Title: Young Asian elephant calves show differentiated social relationships with conspecifics

Running title: Differentiated calf-conspecific social relationships in Asian elephants

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Data availability statement
The raw data will be uploaded on Dryad or the publicly available JNCASR repository after acceptance and are available immediately to the reviewers as uploaded files.

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Conflict of interest
The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Ethical note

Field data collection was observational in nature. Therefore, no animal handling or manipulation was involved. Researchers maintained a minimum distance of 40 m to the elephants to avoid any disturbance. Fieldwork was carried out under permit number PCCF/WL/E2/CR-121/2014-15 dated 09/05/2014, issued by the office of the Principal Chief Conservator of Forests (Wildlife) and Chief Wildlife Warden, Karnataka.

Author contributions

Conceptualization: TR, TNCV; Data Curation: TR; Formal Analysis: TR; Funding Acquisition: TNCV; Investigation: TR; Methodology: TR, TNCV; Project Administration: TNCV; Supervision: TNCV; Validation: TR, TNCV; Writing – Original Draft Preparation: TR; Writing – Review & Editing: TR, TNCV.

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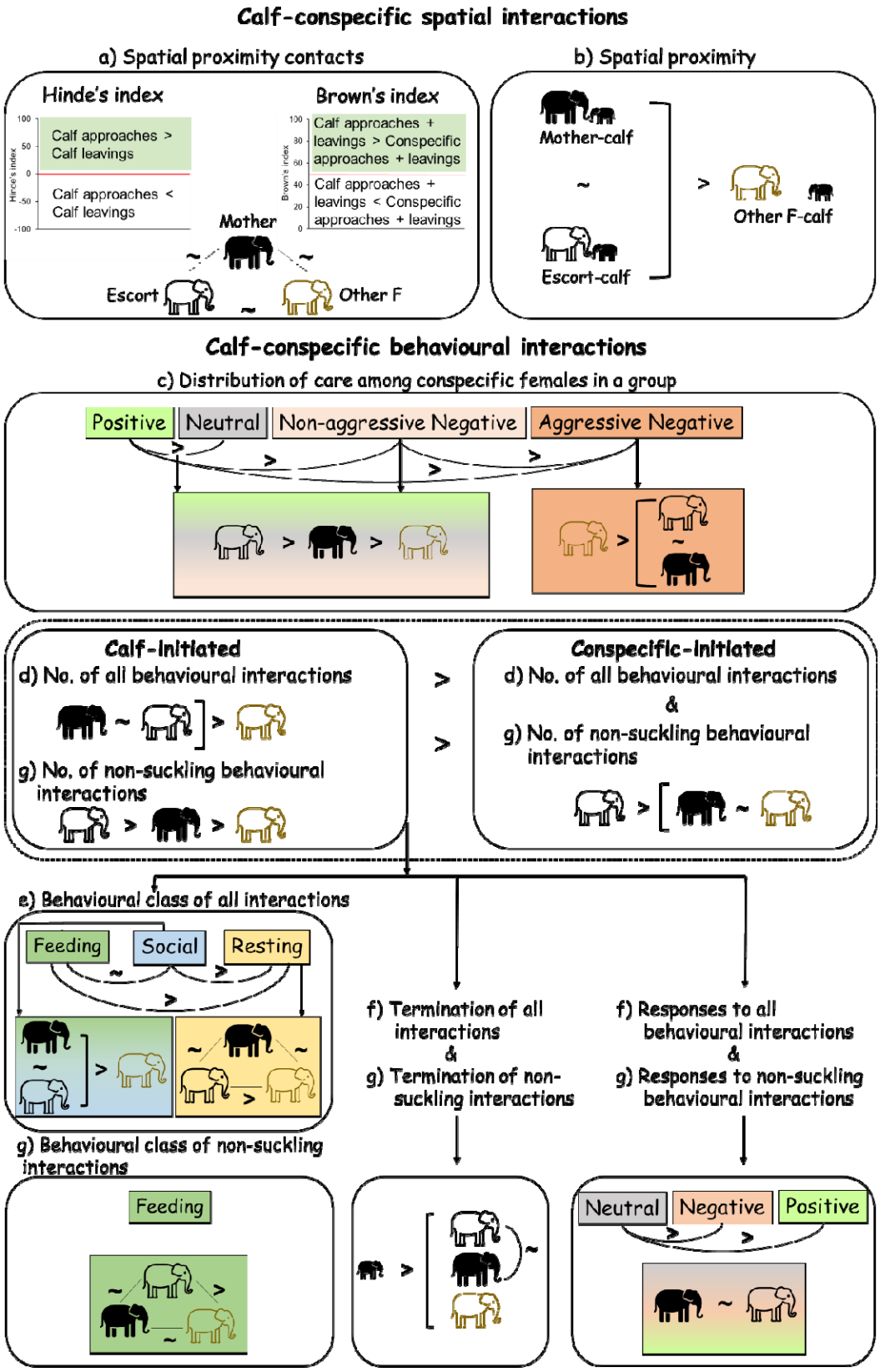
Abstract

Social relationships may increase longevity and reproductive success of individuals, thereby providing crucial benefits in social species. Adults of many social species have differentiated social relationships; however, when and how these relationships form and are maintained are often not understood. We studied spatial and behavioural interactions between young calves (≤6 months old) and conspecific females (≥5 years old) to understand social ontogeny in a wild Asian elephant (*Elephas maximus*) population in Nagarahole and Bandipur National Parks, southern India. We found that elephant groups with calves comprised females – mother and 'escort', who provided active care, and females who did not provide overt, active care – 'other females'. Escorts, apart from coordinating their movement with the calf, provided allomaternal care by initiating positive and helpful interactions with the calf. Other females rarely initiated interactions, which were usually negative, towards calves. Primarily calves, rather than conspecific females, initiated and terminated proximity contacts and behavioural interactions. Calves were near and interacted similarly with their mothers and escorts, under feeding, resting, and social contexts, and almost never interacted with other females. Similarly, we found remarkable similarities between mothers and escorts in their behaviours towards calves, with the primary difference being that escorts did not provide milk. Our results suggest that calves begin to form differentiated social relationships from a young age. The presence of calves and their interactions with escorts might result from existing close social relationship between mothers and escorts or may establish new relationships. Allomaternal care may also reinforce relationship differentiation in such social species. As calf-escort interactions involved behaviours that may potentially be helpful in protection and feeding skill acquisition, the development and survival of calves may be affected by the presence of, and interactions, with allomothers.

Keywords

Allomaternal care, calves, ontogeny, escort, social relationships, Asian elephant

Graphical Abstract



Introduction

The development of social relationships is a central component of the ontogeny of social mammals (Bekoff, 1972). Differentiated social relationships may be beneficial (Connor et al., 2001; Langergraber et al., 2013), and such heterogeneous relationships may exist from a young age itself or form gradually (Berman, 1982a, 1982b; Berman et al., 1997; de Waal, 1990; Roatti et al., 2023). Social relationships involving care are of particular importance to developing individuals. In mammals, young individuals form their closest relationship with their mother, who provides a majority of the care (van Noordwijk, 2012). In some species, parental care may be supplemented by alloparental care or allocare, which refers to care contributed by conspecifics apart from the biological parent(s) in raising offspring that are not one's own. Alloparental care is documented in over 100 social mammals, such as primates, lions, cetaceans, mongooses, dogs, and elephants, and include behaviours such as babysitting or accompanying the young one, carrying, active food provisioning, allosuckling, and defending against conspecifics or predators that result in direct interactions between allocarers and the young one (Brotherton et al., 2001; Clutton-Brock et al., 2000; Erb & Porter, 2020; Estes & Goddard, 1967; Gadgil & Nair, 1984; Gero et al., 2013; Hill & Campbell, 2014; Hodge, 2005; Hrdy, 1976; Lee, 1987; Pal et al., 2021; Pusey & Packer, 1994; Rood, 1978; Rowell et al., 1964; Whitehead, 1996; Xiang et al., 2019). Allocare may be provided by one or more or all the members of a social group, and allocarers may be generalised or may specialise in caretaking tasks (Erb & Porter, 2020; Garber, 1997; Gero et al., 2009). Allocare may be distributed among group members, and young ones may solicit help from specific allocarers and/or allocarers may approach specific young ones to initiate affiliative interactions (Brotherton et al., 2001; Gilchrist, 2004). Ultimately, allocarers can interact differently than other conspecifics with the young ones and *vice versa*, forming the basis for the development of differentiated social relationships from a young age. In this paper, we report on differentiated relationships between adult female conspecifics and calves in the Asian elephant.

Among social mammals, primates are known for their highly differentiated social relationships (Berman, 1982a, 1982b; Roatti et al., 2023; Silk et al., 2009, 2010). While adult female elephants show differentiated social structure similar to many primates (Archie et al., 2011; de Silva et al. 2011; Nandini et al., 2017, 2018; Wittemyer et al., 2005), when and how relationships form and become differentiated are not well-studied. Elephants live in

matrilineal societies with female philopatry and male dispersal (Archie et al., 2005; Vidya & Sukumar, 2005). Males associate only temporarily with female groups after dispersal (Keerthipriya et al., 2021) and do not provide parental care (McKay, 1973). Female elephants give birth to a single calf at a time; twins are rare. Calves are precocial at birth but are nutritionally and socially dependent on their mothers (Gadgil & Nair, 1984; Lee & Moss, 2011; Nair, 1989; Revathe et al., 2020). Young individuals (≤2.5 years of age) face high predation risk from lions in Africa (Loveridge et al., 2006) and tigers in India (Williams, 1950). Young ones are weaned at only 4-5 years of age or after the birth of a sibling (Mar et al., 2012) and constantly associate with the mother until then. Thus, female elephants invest heavily in their young for an extended duration, exceeded only by certain great apes and cetaceans among social mammals (Mann, 2019; van Noordwijk et al., 2018).

Allomaternal care has been conjectured to be important in the evolution and cohesiveness of female elephant societies (Dublin, 1983; Gadgil & Nair, 1984) and has been documented in many African and Asian elephant populations (Dublin, 1983; Eisenberg, 1980; Gadgil & Nair, 1984; Jayantha et al., 2009; Lee, 1987; Lee & Moss, 2011; Rapaport & Haight, 1987; Vidya, 2014; Woodford & Trevor, 1970). However, there are only a few detailed studies of calf-conspecific interactions in elephants (Lee, 1987; Lee & Moss, 2011 on African savannah elephants (*Loxodonta africana*); Gadgil & Nair, 1984 on semi-captive Asian elephants (*Elephas maximus*); Chelluri 2009 on wild African forest elephants (*Loxodonta cyclotis*); Webber 2017 on wild Asian elephants in Uda Walawe, Sri Lanka, and captive Asian and African savannah elephants) and hardly any studies detailing and quantifying allomaternal care and the development of differentiated relationships (but see Lee, 1987; Lee & Moss, 2011). To understand the development of differentiated relationships in the Asian elephant, we studied calf-conspecific social interactions, including allomaternal interactions, in a long-term monitored wild Asian elephant population in southern India (Kabini Elephant Project: Keerthipriya and Vidya, 2022; Vidya et al., 2014).

Calves are individuals under 1 year of age (there is high mortality until that time; Kabini Elephant Project, unpublished data). In this population, females are organized into distinct clans, with the clan being the most inclusive level of social organization (Nandini et al., 2018). Fission-fusion dynamics are seen within clans (Nandini et al., 2017, 2018); as a result, all the females of a clan are not always together. A set of females seen together in the field is referred to as a group (Nandini et al., 2018; equivalent to ‘party’ in the primate literature; see

Methods). Group size and composition change over time due to the splitting (fission) and rejoining (fusion) of groups.

We investigated the ontogeny of social relationships by comparing behaviours of different categories of females (that were at least 5 years old) towards calves up to 6 months of age and *vice versa*. We examined 1) whether proximity contacts and interactions were initiated and terminated primarily by adult and subadult female conspecifics or calves (questions a, d, and f below), 2) how care (and hence, calf-conspecific interactions) was distributed among female conspecifics in the group and whether individuals that showed one type of care (escorting, see below) also provided other care (questions b, c, d, f), and 3) whether certain kinds of behavioural interactions were associated with specific categories of conspecifics (questions e, g). Specific questions are listed below, and the predictions follow.

a) Do calves initiate and terminate more proximity contacts towards conspecifics or *vice versa*, and is there a difference across conspecific categories (mothers, escorts, other females; see below) in proximity contact initiation?

b) How do calf age-class and conspecific category affect calf-conspecific proximity?

c) How is care distributed among the females in a group? Specifically, is there a difference across conspecific categories in the number and nature of interactions (i.e., positive / neutral / negative) initiated towards a calf?

d) Do calves initiate more behavioural interactions towards conspecifics or *vice versa*, and is this affected by calf age-class and conspecific category?

e) Do calves initiate a greater number of interactions of certain behavioural classes (feeding / resting / social) towards particular conspecific categories?

f) Do calves terminate interactions more frequently than do conspecifics or *vice versa* and is there a difference across conspecific categories in the kinds of responses shown towards calf-initiated interactions?

g) Does the pattern of results of questions b)-f) remain unchanged when only non-suckling interactions rather than all interactions initiated by calves are considered?

