Social significance of trunk use in captive Asian elephants

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Running head: Social significance of trunk use

Tactile behaviour plays an important role in maintaining social relationships in several mammalian species. Touching with the tip of the trunk is a common social behaviour among Asian elephants (*Elephas maximus*). This is considered an affiliative behaviour; however, few studies have investigated it in detail. Therefore, this study aimed to determine whether this is an affiliative behaviour and whether it has other functions. We directly observed a group of captive female Asian elephants in Thailand. We found that the elephants usually touched each other with their trunks shaped in a U (U-type) or S (S-type) shape. The S-type shape was observed mainly when the elephants touched the lips of other elephants; however, this behaviour was occasionally observed in agonistic or play contexts, where it appeared to be a threat or dominant behaviour, particularly within adults. In contrast, the U-type shape was more frequently observed when the elephants were disturbed, where it appeared as a gesture for reassurance. We found that the U-type touch on the genitals may be used for interacting with neonates. Therefore, we suggest that despite the S-type touch having a tactile component, it may be a rare behaviour in Asian elephants that is similar to visual threat displays in other mammals. However, the U-type touch is similar to social grooming behaviour in primates or flipper rubbing in dolphins and can be used as an indicator of

affiliative relationships. Asian elephants change the shape of their trunk while touching others depending on their motivation and the situation, thereby demonstrating that the nuances of trunk use can assist in understanding the social relationships between individuals.

KEY WORDS: Asian elephant, touch with trunk, function, affiliative, aggressive.

INTRODUCTION

In various animal species, social relationships are regulated by tactile behaviours. Social grooming is one such tactile behaviour that has been frequently studied in various mammalian species (Spruijt et al. 1992). In most species, the primary function of grooming is to maintain healthy skin by removing parasites (Spruijt et al. 1992). However, social grooming has several additional functions, such as reconciliation and consolation following an aggressive interaction (Nakamura & Sakai 2013) and the maintenance of social bonds (Dunbar 1991, 2010; Nakamura & Sakai 2013). Thus, it is an indicator of affiliative relationships (McCowan et al. 2008; Kasper & Voelkl 2009). Dolphins exhibit a tactile behaviour termed flipper rubbing, which has functions similar to those of social grooming in primates (Sakai et al. 2006; Tamaki et al. 2006). Thus, tactile interactions are utilized for various purposes and are important for establishing and maintaining social relationships.

Elephant societies exhibit complexity similar to that of primate and cetacean societies (Poole & Moss 2008). The societies of both Asian (*Elephas maximus*) and African (*Loxodonta* spp.) elephants are centred on maternal groups. The female elephants live in a natal (family) group throughout their lives, whereas the males leave the group when they become sexually mature. However, the family groups temporarily reunite and then separate again. Longitudinal studies in wild African elephants have revealed that they have a hierarchical social structure (Wittemyer et al. 2005), whereas Asian elephants tend to form smaller groups with a looser association (de Silva et al. 2011). Asian elephants use vocal, seismic (Payne et al. 1986; O'Connell-Rodwell 2007; Nair et al. 2009; de Silva, 2010) and chemical (Rasmussen 1999) communication to maintain their complex social structure. Tactile behaviour is an important and prominent behaviour between them (Vidya & Sukumar 2005); however, few studies have investigated this behaviour to date.

Asian elephants show various tactile behaviours (Gadgil & Nair 1984; Makecha et al. 2012). Mostly, they use their trunks to touch other individuals (Gadgil & Nair 1984; Makecha et al. 2012), which serves not only as a form of tactile communication but also as a form of chemical communication (Garaï 1992; Makecha et al. 2012). Asian elephants have an excellent sense of smell and receive chemical information by touching body orifices or glands (Rasmussen & Krishnamurthy 2000). Some studies have shown that elephants touch the genitals and interdigital glands to assess the oestrus state of females (Slade et al. 2003; Thitaram et al. 2009). Other behavioural studies have suggested that touching with the trunk is an affiliative behaviour (Garaï 1992; Makecha et al. 2012). For example, touching the lips or mouth of another individual with the trunk is associated with investigation of food, reassurance, affirmation of affiliative relationships and individual recognition (Garaï 1992; Langbauer 2000; Sukumar 2003; Plotnik & de Waal 2014). In addition, touching the genitals of another individual provides reassurance or an exchange of information regarding health or reproductive state (Garaï 1992; Sukumar 2003; Kurt & Garaï 2006). However, to date, only a few studies have systematically investigated the precise function of the various types of elephant trunk touches.

Elephant trunks have a function similar to that of human and primate hands (Onodera & Hicks 1999; Martin & Niemitz 2003). Elephants use their trunks to feed and communicate in a manner similar to how primates use their hands for the same purposes. Elephant trunks are flexible; therefore, elephants can change their trunk shape depending on their requirements, such as for grabbing or reaching out. However, both Asian and African elephants can communicate with each other by changing their trunk shape, just as humans can change their hand shape to convey various intentions (McNeill 1992; Moss et al. 2011). African elephants entwine their trunks with one another as a greeting or during play (Moss et al. 2011). Garaï (1992, p. 14) reported that Asian elephants sometimes touched the mouths of other elephants using a complicated twisting of the trunk, which she speculated is used to prevent aggressive behaviour from escalating. Therefore, it is possible that elephants change their trunk shape to convey different intentions to the recipients. Deciphering complex behaviours, such as the form and function of elephant trunk use, will provide us with a better understanding of the social relationships among Asian elephants.

The aim of our study was to investigate the various functions of Asian elephant trunk touching by recording the trunk shape and any associated behaviours. In the present report, we examined the relationship between the types of trunk touch and the proximity between individuals, which is frequently used as an index of affiliative relationships among primates and elephants (Garaï 1992; Schel et al. 2013). We also investigated the behavioural context around trunk touching (play and aggression) to understand the nature of this type of tactile communication among Asian elephants.

METHODS

Study site

We collected behavioural data from the Surin Elephant Study Centre in Ban Ta Klang Elephant Village, Surin Province, Thailand (15°15′59.7″N, 103°29′48.3″E), which is managed by the Zoological Park Organization and the Surin Provincial Administration Organization. This village is home to the Guay tribe, who are known for their skills in caring, training and working with elephants. This region experiences three seasons: summer (February–April), rainy (May–October) and winter (November–January) (Polthanee & Promkhambut 2014). Approximately 200 elephants have been registered at the Centre by their mahouts, Approximately 40 elephants work at elephant shows or provide rides for tourists, whereas others work in volunteer programmes (e.g. allowing visitors to experience the lifestyle of a mahout). The elephants at the Centre also participate in ceremonies or parades in other regions of Thailand. When the elephants have no work, they are chained in front of the mahout's house or sheltered in the village and are taken on walks for bathing a few times each day.

Research periods and subjects

The present research was conducted between July and September 2012 (Period 1) and between December 2012 and March 2013 (Period 2). We observed the group of elephants that was involved in the Surin Project volunteer programme, which was started in 2009 by the Save Elephant Foundation. This group usually included 10–13 elephants. During our study period, some elephants left or newly joined the group. We observed a total of 17 elephants (16 females and one male; Table 1).

All elephants under observation were born in captivity, but their life histories before joining the project differed. Some elephants were used for working in shows, whereas others were used for street begging (walking the city streets to obtain money from tourists by providing them the experience of feeding elephants, etc.). In addition, some elephants were cared for by only one mahout or his family members for their entire lives, whereas others were cared for by different mahouts.

We identified each individual elephant by their body size or body characteristics (e.g. ear or tail shape and pink pigmentation on their ears and trunks). We categorised the elephants into four age classes: neonate (birth to 2 years), juvenile (3–10 years), subadult (11–15 years) and adult (> 15 years). The neonates were usually tied to their mother with a rope (approximately 2 m) around their necks.

Behavioural observations

Our subjects were taken for a walk around the village and/or spent time at an enclosure in the village for 3–6 hr per day, following the weekly schedule of the Surin Project. The mahouts usually stayed around their elephants and occasionally interacted with their elephants during activities. The volunteers and staff of the Surin Project also walked with the elephants, although they always maintained a greater distance between themselves and the elephants than the mahouts and did not interact with the elephants. During their walks, the elephants occasionally stopped walking to eat bark in the forest or the sugar cane that had been scattered for them in advance. During their time at the enclosure, the volunteers and staff did not stay in the enclosure, whereas the mahouts remained near their own elephants or at the shelter in the enclosure. All observations were conducted by S. Yasui, who also conducted the preliminary observations of the same study group from December 2011 to March 2012. All elephants showed little interest in the observer during the study periods, indicating that the observer had almost no influence on their behaviours.

The daily schedule comprised one activity (e.g. a walk or enclosure time) in the morning and one activity in the afternoon. All subjects walked or spent time in the enclosure together except when they showed health problems or were required to work elsewhere. Focal animal sampling (Altmann 1974) was conducted on one target animal during each activity, using a total of 10 females. All social behaviour relating to the focal animal were recorded continuously (Martin & Bateson 1993) using an IC digital voice recorder (SONY ICD-UX523) and a video camera (SONY HDR-550V), and the names and postures of the actor and recipient were also noted. All observation data on the elephants during both study periods are provided in Table 1. The total observation time was 271.9 hr. Each subject was observed 17–23 times (average 20.2 ± 1.89) for an average duration of 1.34 ± 0.58 hr. The distance between the target animal and the observer was 2–30 m. All subjects were under the authority of their mahouts. At few instances, the mahouts attempted to stop interactions, particularly severe aggressive interactions, between the elephants using vocal commands or physical contact. All observations were made following the guidelines on the ethics of animal studies of the Wildlife Research Centre of Kyoto University.

