Asian elephants (*Elephas maximus*) reassure others in distress

Contact directed by uninvolved bystanders toward others in distress, often termed consolation, is uncommon in the animal kingdom (thus far only demonstrated in the great apes, canines, and corvids). Whereas the typical agonistic context of such contact is relatively rare within natural elephant families, other causes of distress may trigger similar, other-regarding responses. In a study carried out at an elephant camp in Thailand, we found that elephants affiliated significantly more with other individuals through directed, physical contact and vocal communication following a distress event than in control periods. In addition, bystanders affiliated with each other, and matched the behaviour and emotional state of the first distressed individual, suggesting emotional contagion. The initial distress responses were overwhelmingly directed toward ambiguous stimuli, thus making it difficult to determine if bystanders reacted to the distressed individual or showed a delayed response to the same stimulus. Nonetheless, the directionality of the contacts and their nature strongly suggest attention toward the emotional states of conspecifics. The elephants' behaviour is therefore best classified with similar consolation responses by apes, possibly based on convergent evolution of empathic capacities.

Asian elephants (*Elephas maximus*) reassure others in distress

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Introduction

Most empirical evidence for how animals react to others in distress comes from the study of conflict resolution (de Waal & van Roosmalen, 1979; de Waal & Aureli, 1996; de Waal, 2000). Peacekeeping mechanisms have evolved to manage conflict (see de Waal, 1996; de Waal, 2000 for a review) in animal societies, including reconciliation (i.e. affiliative physical contact between former opponents soon after a conflict) and consolation (i.e. affiliative physical contact from an uninvolved bystander directed toward a recipient of aggression). The former is much more common than the latter in the animal kingdom, possibly due to differences in the complexity of underlying cognitive mechanisms (de Waal & Aureli, 1996; de Waal, 2008). Although reconciliation appears to be self-interested for all individuals involved (due to the need to maintain valuable relationships - de Waal, 2000), the significance of consolation for the bystander is still unclear. Recent work trying to identify the adaptive function(s) of consolation has focused on a) the identity of bystanders and their relationships with the consolation recipient (Romero, Castellanos & de Waal, 2010; Romero & de Waal, 2010; Romero, Castellanos & de Waal, 2011), b) the physiological changes in distressed individuals consoled by bystanders (Koski & Sterck, 2007; Fraser, Stahl & Aureli, 2008), and c) possible benefits to the consolers themselves (Koski & Sterck, 2007; Koski & Sterck, 2009). All of these possible functions for such affiliative behaviour suggest that the parties involved initiate or accept contact as a way of mitigating emotional stress responses (de Waal, 2008; Koole, 2009).

Because of these functional uncertainties, some scientists remain reluctant to use functional or motivational terminology, such as consolation; instead, the aforementioned behaviour is sometimes described as "third-party affiliation" (a descriptive term that specifies only directed, physical contact with a distressed individual, e.g., Call, Aureli & de Waal, 2002; Koski & Sterck, 2007; Seed, Clayton & Emery, 2007). However, other studies argue that the mammalian capacity for empathy underlies consolation (Preston & de Waal, 2002), and compare

the morphology and motivation of the behaviour with "sympathetic concern" in humans (Clay & de Waal, 2013; Romero, Castellanos & de Waal, 2010). In general, demonstrations of consolation in animals are rare, with empirical evidence thus far provided only for the great apes, canines, and certain corvids (de Waal & van Roosmalen, 1979; de Waal & Aureli, 1996; Palagi, Paoli & Tarli, 2004; Cordoni, Palagi, Borgognini Tarli, 2006; Mallavarapu et al., 2006; Seed, Clayton & Emery, 2007; Cools, van Hout & Nelissen, 2008; Palagi & Cordoni, 2009; Fraser & Bugnyar, 2010; Romero, Castellanos & de Waal, 2010; Romero & de Waal, 2010), but not for monkeys or any other species (e.g. de Waal & Aureli, 1996; Schino et al., 2004; Watts, Colmenares & Arnold, 2000, but see Call, Aureli & de Waal, 2002; Wittig et al., 2007). This rarity may be due to the potential cognitive underpinnings of consolation, or species-specific social dynamics that determine how animals mitigate social strife in a variety of relationships. In some monkey societies, for example, it may be too risky or dangerous to associate with victims of aggression due to the rigidity of linear hierarchies (de Waal & Aureli, 1996; de Waal, 2000).