From preliminary field observations, we found that some non-mother females showed coordinated movement with the calf beyond that resulting from coordinated group movement. We termed these females ‘escorts’ (see Methods). In our study population, at least one escort was present in around three-fourths of the female group sightings that had a calf (Revathe,

2022). Therefore, we used mother, escort, and other females (i.e., non-mother and non-escort) as the conspecific categories.

Predictions

1) Are proximity contacts and interactions initiated and terminated primarily by female conspecifics or calves? (*Questions a, d, f)*

The frequency of initiation of spatial proximity, behavioural interactions, and termination of interactions by young ones is expected to vary with the degree of neonatal development (Hill & Campbell, 2014). As elephant calves are precocial and quick to explore their surroundings after birth (Nair, 1989; Revathe et al., 2020), we expected calves to initiate and terminate more spatial (proximity contacts) and behavioural interactions towards conspecifics than *vice versa*. We expected initiations of behavioural interactions by calves with mothers, escorts, and with other females to increase over the first six months, as calves likely start to learn foraging and social skills while reducing the time spent resting (Revathe et al., 2020) during this period. We did not expect a sex difference in calf behaviours during the initial six months of life.

2) How is care (and hence calf-conspecific interactions) distributed among female conspecifics in the group? (*Questions b, c, d, f)*

We expected calves to initiate more spatial and behavioural interactions with their mother – the reliable/familiar social partner – than with other conspecific categories of females in the group, as group compositions could change due to fission-fusion dynamics. Similarly, as mothers have the highest incentive to be tolerant of and show positive interactions towards their calves, we expected mothers rather than other conspecific categories of females to initiate more spatial and behavioural interactions towards their calves. We further expected mother-calf spatial and behavioural interaction terminations to be lower than those between calves and other conspecific categories of females in the group. We did not have an *a priori* expectation about whether escorts would show more affiliative behaviour towards calves than would other females in the group. As being near calves by coordinating movement might be thought of as a form of care by itself, it was not necessary that escorts would show other forms of care, and other individuals could potentially provide such care.

Question b): We expected the time spent in proximity to conspecific females to show a heterogeneous pattern with increasing age, and hence, skill acquisition (Nair, 1989; Revathe

et al., 2020). We expected the time spent in proximity to mothers and escorts to decrease, although not by much, as calves still need protection in the first six months of life, but we expected the time spent in proximity to other females to increase with age, coinciding with increased familiarity with the group members and exploration during development. It must be noted that it is possible for proximity to decrease but initiation of behaviours to conspecifics to increase over time if calves became generally more active with age. We did not expect a sex-based difference in proximity during the first six months of life.

Question c): We expected the number and nature of interactions initiated by conspecific females towards calves to vary among conspecific categories. Specifically, we expected calves to have more frequent and more positive interactions with mothers and escorts than with other females as that seen in African savannah elephants (Lee, 1987).

3) Are certain kinds of behavioural interactions associated with specific types of conspecifics? *(Questions e, g)*

Question e): Since only mothers provide primary nutritional support in elephants (Lee, 1987; Sukumar, 2003), we expected calves to initiate a greater number of feeding interactions with mothers than with other categories of conspecific females. Based on close association, we expected calves to initiate the highest number of social and resting interactions with mothers, followed by those with escorts, and then with other females. We expected the number of resting interactions with conspecifics to decrease but feeding interactions with conspecifics to increase with age, as the total time spent resting decreases and that spent feeding increases with calf age (Revathe et al., 2020). We expected the number of social interactions to not change much within the first six month of life, as the total time spent in social interactions remained similar during the first year of life (Revathe et al., 2020). We did not expect male and female calves to interact differently with conspecific females during the first few months of life.

Question g): It was possible that nutritional dependence of calves on their mother might mask the presence of otherwise comparable relationships of calves with escorts or other females. To investigate this possibility, we removed suckling interactions and reanalysed our data. We expected that mother-calf behavioural interactions would still be higher than those with other categories of females due to the reliability and safety of one’s mother as an interaction partner.

Methods

Field data collection

We collected field data from December 2015 to June 2018 in Nagarahole and Bandipur National Parks and Tiger Reserves, southern India, where the tiger density is high (Jhala et al., 2008). We carried out field sampling across these two parks following systematic, fixed sampling routes, from ~6:30 AM to ~5:45-6:45 PM (see Nandini et al., 2017 for further details). Female elephant groups were defined as one or more females, often accompanied by young ones, that showed coordinated movement or behaviour and were usually within 50-100 m of one another (Nandini et al., 2017, 2018). We aged, sexed, and identified the individuals seen based on natural physical characteristics (Vidya et al., 2014). The Kabini Elephant Project has recorded hundreds of individually identified elephants since its inception in 2009 (see Vidya et al., 2014). We age-classified individuals as calves (<1 year), juveniles (1-<5 years), subadults (5-<10 years in the case of females and 5-<15 years in the case of males), and adults (>=10 or 15 years, for females and males, respectively). In this study, since we examined calves of different ages, we refer to those less than three months old as newborn calves and to those between 3 and <6 months of age as infant calves.

Most of the behavioural data presented here were collected from around the Kabini backwaters (which separate Nagarahole and Bandipur) because of good visibility. We used focal animal sampling (Altmann, 1974) to record interactions between calves and conspecifics within groups. We recorded observations using a video camera (SONY HDR-XR 100E or SONY HDR-PJ 540E).

We defined escorts based on coordinated movement between calf-conspecific pairs, beyond that required of group members (i.e., any distance less than 50-100 m that the group showed). Thus, one or more non-mother subadult or adult females who moved along with the focal calf (either accompanied by the calf's mother or not) was/were identified as escort(s) in each focal session (Figure 1a) as previously done in whales (e.g., Gero et al., 2009). We refer to females other than the focal calf's mother and escort(s) in a focal session as 'other females' (Figure 1a). Although an escort is a female that showed coordinated movement with the calf, she did not have to necessarily initiate any, and specifically, allocare, interaction towards the calf.

Mother-escort comparisons in their behaviours towards calves and *vice versa* allowed us to understand how comparable allomaternal care (if shown by escorts) was to maternal care, and if it was primarily the escorts, and not other females, that showed allomaternal care (we defined this to require more than coordinated movement with the calf). It should be noted that although, by definition, other females did not show coordinated movement with the focal calf, they were still part of the same group as the focal calf and, hence, could reach the calf to initiate allocare interactions (Figure 1a). Similarly, it was possible for calves to easily go up to other females to initiate interactions. Essentially, it was entirely feasible for conspecific females to show escorting behaviour but not allomaternal care and *vice versa*. Data could not be recorded blindly because our study involved focal animals in the field.

Focal video scoring and data analysis

We used Windows Media Player 12.0 to score focal videos to quantify calf-conspecific proximity and interactions (see below). All the videos were scored by TR. We used only those focals in which all the group members were clearly visible, and in which all three conspecific categories of females (Mother, Escort, Other female) were present for the focal calf because we wanted to make mother-escort, mother-other female, and escort-other female comparisons.

Calf-conspecific proximity contacts

We scored 3 focal videos per calf, recorded on three different days, to look at calf position changes on a second-by-second basis for 20 calves (based on 299 position changes) belonging to 9 focal clans, who were up to 6 months old (Supplementary Material 1). The calf belonged to the same age-class during all 3 focals, and each calf appeared in only one age-class. Each focal lasted 20 minutes (72,000 seconds scored in all), during which we noted down the focal calf's positions in terms of who was near the calf (see Supplementary Material 2). We considered a focal calf to be near a conspecific if the distance between the calf and the conspecific was up to one calf-body length (≤1 m). A calf could be near multiple individuals simultaneously.

We used the Hinde's proximity index (Hinde & Spencer-Booth, 1967; the percentage of approaches made by the calf towards a conspecific minus the percentage of leavings made by that calf away from that conspecific) to find out whether the calf more frequently approached or left a particular conspecific (see Supplementary Material 3). Additionally, we calculated

Brown's proximity index (Brown, 2001) to measure the relative contributions of the calf and conspecific to changes in proximity contacts between the pair (see Supplementary Material 3).

Since these indices could be calculated with all three conspecific categories in each focal only for two calves (as the remaining did not show proximity contact changes with other females), we tested for differences in Hinde's and Brown's indices across conspecific categories (Mother, Escort, Other Female) using the non-parametric Friedman's ANOVA, using the averaged value across focals for each calf and matched for calf identity. We additionally performed ANOVAs on the logit Hinde's index and Brown's index to examine possible differences between only mothers and escorts, for which the sample sizes were larger. Here, conspecific category was a fixed factor with two levels – Mother and Escort. Calf identity was included as a random factor because there were multiple calves, although each calf was sampled only in two or three focals. However, we were not actually interested in variation amongst calves, nor can such variation be tested without many focals per calf. Therefore, in this and all the other following analyses whenever calf identity was used, inferences were not made about calf identity or its interactions. Only calves that had Hinde's and Brown's index values in at least two of their focals were used. Due to low sample size, the effects of calf age and sex on proximity initiation could not be assessed.

Calf-conspecific proximity

During each 20-minute focal, we took a scan every 4 minutes to obtain six independent calf positions in terms of the conspecific(s) who were near the calf (4 minutes was chosen based on how quickly calves changed their positions: this corresponded to 95% of the durations to changes in positions; see Supplementary Material 2). We thus used a total of 360 calf positions (6 positions x 3 focals x 20 calves, of which 10 calves were newborns, less than 3 months old, and 10 calves were infant calves, 3-<6 months old) for this analysis. In order to find out whether calf proximity differed with respect to conspecific category, we carried out an ANOVA on the logit proportion of calf-scans near a conspecific (dependent variable; proportions were logit transformed as they were not normally distributed), with calf age-class (<3 and 3-<6 months) and conspecific category (Mother, Escort, and Other Female) as fixed factors, and calf identity nested within age-class as a random factor.

Calf-conspecific interactions

To examine calf-conspecific interactions, we scored two 30-minute focal videos per calf for the same 20 calves as those used for proximity analyses, during which we noted down all the interactions that occurred between a focal calf and females of the three conspecific categories, the identities of the initiator and terminator of each interaction, and the duration of the interaction. Behaviours were classified into three classes: feeding-related (sucking from a conspecific, taking plucked grass from a conspecific, sniffing grass from the mouth of a conspecific, etc.), resting-related (calf leaning against a conspecific, calf lying down near/under a conspecific, and calf sliding off an individual to lie down), and social (for e.g., touching a conspecific, rubbing against a conspecific, conspecific standing guard over a calf etc.; see Supplementary Material 4). We also noted down whether conspecific-initiated interactions, as well as the responses shown by conspecifics towards calf-initiated interactions, were positive (for e.g., rushing towards a calf when the calf was in distress, stopping one's activity to allow the calf to suck, keeping the calf within reachable distance, etc.), negative (for e.g., lashing out at a calf, kicking a calf, pushing a calf, etc.), or neutral (see Supplementary Material 4). Conspecifics did not always show a response, and no response was also included under the category 'neutral' during analysis.

Initiation of interactions

In order to find out whether calves initiated more interactions towards conspecifics or *vice versa* and to find out whether there was a difference amongst mothers, escorts, and other females in the numbers of interactions that calves initiated towards them and the numbers of interactions that they initiated towards calves, we ran a nested ANOVA on the log-transformed numbers of calf-conspecific interactions (as they were not normally distributed), with calf age-class (<3, 3-<6 months), initiator category (Calf, Conspecific), and conspecific category (Mother, Escort, and Other Female) as fixed factors, and calf identity nested within age-class as a random factor. We also tested interaction effects.