Definitions and terminology

We use the term 'touch' to refer only to the physical contact made with the tip of the elephant trunk. It has been shown that elephants exhibit social behaviours more frequently when they become excited (Garaï 1992; Plotnik & de Waal 2014). Therefore, we defined an excited situation as one in which the focal animal made any vocalisation combined with excited postures (head or tail raised and ears extended). This excited situation ended when the subject returned to the normal posture (de Silva et al. 2011; Moss et al. 2011). We used the modified versions of ethograms presented in previous studies for our observations (Table 2; Olson 2004; Moss et al. 2011).

Data analysis

Initially, we determined whether there were any differences in the observed number of times elephants touched different body parts and whether there were any age-related differences in the number of times elephants touched or received touches. We examined differences in touch frequencies between individuals and pairs of elephants. To calculate the touch frequency for each individual, the observed number of times that the focal animal touched or received touches was divided by the focal time. In contrast, differences in the touch frequencies of pairs were calculated using the following formula: $(O_{AB\text{-}A} + O_{AB\text{-}B}) / (T_{AB} + T_{BA})$, where

$O_{AB\text{–}A}$ indicates the number of times that A touched B when A was the focal animal, $O_{AB\text{–}B}$ indicates the number of times that A touched B when B was the focal animal, T_{AB} indicates the time during which both A and B were in the study group with A as the focal animal and T_{BA} indicates the same measurement with B as the focal animal.

We also examined whether touches were correlated with the proximity index for each pairs of elephants, which was calculated using the formula: $(P_{AB} + P_{BA}) / (T_{AB} + T_{BA})$, where P_{AB} indicates the time when A and B were in proximity to each other with A as the focal animal and P_{BA} indicates the same measurement with B as the focal animal. In this context, proximity refers to when either of the two individuals could touch the body of the other. Four individuals (Thong deng, Soi thong, Tuk or Kham koon) were excluded from the present analysis as they stayed in the same group for < 10 hr during each focal observation period. In addition, we did not include proximity data between Kaem sean and Nopa gao as they were tied to each other.

We then examined whether the frequency of touching increased when the elephants were excited. In the present analysis, we distinguished between excited situations in which the mahout interacted with the elephants, for example, using vocal commands or physical contact to calm their elephants (excited with mahouts) and those in which there was no interaction between the mahout and the elephant (excited). We also distinguished between normal situations in which the mahouts held the ears of their elephants to direct them (normal with mahouts) and those that did not require the ears to be held (normal). Thus, we compared the frequency of touches between four situations: normal, normal with mahouts, excited and excited with mahouts. In addition, we categorised the excited situations according to the perceived cause of the excitement (i.e. disturbance and play; see Table S1 of supplemental material for definitions) and compared the frequency of touches between the normal situations and each of these categories. We examined whether both the actor and recipient of the touches were excited or only one of these was excited.

To interpret the social context of the touches, we investigated the social behaviours that occurred just before and after the touch. We also investigated the relationship between the context of the touches and pair types: with or without adults, subadults and ‘young’ (juveniles and neonates). Here, each category indicates that one or both individuals of the pair belonged to that age category, for example, ’with adults’ indicates that one or both individuals of the pair were adults.

We also investigated whether the actor exhibited a threat posture during the touch.

We conducted all analyses using generalised linear mixed-effect models [GLMER function using the lme4 package in R software (Version 2.15.3)]. GLMER fits the model using the maximum likelihood method. The best model was then selected from all possible models with or without each explanatory variable based on the Akaike information criterion (AIC, Akaike 1974). The model with the lowest AIC value was chosen as the best model. Multiple pair-wise comparisons were then performed using Tukey's method with the GLHT function in the multcomp package. To examine the frequency at which elephants touched different body parts, we included the observed times of touch as a response variable, body part as an explanatory variable and log (focal time) as an offset. We also included animal identification (ID) as a random effect to avoid pseudo-replication (Hurlbert 1984). To analyse the effect of age on touch frequencies, we included the observed number of touches as the response variable, age class as an explanatory variable, log (focal time) as an offset and animal ID as a random effect. We tested the relationship between each touch and the proximity index by including the observed number of touches as the response variable, the proximity index as an explanatory variable, log (time when the two individuals in each pair remained in the study group) as an offset and pair ID as a random effect. To investigate the effect of excitement on touch frequency, we included the observed number of touches as the response variable, the situation (normal with mahout, normal, excited with mahout or excited) as an explanatory variable, log (focal time) as an offset and animal ID as a random effect. The Poisson distribution and a log link function were used for these analyses.

We categorised all social behaviours into one of the four groups: movement, touch/smell, aggression or play (see Table 2). To compare the effect of social behaviours on touch frequencies, we included the occurrence of a social behaviour (1 = yes or 0 = no) as the response variable, the touch type as an explanatory variable, and pair ID as a random effect. We also investigated the effect of pair type (with or without adults, subadults and young) on social behaviour by including the occurrence of a social behaviour (1 = yes or 0 = no) as the response variable, the pair type as an explanatory variable, and pair ID as a random effect. We also included command (whether the mahouts used a vocal command to stop interactions following the touch as an explanatory variable to investigate the effect of interactions with the mahouts. The binomial distribution and a logit link function were used for these analyses.

In addition, we also analysed the difference in the touch type between pair types by including the observed number of U-type lip touches as the response variable, the observed number of U-type genital touches and pair type (with or without adults, subadults, juveniles and neonates) as explanatory variables, and pair ID as a random effect. The Poisson distribution and a log link function were used for this analysis.

RESULTS

Overview

In most cases, the 10 female elephants touched the body parts of other elephants with their trunks in a U-shape (U-type, Fig. 1a), but occasionally with their trunks in an S-shape (S-type, Fig. 1b). All elephants performed or received both U-type and S-type touches during the study. The elephants performed S-type touches on 187 occasions when touching others' lips (193 times) and on 4 occasions when touching others' genitals.

The observed frequency of touches differed between body parts (Fig. 2). We distinguished between touches to the lips and mouth by observing whether the elephants touched around the mouth (lips) or inside the mouth (mouth). Recipients opened their mouths during mouth touches whereas they usually closed their mouth during lip touches. All subjects performed touches to all body parts, despite the varying body size of the focal animals. The elephants touched the lips and genitals of other elephants more frequently than any other parts of the body (Fig. 2, lips vs all other body parts, $P < 0.01$; genitals vs all other body parts, $P < 0.01$). Therefore, we specifically focused on these two touches. In 83 of 193 S-type touches, the elephants performed a U-type touch either before or after the S-type touch at the same distance from the recipient. Thus, it appeared as natural and easy for the elephants to touch with their trunks in the U-type shape; however, they also sometimes touched with their trunks in the S-type shape. The observed number of each touch type during each focal period is shown in Table 3. As observed, individuals that performed or received U-type touches frequently did not typically perform or receive S-type touches frequently.

Differences between pairs in touch frequency are shown in Table 4. Of the top 10% of pairs that performed U-type lip touches, five also ranked in the top 10% for U-type genital touches. In contrast, of the top 10% of pairs that performed S-type lip touches, only one pair ranked in the top 10% for U-type genital touches, and no pair ranked in the top 10% for U-type lip touches. In Table 4, the individuals are arranged according to age (oldest to youngest). For all touch types, younger individuals touched older individuals at an almost identical frequency to older individuals touching younger individuals in the top 10% of pairs. The subadults received S-type lip touches more frequently than the adults (N = 10; adults vs subadults: coefficient = − 1.41 ± 0.57, z = − 2.47, P = 0.04; adults vs juveniles: coefficient = − 0.76 ± 0.59, z = − 1.29, P = 0.40; subadults vs juveniles: coefficient = 0.66 ± 0.0.58, z = 1.13, P = 0.50). However, there was no relationship between age class and the frequency of receiving U-type lip and U-type genital touches). One mother (Kaem sean) only gave U-type lip touches 0.07 times/hr and U-type genital touches 0.14 times/hr to her son, Nopa gao, despite them usually being attached to each other with a rope. Kanoon performed the highest frequency of U-type touches to Nopa gao (U-type lip: 0.99 times/hr; U-type genital: 2.55 times/hr). Kaem sean did not give any S-type lip touches to her son.

Relationship between touches and proximity

We found that the proximity index was not related to the occurrence of aggressive behaviours (N = 74). In addition, we did not observe any aggressive behaviours between pairs whose proximity index was > 0.15. Therefore, we used the data from all 74 pairs in our analyses. The models for U-type lip touches and U-type genital touches, including the proximity index, were chosen as the best models (Fig. 3, U-type lip: coefficient = 7.84 ± 1.16; U-type genital: coefficient = 8.47 ± 0.87). In contrast, the model that included the proximity index was not selected as the best model for S-type touches. Therefore, proximity is not necessarily related to the frequency of S-type touches.

Relationship between touches and excitement

For the 10 focal animals, frequencies of all touch types were relative to the situation (Table 5a). Elephants performed U-type lip and U-type genital touches more frequently when they were excited (excited and excited with mahouts) than under normal situations (normal and normal with mahouts), with a significant difference between normal and excited. The frequency of U-type genital touches was not related to the type of situation either with or without interaction with the mahouts, and the frequency of S-type lip touches did not significantly differ between normal and excited situations which involved no interaction with the mahouts.

