, it limited our ability to assess the variability in cooperative tendencies based on relationship quality (i.e., tolerance - Melis et al. 2006; Hare et al. 2007). The danger and difficulty of working with a forest-dwelling social mammal of the Asian elephant's intelligence and size makes expanding such work to wild populations or avoiding experimental limitations increasingly difficult, but we hope to collaborate with colleagues to formulate plans for continuing this work on larger populations elsewhere.

Convergent Cognitive Evolution

Studies of cognitive complexity in intelligent species aim to better understand the cognitive underpinnings of social behavior across taxa, and, along the same lines, to recognize the common factors affecting convergent cognitive evolution in distantly related species. Elephants are interesting because, like dolphins, they exhibit social complexity on a par with that of the Great Apes, and in some cases (discussed previously), greater than that of monkeys (Gallup 1983; de Waal 1996; Poole 1996; Bates et al. 2008). This is even more peculiar considering that the approximate time of evolutionary divergence from a common ancestor of humans and the Great Apes (4-6 myo – e.g., Patterson et al. 2006; Hobolth et al. 2007) and the Great Apes and old world monkeys (35-30 myo - Steiper et al. 2004) is far less than the ~ 103 myo divergence of Great Apes and elephants from a shared common ancestor (Murphy et al. 2001). Although much of the variation and connectivity within and between Great Ape and monkey behavior is explained through cladistic relationships, this is most likely not the case for similarities in behavior between primates and non-primates, including dolphins, corvids and elephants (Marino 2002; Emery and Clayton 2004; Poole and Moss 2008; Byrne et al. 2009), with high levels of phylogenetic divergence. In these species, we see similarities in behavior such as complex cooperation, consolation, problem-solving skills, mirror self-recognition and, in some species, the capacity for cognitive empathy. In addition, we see similarities in brain functionality, despite differences in brain morphology (e.g., Shoshani 1998; Shoshani et al. 2006; Marino et al. 2007; Hakeem et al. 2009). The resulting cognitive complexity across these distantly related species suggests commonalities in the environmental pressures under which these species evolved. Unfortunately, we only have evidence for similarities in these different species' behavior; we know virtually nothing about the underlying pressures driving convergent cognitive evolution (Marino 2002). Most likely, it is in fact rooted in the need for complex sociality– a common factor across all of these species – that led to similar psychological capacities. Clearly, much more research in these non-primate species is needed to gain a better understanding of cognitive evolution in general.

A Note on Conservation

The Asian elephant is listed on the IUCN (the International Union for the Conservation of Nature) Red List as “Endangered” (March 2010), just two levels below “Extinct in the Wild.” Estimates put wild Asian elephant numbers at between 37,000-50,000 as of 1997, and numbers within Thailand alone between 1,200-1,500 (Lair 1997). Human-elephant conflict – i.e., the pressures of human encroachment, poaching, resource conflict, elephant habitat destruction, and elephant crop raiding (Lair 1997; Zhang and Wang 2003) on both species – is a serious concern throughout Asia, with various agencies collaborating to develop new techniques for reconciling human and elephant needs. But as human population numbers continue to increase, wild elephant numbers will inevitably decline further. As scientists that work both in range countries and in the laboratory with animal species that face serious threat of extinction in the wild, we are obligated to use our research to educate the public. This comes through the implementation of conservation programs that focus on the social and cognitive complexity of the animals in general and teach better understanding of how this complexity relates to the elephant’s natural behavior. Our study of elephant cognition, for instance, has important implications for understanding the ecological needs of elephants in the wild. Hopefully, it provides important discussion points for assessing how best to approach human-elephant conflict concerns by attempting to actively seek conflict resolution through a scientific understanding of an animal’s behavior. Through future studies on elephant cognition with the combination of both ethological and experimental procedures, we hope to contribute both to a further understanding of the evolution of complex social behavior and the convergence of complex cognition across species, as well as to the international effort to conserve this remarkable species in the wild.

References

Akçay E., et al. 2009. A theory for the evolution of other-regard integrating proximate and ultimate perspectives. *Proceedings of the National Academy of Sciences U.S.A.* 106:19061-19066.

Altmann J. 1974. Observational study of behaviour: sampling methods. *Behaviour* 49:227-265.

Arnold K., Whiten A. 2001. Post-conflict behaviour of whild chimpanzees (*Pan troglodytes schweinfurthii)* in the Budongo Forest, Uganda. *Behaviour* 138:649-690.

Aureli F. 1997. Post-conflict anxiety in nonhuman primates: the mediating role of emotion in conflict resolution. *Aggressive Behavior* 23:315-328.

Aureli F., Cords M., van Schaik C. P. 2002. Conflict resolution following aggression in gregarious animals: a predictive framework. *Animal Behaviour* 63:1-19.

Aureli F., de Waal F. B. M. 2000. *Natural Conflict Resolution*. Berkeley (CA): University of California Press.

Axelrod R., et al. 2006. Evolution of cooperation among tumor cells. *Proceedings of the National Academy of Sciences U.S.A.* 103:13474-13479.