Conspecific-initiated interactions: frequency in different contexts

We then classified conspecific-initiated interactions towards calves into four different interaction types (Supplementary Material 4, Table 2) from the perspective of the calf, namely positive (potentially benefitting the calf; such as checking the calf, chaperoning the calf), neutral (no obvious benefit to the calf; such as sniffing the calf), and negative (not benefitting the calf, or at least not in the immediate interest of the calf). Since not all the negative interactions cause physical distress, we also split them into non-aggressive negative

(not causing physical distress, such as nudging the calf to move, mother nudging the calf towards the escort) and aggressive negative (causing physical distress, such as kicking the calf, lashing out at the calf) interactions. We found that most of the calf-conspecific interactions were initiated by calves (see Results); hence, we could not use ANOVA to test the effect of conspecific category on interaction type with calves. We, therefore, used an R x C test of independence using *G*-test to test the null hypothesis that interaction type with calves was independent of conspecific category by combining interactions across all focals (of all calves) in each conspecific category and interaction type.

Calf-initiated interactions: frequency in different contexts, and terminations and types of responses shown by conspecifics

To understand social preferences of calves, we examined whether the number of calf-initiated interactions varied based on conspecific category for the different behavioural classes. To do so, we carried out a nested ANOVA on the log-transformed numbers of calf-initiated interactions, with calf age-class, conspecific category, and behavioural class of interaction (Feeding, Resting, and Social) as fixed factors, and calf identity nested within age-class as a random factor.

For each focal, we also calculated the proportion of calf-initiated interactions towards females of a conspecific category terminated by females of that category (calves that did not initiate any interaction towards females in a focal were not included in the analysis). These proportions of calf-initiated interactions terminated by mothers and escorts were compared. Terminations by other females were not used as only two calves initiated interactions with all three conspecific categories of females in all their focals. We carried out a nested ANOVA on the logit-transformed proportions of calf-initiated interactions terminated by conspecifics, with calf age-class (<3 and 3-<6 months) and conspecific category (Mother, Escort) as fixed factors and calf identity nested within age-class as a random factor.

We also calculated the proportions of calf-initiated interactions towards mothers and escorts that elicited positive, neutral, or negative responses from that conspecific category (these proportions would add up to 1 for each conspecific category; therefore, the proportion of negative responses was not included in the analysis). Again, as above, responses by other females could not be compared as calves did not initiate sufficient interactions towards them. To see if mothers and escorts showed similar types of responses, we ran a nested ANOVA on

the logit proportions of calf-initiated interactions that elicited a positive or a neutral response, with calf age-class, conspecific category, and type of response (Positive, Neutral) as fixed factors, and calf identity nested within age-class as a random factor.

Calf-conspecific non-suckling interactions

We modified the original dataset by removing all the suckling-related interactions that the focal calves initiated towards the conspecifics and investigated whether the pattern of social preferences of calves remained the same even when suckling was not considered. The same analyses that were performed on calf-initiated interactions were also performed on this modified dataset.

Thus, to check whether females of different conspecific categories behaved in a similar manner towards calves, we compared conspecific-initiated interactions towards calves, proportion of calf-initiated interactions that were terminated by conspecifics, and the proportion of calf-initiated interactions that elicited different kinds of responses, across the conspecific categories.

To check whether calves behaved in a similar manner towards different categories of conspecific females, we compared calf proximity initiation and leaving, calf proximity, and the number of calf-initiated interactions – overall and under different behavioural classes, across the conspecific categories.

The ANOVAs were carried out by obtaining sums of squares using Statistica (7.0, StatSoft, Inc. 2004), and carrying out the *F* test calculations based on Neter *et al*. (1990, Chapter 27, pgs. 1010-1029).

Results

a) Do calves initiate and terminate more proximity contacts towards conspecifics or *vice versa*, and is there a difference across conspecific categories (mothers, escorts, other females) in proximity contact initiation?

There was no significant difference in the Hinde's (Friedman ANOVA: χ^2= 2.000, N=7, df=2, P=0.368, Figure 1b) or Brown's (Friedman ANOVA: χ^2= 4.571, N=7, df=2, P=0.102,

Figure 1c) proximity indices among mothers, escorts, and other females. ANOVAs on the logit Hinde's index with mothers and escorts based on data from a larger number of calves (17 calves, 44 focals) also showed no significant effect of conspecific category ($F_{1,16}$=3.849, P=0.067, Figure 1d). However, the average Hinde's index of the calves with their mothers was not significantly different from zero, suggesting that calves approached and left their mothers to similar extents, while the Hinde's index with the escorts was significantly greater than zero, suggesting that calves were more likely to approach than to leave escorts (confidence intervals in Figure 1d). The average Brown's proximity indices of calves with the mother, escort, and other females were greater than 50 (Figure 1c,e), indicating that calves contributed more than their conspecifics to changes in proximity. However, there was no significant effect of conspecific category (mothers and escorts) on this index either (ANOVA on logit Brown's index: $F_{1,16}$=0.888, P=0.360; 17 calves, 44 focals; Figure 1d).

a.

b. c.

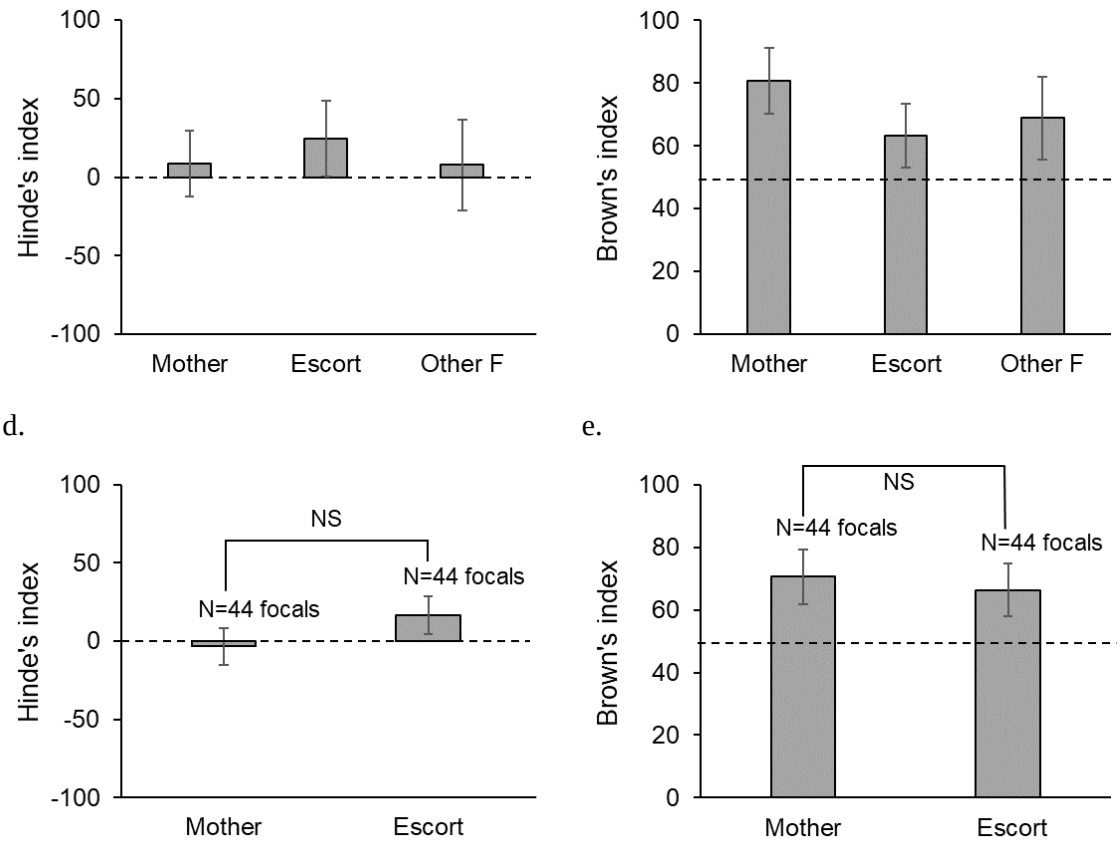


Figure 1. a) Photo of an elephant group showing the positions of group members. Left to Right: other female, mother, calf, escort, other female. Photo: Divya Choudhary, © Kabini Elephant Project; b) average Hinde's and c) average Brown's proximity indices of 7 calves for which data were available with all three conspecific categories; d) Hinde's and e) Brown's indices of 17 calves with mothers and escorts. Error bars are 95% CI. Dashed lines indicate the expected Hinde's index of 0 and expected Brown's index of 50 in the respective graphs.

b) How do calf age-class and conspecific category affect calf-conspecific proximity?

Calves were within reachable distance of at least one female conspecific almost all the time (average proportion of scans near at least one female conspecific ± 95% CI: newborn calves: 0.978 ± 0.022; infant calves: 0.930 ± 0.030). There was no significant effect of calf age-class on the proportion of scans when calves were near conspecific females (ANOVA: $F_{1,18}$=0.205, P=0.656), with newborn calves and infant calves spending similar proportions of scans near conspecific females (average of the proportion of scans near mother, escort, and other

females ± 95% CI = 0.475 ± 0.076 for newborn calves and 0.439 ± 0.069 for infant calves; these values were lower than the average proportion of scans near at least one female conspecific because of averaging across conspecific categories, with other females not spending much time near calves). However, there was a significant main effect of conspecific category ($F_{2,36}$=103.315, P<0.001), and its interaction with calf age-class ($F_{2,36}$=8.139, P=0.001; Figure 2).

The proportions of scans in which calves were near their mothers or escorts (which were not significantly different from each other; P=0.529) were significantly higher than that near other females (mother versus other females: P<0.001; escort versus other females: P<0.001). Newborn calves spent a greater proportion of their time near mothers than escorts (P=0.043) or other females (P<0.001), and a greater proportion of their time near escorts than other females (P<0.001; Figure 2). Infant calves spent a similar proportion of their time near mothers and escorts (P=0.642), but these were higher than that spent near other females (P<0.001 for both the comparisons, Figure 2). Newborn calves spent a significantly greater proportion of time near their mothers than infant calves did (P=0.015), but both spent similar proportions of time near their escorts (P=0.871) and near other females (P=0.529; Figure 2). When tested for infant calves separately, there was no effect of calf sex on the proportion of scans spent near conspecifics (Supplementary Material 5).

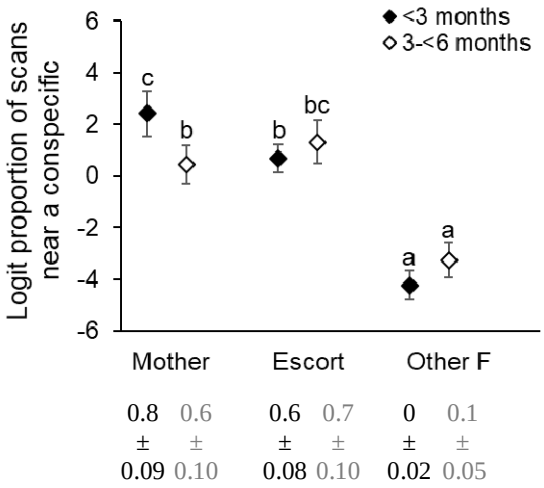


Figure 2. Logit proportions of scans that a calf spent near the three conspecific categories of females. Error bars are 95% CI. In this and the following graphs, letters above the data points

indicate pattern of statistical significance based on Tukey's HSD tests (a<b<c), unless otherwise specified. Shared letters above the bars indicate no significant difference between comparisons. The untransformed value (average ± 95% CI) is shown below the graph for each category. (Averaging was done over all the focals of all the calves in the category in this and the following graphs.)

c) How is care distributed among the females in a group? Specifically, is there a difference across conspecific categories in the number and nature of interactions (i.e., positive / neutral / negative) initiated towards a calf?

We observed 93 positive, 10 neutral, 35 non-aggressive negative, and 10 aggressive negative conspecific-initiated interactions towards calves. The non-aggressive negative interactions included only nudge (to make the calf move from a spot), whereas the aggressive negative interactions included kick, push, pull trunk, beat with tail, and lash (Supplementary Material 4, Table 1). We found that the type of conspecific-initiated interactions towards calves was dependent on conspecific category ($G_{\text{corrected}}$ = 45.930, P<0.001). Escorts initiated a majority (77.4%) of the 93 positive interactions towards calves, mothers initiated 20.4% of them, and other females initiated only 2.2% of them. Escorts also initiated most of the 10 neutral interactions (80%) towards calves, whereas mothers and other females initiated only one neutral interaction each in total. Escorts also initiated a majority (60%) of the 35 negative non-aggressive interactions towards calves, followed by mothers (31.4%), and other females (8.6%). Aggressive negative interactions towards calves were rare (10 interactions), and mostly (90%) initiated by other females; one interaction was initiated by a mother and none by an escort.

d) Do calves initiate more behavioural interactions towards conspecifics or *vice versa*, and is this affected by calf age-class and conspecific category?