In 347 of 635 excited events, we could identify the cause of excitement, which included disturbance, play and interaction by the mahouts. The definitions of each of these are provided in Table S1 (supplemental material). In our analyses, we examined the touch frequencies in each of these situations by including normal, disturbance and play events that were observed for a sufficient time and were unrelated to human interaction, as well as normal, disturbance and play situations involving interaction with mahouts. The model comprising these detailed situations was selected as the best model for all touch types (Table 5b). U-type lip and genital touches were observed significantly more frequently during disturbance and play than during normal situations ($P < 0.01$). In addition, S-type lip touches were observed more frequently during disturbance and play involving interaction no interaction with the mahouts than during normal situations involving interaction with the mahouts ($P < 0.05$), whereas was no significant difference existed among disturbance, play and normal situations involving no interactions with the mahouts.

During disturbances, both the actor and recipient were excited for 49.99% ± 21.22% of U-type lip touches and 45.85% ± 19.48% of U-type genital touches. During play, both the actor and recipient were excited for 71.43% ± 45.18% ($N = 10$)

of U-type lip touches and 44.27% ± 39.80% of U-type genital touches.

Behavioural context before and after touches

There was no significant difference between touch types in the proportion of play behaviour observed before or after touches (Fig. 4, U-type lip: $N = 1444$; S-type lip: $N = 193$; U-type genital: $N = 807$). When analysing the proportion of touches in which aggressive behaviour occurred before the touches, the model that included touch type was selected as the best model. A higher proportion of aggressive behaviour occurred before S-type lip touches than before U-type lip and genital touches (Fig. 4, S-type lip vs U-type genital: coefficient = − 3.64 ± 1.07, $z = 3.41$, $P < 0.01$; U-type lip vs U-type genital: coefficient = 0.11 ± 1.24, $z = 0.09$, $P = 0.99$; U-type lip vs S-type lip: coefficient = − 3.54 ± 0.79, $z = -4.45$, $P < 0.01$).

Aggressive behaviour was never observed after U-type genital touches; therefore, we used only the data for U-type lip and S-type lip touches to investigate the relationship between touch types and aggressive behaviour after the touch. The model that included touch type was selected as the best model, and it was found that a higher proportion of aggressive behaviour occurred after S-type lip touches than after U-type lip touches (Fig. 4, U-type lip: coefficient = − 3.90 ± 0.63;

S-type lip: coefficient = − 2.27 ± 0.25). The results of the analyses of all social behaviours before and after touches are shown in Table S2 (supplemental material).

The elephants exhibited a higher proportion of threatening postures during S-type lip touches than during U-type lip and genital touches (S-type lip vs U-type genital: coefficient = 3.48 ± 0.25, $z = 13.73$, $P < 0.01$; U-type lip vs U-type genital: coefficient = 0.09 ± 0.17, $z = 0.52$, $P = 0.86$; U-type lip vs S-type lip: coefficient = − 3.38 ± 0.79, $z = -14.87$, $P < 0.01$).

S-type lip touches were not observed in neonates; therefore, they were excluded from this analysis. Play behaviour occurred before S-type lip touches at a higher frequency in the pairs with young individuals than in those without young individuals (Fig. 5, with young: $N = 111$, coefficient = 2.46 ± 1.95, without young: $N = 82$, coefficient = − 4.39±1.01) but at a lower frequency in pairs with adults than in those without adults (with adults: $N = 91$, coefficient = − 4.50 ± 1.01; without adults: $N = 102$, coefficient = 2.66 ± 1.05). There was no relationship between the occurrence of subadults in a pair (with subadults: $N = 131$; without subadults: $N = 62$) and the frequency of play behaviour before S-type lip touches. The frequencies of play behaviour after S-type lip touches were neither related to any pair type nor to vocal commands from the mahouts.

The frequency of aggressive behaviour before and after S-type lip touches was not related to any pair type. The frequency of aggressive behaviour after S-type lip touches was also unrelated to vocal commands from the mahouts.

U-type touch interaction with neonates

As shown in Fig. 6, pairs that included neonates had a tendency to perform fewer U-type lip touches and more U-type genital touches than pairs without neonates. The model that included U-type genital touches and pair type with neonates was selected as the best model (U-type genital: coefficient = 0.05 ± 0.01; pair type with neonates: N = 30, coefficient = − 0.80 ± 0.39; pair type without neonates: N= 84, coefficient = 1.71 ± 0.43). U-type genital touches were observed in 14 of 30 pairs with neonates. In 70.80% ± 7.81% of these touches, it was the elders (those older than neonates) who touched the genitals of the neonates.

DISCUSSION In this study, we found that the female Asian elephants touched the lips of other individuals using two different trunk shapes: U-shaped trunks and S-shaped trunks. To the best of our knowledge, this is the first study to analyse the functions of different touch types in elephants.

As shown in Tables 3 and 4, touch frequencies varied between individuals and pairs; therefore, we included animal ID or pair ID as a random factor in all analyses. Only one of the analysed variables was affected by age: the subadults received S-type lip touches more frequently than the adults. This could be related to the time when the subadults had been in the study group, as will be discussed later.

We determined whether the U-type and S-type touches were affiliative behaviours by investigating the relationship between these touches and the proximity index. In our study group, the proximity indices were not positively correlated with aggressive behaviours. In addition, pairs with high proximity indices did not exhibit any aggressive behaviour. These findings confirmed that the proximity index was an appropriate affiliative index in our study group. Further, we found that the frequencies of U-type lip and genital touches were positively correlated with the proximity index, whereas the frequency of S-type lip touches was not, which may suggest that the U-type lip and genital touches are affiliative. This supports previous studies on captive Asian elephants that used trunk tip touches as indicators of affiliative or investigative behaviours (Garaï 1992;

Slade-Cain et al. 2008; Makecha et al. 2012). Similarly, in African elephants, studies have described mouth and genital touches as types of greeting behaviours (Moss 1988; Moss et al. 2011).

Next, we examined whether the touches were used more frequently when the elephants were excited. U-type lip and genital touches were observed more frequently during excited situations than during normal situations and were frequently used when elephants became excited because of disturbance. Furthermore, for many of the U-type touches, both the actor and the recipient were excited. These findings might suggest that the elephants touch the lips or genitals of other individuals with U-shaped trunks to reassure others and themselves during disturbances. Similarly, in a captive group of four Asian elephants, Garai (1992) reported that lip and genital touches occurred more frequently during arousal than during non-arousal. Furthermore, Plotnik and de Waal (2014) showed that captive Asian elephants frequently touched the genitals and mouths of other individuals following stressful situations. Our results supported these patterns and also showed that the trunk touch type varied between circumstances. Therefore, as with humans and non-human primates (Hertenstein et al. 2006), physical contact between elephants appears to provide reassurance and comfort.

Further, we found that female Asian elephants frequently used U-type touches when they became excited during play. This might suggest that U-type lip and genital touches are part of their play behaviour. In addition, S-type lip touches were observed more frequently when elephants were excited during play than during normal situations, despite there being no relationship between this and disturbance. Therefore it appears that female Asian elephants do not use S-type touches for reassurance but as a playful behaviour.

We also considered the effect of interactions with the mahouts on elephant behaviour during these analyses. Under normal conditions, the elephants showed less U-type and S-type lip touches when the mahouts pulled their ears than when they did not. Mahouts usually pulled the ears of their elephants to direct them when walking and it is possible that by doing so, mahouts affected the activity of these elephants, resulting in elephants interacting less frequently with others while walking than during other situations, such as during feeding or bathing. U-type lip touches were also observed less frequently during excited situations involving interactions with the mahouts than those involving no such interaction. to compare, the frequency of U-type genital touches was not significantly different between excited situations and normal situations with and without interactions of the mahouts. These results may indicate that U-type genital touches were not as greatly affected by interactions with the mahouts as U-type and S-type lip touches. However, additional systematic studies are required to better understand the relationship between elephants and their mahouts.

In addition, we investigated whether the touches were related to aggression or play. Aggressive behaviour rarely occurred before or after U-type lip and genital touches, and the elephants also rarely displayed threatening postures during these touches. In contrast, the elephants exhibited aggressive behaviour more frequently before and after S-type lip touches, during which the actors typically adopted threatening postures. These findings support the results of the first analysis that investigated the relationship between U-type touches and the proximity index and may suggest that S-type lip touching is a more aggressive behaviour than U-type touching. Garaï (1992) reported that mouth touching, which includes touches with complex trunk twisting, was often observed in pairs of captive Asian elephants that showed frequent aggressive interactions and suggested that this may reduce aggressive motivation. Because the actors of S-type lip touches usually showed threatening postures, it might be difficult to consider this as appeasement behaviour. However, both types of mouth touches in Garaï's study and S-type lip touches in our study were associated with aggressive behaviour. It was occasionally difficult to observe whether the elephants were touching the other elephants inside or around the mouth as the actor's trunk tip was hidden by the recipient's trunk. Thus, it is possible that the S-type lip touch in the present study and the mouth touch with twisted trunk in Garaï's study refer to the same behaviour.

As shown in Fig. 4, the likelihood of S-type lip touches escalating to aggressive behaviour was not very high. Furthermore, this behaviour was never observed in neonates, which are much smaller and weaker than the others. Thus, we may suggest that female Asian elephants change their trunk shape during lip touching, a frequently observed affiliative interaction, to show dominance both visually and tactually. In this study, the subadults received S-type lip touches more frequently than the adults, further supporting this interpretation, as two of the three subadults were the newest members of the group and so may have needed to find their places in the dominance hierarchy.