Axelrod R., Hamilton W. D. 1981. The evolution of cooperation. *Science* 211:1390-1396.

Bates L. A., Byrne R. W. 2007. Creative or created: using anecdotes to investigate animal cognition. *Methods* 42:12-21.

Bates L. A., Lee P. C., Njiraini N., Poole J. H., Sayialel K., Sayialel S., Moss C. J., Byrne R. W. 2008. Do elephants show empathy? *Journal of Consciousness Studies* 15:204-225.

Bates L. A., Sayialel K. N., Njiraini N. W., Moss C. J., Poole J. H., Byrne R. W. 2007. Elephants classify human ethnic groups by odor and garment color. *Current Biology* 17:1938-1942.

Bates L. A., Sayialel K. N., Njiraini N. W., Poole J. H., Moss C. J., Byrne R. W. 2008. African elephants have expectations about the locations of out-of-site family members. *Biology Letters* 4:34-36.

Bischof-Köhler D. 1991. The development of empathy in infants. Pages 245-273 in *Infant Development: Perspectives from German Speaking Countries*, edited by M. E. Lamb et al. London: Lawrence Erlbaum.

Boesch C. 1994. Cooperative hunting in wild chimpanzees. *Animal Behaviour* 48:653-667.

Boesch C., Boesch-Achermann H. 2000. *The Chimpanzees of the Tai Forest*. Oxford: Oxford University Press.

Bradshaw G. A., Schore A. N. 2007. How elephants are opening doors: developmental neuroethology, attachment and social context. *Ethology* 113:426-436.

Brosnan S. F., de Waal F. B. M. 2002. A proximate perspective on reciprocal altruism. *Human Nature* 13:129-152.

Brosnan S. F., de Waal F. B. M. 2003. Monkeys reject unequal pay. *Nature* 425:297-299.

Brown J. L. 1983. Cooperation: A biologist's dilemma. *Advanced Study of Behavior* 13:1-37.

Brown J. L. 2000. Reproductive endocrine monitoring of elephants: An essential tool for assisting captive management. *Zoo Biology* 19:347-367.

Brown J. L., Wemmer C. M., Lehnhardt J. 1995. Urinary cortisol analyses for monitoring adrenal activity in elephants. *Zoo Biology* 13:533-542.

Byrne R. W., Bates L. A., Moss C. J. 2009. Elephant cognition in primate perspective. *Comparative Cognition and Behavior Reviews* 4:1-15.

Caldwell M. C., Caldwell D. K. 1966. Epimeletic (care-giving) behavior in Cetacea. Pages 755-789 in *Whales, Dolphins, and Porpoises*, edited by K. S. Norris. Berkeley: University of California Press.

Call J., Aureli F., de Waal F. B. M. 2002. Postconflict third party affiliation in stumptailed macaques. *Animal Behaviour* 63:209-216.

Call J., Tomasello M. 2008. Does the chimpanzee have a theory of mind? 30 years later. *Trends in Cognitive Sciences*. 12:187-192.

Chalmeau R. 1994. Do chimpanzees cooperate in a learning task? *Primates* 35:385-392.

Chalmeau R., Gallo A. 1996. What chimpanzees (*Pan troglodytes*) learn in a cooperative task. *Primates* 37:39-47.

Chalmeau R., Visalberghi E., Gallo A. 1997. Capuchin monkeys (*Cebus apella*) fail to understand a cooperative task. *Animal Behaviour* 54:1215-1225.

Cheney D. L., Seyfarth R. M. 1989. Redirected aggression and reconciliation among vervet monkeys (*Cercopithecus aethiops*). *Behaviour* 110:258-275.

Chevalier-Skolnikoff S., Liska J. 1993. Tool use by wild and captive elephants. *Animal Behaviour* 46:209-219.

Cools A. K. A., Van Hourt A. J. M., Nelissen M. H. J. 2008. Canine reconciliation and third-party-initiated postconflict affiliation: Do peacemaking social mechanisms in dogs rival those of higher primates? *Ethology* 114:53-63.

Cordoni G., Palagi E. 2008. Reconciliation in wolves (*Canis lupus*): new evidence for a comparative perspective. *Ethology* 114:298-308.

Cordoni G., Palagi E., Borgognini Tarli S. M. 2004. Reconciliation and consolation in captive lowland gorillas (*Gorilla gorilla gorilla*). *Folia Primatologica* 75:79.