Of the total of 1332 interactions between calves and their mothers, escorts, and other females in their groups that we observed during the total focal duration of 1200 minutes, calves initiated 1184 interactions. Most of these interactions were of very short duration (average duration of interaction ± 95% CI: calf-initiated: 20.4 ± 4.14 seconds; conspecific-initiated: 24.0 ± 14.5 seconds; Supplementary Material 6). We found significant main effects of initiator category, calf age-class, and conspecific category on the log number of calf-conspecific interactions (Table 1).

Calves initiated significantly more interactions towards conspecific females (average number of interactions ± 95% CI per 30-min focal: 29.60 ± 4.931) than conspecific females initiated towards calves (3.70 ± 1.634; Table 1, Figure 3a). Newborn calves were involved in a significantly greater number of interactions (39.4 ± 8.87) with conspecific females (initiated by either) than were infant calves (27.3 ± 6.64; Table 1). The numbers of calf-mother (14.88 ± 3.644) and calf-escort (16.95 ± 3.814) interactions were similar (95% CI around difference between means for conspecific category: 0.312; Tukey's HSD: $P>0.05$), and both were significantly higher ($P<0.05$ for both) than the number of calf-other female interactions (1.48 ± 0.848).

There was also a significant interaction effect between initiator and conspecific categories (Table 1). Calves initiated similar numbers of interactions towards mothers and escorts (95% CI around difference between means for initiator category x conspecific category: 0.348; $P>0.05$; Figure 3a), and a smaller number of interactions towards other females ($P<0.05$ for both the comparisons; Figure 3a). On the other hand, escorts initiated a greater number of interactions towards calves than mothers or other females did ($P<0.05$ for both the comparisons; previous paragraph, Figure 3a), with the latter two not being significantly different from each other ($P>0.05$; Figure 3a). When tested separately, there was no effect of calf sex on the numbers of calf-conspecific interactions involving infant calves (Supplementary Material 7).

Table 1. Results of the nested ANOVA on the log numbers of all calf-conspecific interactions. Calf ID (random factor) was nested within age-class, and age-class, initiator category, and conspecific category were fixed factors. Significant *P* values are marked in bold. The asterisks in the *P* values column indicate significance in the ANOVA on the log numbers of non-suckling calf-conspecific interactions (see Supplementary Material 8) for comparison. (Inferences should not be drawn about Calf ID or its interactions in this and the following tables as each calf was sampled in only two focals.)

Effect	Effect (F/R)	*SS*	*df*	*MS*	*F*	*P*
Calf ID(age-class)	Random	12.932	18	0.718	1.499	0.102*
Age-class	Fixed	4.573	1	4.573	6.366	**0.021***
Initiator category	Fixed	97.587	1	97.587	164.480	**<0.001***

Conspecific category	Fixed	79.952	2	39.976	61.366	**<0.001***
Calf ID(age-class) x Initiator category	Random	10.679	18	0.593	1.238	0.243
Calf ID(age-class) x Conspecific category	Random	23.452	36	0.651	1.359	0.112*
Age-class x Initiator category	Fixed	0.962	1	0.962	1.621	0.219
Age-class x Conspecific category	Fixed	2.345	2	1.172	1.800	0.180
Initiator category x Conspecific category	Fixed	36.471	2	18.236	68.065	**<0.001***
Calf ID(age-class) x Initiator category x Conspecific category	Random	9.645	36	0.268	0.559	0.977
Age-class x Initiator category x Conspecific category	Fixed	1.350	2	0.675	2.520	0.095
Error	_	57.516	120	0.479	_	_

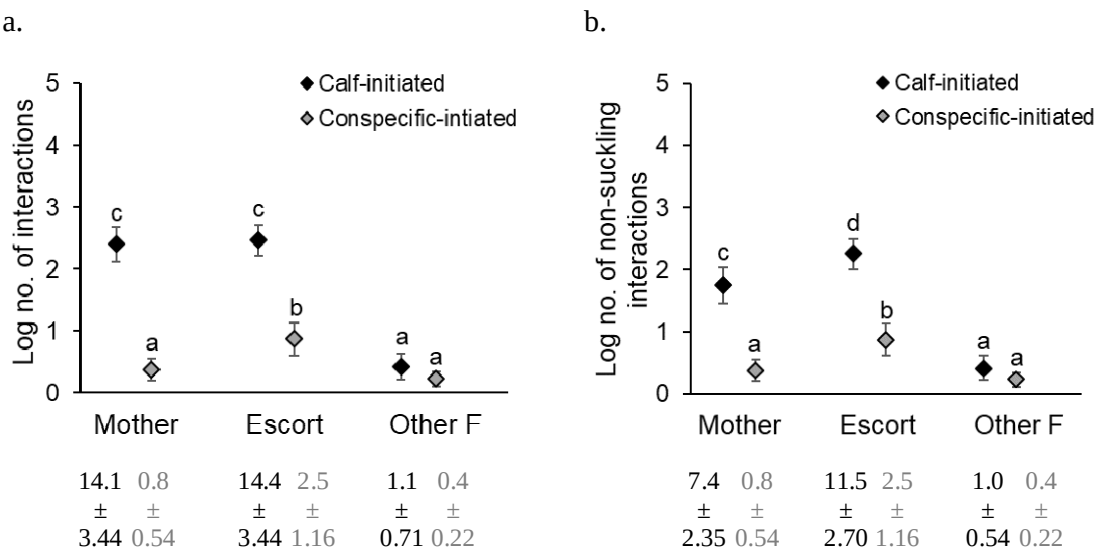


Figure 3. Log numbers of a) all interactions and b) non-suckling interactions initiated by calves towards the three conspecific categories of females, and the log numbers of interactions initiated by these conspecific females towards calves per focal. Error bars are 95% CI. The untransformed number of interactions (average ± 95% CI) for each category is shown below the X-axis.

g) Non-suckling interactions

The ANOVA on non-suckling interactions showed almost the same pattern of results as that on all the interactions, with calves initiating a higher number of interactions towards conspecific females than *vice versa* (794 non-suckling interactions, see Supplementary Material 8, 9). The interaction between initiator and conspecific categories was also

significant. However, calves initiated more non-suckling interactions towards escorts than towards their mothers (95% CI around difference between means for initiator category x conspecific category: 0.444; $P<0.05$; Figure 3b).

e) Do calves initiate a greater number of interactions of certain behavioural classes (feeding / resting / social) towards particular conspecific categories?

Among the 1184 calf-initiated interactions were 539 feeding interactions, 89 resting interactions, and 556 social interactions. The log number of calf-initiated interactions was significantly affected by the behavioural class of interaction, conspecific category, their interaction, and calf identity (Table 2). Calves initiated more interactions towards mothers and escorts than towards other females as seen above (Initiator category x Conspecific category in Table 1, Figure 3a). This pattern was also found separately in feeding (95% CI around difference between means for behavioural class x conspecific category: 0.502; Mother versus Other Females: $P<0.05$; Escort versus Other Females $P<0.05$, Figure 4a) and social interactions (Mother versus Other Females: $P<0.05$; Escort versus Other Females $P<0.05$, Figure 4a), but the number of resting-related interactions initiated by calves was higher only towards escorts than towards other females ($P<0.05$), and was similar between mothers and other females ($P>0.05$) and mothers and escorts ($P>0.05$, Figure 4a).

Newborn and infant calves initiated similar numbers of interactions towards conspecific females (in keeping with the lack of an Age-class x Initiator category effect in Table 1). Calves initiated similar numbers (average ± 95% CI per 30-minute focal) of feeding (13.48 ± 3.473) and social interactions (13.90 ± 3.308; 95% CI around difference between means for behavioural class: 0.310; Tukey's HSD: $P>0.05$) towards conspecific females, which were both significantly higher than resting-related interactions (2.23 ± 1.208; $P<0.05$ for both the comparisons); this pattern was not different across calf age-classes (Table 2). There was no effect of sex on the number of calf-initiated interactions for infant calves examined separately (see Supplementary Material 10).

Table 2. Results of the nested ANOVA on the log number of calf-initiated interactions towards the three conspecific categories of females. Significant *P* values are marked in bold. The asterisks in the *P* values column indicate significance in the ANOVA on the log numbers of calf-initiated non-suckling interactions (see Supplementary Material 11) for comparison.

Effect	Effect (F/R)	*SS*	*df*	*MS*	*F*	*P*
Age-class	Fixed	1.151	1	1.151	1.153	0.297
Calf ID(Age-class)	Random	17.973	18	0.999	2.171	**0.005***
Behavioural-class	Fixed	52.362	2	26.181	27.138	**<0.001***
Conspecific category	Fixed	86.172	2	43.086	59.997	**<0.001***
Behavioural-class* Conspecific category	Fixed	22.078	4	5.519	11.206	**<0.001***
Age-class*Behavioural-class	Fixed	1.379	2	0.689	0.715	0.496
Age-class*Conspecific category	Fixed	0.539	2	0.269	0.375	0.690
Age-class*Behavioural-class*Conspecific category	Fixed	2.166	4	0.542	1.100	0.363
Calf ID(Age-class)*Behavioural-class	Random	34.730	36	0.965	2.098	**0.001***
Calf ID(Age-class)*Conspecific category	Random	25.853	36	0.718	1.561	**0.031***
Calf ID(Age-class)*Behavioural-class*Conspecific category	Random	35.464	72	0.493	1.071	0.353
Error	_	82.788	180	0.460	_	_

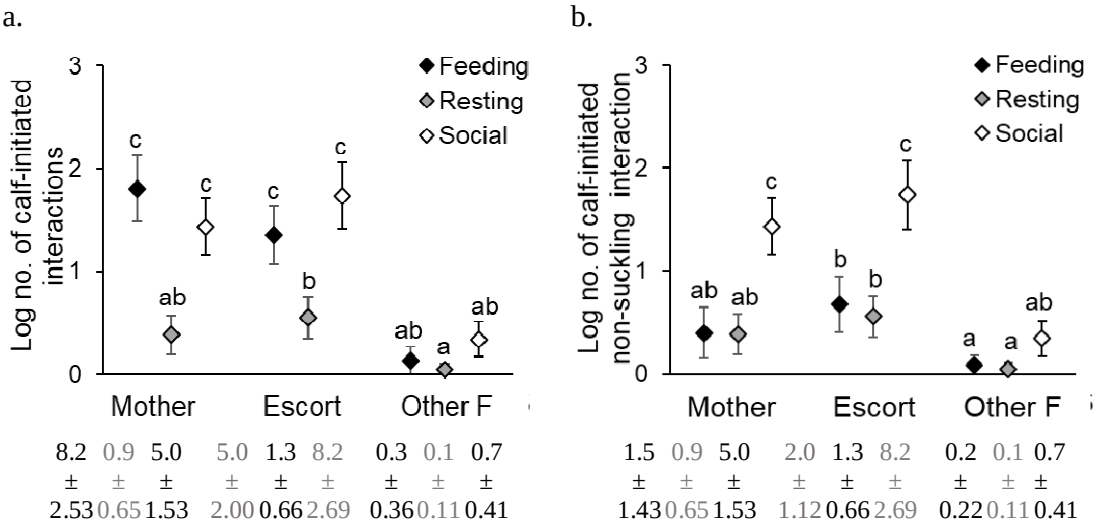


Figure 4. Log numbers of a) all calf-initiated interactions and b) calf-initiated non-suckling interactions of three behavioural classes towards the three conspecific categories of females. Error bars are 95% CI. Untransformed numbers (average ± 95% CI) are shown below the graphs.

g) Non-suckling interactions

The ANOVA on the log number of calf-initiated non-suckling interactions (149 interactions) also showed similar results (Supplementary Material 11). However, since the number of feeding-related interactions (average ± 95% CI per 30-minute focal: 3.72 ± 2.451) was lowered because of the removal of suckling or attempts to suckle, these were significantly smaller than the number of social interactions (13.90 ± 3.308; 95% CI around difference between means for behavioural class: 0.342; Tukey's HSD: $P<0.05$) and similar to the number of resting interactions (2.23 ± 1.208; $P>0.05$, Figure 4b). The number of non-suckling feeding interactions initiated by calves was higher towards escorts than other females (95% CI around difference between means for behavioural class: 0.452; $P<0.05$) and similar towards mothers and escorts ($P>0.05$, Figure 4b) as before, but was also not different between mothers and other females ($P>0.05$; however, the sample size of interactions with other females was very small), unlike that in the case of all calf-initiated feeding interactions (see Figure 4a,b).

f) Do calves terminate interactions more frequently than conspecifics or *vice versa* and is there a difference across conspecific categories in the kinds of responses shown towards calf-initiated interactions?