Play behaviour occurred before S-type lip touches at a higher frequency in pairs without adults than in pairs with adults. Therefore, it may be possible that this touch type also functions as a play behaviour, particularly among young individuals, but then develops into aggressive behaviour among adults. Similar behavioural changes as a consequence of maturation are observed in other species; for example, 'chase' and 'kick' behaviours in primates (Nishida et al. 2010; Cordoni & Palagi 2011). There are few studies on the change in these behaviours from the development viewpoint, though Nishida (2003) revealed that in wild chimpanzees the reaction of recipients to such behaviours change depending on the actors' age.

Finally, we examined whether there were any differences in the behaviours depending on the age classes of the pairs. We found that the pairs that included neonates used U-type genital touches more frequently than the pairs without neonates. Previous studies on genital touches in Asian elephants have mainly focused on reproductive behaviour (Meyer et al. 2008; Slade-Cain et al. 2008). However, our results suggest that U-type genital touches may have an additional function unrelated to reproductive behaviour. Elders touched the genitals of neonates more frequently than neonates touched the genitals of the elders. Therefore, it is possible that this behaviour was performed to assess the health of the neonates while demonstrating affiliative relationships, as some previous studies have suggested for both Asian and African elephants (Sukumar 2003; Moss et al. 2011).

In this study, the elephants used U-type lip and genital touches during affiliative interactions and disturbance, possibly for reassurance. Both touches were observed frequently, as noted in previous studies (Garaï 1992; Makecha et al. 2012). Therefore, we recommend that more research is conducted on this topic, because it might be possible that U-type touches in Asian elephants are comparable with social grooming in primates or flipper rubbing in dolphins (Nakamura & Sakai 2013) as female Asian elephants also appear to use these touches as indicators of affiliative relationships. We did not focus on the functions of these touch types from the viewpoint of chemical communication. Sexual maturation or dominance rank may be related to touch type; however, we were unable to obtain this information on our subjects. Therefore, it is also possible that each trunk touch type has additional functions, such as individual recognition or investigation of food, which requires further research.

S-type lip touches were observed in agonistic interactions and appeared to be related to dominant behaviour. Animals often threaten opponents using visual displays or vocalisations (Deag 1977; Randall 2001), and animals occasionally place a part of their body over an opponent's body, such as mounting, to show dominance (Maslow 1936; Goodwin et al. 1997). Both Asian and African elephants place their head over another elephant's head or back to show dominance (Olson 2004; Moss et al. 2011). However, in the case of S-type lip touches, the actors touch the lips of recipients and do not put their weight on the bodies of recipients. Thus, this behaviour appears to be intermediate between a visual threat display and physical dominance behaviour and may be used as an initial step in an agonistic interaction, –similar examples of which are rare in other mammals. Because trunk touching does not hurt the recipient, it may also be possible for young individuals to use S-type lip touches as one of their play behaviours. During play, it is common to act out dominant or submissive roles, and thus it is reasonable to assume that Asian elephants may use S-type lip touches as one of their play behaviours. However, we need to collect more data and perform more detailed analyses to understand the reason for these elephants exhibiting this behaviour.

Some previous studies have reported the laterality of elephant trunks (Martin & Niemitz 2003; Haakonsson & Semple 2009). For example, Martin and Niemitz (2003) reported that wild Asian elephants have a side preference for twisting their trunk when they grab grasses, and Haakonsson and Semple (2009) reported that captive Asian elephants have a side preference during feeding, trunk swinging, self-touching and sand bathing. These side preferences are considered to be related to the brain hemisphere. In the present study, we did not consider the side to which the subjects twisted their trunks during S-type touches. However, it is possible that the elephants also have a side preference for these touches, which is related to their side preference during feeding.

The present study had several limitations. Our subjects were born in captivity and had lived and worked with their mahouts since they were young. During our observations, the mahouts usually stayed around their elephants, and we found that interactions with the mahouts influenced the social behaviours of these elephants to some extent. Furthermore, it should be noted that the mere existence of mahouts and/or the relationship with them, may affect the social behaviour of the elephants, most of whom do not have as much social experience as wild elephants. Therefore, we need to confirm these results in wild Asian elephants to understand Asian elephant societies.

Though the present preliminary investigation into the role(s) of trunk touching in social relationships between Asian elephants, we demonstrated a novel social ability of this species that will assist in understanding relationships between individuals and their societies.

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REFERENCES Akaike H. 1974. A new look at the statistical model identification. IEEE Trans Automat Contr. 19:716–723.

Altmann J. 1974. Observational study of behaviour: Sampling methods. Behaviour. 49:227–267.

Cordoni G, Palagi E. 2011. Ontogenetic trajectories of chimpanzee social play: Similarities with humans. PloS One. 6:e27344.

Deag JM. 1977. Aggression and submission in monkey societies. Anim Behav. 25: 465–474.

de Silva S. 2010. Acoustic communication in the Asian elephant, *Elephas maximus maximus*. Behaviour. 147:825–852.

de Silva S, Ranjeewa ADG, Kryazhimskiy S. 2011. The dynamics of social networks among female Asian elephants. BMC Ecology. 11:17.Dunbar RI. 1991. Functional significance of social grooming in primates. Folia Primatologica. 57:121–131.

Dunbar RI. 2010. The social role of touch in humans and primates: Behavioural function and neurobiological mechanisms. Neurosci Biobehav Rev. 34:260–268.

Gadgil M, Nair P. 1984. Observation on the social behaviour of free ranging groups of tame Asiatic elephant (*Elephas maximus* Linn). Proc Indian Acad Sci. 93:225–233.

Garaï ME. 1992. Special relationships between female Asian elephants (*Elephas maximus*) in zoological gardens. Ethology. 90:187–205.

Goodwin D, Bradshaw JWS, Wickens SM. 1997. Paedomorphosis affects agonistic visual signals of domestic dogs. Anim Behav. 53:297–304.

Haakonsson JE, Semple S. 2009. Lateralisation of trunk movements in captive Asian elephants (*Elephas maximus*). Laterality. 144:413–422.

Hertenstein MJ, Verkamp JM, Kerestes AM, Holmes RM. 2006. The communicative functions of touch in humans, nonhuman primates, and rats: A review and synthesis of the empirical research. Genet Soc Gen Psychol Monogr. 132:5–94.

Hurlbert SH. 1984. Pseudoreplication and the design of ecological field experiments. Ecol Monogr. 54:187–211.

Kasper C, Voelkl B. 2009. A social network analysis of primate groups. Primates. 50:343–356.

Kurt F, Garaï ME. 2006. The Asian elephant in captivity: A field study. Cambridge India: Foundation Press.

Langbauer WR Jr. 2000. Elephant communication. Zoo Biol. 19:425–445.

Makecha R, Fad O, Kuczaj SA. 2012. The role of touch in the social interactions of Asian elephants (*Elephas maximus*). Int J Comp Psychol. 25:60–82.

Martin F, Niemitz C. 2003. "Right-trunkers" and "left-trunkers": side preferences of trunk movements in wild Asian elephants (*Elephas maximus*). Int J Comp Psychol. 117:371–379.

Martin P, Bateson P. 1993. Measuring behaviour: An introductory guide. Cambridge: Cambridge University Press.Maslow AH. 1936. The role of dominance in the social and sexual behaviour of infra-human primates: III. A theory of sexual behaviour of infra-human primates. Pedagog Semin J Genet Psychol. 48:310–338.

McCowan B, Anderson K, Heagarty A, Cameron A. 2008. Utility of social network analysis for primate behavioural management and well-being. Appl Anim Behav Sci. 109:396–405.

McNeill D. 1992. Hand and mind: What gestures reveal about thought. Chicago: University of Chicago Press.

Meyer JM, Goodwin TE, Schulte BA. 2008. Intrasexual chemical communication and social responses of captive female African elephants, *Loxodonta africana*.

Anim Behav. 76:163–174.

Moss CJ. 1988. Elephant memories: Thirteen years in the life of an elephant family. New York: William Morrow and Co. Inc.

Moss CJ, Croze H, Lee PC, editors. 2011. The Amboseli elephants: A long-term perspective on a long-lived mammal. Chicago: University of Chicago Press.

Nair S, Balakrishnan R, Seelamantula CS, Sukumar R. 2009. Vocalizations of wild Asian elephants (*Elephas maximus*): structural classification and social context. J Acoust Soc Am. 126:2768–2778.

Nakamura M, Sakai M. 2013. Social touch in apes and dolphins. In: Yamagiwa J, Karczmarski L, editors. Primates and cetaceans: Field research and conservation of complex mammalian societies. Tokyo: Springer Japan; p. 355–383.

Nishida T. 2003. Harassment of mature female chimpanzees by young males in the Mahale Mountains. Int J Primatol. 24:503–514.

Nishida T, Zamma K, Matsusaka T, Inaba A, McGrew WC. 2010. Chimpanzee behaviour in the wild. An audio-visual encyclopaedia. Tokyo: Springer Japan.

O'Connell-Rodwell CE. 2007. Keeping an "ear" to the ground: seismic communication in elephants. Physiology. 22:287–294.

Olson D. 2004. Elephant husbandry resource. Lawrence (KS): Allen Press.