Crawford M. P. 1937. The cooperative solving of problems by young chimpanzees. *Comparative Psychology Monographs* 14:1-88.

de Waal F. B. M. 1982. *Chimpanzee Politics: Power and Sex Among Apes*. Baltimore: Johns Hopkins University Press.

de Waal F. B. M. 1989. Food sharing and reciprocal obligations among chimpanzees. *Journal of Human Evolution* 18:433-459.

de Waal F. B. M. 1996. *Good Natured*. Cambridge: Harvard University Press.

de Waal F. B. M. 1997. The chimpanzee's service economy: food for grooming. *Evolution of Human Behavior* 18:375-386.

de Waal F. B. M. 2001. *The Ape and the Sushi Master*. New York: Basic Books.

de Waal F. B. M. 2003. On the possibility of animal empathy. Pages 379-399 in *Feelings and Emotions: The Amsterdam Symposium*, edited by T. Manstead et al. Cambridge: Cambridge University Press.

de Waal F. B. M. 2008. Putting the altruism back into altruism: the evolution of empathy. *Annual Review of Psychology* 59:4.1-4.22.

de Waal F. B. M., Aureli F. 1996. Consolation, reconciliation, and a possible cognitive difference between macaques and chimpanzees. Pages 80-110 in *Reaching Into Thought: The Minds of the Great Apes*, edited by A. E. Russon, K. A. Bard and S. T. Parker. Cambridge (UK): Cambridge University Press.

de Waal F. B.M., van Roosmalen A. 1979. Reconciliation and consolation among chimpanzees. *Behavioral Ecology and Sociobiology* 5:55-66.

de Waal F. B. M., Yoshihara D. 1983. Reconciliation and redirected affection in rhesus monkeys. *Behaviour* 85:224-241.

Douglas-Hamilton I., Bhalla S., Wittemyer G., Vollrath F. 2006. Behavioural reactions of elephants towards a dying and deceased matriarch. *Applied Animal Behavior Science* 100:87-102.

Douglas-Hamilton I., Douglas-Hamilton O. 1975. *Among the Elephants*. New York: Viking Press.

Douglas-Hamilton I., Douglas-Hamilton O. 1992. *Battle for the Elephants*. New York: Viking Adult.

Drea C. M., Carter A. N. 2009. Cooperative problem solving in a social carnivore. *Animal Behaviour* 78:967-977.

Dugatkin L. A. 1997. *Cooperation Among Animals: An Evolutionary Perspective*. New York: Oxford University Press.

Eisenberg N. 2000. Emotion, regulation, and moral development. *Annual Review of Psychology* 51:665-697.

Eisenberg N., Mussen P. H. 1989. *The Roots of Prosocial Behavior in Children*. Cambridge: Cambridge University Press.

Emery N. J., Clayton N. S. 2004. The mentality of crows: convergent evolution of intelligence in corvids and apes. *Science* 306:1903-1907.

Fehr E., Fischbacher U. 2003. The nature of human altruism. *Nature* 425:785-791.

Fowler M. E., Mikota S. M. 2006. *Biology, Medicine, and Surgery of Elephants*. Ames (IA): Blackwell Publishing.

Fraser O. N., Stahl D., Aureli F. 2008. Stress reduction through consolation in chimpanzees. *Proceedings of the National Academy of Sciences U.S.A*. 105:8557-8562.

Gadagkar R. 1997. *Survival Strategies: Cooperation and Conflict in Animal Societies*. Cambridge: Harvard University Press.

Gallup Jr. G. G. 1970. Chimpanzees: self-recognition. *Science* 167:86-87.

Gallup Jr. G. G. 1982. Self-awareness and the emergence of mind in primates. *American Journal of Primatology* 2:237-248.

Gallup Jr. G. G. 1983. Toward a comparative psychology of mind. Pages 473-510 in *Animal Cognition and Behavior*, edited by R.L. Mellgren. New York: North-Holland.

Goodall J. 1968. The behaviour of free-living chimpanzees in the Gombe Stream Reserve. *Animal Behaviour Monographs* 1:161-311.

Goodall J. 1986. *The Chimpanzees of Gombe*. Cambridge (MA): Harvard University Press.

Goodall J. 1990. *Through a Window: My Thirty Years with the Chimpanzees of Gombe*. Boston: Houghton Mifflin.

Gordon J. A. 1966. Elephants do think. *African Wildlife* 20:75-79.

Griffin D. 1976. *Question of Animal Awareness*. New York: Rockefeller University Press.

Hakeem A. Y., Sherwood C. C., Bonar C. J., Butti C., Hof P. R., Allman J. M. 2009. Von Economo neurons in the elephant brain. *The Anatomical Record* 292:242-248.

Hammerstein P. 2003. Why is reciprocity so rare in social animals? A protestant appeal. Pages 83-94 in *Genetic and Cultural Evolution of Cooperation*, edited by P. Hammerstein. Boston: MIT Press.

Harcourt A. H., de Waal F. B. M. 1992. *Coalitions and Alliances in Humans and Other Animals*. Oxford: Oxford University Press.

Hare B., Call J., Tomasello M. 2001. Do chimpanzees know what conspecifics know? *Animal Behaviour* 61:139-151.

Hare B., Melis A. P., Woods V., Hastings S., Wrangham R. 2007. Tolerance allows bonobos to outperform chimpanzees on a cooperative task. *Current Biology* 17:619-623.

Hare B., Tomasello M. 2005. Human-like social skills in dogs? *Trends in Cognitive Sciences* 9:439-444.