Elephants are interesting study species because of their complex social behaviour and close bonding with family members (Douglas-Hamilton & Douglas-Hamilton, 1975; Moss, 1988; Poole, 1996; Schulte, 2000; Payne, 2003; Bates et al., 2008). They often act as allomothers toward others' offspring, and respond immediately to the vocalisations of these individuals (e.g. in response to infant distress – Lee, 1987; Bates et al., 2008). They are also known for their "targeted helping," or directed assistance that takes the specific needs of others into account (e.g. helping to lift and coordinated bracing of injured, dying or otherwise prostrate family members – Douglas-Hamilton et al., 2006; Bates et al., 2008). Targeted helping is viewed as a sign of empathic perspective taking (e.g., Preston & de Waal, 2002; de Waal, 2008).

In the present study, we aim to assess the affiliative tendencies of Asian elephants (*Elephas maximus*) toward conspecifics in response to distress, using similar methodology to that used in the conflict resolution literature. To our knowledge, this is the first systematic

investigation of distress-related affiliation in elephants based on a priori hypotheses (but see Bates et al., 2008 and Hart, Hart & Pinter-Wollman, 2008 for other possible displays of empathy and stress-related emotional responses).

Relative to chimpanzees (de Waal, 1982; de Waal & Aureli, 1996), elephants do not often engage in conflict within their herd, which consists primarily of related females and immature offspring (Douglas-Hamilton & Douglas-Hamilton, 1975; Moss, 1988; Poole, 1996; Payne, 2003; de Silva, Ranjeewa & Kryazhumskiy, 2011). Thus, we measured how elephants affiliate or reassure others as a response to an individual's distress irrespective of its cause. We recognise that our inability to identify a clear stimulus for each distress event makes it difficult to differentiate between cases where individuals are reacting to the stimulus or to another elephant's distress. Because of this, it is unclear if all or most cases of affiliative contact can be classified as "consolation" in the way this label is used in post-conflict studies (e.g., Call, Aureli & de Waal, 2002; Preston & de Waal, 2002; Koski & Sterck, 2007; Seed, Clayton & Emery, 2007; Cools, van Hout & Nelissen, 2008; Fraser, Stahl & Aureli, 2008; Koole, 2009; Koski & Sterck, 2009; Fraser & Bugnyar, 2010; Romero, Castellanos & de Waal, 2011). Instead, we refer to the elephants' affiliation with others as "reassurance" to note our focus on both affiliative contacts and emotional responses. We use this term instead of "consolation" to avoid implying the potential function of the elephants' behaviour.

This study then is a first attempt to distinguish the affiliative tendencies of elephants in response to behaviourally identified stress. Based on the aforementioned social complexity of and targeted helping in elephants, we predicted that reassurance behaviour toward distressed individuals should be identifiable through an assessment of physical and vocal contacts. If elephants are responsive to the distress of others, they should be expected to make physical or vocal contact with stressed conspecifics, and do so sooner than in control periods during which the conspecifics do not display distress. In addition, we might expect emotional contagion –

bystanders' adoption of the emotional state of those in distress - to be part of such a reaction if the elephants' affiliative behaviour is part of a more complex, emotionally driven social response (cf., Zahn-Wexler, Hollenbeck & Radke-Yarrow, 1984; Zahn-Waxler & Radke-Yarrow, 1990; Zahn-Waxler et al., 1992; de Waal, 2003; de Waal, 2008; Clay & de Waal, 2013). Thus, we predicted that the elephants' behavioural and emotional responses would mimic physically and follow temporally those of distressed conspecifics. Due to the close social bonding within matriarchal elephant herds and multiple descriptions of emotional reactivity in elephants (e.g., Moss, 1988; Poole, 1996; Schulte, 2000; Payne, 2003; Bates et al., 2008), we also considered that emotional contagion – known of many mammals (cf., de Waal, 2003; de Waal, 2008) – might lead to affiliative interactions among bystanders as well. Thus, we also predicted that bystanders to distress would make physical or vocal contact with one another, in addition to, or instead of contact with the first stressed individual.

Materials and methods

Ethics statement

This project was approved by the National Research Council of Thailand and Emory University's Institutional Animal Care and Use Committee (ID 219-2007Y).