Onodera S, Hicks TP. 1999. Review: Evolution of the motor system: Why the elephant's trunk works like a human's hand. Neuroscientist. 5:217–226.

Payne KB, Langbauer WR Jr, Thomas EM. 1986. Infrasonic calls of the Asian elephant (*Elephas maximus*). Behav Ecol Sociobiol. 18:297–301.

Plotnik JM, de Waal FBM. 2014. Asian elephants (*Elephas maximus*) reassure others in distress. PeerJ. 2:e278.

Polthanee A, Promkhambut A. 2014. Impact of climate change on rice-based cropping systems and farmers' adaptation strategies in northeast Thailand. Asian J Crop Sci. 6:262–272.

Poole JH, Moss CJ. 2008. Elephant sociality and complexity: the scientific evidence, In: Wemmer C, Christen CA, editors. Elephants and ethics: towards a morality of coexistence. Baltimore: John Hopkins University Press; p. 69–98.

Randall JA. 2001. Evolution and function of drumming as communication in mammals. Am Zool. 41:1143–1156.

Rasmussen LEL. 1999. Evolution of chemical signals in the Asian elephant, *Elephas maximus*: behavioural and ecological influences. J Biosci. 24:241–

251.

Rasmussen LEL, Krishnamurthy V. 2000. How chemical signals integrate Asian elephant society: The known and the unknown. Zoo Biol. 19:405–423.

Sakai M, Hishii T, Takeda S, Kohshima S. 2006. Flipper rubbing behaviours in wild bottlenose dolphins (*Tursiops aduncus*). Mar Mam Sci. 22:966–978.

Schel AM, Rawlings B, Claidiere N, Wilke C, Wathan J, Richardson J, Pearson S, Herrelko ES, Whiten A, Slocombe K. 2013. Network analysis of social changes in a captive chimpanzee community following the successful integration of two adult groups. Am J Primatol. 75:254–266.

Slade BE, Schulte BA, Rasmussen LEL. 2003. Oestrous state dynamics in chemical communication by captive female Asian elephants. Anim Behav. 65:813–819.

Slade-Cain BE, Rasmussen LEL, Schulte BA. 2008. Estrous state influences on investigative, aggressive, and tail flicking behaviour in captive female Asian elephants. Zoo Biol. 27:167–180.

Spruijt BM, van Hooff JA, Gispen WH. 1992. Ethology and neurobiology of grooming behaviour. Physiol Rev. 72:825–852.

Sukumar R. 2003. The living elephants: evolutionary ecology, behaviour, and conservation. New York: Oxford University Press.

Tamaki N, Morisaka T, Taki M. 2006. Does body contact contribute towards repairing relationships? The association between flipper-rubbing and aggressive behaviour in captive bottlenose dolphins. Behav Prosses. 73:209–215.

Thitaram C, Chansitthiwet S, Pongsopawijit P, Brown JL, Wongkalasin W, Daram P, Roongsri R, Kalmapijit A, Mahasawangkul S, Rojanasthien S, et al. 2009. Use of genital inspection and female urine tests to detect oestrus in captive Asian elephants. Anim Reprod Sci. 115:267–278.

Vidya TNC, Sukumar R. 2005. Social and reproductive behaviour in elephants. Curr Sci. 89:1200–1207.

Wittemyer G, Douglas-Hamilton I, Getz WM. 2005. The socioecology of elephants: analysis of the processes creating multitiered social structures. Anim Behav. 69:1357–1371.

APPENDICES

Table S1.

Reasons for excitement

Reason	Description	No. of events (with and without mahout interactions)
Disturbance	Elephants were disturbed by the sounds of cars or firecrackers, other species such as dogs or buffaloes and other elephants' vocalisations	234 (87, 147)
Play	Elephants became excited during bathing or dusting or before feeding	64 (20, 44)
Mahout's interaction	Elephants reacted to interactions with their mahouts	49 (49, 0)
Unknown	We were unable to identify the reason why elephants became excited.	288 (93, 195)

Table S2.

The social behaviours that occurred before or after touches. The percentages were calculated using the fomula $N_{\text{before or after}}/N_{\text{touch}} \times 100$ (where $N_{\text{before or after}}$ = the number of times that behaviouroccurred in each category before or after the touches and N_{touch} = the total number of touch events). * indicates that the rates were significantly different (GLMER followed by Tukey's test). We did not perform statistical analyses for 'unknown'.

Timing	Touch	Categories of behaviours before or after touch (%)				
		Movement	Play	Aggression	Touch or smell	Unknown
Before	U-type lip (*N*= 1444)	45.2	2.2	0.1	51.0	1.5
	U-type genital (*N*= 807)	41.9	1.9	0.1	54.2	1.9
	S-type lip (*N*= 193)	35.2	7.8	5.2	51.2	0.6
After	U-type lip (*N*= 1444)	40.2	2.8	0.2	52.6	4.3
	U-type genital (*N*= 807)	40.5	1.6	0.0	52.3	5.6
	S-type lip (*N*= 193)	30.6	5.7	9.3	50.3	4.1

Table 1.

Subjects included in this study. The individuals with bold characters were the focal animals for this study. o indicates that the individual stayed in the group during the particular period while × indicates that they did not stay in the group during that particular period. * means that the individual joined or left the group in the middle of the period.

Name (Abbreviations)	Sex	Age (years)	Age class	Relationship	Period1	Period2	Focal time (hr)
Kaem sean (KS)	F	26	Adult		o	o	25.0
Fah sai (FS)	F	23	Adult		o	o	28.4
Mem (ME)	F	20	Adult		o	o	30.2
Euang loaung (EL)	F	18	Adult		o	o	26.2
Sai faa (SF)	F	15	Subadult		o	o	25.2
Kanoon (KN)	F	13	Subadult		o	o	24.7
Gem (GE)	F	11	Subadult		o	o	27.4
Nong nung (NO)	F	9	Juvenile		o	o	28.4
Nung ning (NU)	F	9	Juvenile		o	o	28.0
Teng mo (TM)	F	7	Juvenile		o	o	28.4
Nopa gao	M	1	Neonate	Kaem sean's son	o	×	–
Ploy	F	17	Adult		×	o	–
Khwan	F	1	Neonate	Ploy's daughter	×	o	–
Thong deng	F	19	Adult		*	×	–
Soi thong	F	0.67	Neonate	Thong deng's daughter	*	×	–
Tuk	F	10	Juvenile		*	×	–
Kham koon	F	5	Juvenile		×	*	–

Table 2.

Ethogram of social behaviours.

Behavioiur	Definition
MOVEMENT	
Approach	Move towards other individual such that they can touch each other (reach distance)
Leave	Move away from the reach distance of other individual
Follow	Walk behind other individual while maintaining the reach distance
TOUCH OR SMELL	
Touch	Touch other elephant's body (lip, genitals, body, head, mouth, ear, leg, tail, trunk, trunk tip) with the trunk tip
Touch with other body parts	Touch other elephant's body with other body parts, such as body, tail, leg
Trunk toward	Move trunk towards other elephant
AGGRESSION	
Head butt	Thump head against other elephant's head or body
Trunk hit	Slap other elephant's head or body with trunk
Kick	Kick other elephant's body with foreleg or hind leg
Trunk/head over head	Put trunk or head on other elephant's head
Trunk/head over back-aggressive	Put trunk or head on other elephant's back when the recipient is standing
Push-aggressive	Push other elephant's head with raised head
Push with tush	Push other elephant's body with tush
PLAY	
Mount	Put forelegs on other elephant's body from behind or side
Trunk/head over back -play	Put trunk or head on other elephant's back when the recipient is sitting
Push-play	Push other elephant's head or body with head or body without raised head
Rub	Rub head or body against other elephant's head or body
VOCALISATION	
Trunk smack	Hit ground with trunk outside and make sound
Air burst	Blow air from trunk and make noise
Other vocalisation	Rumble, growl, trumpet, squeak, chirp
POSTURE	
Threat posture	Raise head and extend ears towards opponent

Table 3.

Observed times and frequencies of touches in each focal animal.

Focal animal	U-type lip			U-type genital			S-type lip		
	N (times)	Act (times/hr)	Receive (times/hr)	N (times)	Act (times/hr)	Receive (times/hr)	N (times)	Act (times/hr)	Receive (times/hr)
KS	85	1.68	1.72	25	0.32	0.76	10	0.24	0.16
FS	226	4.43	3.52	96	1.13	2.25	25	0.60	0.28
ME	63	1.19	0.89	101	2.75	0.60	6	0.13	0.07
EL	197	3.06	4.47	67	1.11	1.45	3	0.00	0.11
SF	138	3.22	2.27	45	0.91	0.87	41	0.36	1.27
KN	138	2.87	2.71	169	4.57	2.18	23	0.36	0.57
GE	198	4.49	2.74	102	3.40	0.33	8	0.07	0.22
NO	151	2.46	2.85	52	1.20	0.63	21	0.18	0.56
NU	116	2.29	1.86	34	0.68	0.54	54	1.48	0.50
TM	132	2.25	2.39	118	0.77	3.31	2	0.04	0.04

Table 4

Observed touch frequencies for each pair. 'Other' shows the average frequency with which the animals other than the focal animals performed touches with the focal animal. The values that rank in the top 10% are highlighted.