Terminations

Calves themselves terminated most (N=868) of the interactions that they initiated (N=1184), while conspecifics terminated the remaining. We found that mothers and escorts terminated similar proportions of calf-initiated interactions towards them (P=0.271; Figure 5, Supplementary Material 12). The same pattern was seen in the termination of non-suckling interactions (Supplementary Material 12). In both the cases, mothers and escorts terminated similar proportions of interactions initiated by newborn and infant calves.

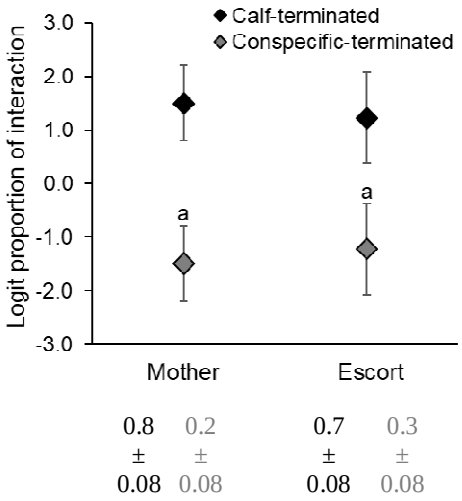


Figure 5. Logit proportions of calf-initiated interactions with their mothers and escorts that were terminated by the calves and by the conspecific females for all calf-initiated interactions. Error bars are 95% CI. Letters indicate pattern of statistical significance based on ANOVA. Proportions of calf-initiated interactions terminated by the calf and mother, and by the calf and escort, respectively, (average ± 95% CI) are shown below the graph.

Responses by conspecifics

Calves received different types of responses, but most of their interactions did not elicit a response from conspecific females (885 out of 1184 calf-initiated interactions received no response). There were more negative (192) than positive (107) responses overall, but only 17 of the 192 negative responses were aggressive, such as kick, lash, push, pull trunk, and beat with tail.

We found that the proportions of calf-initiated interactions towards mothers and escorts that elicited a neutral response (about 80%) were significantly higher than the proportion that elicited a positive response from them (about 10%; $P<0.001$; Figure 6, Supplementary Material 13). There was no significant effect of conspecific category or its interaction with response type (Figure 6, Supplementary Material 13) on the proportion of calf-initiated interactions that elicited a response. The same pattern of results was seen in the case of responses to calf-initiated non-suckling interactions also (Supplementary Material 13). Mothers (0.36% of the 563 calf-initiated interactions towards mothers) and escorts (1.39% of the 577 calf-initiated interactions towards escorts) showed a much smaller proportion of

aggressive responses than other females (15.91% of the 44 calf-initiated interactions towards other females) towards the calf-initiated interactions.

When we pooled together negative responses to calf-initiated interactions and negative conspecific female-initiated interactions towards calves across focals, we found that calves less than 6 months of age received the lowest rate of aggression from their mothers (0.15/h), followed by escorts (0.4/h). Calves received the highest rate of aggression from other females (0.8/h), despite calves spending the least proportion of time near other females.

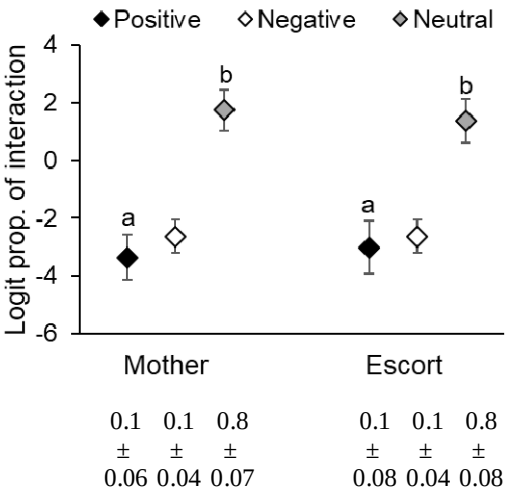


Figure 6. Logit proportions of all calf-initiated interactions with their mothers and escorts that elicited a positive, neutral, and negative response from them. Error bars are 95% CI. Letters above the data points indicate patterns of statistical significance (a<b). Proportions of interactions that elicited a positive, neutral, and negative response from mothers and escorts are written below the graph (average ± 95% CI).

Discussion

We examined the relationship between calves that were up to 6 months old and conspecific females (that were at least 5 years old) to understand the ontogeny of social relationships in wild Asian elephants. Through analysing calf-female spatial and behavioural interactions, we found that both conspecific-initiated and calf-initiated interactions towards each other were

heterogenous. Females who showed coordinated movement with a calf (i.e., escorts) also showed other positive behavioural interactions with the calf as much as or more than the calf's mother, and mothers and escorts showed similar behaviours towards calves. Therefore, escorts are allomothers in the study population. Other females did not show coordinated movement and engaged in more negative than positive interactions with calves. Thus, our study on social ontogeny shows that differentiated social relationships exist from a young age in Asian elephants.

Primarily calves initiated and terminated proximity contacts and behavioural interactions

Proximity

As expected based on the precociality hypothesis (Hill & Campbell, 2014), we found that calves were responsible for initiating more changes in proximity with mothers, escorts, and other females than *vice versa* from a young age. Offspring have been found to contribute more to proximity changes than mothers in other precocial species such as belugas (Hill & Campbell, 2014), Saharan arrui (Cassinello, 1997), and sorraia horses (Heitor & Vicente, 2008). We further found that calves approached their mothers, escorts, and other females more frequently than they left them. Contrary to this, calves left their mothers more often than they approached them during the first 6 months of life in the African savannah elephant (Douglas-Hamilton 1972). However, the distance at which approaches and leavings by calves were defined in that study was 5 m, whereas we used a distance of one calf body length, which is about 1 m. Results from the African savannah elephants hint at the possibility that calves engage in different behaviours when they are within 1 m than when within 5 m of the mother, as calves were more likely to have an age mate as a neighbour in the latter scenario than in the former (Lee, 1987). This suggests that calves might engage in play when they are at a 5-m distance, resulting in them leaving their mothers more than they approach them. It is further possible that the group's social environment – i.e., the number of individuals of different age-sex classes and the risk posed by them to the calves – may dictate conspecific female-calf approach-leave behaviour (e.g., Berman et al., 1997).

Behavioural interactions

As expected, we also found that calves initiated and terminated most of the behavioural interactions. Similar results were reported by Gadgil and Nair (1984) in semi-captive Asian elephants (birth to 1.25 years) and by Lee (1986) in the Amboseli elephants (birth to 5 years). Contrary to our expectation, the number of interactions initiated by calves decreased within

the first six months of life, which may be a result of their increasing independence (e.g., Guarino et al., 2017; Lee, 1987). This would be consistent with the calf exploring its physical rather than social environment, as the proportion of time spent near the mother also decreased. As expected, males and females did not differ in the number of interactions initiated, consistent with previous studies (Förster & Cords, 2005; Lee, 1987), although differences between the sexes may develop with age, as found in play behaviours in the African savannah elephant (Lee & Moss, 2014).

Calf-conspecific interactions were heterogeneously distributed among female conspecifics in the group

Proximity

Calves had non-random neighbours and were often positioned between their mothers and escorts, as previously observed in semi-captive Asian elephants (Gadgil & Nair, 1984). As young individuals face predation risk from tigers (Williams, 1950), being positioned near conspecific females in addition to the mother might further reduce the risk of predation (see Lee, 1987). Overall, calves showed similar proximity with mothers and escorts, but we do not have similar comparisons from other elephant populations. As expected, newborn calves spent a greater proportion of time near their mothers than near escorts, which was also seen in semi-captive elephants (Gadgil & Nair, 1984). As the calves grew (to 3-<6 months of age), they spent more time away from their mothers as expected; this period coincided with an increase in trunk motor skills and adult-like feeding behavioural expression (Revathe et al., 2020). Increase in skill competence has been found to be associated with an increase in mother-offspring distance in other species also (e.g., van Noordwijk & van Schaik, 2005). Seeking out other social partners, such as age-mates, for play, might also result in decreasing time spent near one's mother (e.g., Arroyo-Rodríguez et al., 2007). An effect of calf age on mother-calf proximity has also been reported in wild African savannah elephants (Lee 1986) and wild and captive Asian elephants in Sri Lanka and UK facilities, respectively (Webber 2017).

Contrary to our expectation, the proportion of time spent near escorts did not decrease significantly at least till 6 months of age. It is possible that escorts continue to actively keep track of and accompany calves as calves age, perhaps to support maternal foraging freedom while ensuring calf protection, as suggested in cetaceans (Whitehead, 1996). Frequent care from alloparents during later stages of infant development has also been seen in other species

(O'Brien & Robinson, 1991; Pal et al., 2021). However, our results from the Hinde's index (albeit for calves of all ages up to 6 months) that calves were more likely to approach than to leave escorts suggest that calves may be following escorts rather than escorts moving along with calves. More data are required to differentiate between these scenarios.

Against our expectation, the proportion of time spent in proximity to other females did not increase with calf age. Whether heterogeneity in calf-conspecific female (≥5 years) relationships is maintained as calves grow up (e.g., Berman, 1982a; Wey & Blumstein, 2010) or whether it reduces with age (Berman, 1982b; Roatti et al., 2023) remains to be seen. Overall, our findings are in line with that found in the African savannah elephant, in which the mother-calf distance increased but the distance between calves and other conspecific females did not vary much with calf age (Douglas-Hamilton 1972, Lee, 1987). As expected, and in line with a previous study (Webber 2017), we did not find sex-based differences in calf-female conspecific proximity at the young ages we examined.

Only females who escorted calves provided allomaternal care

Behavioural interactions

Contrary to our expectation, and despite mothers and escorts spending similar proportions of time near calves, escorts initiated more interactions (of all kinds) towards calves than did mothers. They also initiated the highest proportion of positive interactions and initiated more positive than negative interactions. Mothers also initiated more positive than negative interactions as expected, but the difference was small. As lactation is energetically expensive and requires increased time spent foraging (Wisniewska et al., 2015) and as primarily mothers provide milk in elephants (including in the study population), other caretaking behaviours might be shared with escorts, leading to more positive interactions from escorts than mothers. A previous study in the Kabini elephant population found that females in certain clans had their first- or second-order relatives as their top associates (Nandini, 2016). If such females are escorts, they might accrue indirect fitness benefits through positive interactions with calves.

Unlike African savannah elephant calves (≤12 months old) that had been found to interact with their mothers more frequently than with any other age-sex class (Lee 1986, 1987), we found that calves (<6 months) interacted with their mothers and escorts at similarly high rates. Mothers and escorts showed similar extents of positive responses (that often required

them to stop feeding) to calf-initiated interactions, terminated comparable proportions of calf-initiated interactions, and rarely directed aggression towards the calf. Mothers showed even lower aggression towards calves than did escorts, but this was not statistically significant. Mothers and escorts, but not other females, also guarded calves during long periods of calf resting. Whether the time spent showing positive responses translated into feeding costs for mothers and escorts and/or other significant costs associated with caretaking behaviours for escorts remains to be seen. It would also be important to separate interactions that necessitated a response (many interactions initiated by a calf did not require a response and did not receive one) and then compare the responses of conspecific females. The actual responses that were neutral may serve to reassure presence; this needs to be further examined. As calves <6 months old are probably in a crucial stage of learning and development, mothers and escorts may be tolerant of calf interactions through which calves explore and understand their physical and social environment and learn survival skills. Whether this changes when calves attain foraging and/or social independence, as that found in great apes (Mikeliban et al., 2021) – who have learning-intensive, prolonged developmental period similar to elephants – remains to be seen.

Other females initiated fewer interactions and more negative than positive or neutral interactions than escorts did towards calves. Some of the differences in the responses of conspecifics to calves could have arisen from the fact that calves initiated similar numbers of interactions with their mothers and escorts but far fewer interactions (almost 14 times less frequent than with escorts) with other females. However, this would not explain the higher frequency of negative interactions by other females towards calves. The fact that not all the females other than the calf's mother interacted positively – or interacted at all – with calves suggests that either conspecific females and/or the calves may actively shape their relationship, perhaps as a result of the differences in relatedness/familiarity between mothers and other conspecific females (e.g., Berman, 1982b; Dunayer & Berman, 2017). Differences in female reproductive status might also contribute to the differential nature of escort and other female interactions with calves, as females who were escorts did not have a calf of their own during the study period. However, not all the other females had a calf either during the study period.