(a) Study area and subjects

This study was conducted at the Elephant Nature Park (the "Park") in the Mae Tang district of Chiang Mai province, Thailand. Although the Park owns many of the elephants on-site, some are leased or contracted so that the general elephant population changed regularly during the study period. The data in this study refer to 26 elephants with approximate ages ranging from 3-60 years old, although due to unverifiable records, ageing elephants precisely was impossible. Although genetic tests on the relatedness of the elephants were never done, it is reasonable to conclude based on the relayed 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

111 care of by one or two mahouts (elephant caretakers) every day. Adult male elephants (n = 4) were
112 completely excluded from the study as they were regularly prevented, for safety and husbandry
113 reasons, from participating in most of the natural, social interactions within groups. When a
114 female was first brought to the Park, she was generally allowed to integrate with a smaller group
115 of elephants. In this study, these smaller, family-like social groups (generally of n = 5 – 7
116 individuals) were labeled “pseudo-families” because they consisted of closely bonded individuals
117 akin to a family group but devoid of genetic relatedness. There was no single herd at the Park, but
118 six individual pseudo-family groups that interacted at specific times during the day. These groups
119 were delineated based on interviews with the Park mahouts during data collection but prior to
120 data analysis.

121 Each day, elephants followed a specific routine established by Park management.
122 Mahouts moved their elephants to a specific location on the property, as a pseudo-family group,
123 beginning at 0700 hours. They ate at a central location at 1130 hours – fed either by their mahouts
124 or visiting tourists – bathed communally at 1300 hours and 1630 hours, and returned to their
125 night shelters, in which they were tethered for the night, at 1700 hours. Mahouts moved elephants
126 with vocal commands or by grasping their ears or legs and walking them to different locations on
127 the property. Throughout the day, elephants were left to graze or play in various parts of the
128 property within their social groups. Although individual elephants were generally allowed to
129 interact with members of other pseudo-family groups, the mahouts often intervened at
130 unpredictable times to separate volatile pairings.

131 (b) Defining Distress

132 Because there is very little literature on Asian elephant behaviour in general (but see Sukumar,
133 2003; Sukumar, 2006; de Silva, Ranjeewa & Kryazhimskiy, 2011), the more detailed literature on
134 African elephant behaviour (*Loxodonta* genus - e.g., Douglas-Hamilton & Douglas-Hamilton,
135 1975; Moss, 1988; Poole, 1996; Payne, 2003) is often applied to Asian elephants as well because

of their relatively close phylogenetic proximity (Payne, 2003). Douglas-Hamilton and Douglas-Hamilton (1975) and Lee (1987) describe distress in individual elephants, specifically infants, based on specific vocalisations 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). Roars, rumbles, and trumpets 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) a comprehensive ethogram of elephant behaviour with specific attention to those behaviours occurring when an infant or adult is distressed or agitated (adapted and expanded from Olson, 2004), we define a distress event in elephants as follows:

A distress event is one resulting from an unseen or seen negative stimulus (e.g. negative mahout intervention, conspecific intimidation or aggression, pseudo-family group separation, environmental threat or accident) that causes an individual 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 vocalisations, specifically trumpets, roars and rumbles).

(c) General Data Collection

We chose locations on the property from which to collect data to ensure both a full view of pre-selected pseudo-family groups and the observer's safety. These locations included viewing platforms constructed specifically for observations, and in fields in close proximity to mahouts. 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 approximately 55 acres in total size,

but only 30 acres were observable for this study. The property was divided into four grids for observation purposes, and an observation location was chosen within a grid based on the aforementioned factors.

On average, data were collected during 1-2 week periods each month from April, 2008 – February, 2009. General observation periods ran for no less than 30 minutes and no more than 180 minutes per session from 0730 – 1030 and from 1400 – 1630, with scan samples taken every 10 minutes. Data on proximity distance only were collected for relationship quality within elephant groups. All observation periods began after 10 minutes of no mahout interference on elephant behaviour, and individual scan samples were cancelled if such interference occurred within a given 10-minute period. All-occurrence sampling was used for distress behaviours and the reactions of others to these behaviours (Altmann, 1974). In addition, if an interaction was clearly and completely observed outside these specific observation periods, the same data were collected ad-libitum (<20% of total cases), and a subsequent control observation period (see below) was scheduled.