(a) U-type lip

		Recipient										
		KS	FS	ME	EL	SF	KN	GE	NO	NU	TM	Other
Actor	KS		0.31	0.02	0.25	0.11	0.42	0.16	0.14	0.02	0.06	0.10
	FS	0.17		0.16	**1.63**	0.20	0.21	0.07	**1.50**	0.18	0.11	0.03
	ME	0.02	0.05		0.16	0.23	0.22	0.05	0.21	0.00	0.04	0.14
	EL	0.21	**0.88**	0.07		**1.13**	0.02	0.08	0.21	0.18	0.11	0.05
	SF	0.04	0.35	0.02	**1.54**		0.07	0.10	0.19	0.33	0.08	0.26
	KN	**0.76**	0.14	0.04	0.02	0.14		0.08	0.08	0.10	0.31	0.23
	GE	0.20	0.04	0.09	0.08	0.16	0.18		0.16	0.04	**2.67**	0.01
	NO	0.18	**0.99**	0.12	0.24	0.21	0.12	0.07		0.27	0.07	0.01
	NU	0.02	0.33	0.02	0.31	0.25	0.14	0.23	0.44		0.45	0.00
	TM	0.15	0.20	0.05	0.11	0.00	0.29	**1.63**	0.13	**0.74**		0.00
	Other	0.14	0.03	0.14	0.23	0.07	0.27	0.04	0.06	0.01	0.01	

(b) U-type genital

		Recipient										
		KS	FS	ME	EL	SF	KN	GE	NO	NU	TM	Other
Actor	KS		0.02	0.00	0.04	0.02	**0.32**	0.02	0.00	0.02	0.00	0.02
	FS	0.00		0.00	**0.44**	0.04	0.02	0.05	**0.48**	0.04	0.02	0.00

		KS	FS	ME	EL	SF	KN	GE	NO	NU	TM	Other
	ME	0.15	0.28		0.09	0.14	0.31	0.02	0.03	0.07	0.07	0.55
	EL	0.04	0.56	0.00		0.29	0.02	0.02	0.02	0.04	0.00	0.08
	SF	0.00	0.20	0.02	0.41		0.11	0.04	0.02	0.08	0.00	0.14
	KN	0.56	0.08	0.06	0.15	0.11		0.12	0.16	0.14	0.24	0.98
	GE	0.00	0.04	0.07	0.02	0.04	0.16		0.04	0.04	2.98	0.01
	NO	0.00	0.77	0.02	0.11	0.04	0.06	0.04		0.04	0.04	0.05
	NU	0.04	0.16	0.00	0.06	0.06	0.22	0.05	0.04		0.05	0.01
	TM	0.04	0.07	0.00	0.02	0.02	0.20	0.20	0.00	0.15		0.01
	Other	0.04	0.02	0.15	0.11	0.07	0.16	0.01	0.05	0.00	0.02	

(c) S-type lip

		Recipient										
		KS	FS	ME	EL	SF	KN	GE	NO	NU	TM	Other
Actor	KS		0.02	0.02	0.00	0.00	0.20	0.08	0.00	0.00	0.00	0.00
	FS	0.17		0.00	0.00	0.22	0.19	0.09	0.00	0.02	0.00	0.00
	ME	0.02	0.00		0.00	0.08	0.06	0.02	0.03	0.00	0.00	0.00
	EL	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.02	0.02	0.00
	SF	0.02	0.02	0.00	0.00		0.00	0.04	0.08	0.21	0.00	0.00
	KN	0.02	0.14	0.06	0.02	0.00		0.02	0.00	0.02	0.00	0.02
	GE	0.08	0.00	0.00	0.00	0.06	0.00		0.00	0.00	0.02	0.00
	NO	0.00	0.00	0.00	0.00	0.00	0.02	0.02		0.14	0.02	0.00
	NU	0.04	0.05	0.00	0.09	0.68	0.02	0.07	0.43		0.00	0.00
	TM	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02		0.00

Other	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table 5.

Statistical results of the generalised linear mixed-effect models followed by Tukey's test for the analyses of excited situations. m refers to situations with interactions by the mahouts. * indicates $P < 0.05$ and ** indicates $P < 0.01$.

	U-type lip			U-type genitals			S-type lip		
(a) Excited or normal situations	Coefficient	*z*	*P*	Coefficient	*z*	*P*	Coefficient	*z*	*P*
Normal(m) vs. normal	− 0.90 ± 0.14	− 6.43	**	0.05 ± 0.12	0.42	0.98	− 1.77 ± 0.59	− 3.02	*
Normal(m) vs. excited(m)	− 1.91 ± 0.16	− 11.67	**	− 1.35 ± 0.16	− 8.54	**	− 0.91 ± 0.82	− 1.11	0.66
Normal(m) vs. excited	− 2.21 ± 0.15	− 14.38	**	− 1.33 ± 0.15	− 9.06	**	− 2.03 ± 0.66	− 3.10	*
Normal vs. excited(m)	− 1.01 ± 0.09	− 10.64	**	− 1.40 ± 0.12	− 11.78	**	0.86 ± 0.58	1.47	0.43
Normal vs. excited	− 1.31 ± 0.08	− 17.06	**	− 1.38 ± 0.11	− 13.13	**	− 0.26 ± 0.31	0.31	0.82
Excited(m) vs. excited	− 0.30 ± 0.11	− 2.63	*	0.02 ± 0.15	0.13	0.99	− 1.12 ± 0.65	− 1.72	0.29
(b) Detailed situations	Coefficient	*z*	*P*	Coefficient	*z*	*P*	Coefficient	*z*	*P*
Normal(m) vs normal	− 0.91 ± 0.14	− 6.48	**	0.09 ± 0.12	0.73	0.97	− 1.75 ± 0.59	− 3.00	*
Normal(m) vs disturbance(m)	− 2.22 ± 0.18	− 12.69	**	− 1.55 ± 0.18	− 8.49	**	− 1.17 ± 0.92	− 1.27	0.78
Normal(m) vs disturbance	− 2.50 ± 0.17	− 14.33	**	− 1.09 ± 0.21	−5.19	**	− 2.32 ± 0.74	− 3.15	*
Normal(m) vs play(m)	− 1.96 ± 0.22	− 8.81	**	− 1.31 ± 0.25	− 5.29	**	− 1.61 ± 0.92	− 1.75	0.47
Normal(m) vs play	− 2.01 ± 0.30	− 6.66	**	− 1.29 ± 0.37	− 3.46	**	− 2.89 ± 0.77	− 3.74	**
Normal vs disturbance(m)	− 1.31 ± 0.11	− 11.65	**	− 1.64 ± 0.15	− 10.98	**	0.59 ± 0.71	0.82	0.96
Normal vs disturbance	− 1.59 ± 0.11	− 14.26	**	− 1.18 ± 0.18	− 6.48	**	− 0.56 ± 0.46	− 1.23	0.80
Normal vs play(m)	− 1.05 ± 0.18	− 5.96	**	− 1.40 ± 0.22	− 6.31	**	0.15 ± 0.71	0.21	0.99
Normal vs play	− 1.10 ± 0.27	− 4.06	**	− 1.38 ± 0.36	− 3.84	**	− 1.13 ± 0.51	− 2.21	0.21
Disturbance(m) vs disturbance	− 0.27 ± 0.15	− 1.82	0.42	0.46 ± 0.23	2.02	0.30	− 1.15 ± 0.84	− 1.37	0.72
Disturbance(m) vs play(m)	0.26 ± 0.20	1.26	0.78	0.24 ± 0.26	0.95	0.92	− 0.44 ± 1.00	− 0.44	0.99
Disturbance(m) vs play	0.21 ± 0.29	0.73	0.97	0.26 ± 0.38	0.69	0.98	− 1.72 ± 0.87	− 1.97	0.33
Disturbance vs play(m)	0.53 ± 0.20	2.62	0.08	− 0.22 ± 0.28	− 0.77	0.97	0.71 ± 0.84	0.85	0.95

Disturbance vs play	0.49 ± 0.29	1.69	0.50	− 0.20 ± 0.40	− 0.49	0.99	− 0.57 ± 0.68	− 0.85	0.95
Play(m) vs play	− 0.05 ± 0.32	− 0.14	1.00	0.02 ± 0.42	0.04	1.00	− 1.28 ± 0.87	− 1.47	0.65

Fig. 1. － Examples of (a) U-type lip and (b) S-type lip touches.

Fig. 2. － Mean frequency of touches to each body part. The values are individual means ± SD.

Fig. 3. － Relationships between the percentage of time in proximity to an individual and the number of times (a) U-type lip, (b) U-type genital and (c) S-type lip touches were performed.

Fig. 4. － Proportion of times that play or aggressive behaviours occurred (a) before and (b) after the touches.

Fig. 5. － Proportion of times that play or aggressive behaviours occurred (a) before and (b) after S-type touches between pairs with and without young.

Fig. 6. － Relationship between the number of times U-type lip and U-type genital touches occurred in pairs with or without neonates.