Calves interacted similarly with mothers and escorts under different contexts and even more so with escorts when suckling was not considered

Calves interacted similarly with mothers and escorts in feeding, resting, and social contexts. Feeding interactions involved passive food sharing behaviours such as calves taking grass that had been scraped off the ground from a conspecific or feeding in the same spot as the conspecific. These behaviours required social tolerance and close contact between calves and conspecifics, which are prerequisites for social transmission of knowledge and skills (van Schaik, 2003), and were almost always initiated towards mothers and escorts, and almost never towards other females. Social interactions through which calves probably sought protection (from heat or predation) were also primarily with mothers and escorts, and such interactions interfered with the conspecific's foraging, as they partly restricted their leg movement (feeding requires kicking at and scraping short grass with the foot around the Kabini backwaters). Close proximity and interactions with escorts may contribute to not just protection of young ones but also social learning opportunities in this long-lived species with a prolonged developmental period.

We found that suckling interactions accounted for about half of the calf-initiated interactions with their mothers. Calves also sucked from escorts and rarely from other females, but these were non-lactating females; thus, calves received milk only from their mothers. Calves were quickly rejected by other females the few times calves tried to suck from them, as was seen in the African savannah elephant (Lee, 1987). This is expected as lactation is energetically costly. Calves initiated more non-suckling interactions towards their escorts than even their mothers, despite similar calf-mother and calf-escort proximity. Furthermore, almost all the play interactions with conspecific females (≤5 years) were also initiated towards escorts, but the most common social interactions included rubbing against a conspecific and touching a conspecific. Tactile communication between mothers or allomothers and newborn calves may serve to monitor the well-being of developing calves and aid in adjusting maternal or allomaternal care (Gadgil et al., 1985).

We do not yet know if escorts are more closely related or more familiar to calves than other females, and whether this drives the difference in interactions. In many species, interactions of developing individuals with familiar/related individuals are more frequent than that with unfamiliar/unrelated individuals (Bădescu et al., 2015; Berman, 1982a; Konrad et al., 2019; Lee, 1987). Allomaternal care may, therefore, reinforce existing relationship differentiation. It is also possible that escorts were younger than other females, and were, therefore, preferred by calves (see Lee, 1987). Since our study included 20 calves from 9 elephant clans, our

results are generalizable. However, we did not have enough sample size to test the effect of calf age and sex within the same model. The effect of sex should be investigated with more data points.

In summary, we found that elephant groups with calves comprised females who provided active care (mother and escort) and those who did not provide overt, active care (other females). Thus, there is heterogeneity in the quantity and quality of interactions between calves and conspecific females from a young age. It is possible that although other females do not show overt care, they may still participate in cooperative defense of calves against predators (see McComb et al., 2011). Overall, there were remarkable similarities between mothers and escorts in their behaviours towards calves and in the behaviours of calves towards them, with the primary difference being that escorts did not provide milk. Moreover, females who were classified as escorts in a focal (based on coordinated movement) always provided other forms of allomaternal care during that focal. The presence of calves and their interactions with escorts in the group might increase close social interactions between mothers and escorts, which may establish new relationships or strengthen existing relationships (Gadgil & Nair, 1984; Lee, 1987). As calf-escort interactions involved behaviours that may potentially be helpful in feeding skill acquisition and protection, the development and survival of calves may be affected by the presence of, and/or interactions, with allomothers (Hrdy 1976, Lee 1987, Hodge 2005).

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Supplementary Material

Supplementary Material 1. Details of focal calves.

Supplementary Material 1, Table 1. Details of focal calves including their clan identities, age-class (at the time of sampling), and sex that were sampled to get durations of calf positions, calf proximity, and calf behavioural interactions data.

S.No.	Calf identity	Clan identity	Calf sex	Calf age-class
1	Genette_2017_F	Patricia	F	<3 months
2	Georgina_2017_F	Patricia	F	<3 months
3	Ilaena_2016_F	Menaka	F	<3 months
4	Alena_2017_M	Alexandra	M	<3 months
5	Amarilla_2016_M	Osanna	M	<3 months
6	Gemini_2017_M	Patricia	M	<3 months
7	Iliora_2015_M	Menaka	M	<3 months
8	Ipomoea_2018_M	Victoria	M	<3 months
9	Kai_2016_M	Nakshatra	M	<3 months
10	Kasturi_2018_M	Kasturi	M	<3 months
11	Floppy_ears_2018_F	Victoria	F	3-<6 months
12	Marlene_2015_F	Tilottama	F	3-<6 months
13	Namrata_2017_F	Nakshatra	F	3-<6 months
14	Suhrita_2016_F	Victoria	F	3-<6 months
15	Zarin_2015_F	Victoria	F	3-<6 months
16	Camila_2017_M	Patricia	M	3-<6 months
17	Kausalya_2015_M	Kasturi	M	3-<6 months
18	Orlanda_2015_M	Lisa	M	3-<6 months
19	Valerie_2016_M	Victoria	M	3-<6 months
20	Vanessa_2015_M	Victoria	M	3-<6 months

Supplementary Material 1, Table 2. Details of focal calves, including their clan identities and age-, sex-class that were sampled to get durations of calf positions to calculate the time to independence of calf positions.

Calf identity	Clan identity	Calf sex	Calf age (in months)	Calf age-class	No. of different calf positions
Kausalya_2015_M	Kasturi	M	4.33	<6 months	25
Kausalya_2015_M	Kasturi	M	4.43	<6 months	12
Kausalya_2015_M	Kasturi	M	4.97	<6 months	18
Hannah_2016_F	Tilottama	F	3.80	<6 months	16
Hannah_2016_F	Tilottama	F	3.97	<6 months	20
Hannah_2016_F	Tilottama	F	4.63	<6 months	22
Vanessa_2015_M	Victoria	M	5.23	<6 months	6
Vanessa_2015_M	Victoria	M	5.73	<6 months	27
Vanessa_2015_M	Victoria	M	5.97	<6 months	45
Genette_2017_F	Patricia	F	0.10	<6 months	22
Genette_2017_F	Patricia	F	1.00	<6 months	8
Genette_2017_F	Patricia	F	1.17	<6 months	22
Leena_2017_F	Lisa	F	3.37	<6 months	15
Leena_2017_F	Lisa	F	3.60	<6 months	9
Leena_2017_F	Lisa	F	4.00	<6 months	32

Supplementary Material 2. Calf position codes and duration to independence of positions.

Supplementary Material 2, Table 1. Focal calf's position codes and their descriptions. Mother refers to the focal calf's mother; escort/s refers to the focal calf's escort/s; other female/s refers to females (≥ 5 years) other the focal calf's mother or escorts in a group; conspecific male refers to males (≥ 5 years) in a group; juvenile refers to a female or a male juvenile in the group; and another calf refers to a female or a male calf other than the focal calf in the group. Near refers to the focal calf standing/sitting/lying down within one calf body length of any of the conspecifics. The order in which conspecific categories (Calf/Juvenile/Mother/Escort/Other female/Male) appear in the position code do not signify anything.

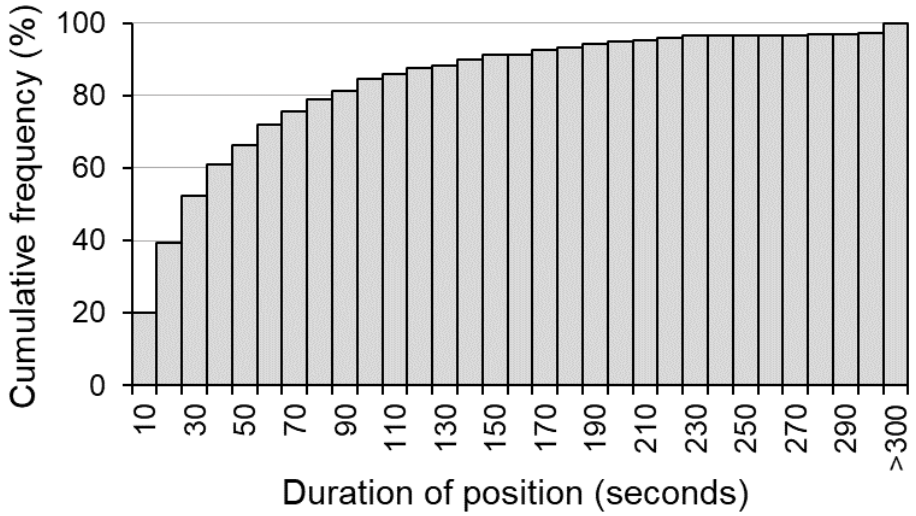
S.No.	Focal calf position code	Code description
1	ALO	Alone
2	SNC	Near another calf
3	SCE	Near another calf and an escort
4	CCJ	Near another calf and a juvenile
5	FCJ	Near another calf, a juvenile, and an other female
6	SCM	Near another calf and the mother
7	CCC	Near another calf and two other females
8	SNE	Near an escort and not near any other individual
9	ESC	Near an escort and another calf
10	SEE	Near two escorts
11	SEC	Near an escort and an other female
12	EFC	Near an escort, an other female, and another calf
13	EFJ	Near an escort, an other female, and a juvenile
14	ECC	Near an escort and two other females
15	SNJ	Near a juvenile
16	SJE	Near a juvenile and an escort
17	SJJ	Near two juveniles
18	SJM	Near a juvenile and the mother

S.No.	Focal calf position code	Code description
19	SML	Near a conspecific male
20	SME	Near a conspecific male and an escort
21	SMM	Near a conspecific male and the mother
22	SMF	Near a conspecific male and an other female
23	MFE	Near a conspecific male, an other female, and an escort
24	SNM	Near the mother and not near any other individual
25	SEM	Near an escort and the mother
26	MEC	Near the mother, an escort, and another calf
27	MEE	Near the mother and two escorts
28	MEJ	Near the mother, an escort, and a juvenile
29	MEM	Near the mother, an escort, and a conspecific male
30	MEF	Near the mother, an escort, and an other female
31	SMC	Near the mother and an other female
32	MFC	Near the mother, an other female, and another calf
33	MFJ	Near the mother, an other female, and a juvenile
34	MCC	Near the mother and two other females
35	MCO	Near the mother, two other females, and a calf
36	SCO	Near an other female and not near any other individual
37	SFC	Near an other female and another calf
38	FEE	Near an other female and two escorts
39	SFJ	Near an other female and a juvenile
40	SCC	Near two other females

While a focal calf could be near other calves or juveniles or subadult/adult males (as in the table above), as we were not interested in looking at these contacts, we did not include them in the analysis. Only changes in calf positions when alone or involving conspecific females were considered for the analysis.

Durations of calf positions

We constructed cumulative frequency distributions of durations of calf positions, calculated from second-to-second scoring of calf position changes for calves <6 months of age. Position changes were included irrespective of whether the calf or the conspecific moved to bring about the change. We found that 95% of the calf positions (near conspecific females ≥5 years or alone) changed within 200-210 seconds for calves <6 months (see figure below). Therefore, we considered two subsequent calf positions to be independent if they were separated by 4 minutes.



Supplementary Material 2, Figure 1. Cumulative frequency distributions of the time durations of calf positions for calves that were <6 months of age.

Supplementary Material 3. Details of Hinde's and Brown's proximity indices.

We examined calf-conspecific proximity initiations using Hinde's proximity index and Brown's proximity index.

Hinde's proximity index

Hinde's proximity index (Hinde and Spencer-Booth 1967) was originally developed as a measure to understand the dynamics of mother-infant relationships in primates. Whenever the calf's position changed, we recorded the time and whether the change was due to the calf's or conspecific's movement. An approach (*Ap*) was recorded when the distance between a calf-conspecific pair decreased from >1 to ≤1 calf-body length (either due to the calf's action – Ap_c or conspecific's action – Ap_{cf}), while a leaving (*L*; L_c when a calf left, and L_{cf} when conspecific left) was recorded when the calf-conspecific distance increased from ≤1 to >1 calf-body length. Hinde's proximity index for each calf-conspecific pair was calculated as follows to see whether calves showed more approaches or leavings towards each conspecific category:

Hinde's index = the percentage of approaches (% Ap_c) made by a young one (calf here) towards a conspecific – the percentage of leavings made by that young one away from that conspecific (% L_c).