(d) Post-distress data collection - PD and MC observations

Although the human staff responsible for the elephants' care artificially constructed the pseudo-family groups over several years, we focused on spontaneous, affiliative behaviour reflective of natural, social interactions (de Waal, 1982; Sukumar, 2003; Sukumar, 2006; de Silva, Ranjeewa, Kryazhimskiy, 2011). Post-distress data for this study were collected at the Park on 26 semi-free ranging individuals in six pseudo-family groups following the PC (post-conflict, or PD, post-distress) / MC (matched-control) methodology developed for reconciliation and consolation behaviour in primates (de Waal & Yoshihara, 1983; see Materials and methods for details).

The PD period was an observation period in which all approach and affiliative behaviour was recorded (as was all data on potential stimuli for distress, individuals present within 50 m, and date, time and weather), for a 10-min block following the first distress display. Because

188 elephant interactions may involve multiple distressed individuals (Lee, 1987), the first individual
189 to vocalise, or display a distress behaviour was labeled the victim and thus the focal individual in
190 each PD period. If more than one individual responded simultaneously, the rarest case (if known,
191 the least-often distressed individual) was chosen for observation. Each PD period was compared
192 to an MC (matched control) period, or another 10-min block of observation taken of the victim
193 and bystanders on the next possible day following the PD. An MC period was selected when as
194 many variables from the PD – in prioritised order: high percentage of original individuals present,
195 location, time of day and weather – could be maintained, and, most importantly, no new distress
196 event occurred in the 30 minutes prior to (and during) the period of observation. An MC was
197 collected within seven days of its corresponding PD (in 80% of PD/MC cases, the MC was
198 collected within 48 hours). If an MC was conducted when an elephant that had made contact with
199 the distressed individual in the corresponding PD was absent or more than 25 m away, that
200 PD/MC observation was excluded from the analysis to avoid biasing the data in favor of our
201 predictions.
202 (e) Scan-Sampling for Proximity – “Friends” and “Non-Friends”
203 We attempted to differentiate between contact directed toward “friends” (closely-bonded
204 individuals) and “non-friends” by collecting 68 hours of scan-sampling proximity data (for
205 procedure, see Romero & de Waal, 2010). Although mahouts did not interfere with most social
206 interactions within established, elephant pseudo-family groups (and thus we were able to specify
207 controlled parameters for the PD/MC data), they often discriminately prevented outsiders from
208 coming too close to avoid potential conflict. Such conflict between elephants at the Park was also
209 not representative of natural, wild elephant groups (in which conflict is relatively rare), probably
210 due to a high level of unrelatedness within and between pseudo-family groups at the Park. Thus,
211 unfortunately, we were forced to exclude the scan-sampling data (and any measure of relationship
212 quality) from our analysis due to circumstances beyond our control.

(f) Analysis

We used Wilcoxon signed-ranks tests (two-tailed) to analyse the differences between PD and MC pairs because of the relatively small sample size. The data were analysed by focal individual to avoid biasing the data toward any particularly well-represented focal elephant. In addition, the McNemar test was used to assess the presence or absence of elephant bunching behavior within PD/MC observations (Siegel & Castellan, 1988). All tests were two-tailed, and P-values were compared to an alpha level of $\alpha = 0.05$.

Results

(a) Physical affiliation following distress

To assess reassurance behaviour, we first recorded the timing of the first affiliative interaction between the victim (the first individual in a group to display distress behaviour, i.e. vocalisations and body state changes signaling emotional distress or agitation) and any bystander(s), with physical contact and affiliative vocalisations analysed separately. These data were collected during the 10-min PD period and then compared to the timing of the first affiliative interaction in the corresponding MC period. Following standard procedures developed in primate studies (e.g., de Waal & van Roosmalen, 1979; de Waal & Yoshihara, 1983; de Waal & Aureli, 1996; Romero & de Waal, 2010), PD/MC pairings were split into three categories: attracted (pairings in which the first affiliative contact occurred earlier in the PD than in the MC, or no contact occurred in the MC following contact in the PD), dispersed (contact occurred earlier in the MC than in the PD or not at all in the PD), and neutral (affiliative contact times did not differ in the PD and its corresponding MC, or no contact occurred in either) (c.f., de Waal & Yoshihara, 1983; Veenema, Das & Aureli, 1994; Verbeek & de Waal, 1997; Aureli & de Waal, 2000).