Fig. 1

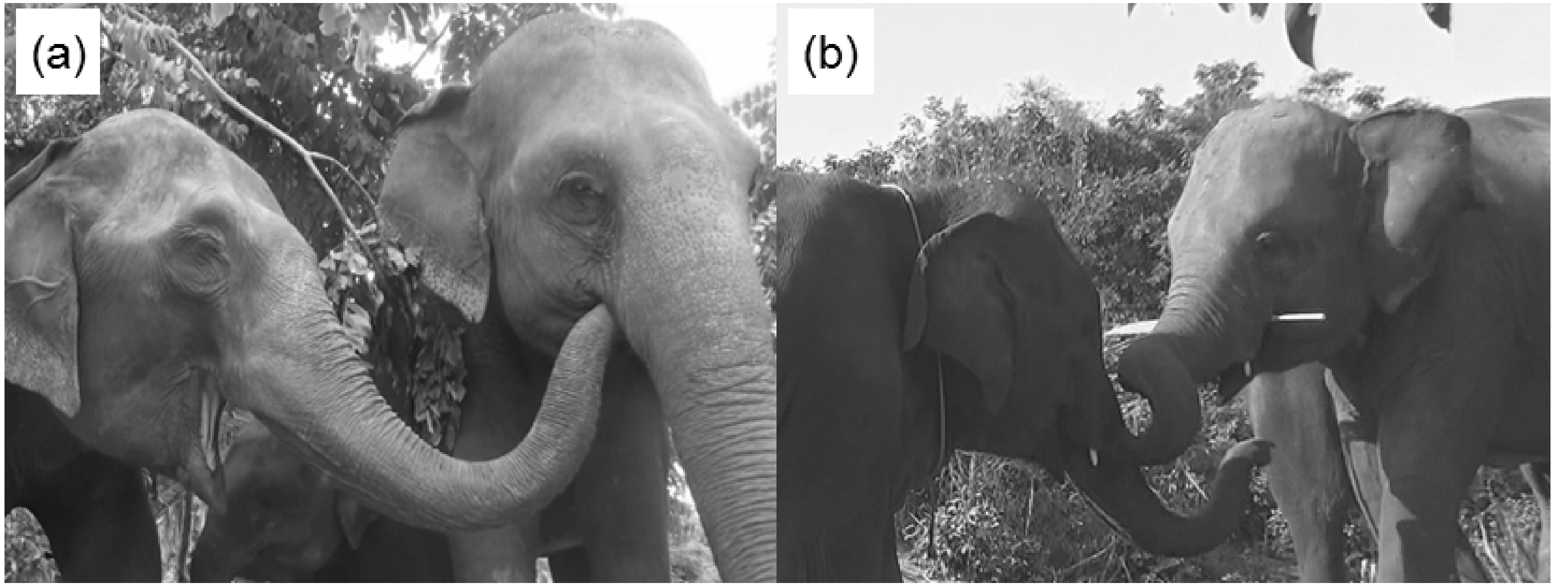
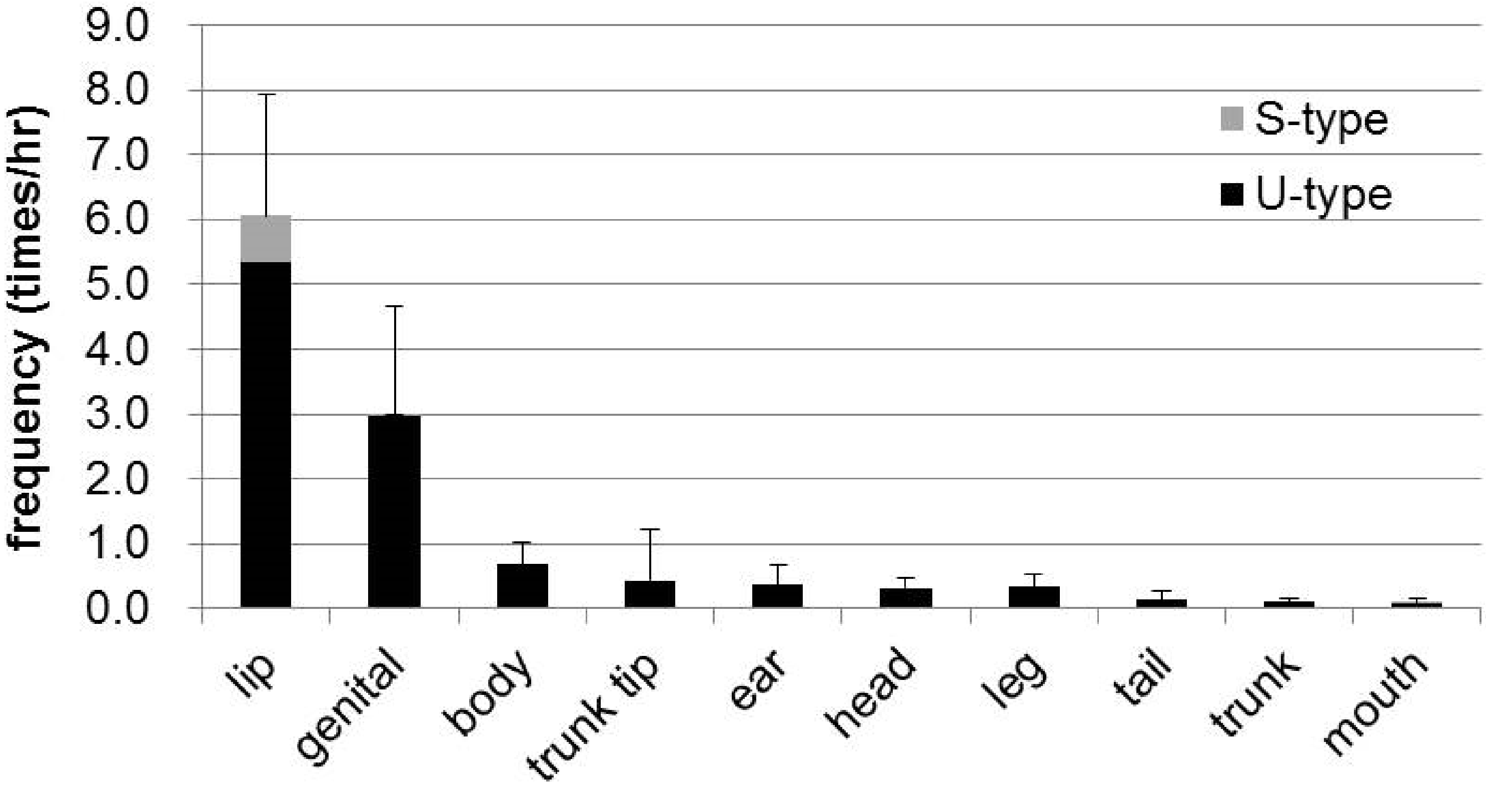
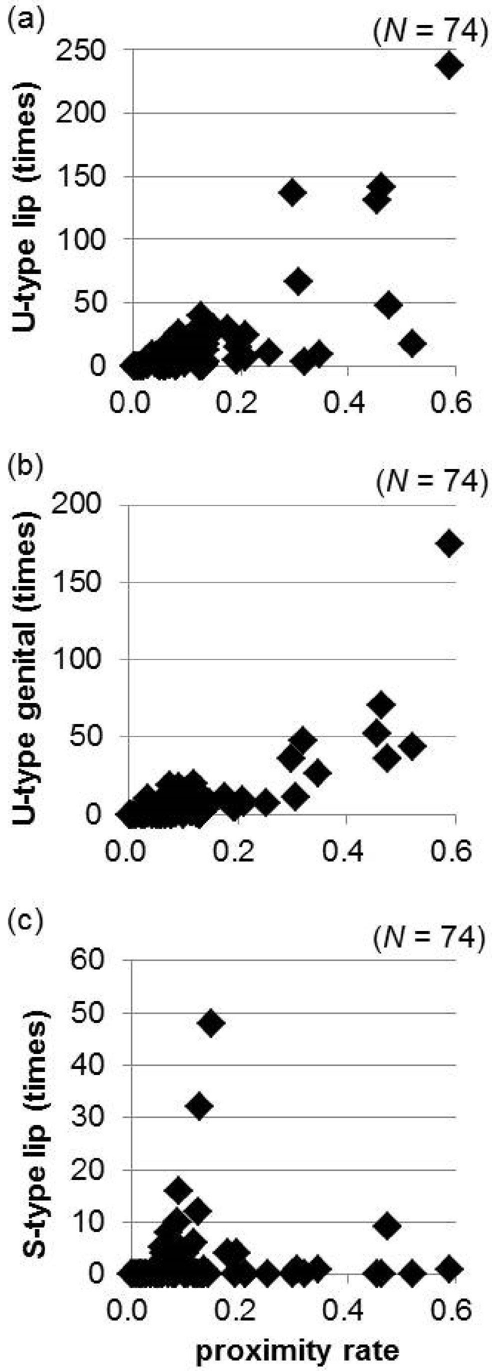


Fig. 2



9.0
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0.0
frequency (times/hr)
S-type
U-type
lip
genital
body
trunk tip
ear
head
leg
tail
trunk
mouth

Fig. 3



(a)
(N = 74)
U-type lip (times)
250
200
150
100
50
0
0.0
0.2
0.4
0.6
(b)
(N = 74)
U-type genital (times)
200
150
100
50
0
0.0
0.2
0.4
0.6
(c)
(N = 74)
S-type lip (times)
60
50
40
30
20
10
0
0.0
0.2
0.4
0.6
proximity rate