% Approaches by a calf towards a conspecific (Ap_c)=

$$\frac{\text{No. of approaches made by a calf towards a conspecific}}{\text{Total no. of approaches made by a calf-conspecific pair towards each other}} \text{ X } 100$$

% Leavings by that calf away from that conspecific (L_c)=

$$\frac{\text{No. of leavings made by that calf away from that conspecific}}{\text{Total no. of leavings made by the calf-conspecific pair away from each other}} \text{ X } 100$$

The index indicates whether the calf more frequently approached or left a particular conspecific. Hinde's proximity index varies between -100 to +100 (Figure). A value of 0 indicates that the young one makes and breaks proximity contacts with a conspecific equally; a negative value indicates that the calf more often leaves than approaches the conspecific, and a positive value that the calf more often approaches than leaves the conspecific. While the

total number of approaches would be similar to the total number of leavings ($Ap = L$ (±1) in a focal) for a calf-conspecific pair (Hinde and Atkinson 1970), the number of approaches by the calf (Ap_c) could differ from the number of leavings by the calf (L_c) for the pair.

Brown's proximity index

Hinde's index does not measure the relative contributions of the calf and conspecific to changes in proximity contacts between the pair. Therefore, we also the calculated Brown's proximity index (Brown, 2001) to measure the relative contributions of the calf and conspecific to changes in proximity contacts between the pair. This calculates the total percentage of changes in proximity contacts that were due to the movement of the calf.

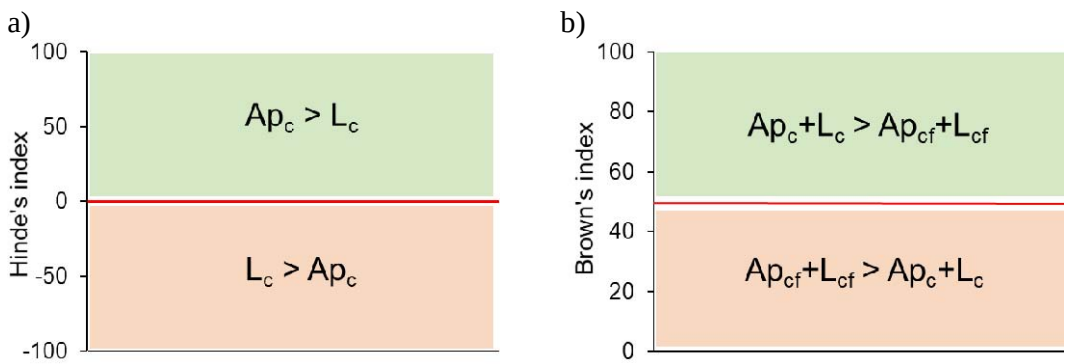
Brown's proximity index = ——————

where,

Ap_c and L_c are as above,

Ap_{cf} is the number of approaches made by the conspecific towards the calf

L_{cf} is the number of leavings made by the conspecific away from the calf.



Supplementary Material 3, Figure 1. A schematic of a) Hinde's and b) Brown's proximity indices.

Brown's index ranges from 0 to 100, with 0 indicating that the calf was not responsible for any of the changes in proximity (numerator will be zero), a value of 50 indicating that young one and conspecific were equally responsible for changes in proximity contacts, any value between 0 and 50 indicating that the conspecific was more responsible for changes in proximity contacts than the young one, a value of 100 indicating that the calf was responsible for all the changes in proximity, and any value between 50 and 100 indicating that the calf was more responsible for changes in proximity contacts than the conspecific. While Brown's

proximity index measures the relative contribution of calves and conspecifics to the changes in proximity contacts, it does not differentiate between calves approaching or leaving a conspecific to a greater extent. Hinde's and Brown's proximity indices complement each other by indicating whether the calf was responsible for making or breaking contact with a particular conspecific and whether the calf or conspecific contributed more to the changes in proximity between them. The values of both the indices may change with the identity of the conspecific (Rowell *et al*. 1964) and the young one's age (Rowell *et al*. 1964, Hinde and Spencer-Booth 1967, Hinde and Atkinson 1970, Douglas-Hamilton 1972), and the indices are not correlated (Brown 2001). The relative contributions of the young one versus the conspecific in proximity contact changes would also differ based on the distance at which approaches and leavings were measured (Brown 2001).

If a focal calf had more than one escort within a focal sample, the Hinde's index and Brown's index were averaged across escorts. Similarly, averages were used when a focal calf had more than one 'other female' with which it was involved in a proximity initiation/termination. As mentioned in the main text, in certain focals, despite the presence of three conspecific categories of females in a focal for a focal calf, there was no proximity initiation/termination between the calf and one or more categories of females. Therefore, average Hinde's and Brown's proximity indices could be calculated only for 7 calves (N: 3 females, 4 males; 3 newborn calves (<3 months), 4 infant calves (3-<6 months)) that each had proximity initiation/termination with all three conspecific categories of females in at least two of their focals. There was no significant difference in the Hinde's (Friedman ANOVA: χ^2= 2.000, N=7, df=2, P=0.368) or Brown's (Friedman ANOVA: χ^2= 4.571, N=7, df=2, P=0.102) proximity indices among mothers, escorts, and other females. ANOVAs on the logit Hinde's index with mothers and escorts based on data from a larger number of calves (17 calves, 44 focals) also showed no significant effect of conspecific category ($F_{1,16}$=3.849, P=0.067). There was no effect of calf ID ($F_{16,54}$=0.992, P=0.479) or its interaction with conspecific category in the ANOVA ($F_{16,54}$=0.724, P=0.757), but inferences cannot be drawn based on these as each calf was sampled only twice. ANOVA on the logit Brown's index with mothers and escorts (17 calves, 44 focals) also showed no significant effect of conspecific category ($F_{1,16}$=0.888, P=0.360), calf ID ($F_{16,54}$=1.484, P=0.140), or their interaction ($F_{16,54}$=0.365, P=0.985).

Supplementary Material 4. Details of behavioural interactions recorded.

As mentioned in the main text, we used focal animal sampling (Altmann, 1974) to record interactions between calves and conspecifics within groups. We recorded observations using a video camera (SONY HDR-XR 100E or SONY HDR-PJ 540E). Focal videos were taken in such a way that a focal calf was always in frame to capture all the calf-conspecific (i.e., subadult or adult female) interactions that occurred. We also ensured that the focal calf's mother was also in the frame, except in cases when the calf ventured far away from its mother, in which case, the mother's behaviours were written down. Calf-initiated interactions, conspecific-initiated interactions, and responses by conspecifics are detailed in the tables below.

Supplementary Material 4, Table 1. Calf-initiated interactions towards mother, escorts, and other females, the frequencies with which they appear in the data, behavioural classes, and descriptions of the interactions.

Code	Interaction	Frequency	Behavioural class	Description
INV	Investigate food	38	Feeding	Investigate another animal's food (in its mouth)/smell the grass that an individual is scraping off, but NOT taking someone else's food (which is TGC).
NDG	Nudge	1	Feeding	Nudge another animal especially when competing for food and feeding very close by and almost always supplanting the animal and feeding there (not dominance related in case of calves).
NPL	Pull at nipple	5	Feeding	Pull or hold nipple.
NPR	Locate nipple correctly	192	Feeding	Try to locate nipple in the correct direction. This includes sniffing in the direction of the nipples also.
NPW	Search for	9	Feeding	Try to locate nipple between the hind legs (also

Code	Interaction	Frequency	Behavioural class	Description
	nipple in the wrong direction			includes trying to suck from there).
SUA	Allosuck	45	Feeding	Suck from the escort/allomother.
SUF	Suck from female	2	Feeding	Suck from a female conspecific other than the mother or escort.
SUM	Suck from mother	137	Feeding	Suck from mother.
TGC	Take grass from a conspecific	89	Feeding	Take grass from a conspecific (and feed on it; PLO if they just throw it away PLO).
TGS	Take grass from a spot	21	Feeding	Feed from the exact spot where another is feeding from (mostly with mothers/escorts).
LEN	Lean	27	Resting	Stand or sit leaning on another animal.
LIE	Lie down	54	Resting	Lie down on land (as opposed to lying in the water, which is bathe BTH).
SLD	Slide	8	Resting	Slide off an individual's leg to lie down.
CHE	Bite	1	Social	Try to chew or bite any body part of another individual.
CHK2	Check	12	Social	Check a conspecific but NOT in dominance.
DST	Express distress	3	Social	Express distress through vocalisations.
EXT	Extend trunk	1	Social	Extend trunk towards a conspecific.
KIC	Kick conspecific	1	Social	Kick a conspecific, even if it misses.
PCL	Play climb	2	Social	Climb/roll on other calves (play).
PSH	Push	16	Social	Push with the head.
PTS	Pass	36	Social	Pass from one side of an older animal to the other through the space between that animal's trunk and forelegs or through the space under its belly.
RUB	Rub	151	Social	Rub against a conspecific (no dominance).

Code	Interaction	Frequency	Behavioural class	Description
SBE	Stand with body contact	46	Social	Stand between the trunk and leg of an escort.
SBM	Stand with body contact	11	Social	Stand between the trunk and leg of the mother.
SNI	Sniff air	62	Social	Sniff the air (could be in the direction of a conspecific or heterospecific).
STE	Stand with escort body contact	46	Social	Stand under the escort
STM	Stand with mother body contact	39	Social	Stand under the mother.
TOU	Touch	129	Social	Touch with trunk in areas apart from the mouth (in mouth would be TRM) and genitals (genitals would be CHK or CHQ), and not in dominance (dominance would be TCH).

Supplementary Material 4, Table 2. Conspecific- (mother, escorts, and other females) initiated interactions towards calves, the frequencies with which they appear in the data, behavioural classes, type, and descriptions of the interactions.

Code	Interaction	Frequency			Behav-ioural class	Type	Description
		Mom	Esc-ort	Other F			
NDG	Nudge	9	21	3	Feeding	Negative non-aggressive	Nudge another animal, especially when competing for food and feeding very close by and almost always supplanting the animal and feeding there (not dominance-related in the case of calves).
KIC	Kick conspecific	0	0	5	Social	Negative aggressive	Kick a conspecific, even if it misses.
LSH	Lash	0	0	1	Social	Negative aggressive	Lash out at a conspecific with the trunk.
NGE	Nudge calf towards escort	2	0	0	Social	Negative non-aggressive	Mother nudges or pushes the calf towards an escort (different from chaperoning because the mother does not walk along with the calf).
PSH	Push	1	0	3	Social	Negative aggressive	Push with the head.
SNI	Sniff air	1	8	1	Social	Neutral	Sniff the air (could be in the direction of a conspecific or heterospecific).
CHK2	Check	0	5	0	Social	Positive	Check a conspecific but NOT in dominance.
CHP	Chaperone	1	8	0	Social	Positive	Follow the calf, or steer the calf while walking, or move in such a way as to place oneself between the calf and males or other group

							members during dominance, or wait for and take the calf along while walking.
Code	Interaction	Frequency			Behav-ioural class	Type	Description
		Mom	Esc-ort	Other F			
CPT	Check for conspecific presence	0	1	0	Social	Positive	Check for a conspecific's presence using the tail.
ETM	Escort calf towards mother	0	8	0	Social	Positive	Escort takes the calf to its mother.
KRD	Keep calf within reachable distance	0	3	0	Social	Positive	Keep the calf within reachable distance by stopping it from moving away (when there is nobody else nearby).
RES	Rescue	1	3	0	Social	Positive	Walk/run towards the calf when distress is expressed and reach the calf.
SMA	Smell anus	1	6	2	Social	Positive	Check the calf by smelling its anus.
STG	Stand guard	3	7	0	Social	Positive	Stand guard while the calf sleeps. The calf should be next to at least one of the legs or the trunk. If the female stands over the calf with the calf in between the four legs, it is always counted as stand guard. If the female is standing next to the calf, it is counted as stand guard only if others are not nearby, for e.g., if others are moving away and the female continues to be near the calf. This

							is to eliminate the case when a calf may be lying down near someone without that individual actively doing anything.

Code	Interaction	Frequency			Behav-ioural class	Type	Description
		Mom	Esc-ort	Other F			
TOU	Touch	5	19	0	Social	Positive	Touch with trunk in areas apart from mouth (in mouth would be TRM) and genitals (genitals would be CHK or CHQ), and not in dominance (dominance would be TCH).
TRM	Trunk in mouth	0	3	0	Social	Positive	Place trunk tip in the mouth.
TRN	Turn towards calf	2	5	0	Social	Positive	Turn towards the calf as the calf experiences distress. Might step forward too but not reach the calf (RES).
WTG	Wait	0	3	0	Social	Positive	Turn towards the direction of and wait for a conspecific to follow, or stop walking and wait for someone to join.
WUC	Wake up calf	6	1	0	Social	Positive	Wake up calf when about to move or when other group members approach.