There were 84 PD/MC observations (and thus 84 distinct initial instances of distress signals) across 18 different focal individuals (mean number of PD/MC observations per

individual = 9.5, range = 1- 38). Within the 84 PD/MC observations, there were a total of 183 focal-bystander dyads, 171 of which involved at least one affiliative physical contact (e.g. Figure 1) during the PD period (93.4%). 53 of the 84 PD/MC observations included affiliative contact by multiple individuals directed toward a single focal individual. 12 of the 84 observations were the result of an identifiable stimulus for distress – either directed aggression or a feature in the environment (e.g. helicopter, human or dog in close proximity) - that caused distress in a single individual. The sample size did not allow for further analysis by stimulus type. In our analysis of affiliative contacts, we were concerned only with the first contacts between bystanders and the focal individual in each of the 84 PD/MC observations. The majority of affiliative contacts occurred within the first minute following distress (Figure 2; see Movie S1 for an example of affiliative contact), and a Wilcoxon signed-ranks test performed on the data by focal individual showed that the difference in frequency of these contacts per individual subject in the first minute of the PD (mean ± SD = 7.50 ± 8.49) versus the MC (mean ± SD = 0.44 ± 0.86) was significant ($Z = 3.56$, $n = 18$, $P < 0.001$).

We categorised attracted and dispersed pairs based on whether or not each interaction was "solicited" (the focal, distressed individual approached a bystander to seek reassurance) or "unsolicited" (a bystander was the first to approach the focal, which is sometimes called "true consolation" in primate studies – Koski & Sterck, 2007; Call, Aureli & de Waal, 2002). When the first affiliative contacts between the focal individual and bystanders in each of the 84 PD/MC observations were analysed (the usual first step in assessing consolation data – e.g., de Waal & van Roosmalen, 1979; de Waal & Yoshihara, 1983; de Waal & Aureli, 1996; Romero & de Waal, 2010), a significant difference was found between the proportion of attracted and dispersed pairs in both unsolicited ($Z = 3.31$, $n = 18$, $P < 0.001$) and solicited contacts ($Z = 2.69$, $n = 18$, $P = 0.007$; Table 1). Across the 18 focal individuals, unsolicited contacts (mean ± SD = 8.83 ± 11.93) occurred significantly more often than solicited contacts (mean ± SD = 1.33 ± 1.71; $Z = 2.47$, $n =$

18, P = 0.014). The two most prevalent types of physical contact given by bystanders were trunk touches to another individual's genitals (38.6% of touches), and trunk touches around or inside another's mouth (35.1%; Figure 3).

(b) Vocal affiliation following distress

Because elephants primarily use acoustic modalities for communication (e.g. Poole, 1996; Payne, 2003; Nair et al., 2009; de Silva, 2010), we also looked at bystanders' vocalisations in response to distressed individuals. In a comparison of first bystander vocalisations in the PD and MC periods, we found that bystanders vocalised earlier following distress than in control periods in a significant number of PD/MC observations (proportion of attracted pairs: mean ± SD = 97.11% ± 8.81%; dispersed pairs: 2.22% ± 8.61%) across 18 focal individuals (incidentally, only three of these focal individuals never had a bystander vocalise when they were distressed: Z = 3.42, N=18, P < 0.001). Bystander elephants most often chirped (a vocalisation often emitted when individuals are in close-proximity to one another – 31.8% of vocalisations) or audibly trunk-bounced (interpreted as a sign of agitation and distress - 24.7% of vocalisations) following distress signals from the focal animal (Olson, 2004; Nair et al., 2009; de Silva, 2010, see Figure 3).

In addition, we assessed differences in the behaviour of bystanders in relation to the behaviour of distressed individuals between PD and MC periods. Vocalisations often signal agitation or excitement in elephants and are usually paired with similarly functioning physical and postural displays (cf., Olson, 2004). Bystanders adopted the agitated behaviour of the originally distressed focal individual in the PD (i.e. ears presented forward with an erect tail, usually followed by vocalisation and simultaneous urination and defecation – Olson, 2004; Bates et al., 2008), yet showed no such signs of agitation or distress in the MC in 157 of the 171 dyads

(91.8%: mean ± SD = 8.72 ± 9.51 dyads per focal individual) in which physical contact occurred (Z = 3.56, n = 18, P < 0.001).