Hart B. L., Hart L. A., McCoy M., Sarath C. R. 2001. Cognitive behaviour in Asian elephants: use and modification of branches for fly switching. *Animal Behaviour* 62:839-847.

Hart B. L., Hart L. A., Pinter-Wollman N. 2008. Large brains and cognition: where do elephants fit in? *Neuroscience and Biobehavioral Reviews* 32:86-98.

Hatfield E., Cacioppo J. T., Rapson R. L. 1994. *Emotional Contagion*. Cambridge (UK): Cambridge University Press.

Hauser M. D., Santos L. R., Spaepen G. M., Pearson H. E. 2002. Problem solving, inhibition and domain-specific experience: experiments on cotton-top tamarins, *Saguinus oedipus*. *Animal Behaviour* 64:387-396.

Hirata S., Fuwa K. 2007. Chimpanzees (*Pan troglodytes*) learn to act with other individuals in a cooperative task. *Primates* 48:13-21.

Hobolth A., Christensen O. F., Mailund T., Schierup M. H. 2007. Genomic relationships and speciation times of human, chimpanzee, and gorilla inferred from a coalescent hidden Markov model. *PLoS Genetics* 3:e7.

Horner V., Whiten A., Flynn E., de Waal F. B. M. 2006. Faithful replication of foraging techniques along cultural transmission chains by chimpanzees and children. *Proceedings of the National Academy of Sciences U.S.A*. 103:13878-13883.

Irie N., Hasegawa T. 2009. Elephant psychology: What we know and what we would like to know. *Japanese Psychological Research* 51:177-181.

Irie-Sugimoto N., Kobayashi T., Sato T., Hasegawa T. 2007. Evidence of means-end behavior in Asian elephants (*Elephas maximus*). *Animal Cognition* 11:1435-1441.

Irie-Sugimoto N., Kobayashi T., Sato T., Hasegawa T. 2008. Relative quantity judgment by Asian elephants (*Elephas maximus*). *Animal Cognition* 12:193-199.

Kappeler P. M., van Schaik C. P. 2006. *Cooperation in Primates and Humans*. Berlin: Springer-Verlag.

Koski S. E., Sterck E. H. M. 2007. Triadic postconflict affiliation in captive chimpanzees: Does consolation console? *Animal Behaviour* 73:133-142.

Krützen M., Mann J., Heithaus M. R., Connor R. C., Bejder L., Sherwin W. B. 2005. Cultural transmission of tool use in bottlenose dolphins. *Proceedings of the National Academy of Sciences U.S.A*. 102:8939-8943.

Lair R. C. 1997. *Gone Astray: The Care and Management of the Asian Elephant in Domesticity*. Rome: Food and Agriculture Organization of the United Nations.

Langbauer Jr. W. R. 2000. Elephant communication. *Zoo Biology* 19:425-445.

Langford D. J. et al. 2006. Social modulation of pain as evidence for empathy in mice. *Science* 312:1967-1970.

Lee P. C. 1987. Allomothering among African elephants. *Animal Behaviour* 35:278-291.

Lee P. C. 1989. Family structure, communal care and female reproductive effort. Pages 323-340 in *Comparative Sociobiology: The Behavioural Ecology of Humans and Other Mammals*, edited by V. Standen and R. A. Foley. Oxford: Blackwell Scientific Publications.

Marino L. 2002. Convergence of complex cognitive abilities in cetaceans and primates. *Brain, Behavior and Evolution* 59:21-32.

Markowitz H. 1982. *Behavioral Enrichment in the Zoo*. New York: Van Nostrand.

Marino L., et al. 2007. Cetaceans have complex brains for complex cognition. *PLoS Biology* 5:e139.

McComb K., Baker L., Moss C. J. 2006. African elephants show high levels of interest in the skulls and ivory of their own species. *Biology Letters* 2:26-28.

McComb K., Moss C., Sayialel S., Baker L. Unusually extensive networks of vocal recognition in African elephants. *Animal Behaviour* 59:1103-1109.

McGrew W. C. 1992. *Chimpanzee Material Culture: Implications for Human Evolution*. Cambridge (UK): Cambridge University Press.

Melis A., Hare B., Tomasello M. 2006. Chimpanzees recruit the best collaborators. *Science* 311:1297-1300.

Melis A., Hare B., Tomasello M. 2006. Engineering cooperation in chimpanzees: tolerance constraints on cooperation. *Animal Behaviour* 72:275-286.

Mendres K. A., de Waal F. B. M. 2000. Capuchins do cooperate: the advantage of an intuitive task. *Animal Behaviour* 60:523-529.

Mesterton-Gibbons M., Dugatkin L. A. 1992. Cooperation among unrelated individuals: evolutionary factors. *Quarterly Review of Biology* 67:267-281.

Moss C. J. 1988. *Elephant Memories*. Chicago: University of Chicago.