Fig. 4

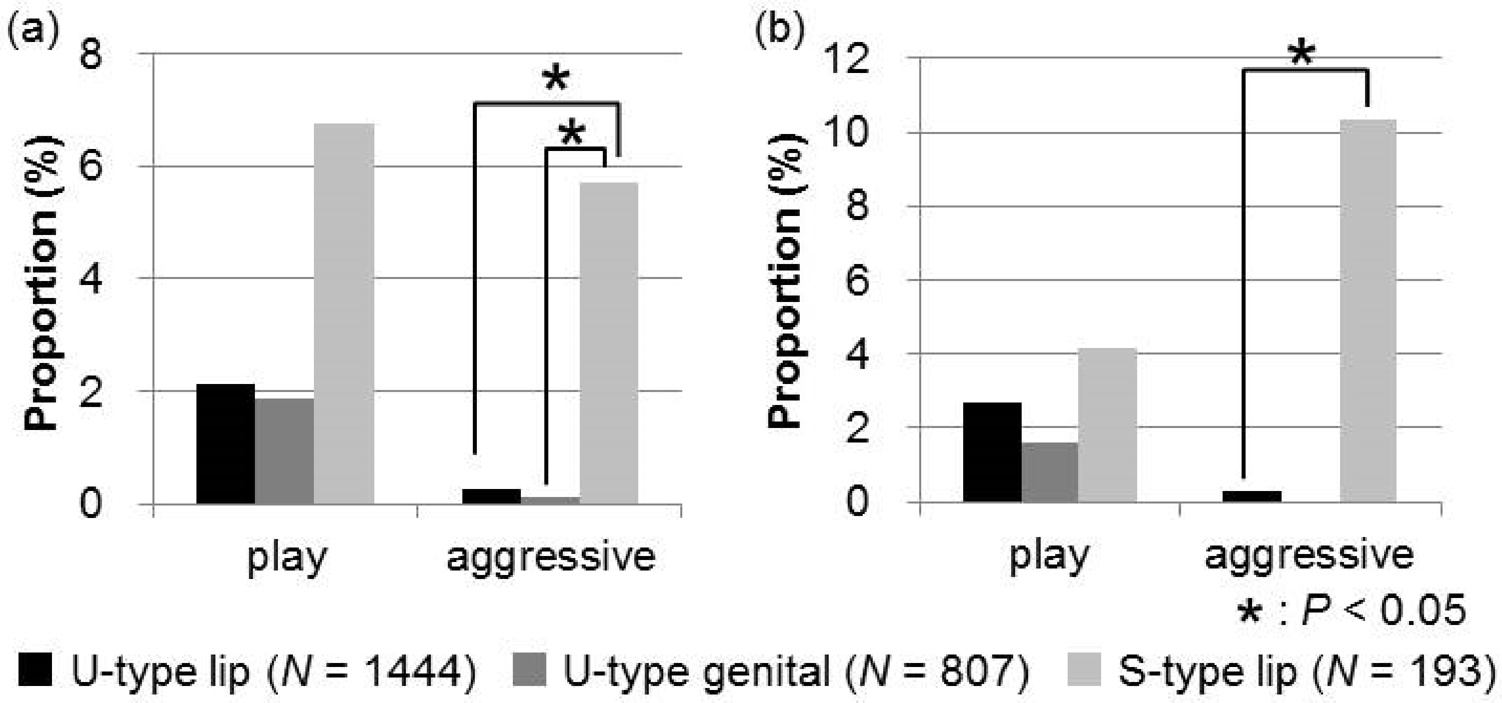
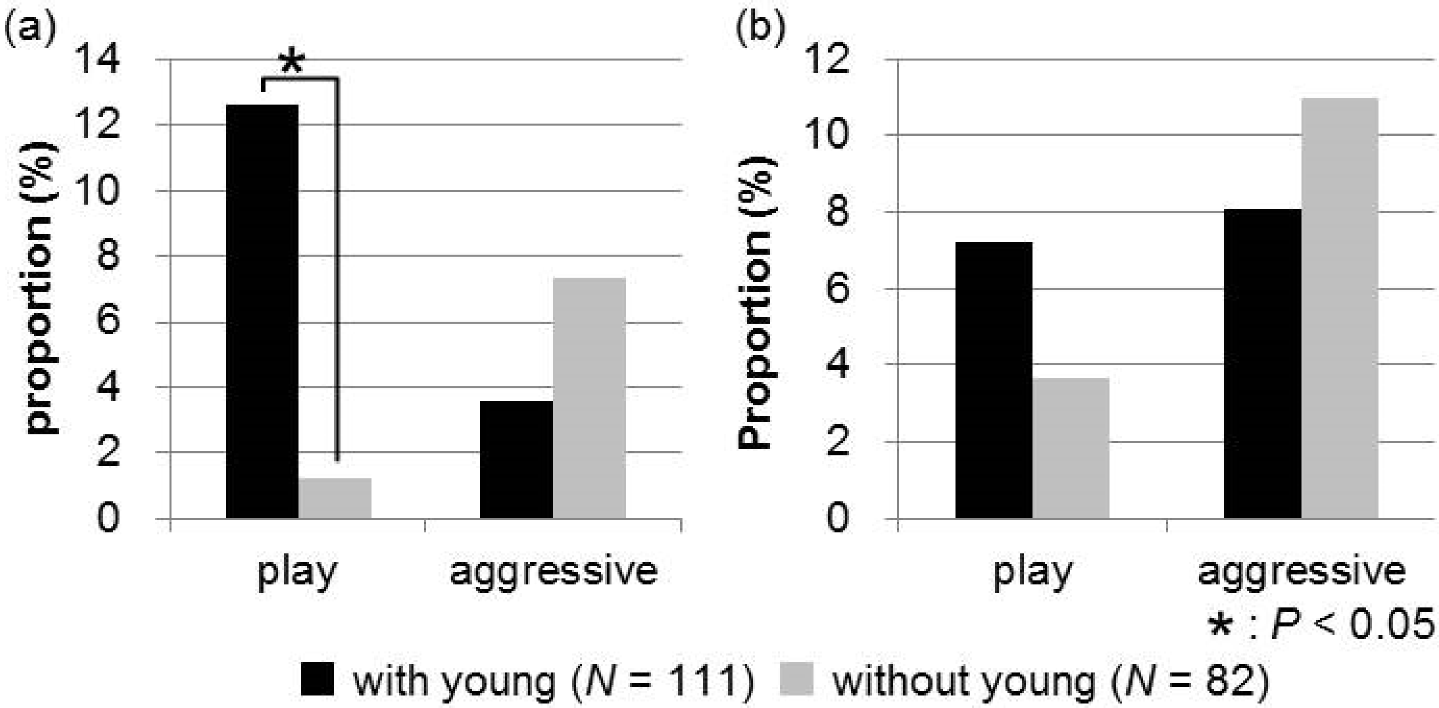
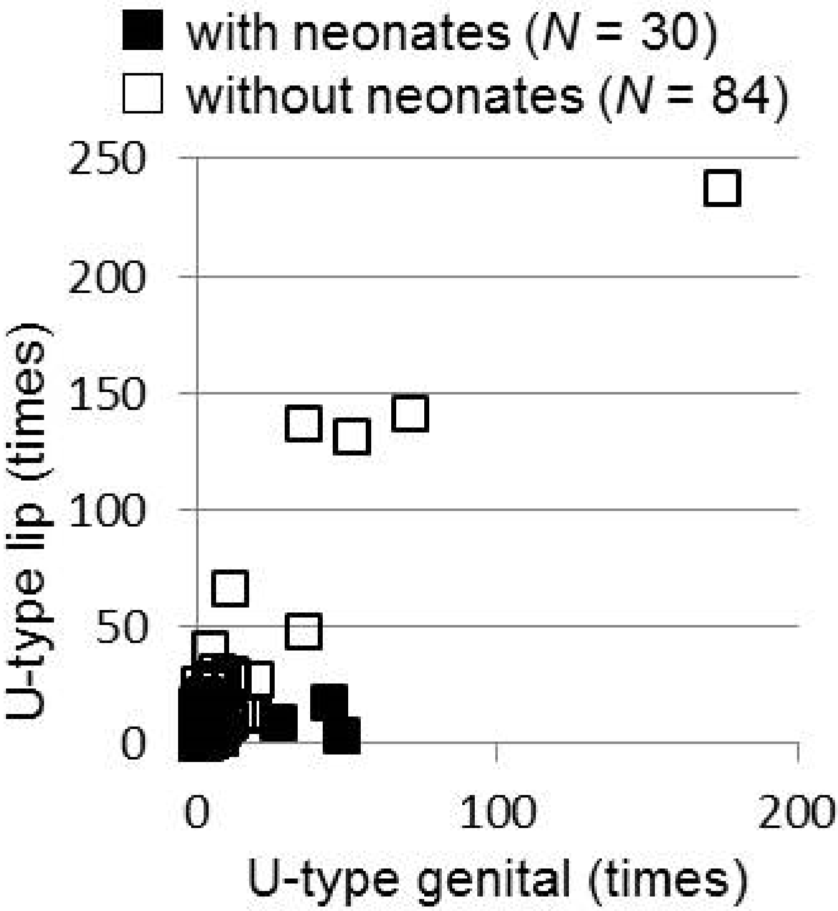

(a)
Proportion (%)
8
6
4
2
0
play
aggressive
*
*
(b)
Proportion (%)
12
10
8
6
4
2
0
play
aggressive
*
* : P < 0.05
U-type lip (N = 1444)
U-type genital (N = 807)
S-type lip (N = 193)

Fig. 5



(a)
proportion (%)
14
12
10
8
6
4
2
0
*
play
aggressive
(b)
Proportion (%)
12
10
8
6
4
2
0
play
aggressive
* : P < 0.05
with young (N = 111)
without young (N = 82)

Fig. 6



with neonates (N = 30)
without neonates (N = 84)
250
200
150
100
50
0
U-type lip (times)
0
100
200
U-type genital (times)