(c) Behaviour among bystanders

The previous results refer to contact by bystanders to a distressed, focal individual, but we also analysed contact between bystanders in PDs in which there were multiple individuals present. Bystander-bystander physical contact occurred in 37 of the 84 PD periods, and, like in victim-bystander contacts, occurred earlier following the victim's distress in the PD period than in the MC in a significant number of interactions across 19 possible bystanders (proportion of attracted pairs: mean ± SD = 97.37% ± 8.36%; dispersed pairs: 2.63% ± 8.36%; Z = 3.85, n = 19, P < 0.001).

Elephants may quickly form a close circle, known as "bunching," around their young in anti-predator defense (e.g., Moss, 1988; Poole, 1996; Bates et al., 2008). Bunching involves the coming together of multiple individuals around the distressed elephant so that all individuals are within trunk's reach of one another (Nair et al., 2009). To systematically assess whether individual signs of distress trigger such behaviour, we looked at the occurrence/non-occurrence of bunching in PD/MC observations. We excluded all observations in which less than four individuals were present (this excluded n = 7 focal individuals altogether). In 30 of the 42 qualifying PD/MC observations, bunching around both juveniles and other adults occurred following distress and never in the corresponding control periods (McNemar change test comparing presence or absence of bunching in PD and control periods: $\chi^2 = 28.03$, df=1, P < 0.001).

Discussion

Here, we set out to study the affiliative responses of elephants to others, and found that they engage in more such responses following distress than during control periods. The elephants engaged significantly more often in unsolicited physical contacts (bystanders approached and affiliated with the first-distressed individual) than in solicited contacts (the first-distressed individual is the initiator of the contact). Bystanders also vocalised toward or in response to distressed individuals, and made contact with each other significantly more often than in controls.

In the study of consolation in animals, the stimulus event is almost always a conflict, and the roles of the individual participants – victim, aggressor, bystander – are clearly differentiated. In the present study, in contrast, the labels of "victim" and "bystander" were applied by labeling the first individual to show distress following a known or unknown stimulus as the "victim", while all nearby individuals were labeled "bystanders." In our study, temporal differences between displays of distress were rather clear within these pseudo-family groups, with the bystanders responding with a considerable delay following the victim's first display of distress. This makes it unlikely that these responses concerned the same stimulus, and suggests that they rather concerned the other's distress. If so, the observed behaviour is to be interpreted in the same way as consolation in primates, including chimpanzees (Romero, Castellanos & de Waal, 2010; Romero & de Waal, 2010). Since our study shows that, across distressed individuals, bystanders initiated affiliative contact more often than did victims, the observed reactions seem similar to "true consolation" in nonhuman primates (de Waal & Aureli, 1996; Romero, Castellanos & de Waal, 2010; Romero & de Waal, 2010).

In studies of consolation, the matching of another's emotional state through emotional contagion (Hatfield, Cacioppo & Rapson, 1994; de Waal, 2003) may imply that the behaviour has empathic underpinnings. In our study, the emotional response of multiple individuals to mostly unknown stimuli could be either contagious (multiple individuals adopt the emotional state of one) or universal (all individuals react with similar emotion to the same stimulus). Substantial

anecdotal evidence of emotional contagion in elephants (e.g., Douglas-Hamilton & Douglas-Hamilton, 1975; Moss, 1988; Poole, 1996; Schulte, 2000; Payne, 2003; Bates et al., 2008) suggests that they do have the capacity for it, and the aforementioned temporal differences between the responses of victims and bystanders suggests emotional contagion in this study as well. However, we acknowledge that both interpretations are possible.

It is important to note that this is the first systematic assessment of post-distress affiliative behaviour in elephants, and that this captive population provided sufficient opportunities to observe this species' social capacity for reassurance. Future studies on wild elephants should confirm these results and those presented in anecdotal reports (e.g., Douglas-Hamilton et al., 2006; Bates et al., 2008; Hart, Hart & Pinter-Wollman, 2008), even though limitations exist on wild Asian elephant social observations (e.g. dense forest cover and the rarity of consistent, large family group sightings – Lair, 1997; Sukumar, 2006; de Silva, Ranjeewa & Kryazhimskiy, 2011). After all, the original studies of consolation in non-human primates were conducted on captive animals (e.g., de Waal & van Roosmalen, 1979; de Waal & Aureli, 1996) and were confirmed only later in the wild (e.g., Wittig & Boesch 2003; Kutsukake & Castles 2004).