Moss C. J., Croze H. J., Lee P. C. in press. *The Amboseli Elephants: A Long-Term Perspective on a Long-Lived Mammal*. Chicago: Chiacgo University Press.

Moss C. J., Poole J. H. 1983. Relationships and social structure of African elephants. Pages 315-325 in *Primate Social Relationships: An Integrated Approach*, edited by R. A. Hinde. Oxford: Blackwell Scientific Publications.

Mulcahy N. J., Call J. 2006. Apes save tools for future use. *Science* 312:1038-1040.

Murphy C. J., Kern T. J., Howland H. C. 1992. Refractive state, corneal curvature, accommodative range and ocular anatomy of the Asian elephant (Elephas maximus). *Vision Research* 32:2013-2021.

Murphy W. J., Eizirik E., O'Brien S., Madsen O., Scally M., Douady C. J., et al. 2001. Resolution of the early placental mammal radiation using Bayesian phylogenetics. *Science* 294:2348-2351.

Nair S., Balakrishnan R., Seelamantula C. S., Sukumar R. 2009. Vocalizations of wild Asian elephants (Elephas maximus): Structural classification and social context. *Journal of the Acoustical Society of America* 126:2768-2778.

Nissani M. 2004. Theory of mind and insight in chimpanzees, elephants, and other animals? Pages 227-262 in *Comparative Vertebrate Cognition: Are Primates Superior to Non-Primates?* Edited by L. J. Rogers and G. T. Kaplan. Berlin: Springer.

Nissani M. 2006. Do Asian elephants (Elephas maximus) apply causal reasoning to tool-use tasks? *Journal of Experimental Psychology: Animal Behaviour Processes* 32:91-96.

Nissani M., Hoefler-Nissani D., Tin Lay U., Wan Htun U. 2005. Simultaneous visual discrimination in Asian elephants. *Journal of the Experimental Analysis of Behavior* 83:15-29.

Noë R. 2006. Cooperation experiments: coordination through communication versus acting apart together. *Animal Behaviour* 71:1-18.

Olson D. 2004. *Elephant Husbandry Resource Guide*. Lawrence (KS): Allen Press.

Osvath M. 2009. Spontaneous planning for future stone throwing by a male chimpanzee. *Current Biology* 19:R190-R191.

Packer C., Gilbert D. A., Pusey A. E., O'Brien S. J. 1991. A molecular genetic analysis of kinship and cooperation in African lions. *Nature* 351:562-565.

Palagi E., Cordoni G. 2009. Postconflict third-party affiliation in *Canis lupus*: do wolves share similarities with the great apes? *Animal Behaviour* 78:979-986.

Palagi E., Cordoni G., Tarli S. B. 2006. Possible roles of consolation in captive chimpanzees (*Pan troglodytes*). *American Journal of Physical Anthropology* 129:105-11.

Palagi E., Paoli T., Borgognini T. S. 2004. Reconciliation and consolation in captive bonobos (*Pan paniscus*). *American Journal of Primatology* 62:15-30.

Parr L. A., de Waal F. B. M. 1999. Visual kin recognition in chimpanzees. *Nature* 399:647-648.

Patterson N., Richter D. J., Gnerre S., Lander E. S., Reich D. 2006. Genetic evidence for complex speciation of human and chimpanzees. *Nature* 441:1103-1108.

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

Payne K., Langbauer Jr. W. R., Thomas E. 1986. Infrasonic calls of the Asian elephant (Elephas maximus). *Behavioral Ecology and Sociobiology* 18:297-301.

Plotnik J. M., de Waal F. B. M., Moore D., Reiss D. 2009. Self-recognition in the Asian elephant and future directions for cognitive research with elephants in zoological settings. *Zoo Biology* DOI:10.1002/zoo.20257.

Plotnik J. M., de Waal F. B. M., Reiss D. 2006. Self-recognition in an Asian elephant. *Proceedings of the National Academy of Sciences U.S.A.* 103:17053-17057.

Poole J. 1996. *Coming of Age with Elephants*. New York: Hyperion Press.

Poole J. 1999. Signals and assessment in African elephants: evidence from playback experiments. *Animal Behaviour* 58:185-193.

Poole J., Granli P. 2010. Waiting. *ElephantVoicess Gestures Database*. http://www.elephantvoices.org/elephantvoices-gestures-database.html?vocalsTask=vocalsDetails&catid=39&vocalsId=113. (Accessed 5 April 2010).

Poole J. H., Moss C. J. 2008. Elephant sociality and complexity: The scientific evidence. Pages 69-98 in *Elephants and Ethics*, edited by C. Wemmer and C. A. Christen. Baltimore: Johns Hopkins University Press.

Poole J., Payne K., Langbauer Jr. W. R., Moss C. J. 1988. The social contexts of some very low frequency calls of African elephants. *Behavioral Ecology and Sociobiology* 22:385-392.

Povinelli D. J., O'Neill D. K. 2000. Do chimpanzees use their gestures to instruct each other? Pages 459-487 in *Understanding Other Minds*, edited by S. Baron-Cohen, H. Tager-Flusberg and D. J. Cohen. Oxford: Oxford University Press.

Preston S. D., de Waal F. B. M. 2002. Empathy: its ultimate and proximate bases. *Behavioral and Brain Sciences* 25:1-72.

Prior H., Schwartz A., Güntürkün O. 2008. Mirror-induced behavior in the magpie (*Pica pica*): Evidence of self-recognition. *PLoS Biology* 6:e202.

Reiss D., Marino L. 2001. Mirror self-recognition in the bottlenose dolphin: a case of cognitive convergence. *Proceedings of the National Academy of Sciences U.S.A.* 98:5937-5942.

Rheingold H. L. 1982. Little children's participation in the work of adults, a nascent prosocial behavior. *Child Development* 53:114-125.

Rensch B. 1957. The intelligence of elephants. *Scientific American* 196:44-49.

Roca A. L., Georgiadis N., Pecon-Slattery J., O'Brien S. J. 2001. Genetic evidence for two species of elephant in Africa. *Science* 293:1473-1477.

Rochat P. 2003. Five levels of self-awareness as they unfold early in life. *Consciousness and Cognition* 12:717-731.

Romanes G. J. 1881. *Animal Intelligence*. London (UK): Kegan Paul.

Romero T., de Waal F. B. M. in press. Chimpanzee (*Pan troglodytes*) consolation behavior: Third party identity as a window on possible function. *Journal of Comparative Psychology*.

Schino G. 1998. Reconciliation in domestic goats. *Behaviour* 135:343-356.

Schulte B. A. 2000. Social structure and helping behavior in captive elephants. *Zoo Biology* 19:447-459.

Seed A. M., Clayton N.S., Emery N. J. 2007. Postconflict third-party affiliation in rooks, *Corvus frugilegus*. *Current Biology* 17:152-158.

Seed A. M., Clayton N. S., Emery N. J. 2008. Cooperative problem solving in rooks (*Corvus frugilegus*). *Proceedings of the Royal Society of London B*. 275:1421-1429.

Seidensticker, J., Lumpkin, S. 1990 (eds). *Asian Elephants: John F. Eisenberg, George M. McKay, and John Seidensticker*. Washington: Friends of the National Zoo and the National Zoological Park.

Shettleworth S. J. 1998. *Cognition, Evolution and Behavior*. Oxford (UK): Oxford University Press.

Shoshani J. 1998. Understanding proboscidean evolution: a formidable task. *Trends in Ecology and Evolution*. 13:480-487.

Shoshani J., Kupsky W. J., Marchant G. H. 2006. Elephant brain part I: Gross morphology, functions, comparative anatomy, and evolution. *Brain Research Bulletin* 70:124-157.

Siebenaler J. B., Caldwell D. K. 1956. Cooperation among adult dolphins. *Journal of Mammalogy* 37:126-128.

Siegel S., Castellan Jr. N. J. 1988. *Nonparametric Statistics for the Behavioral Sciences*. New York: McGraw-Hill.

Skinner B. F. 1965. *Science and Human Behavior*. New York: Free Press.

Smolker R. A., Richards A., Connor R., Mann J., Berggren P. 1997. Sponge carrying by dolphins (Delphinidae, Tursiops sp.): a foraging specialization involving tool use? *Ethology* 103:454-465.

Stanford C. B., Wallis J., Mpongo E., Goodall J. 1994. Hunting decisions in wild chimpanzees. *Behaviour* 131:1-20.

Steiper M. E., Young N. M., Sukarna T. Y. 2004. Genomic data support the hominoid slowdown and an Early Oligocene estimate for the hominoid-cercopithecoid divergence. *Proceedings of the National Academy of Sciences U. S. A.* 101:17021-17026.

Stevens J. R., Hauser M. D. 2004. Why be nice? Psychological constraints on the evolution of cooperation. *Trends in Cognitive Sciences* 8:60-65.

Stone J., Halasz P. 1989. Topography of the retina in the elephant, *Loxodonta africana*. *Brain, Behavior and Evolution* 34:84-95.

Sukumar R. 1989. *The Asian Elephant: Ecology and Management*. Cambridge (MA): Cambridge University Press.

Tinbergen N. 1963. On aims and methods of ethology. *Zeitschrift fur Tierpsychologie* 20:410-433.

Tomasello M., Call J. 1997. *Primate Cognition*. Oxford: Oxford University Press.

Trivers R. L. 1971. The evolution of reciprocal altruism. *Quarterly Review of Biology* 46:35-57.

Trivers R. L. 2004. Mutual benefits at all levels of life. *Science* 304:964-965.

Trivers R. L. 2006. Reciprocal altruism: 30 years later. Pages 67-83 in *Cooperation in Primates and Humans*, edited by P. M. Kappeler et al. Berlin: Springer-Verlag.