This study of post-distress behaviour is unique in that it goes beyond the traditional attention to physical contact. The consistent use of vocalisations by bystanders to distress may serve to reassure others, perhaps independent of or to complement physical touches. Both the overwhelming number of unsolicited contacts, and the prevalence of specific vocalisations (e.g. chirping, which may serve as a reassurance vocalisation used when elephants are in close proximity to each other – Nair et al., 2009; de Silva, 2010) lend support to the notion that elephants use multiple communicative modalities (tactile and acoustic) in their affiliative interactions with others (e.g., Langbauer, 2000; McComb et al., 2000; Douglas-Hamilton et al., 2006; Bates et al., 2008). In addition, a bystander often affiliated physically with a distressed individual by touching or putting its trunk inside the victim's mouth. This may mirror similar

vulnerable contact behaviour seen in chimpanzees, whereby individuals put a finger or a hand into the mouth of a distressed other (de Waal, 1982; de Waal, 1990; Nishida et al., 2010).

Bystander affiliation directed toward others in distress, either in the form of consolation following conflict or reassurance following another stressful event, is rare in the animal kingdom possibly due to the unique cognitive mechanisms that may underlie it. Similarities in the complexity of chimpanzee and elephant social relationships (de Waal, 1982; Payne, 2003; Plotnik et al., 2006; Bates et al., 2008; de Waal, 2008; Byrne, Bates & Moss, 2009; de Waal, 2009; de Silva, Ranjeewa, Kryazhimskiy, 2011; Moss, Croze & Lee, 2011; Plotnik et al., 2011) suggest convergent cognitive evolution that should be further explored through careful analysis of social networks (de Silva, Ranjeewa & Kryazhimskiy, 2011) and these species' use of multi-modal communication in negotiating their physical and social environments.

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Table 1(on next page)

Solicited and unsolicited affiliative contacts for each focal individual across all 183 focal-bystander dyads, within 84 PD/MC observations.

Columns indicate numbers of attracted (A), dispersed (D) and neutral (N) pairs per individual in both solicited (S) and unsolicited (US) contacts. Totals are provided in italics. The Mean ± SD indicates the mean proportion of attracted and dispersed pairs ± the standard deviation.

Focal	A (S)	D (S)	N (S)	A (US)	D (US)	N (US)
AU	3	0	0	11	1	1
BT	3	0	0	7	0	1
F	2	0	0	12	0	1
JB	0	0	0	2	0	0
JK	0	0	0	26	0	2
MB	2	0	0	11	0	0
MD	0	0	0	3	0	0
MEL	3	0	0	0	0	0
MK	0	0	0	2	0	0
ML	1	0	0	0	0	1
MLT	0	0	0	2	0	0
MP	6	0	0	1	0	0
MTK	3	0	0	0	0	0
MVL	0	0	0	3	1	0
SB	0	0	0	0	0	1
TD	0	0	0	2	0	0
TJ	1	0	0	33	1	9
TT	0	0	0	19	4	2
Group	*24*	*0*	*0*	*134*	*7*	*18*
Mean ± SD	100% ± 0			80.31% ± 32.71	3.19% ± 7.23	

Table 1. Solicited and unsolicited affiliative contacts for each focal individual across all 183 focal-bystander dyads, within 84 PD/MC observations. Columns indicate numbers of attracted (A), dispersed (D) and neutral (N) pairs per individual in both solicited (S) and unsolicited (US) contacts. Totals are provided in italics. The Mean ± SD indicates the mean proportion of attracted and dispersed pairs ± the standard deviation.

Figure 1

Physical contact between elephants following distress included trunk touches to the genitals, mouth and the rest of the head (as seen here).

Photograph taken by E. Gilchrist at the Golden Triangle Asian Elephant Foundation, Chiang Rai, Thailand.

Figure 2

Temporal distribution of the first affiliative, physical contacts in PD (closed diamonds) and MC (open squares) periods across all dyads.