Vallortigara G. 2004. Visual cognition and representation in birds and primates. Pages 57-78 in *Comparative Vertebrate Cognition: Are Primates Superior to Non-Primates?* Edited by L. J. Rogers and G. T. Kaplan. Berlin: Springer.

van Schaik C. P., Deaner R. O., Merrill M. Y. 1999. The conditions for tool use in primates: implications for the evolution of material culture. *Journal of Human Evolution* 36:719-741.

van Schaik C. P., van Hooff J. A. R. A. M. 1983. On ultimate causes of primate social systems. *Behaviour* 85:91-117.

Veenema H. C., Das M., Aureli F. 1994. Methodological improvements for the study of reconciliation. *Behavioural Processes* 31:29-38.

Visalberghi E., Quarantotti B. P., Tranchida F. 2000. Solving a cooperation task without taking into account the partner's behavior: the case of capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology* 114:297-301.

Wahaj S. A., Guse K. R., Holekamp K. E. 2002. Reconciliation in the spotted hyena (*Crocuta crocuta*). *Ethology* 107:1057-1074.

Warneken F., Hare B., Melis A. P., Hanus D., Tomasello M. 2007. Spontaneous altruism by chimpanzees and young children. *PLoS Biology* 5:1414-1420.

Watts D. P., Colmenares F., Arnold K. 2000. Redirection, consolation, and male policing: how targets of aggression interact with bystanders. Pages 281-301 in *Natural Conflict Resolution,* edited by F. Aureli and F. B. M. de Waal. Berkeley (CA): University of California Press.

Weaver A. 2003. Conflict and reconciliation in captive bottlenose dolphins (*Tursiops truncatus*). *Marine Mammal Science* 19:836-846.

Whiten A., Goodall J., McGrew W. C., Nishida T., Reynolds V., Sugiyama Y., Tutin C. E. G., Wrangham R. W., Boesch C. 1999. Cultures in chimpanzees. *Nature* 399:682-685.

Whiten A., Horner V., de Waal F. B. M. 2005. Conformity to cultural norms of tool use in chimpanzees. *Nature* 437:737-740.

Williams J.H. 1950. *Elephant Bill*. London: Rupert Hart-Davis.

Wilson E. O. 1975. *Sociobiology: The New Synthesis*. Cambridge: Harvard University Press.

Yerkes R. M., Yerkes A. W. 1929. *The Great Apes: A Study of Anthropoid Life*. New Haven: Yale University Press.

Yokoyama S., Takenaka N., Agnew D. W., Shoshani J. 2005. Elephants and human color-blind deuteranopes have identical sets of visual pigments. *Genetics* 170:335-344.

Zahn-Waxler C., Hollenbeck B., Radke-Yarrow M. 1984. The origins of empathy and altruism. Pages 21-41 in *Advances in Animal Welfare Science*, edited by M. W. Fox and L. D. Mickley. Norwell (MA): Kluwer Academic

Zahn-Waxler C., Radke-Yarrow M. 1982. The development of altruism: alternative research strategies. Pages 109-137 in *The Development of Prosocial Behavior*, edited by N. Eisenberg. New York: Academic Press.

Zahn-Waxler C., Radke-Yarrow M., Wagner E., Chapman M. 1992. Development of concern for others. *Developmental Psychology* 28:126-136.

Zhang L., Wang N. 2003. An initial study on habitat conservation of Asian elephant (*Elephas maximus*), with a focus on human elephant conflict in Simao, China. *Biological Conservation* 112:453-459.

Appendix A

Ethogram for Investigation I

PD/MC recordings

Body State

du = defecation and/or urination
ag = agitated state of any kind; ears out, tail erect
st = regular posture, standing or grazing

Social or Directed Behavior

rn = brisk walk or run toward victim
tm = trunk touch to mouth or in mouth
tt = trunk/trunk touch
tf = trunk to other part of head
tb = trunk to other part of body other than head or genitals
tg = trunk to genital touch
to = trunk over back of other elephant
bf = breast feed
ps = push with head
pb = push with body contact
hr = rest head on other elephant
vt = trumpet
vr = rumble
ts = trunk smack
ab = air burst
vs = roar, scream

Proximity

bc = body contact (if in body contact, don't record px or cm)
px1,2,3,4 = proximity (1: within trunk's reach, 2: within 10m, 3: within 25m, 4: more than 25m)
cm = cluster member (record if more than 2 individuals are within trunk's reach of the victim instead of px)

Appendix B: Additional Conditions for Investigation II

Single release, double rope: After completing the *no-rope control* phase, the second elephant was removed from the test site, and the first-released elephants were released to the two-rope apparatus alone and allowed access to both rope ends. This condition immediately followed the control condition and was conducted to assess the elephants' understanding of the table apparatus itself. Although no elephant ever learned to consistently pull both ropes on their own (either because of the awkwardness of the elephants using their trunks to pick up and pull two ropes or because of their lack of understanding of the workings of the table itself), five of the six elephants immediately approached and began pulling one rope end in the first and all subsequent trials of this condition. SS successfully pulled both ropes in only the first trial, and subsequently refused to participate after his third failed attempt while pulling only a single rope. Such behavior would seem inappropriate if the elephants were simply responding to the contingency of rope tension or reverting back to training phase behavior without understanding that the presence of a partner matters**.**

No-food control: We conducted a final condition of 20 simultaneous release trials without food placed in the buckets to test whether or not the elephants were motivated by the food reward paired with successful completion of the task or acting independently of this reinforcement. SS and KW refused to participate in the task after the eighth trial. We decided to discontinue this condition after the first pairing for husbandry and safety concerns. For the same reason we thought it best to feed elephants in between trials regardless of whether or not they successfully completed the task during test phases (to ensure the elephants did not become agitated and endanger the staff), we decided here to discontinue a condition we believed could further upset the elephants.

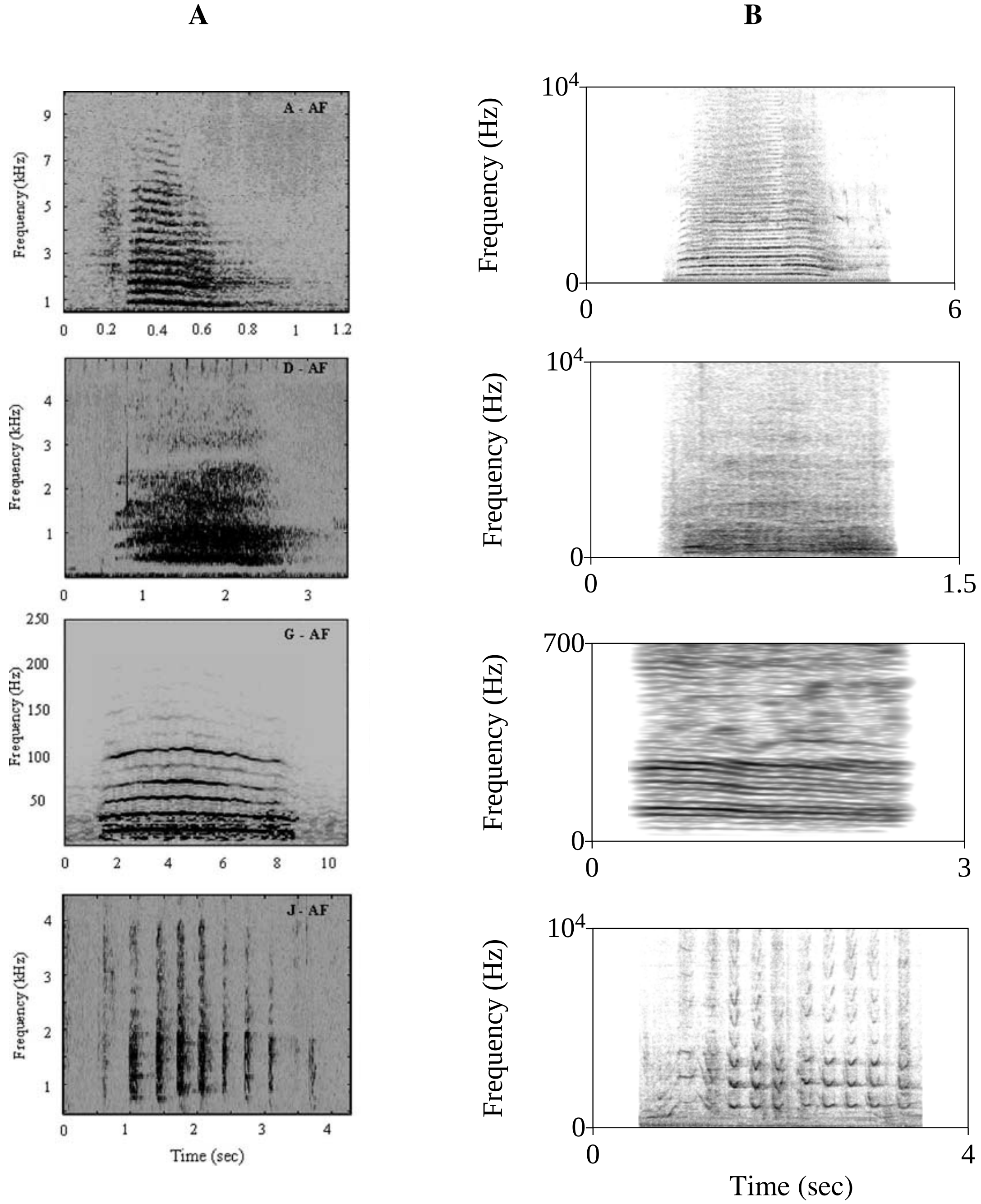

Figure 5. Spectrograms of four vocalization types of elephants in our study (right column - B) and Nair et al. 2009 (left column - A). Rows (from the top): 1 – trumpet, 2 – roar, 3 – rumble, 4 – chirp. Left column reprinted with permission from the authors and the Acoustical Society of America. Column B created with Praat Version 5, with assistance from M. Owren.