The number of first contacts occurred overwhelmingly in the first minute following the distress signal, which is consistent with consolation studies in other species (Aureli, van Schaik & van Hooff, 1989). See Movie S1 for an example of physical and vocal contact.

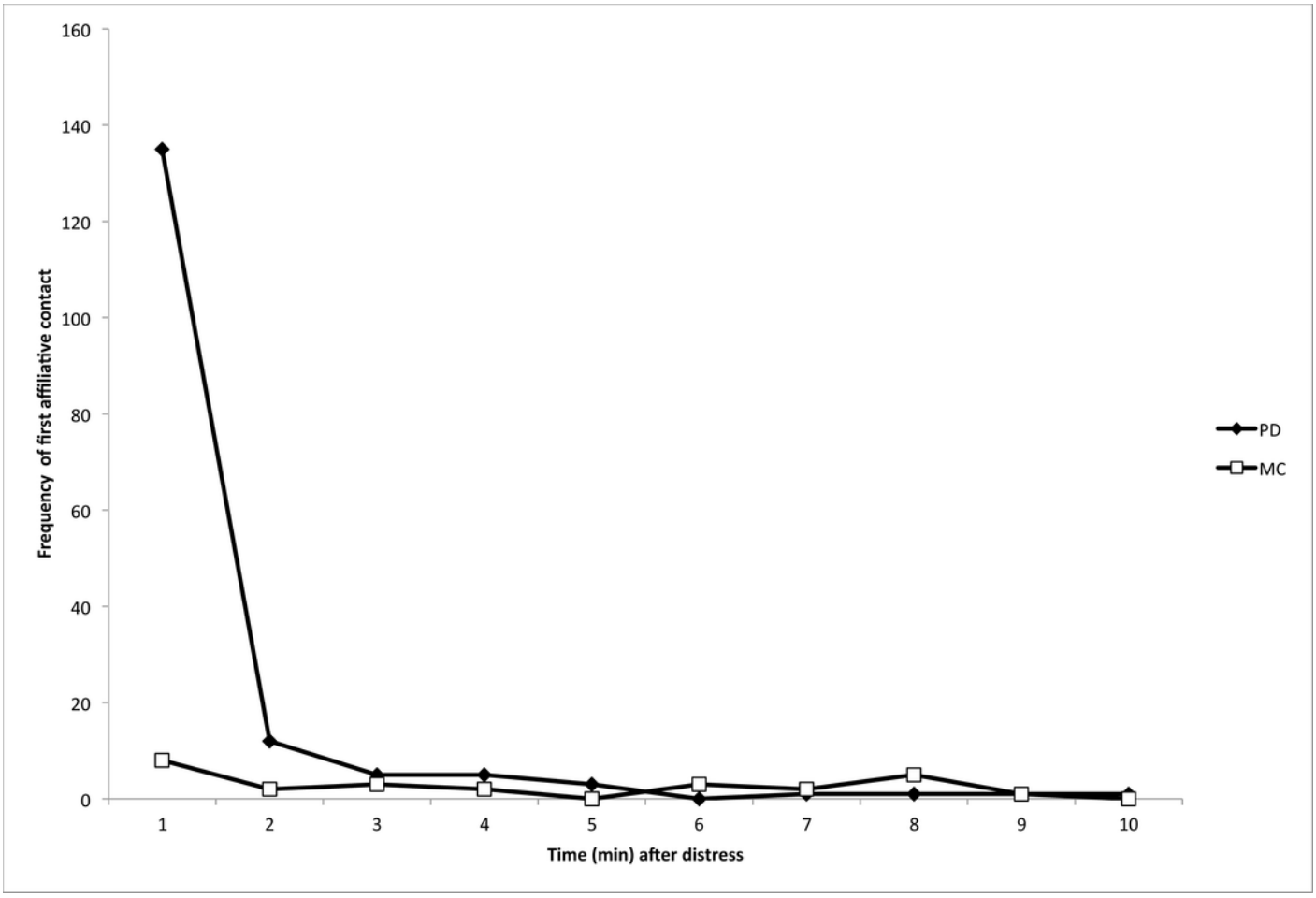

Figure 3

Frequency of each type of first contact or bystander response.

Vocalisations: VC – chirp, TS – trunk smack or trunk bounce, 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 vocalisation or trunk touch as the first affiliative contact or response across all dyads.