It must be noted that as in the case of proximity, it was possible, although uncommon, for more than one conspecific to simultaneously interact with the same calf.

Supplementary Material 4, Table 3. Responses received by the calves to the interactions initiated towards mothers, escorts, and other females, the frequencies with which these responses appear in the data, and the type and the descriptions of the responses.

Code	Response	Frequency	Type	Description
AVO	Avoid	38	Negative	Turn away/walk away.
KIC	Kick	4	Negative	Kick a conspecific even if it misses.
LSH	Lash	4	Negative	Lash out at a conspecific with trunk.
MVL	Move leg	99	Negative	Move leg to stop calf from rubbing/leaning/sucking.
NDG	Nudge	13	Negative	Nudge another animal especially when competing for food and feeding very close by and almost always supplanting the animal and feeding there (not dominance related in the case of calves).
PSH	Push	5	Negative	Push with the head.
PTR	Pull trunk	1	Negative	Pull (hold) the trunk and stop the individual from feeding.
SFT	Shift	25	Negative	Shift body/trunk but not move away from the spot; adjust one's position in such a way that it stops the calf's body contact with the recipient.
TLB	Beat with tail	3	Negative	Beat a conspecific with one’s tail.
NOR	No response	884	Neutral	No response.
SNI	Sniff air	1	Neutral	Sniff the air (could be in the direction of a conspecific or heterospecific).
ATN	Pay attention	3	Positive	Stand next to the calf and watch it (do something); the individual has to stop whatever it is doing and pay attention to the calf.
CCA	Cooperate with calf	14	Positive	Cooperate with calf action by stopping what one is doing.
CSU	Cooperate with suckling	62	Positive	Move foreleg forward or stop feeding for the calf to suck, or stand without moving once the calf starts sucking.

Code	Response	Frequency	Type	Description
RES	Rescue	1	Positive	Walk/run towards the calf when distress is expressed and reach the calf.
SMA	Smell anus	1	Positive	Check the calf by smelling the anus.
STG	Stand guard	16	Positive	Stand guard while the calf sleeps. The calf should be next to at least one of the legs or the trunk. If the female stands over the calf with the calf in between the four legs, it is always counted as stand guard. If the female is standing next to the calf, it is counted as stand guard only if others are not nearby, for e.g., if others are moving away and the female continues to be near the calf. This is to eliminate the case when a calf may be lying down near someone without that individual actively doing anything.
TOU	Touch	2	Positive	Touch with trunk in areas apart from mouth (in mouth would be TRM) and genitals (genitals would be CHK or CHQ), and not in dominance (dominance would be TCH).
TRM	Trunk in mouth	4	Positive	Place trunk tip in the mouth.
WUC	Wake up calf	4	Positive	Wake up calf when about to move or when other group members approach.

Supplementary Material 5. Effect of calf sex on calf-conspecific proximity.

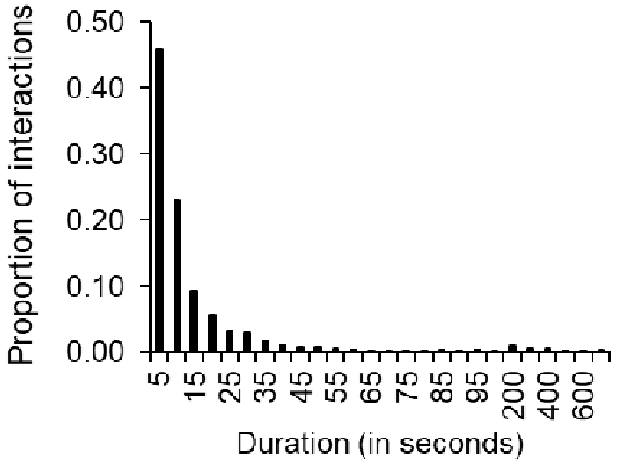
Supplementary Material 5, Table 1. Results of the nested ANOVA on the logit proportion of scans that calves spent near the three conspecific categories of females using 5 female and 5 male infant calves (3-<6 months old). Significant *P* values are marked in bold.

Effect	Effect (F/R)	*SS*	*df*	*MS*	*F*	*P*
Calf sex	Fixed	10.354	1	10.354	2.956	0.124
Conspecific category	Fixed	352.577	2	176.289	32.175	**<0.001**
Calf sex*Conspecific category	Fixed	2.358	2	1.179	0.215	0.809
Calf ID (calf sex)	Random	28.020	8	3.502	0.942	0.490
Calf ID (calf sex)*Conspecific category	Random	87.665	16	5.479	1.473	0.140
Error	_	223.134	60	3.719	_	_

Note: Inferences should not be drawn about Calf ID or interactions with this factor as each calf was sampled in only two focals.

Note: As a calf could have more than one escort and/or other female in a focal, we calculated the proportions of scans that the focal calf spent near each of the three conspecific categories of females as the sum of the number of scans near each of the females in that conspecific category / (total number of females in that conspecific category x 6; where 6 was the number of total scans in each focal). Since calves could simultaneously be near more than one category of conspecifics sometimes, the sum of the three proportions could exceed 1.

Supplementary Material 6. Durations of calf-conspecific interactions.



Supplementary Material 6, Figure 1. Frequency distribution of the durations of calf-conspecific interactions (initiated by either the calf or the conspecific).

Analyses carried out on the durations of interactions (variables: calf-conspecific interactions and calf-initiated interactions under different behavioural classes) gave similar results as those on the numbers of calf-conspecific interactions and numbers of calf-initiated interactions under different behavioural classes. Therefore, they are not reported here.

Supplementary Material 7. Effect of calf sex on the numbers of calf-conspecific interactions.

We ran a nested ANOVA with the log-transformed numbers of calf-conspecific interactions as the dependent variable, calf sex, initiator category (Calf, Conspecific), and conspecific category (Mother, Escort, and Other F) as fixed factors, and calf ID nested within sex as a random factor. We also checked the interaction effects. We could not test the effect of sex for newborn calves, as there were only 3 female (and 7 male) calves. We ran a nested ANOVA with only infant calves (3-<6 months), which contained 5 female and 5 male calves. The effect of calf sex was not significant. However, even these are small sample sizes and it is desirable to test the effects of calf sex on proximity and behavioural interactions with larger sample sizes in the future.

Supplementary Material 7, Table 1. Results of the nested ANOVA on the log no. of all calf-conspecific interactions using 5 female and 5 male infant calves (3-<6 months).

Effect	Effect (F/R)	*SS*	*df*	*MS*	*F*	*P*
Calf ID(calf sex)	Random	7.209	8	0.901	2.195	**0.040**
Calf sex	Fixed	0.074	1	0.074	0.082	0.782
Initiator category	Fixed	58.964	1	58.964	133.247	**<0.001**
Conspecific category	Fixed	27.505	2	13.753	35.559	**<0.001**
Calf ID(calf sex)*Initiator category	Random	3.540	8	0.443	1.078	0.391
Calf ID(calf sex)*Conspecific category	Random	6.188	16	0.387	0.942	0.528
Calf sex*Initiator category	Fixed	0.333	1	0.333	0.753	0.411
Calf sex*Conspecific category	Fixed	0.313	2	0.156	0.404	0.674
Initiator category*Conspecific category	Fixed	20.936	2	10.468	37.391	**<0.001**
Calf ID(calf sex)*Initiator category*Conspecific category	Random	4.479	16	0.280	0.682	0.800
Calf sex*Initiator category* Conspecific category	Fixed	0.204	2	0.102	0.365	0.700
Error	_	24.627	60	0.410	_	_

Note: Inferences should not be drawn about Calf ID or interactions with this factor as each calf was sampled in only two focals.

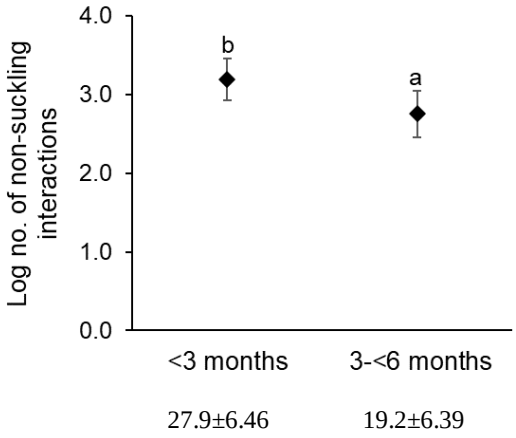
Supplementary Material 8. Non-suckling interactions.

Of the 1184 calf-initiated interactions, there was a total of 794 non-suckling interactions and 390 suckling interactions towards mothers, escort, and other females. The nested ANOVA on the number of non-suckling interactions showed almost the same pattern of results as that on all the interactions. There was a significant main effect of calf age-class, initiator category, and conspecific category on the log number of non-suckling calf-conspecific interactions (Table 1 below). Newborn calves initiated a significantly higher number of non-suckling interactions with conspecific females than infant calves (Figure 1 below). Even after removing suckling interactions, calves continued to initiate a significantly higher number of interactions (average ± 95% CI) towards conspecific females (19.85 ± 3.770) than the latter did towards calves (3.70 ± 1.634). There was again a significant interaction effect between initiator category and conspecific category (Table 1 below). Calves initiated a significantly higher number of non-suckling interactions towards their mothers and escorts than towards other females ($P<0.05$ for both the comparisons), whereas escorts initiated a higher number of interactions towards calves than mothers and other females did ($P<0.05$ for both the comparisons). Unlike the case of all interactions, calves initiated more non-suckling interactions towards escorts than towards their mothers ($P<0.05$). There was a significant effect of calf identity and also its interaction with conspecific category, but the other random factors were not significant.

Supplementary Material 8, Table 1. Results of the nested ANOVA on the log numbers of non-suckling calf-conspecific interactions. Significant *P* values are marked in bold.

Effect	Effect (F/R)	*SS*	*df*	*MS*	*F*	*P*
Calf ID(age-class)	Random	14.521	18	0.807	2.082	**0.010**
Age-class	Fixed	4.596	1	4.596	5.697	**0.028**
Initiator category	Fixed	57.675	1	57.675	103.559	**<0.001**
Conspecific category	Fixed	62.637	2	31.319	44.727	**<0.001**
Calf ID(age-class)*Initiator category	Random	10.025	18	0.557	1.437	0.127
Calf ID(age-class)*Conspecific category	Random	25.208	36	0.700	1.807	**0.009**
Age-class*Initiator category	Fixed	0.952	1	0.952	1.709	0.208
Age-class*Conspecific category	Fixed	2.501	2	1.251	1.786	0.182
Initiator category*Conspecific category	Fixed	19.035	2	9.517	21.867	**<0.001**
Calf ID(age-class)*Initiator category*Conspecific category	Random	15.668	36	0.435	1.123	0.314
Age-class*Initiator category*Conspecific category	Fixed	1.755	2	0.877	2.016	0.148
Error	_	46.503	120	0.388	_	_

Note: Inferences should not be drawn about Calf ID or interactions with this factor as each calf was sampled in only two focals.



Supplementary Material 8, Figure 1. Log numbers of non-suckling interactions between newborn and infant calves and conspecific females. Error bars are 95% CI. Letters above the data points indicate the pattern of statistical significance based on Tukey's HSD tests (a<b). The values of the number of interactions (average ± 95% CI) are shown below the graphs.

Supplementary Material 9. Details of focals that had calf-conspecific interactions.

Supplementary Material 9, Table 1. Numbers of focals (out of 40) in which calves and conspecific females initiated interactions towards each other, and the numbers of all, non-suckling, and suckling interactions initiated by calves towards the three conspecific categories of females in these 40 focals. 74.5% of actual suckling was initiated by calves with the mother, 24.5% was initiated with the escorts, which is much higher than that observed in the Amboseli elephants (3.7% of all suckling bouts with females other than the mother; Lee 1987), and only 1% was initiated with other females.

Variable	Mother	Escort	Other F
No. of focals in which focal calves initiated interactions towards conspecifics	38	40	14
No. of focals in which the conspecifics initiated interactions towards calves	15	25	11
Number of calf-initiated interactions	563	577	44
Number of calf-initiated non-suckling interactions	296	460	38
Number of calf-initiated suckling interactions	267	117	6
Proportion of calf-initiated non-suckling interactions	0.53	0.80	0.86
Proportion of calf-initiated suckling interactions	0.47	0.20	0.14

Supplementary Material 10. Effect of calf sex on the numbers of calf-initiated interactions under different behavioural classes.

As mentioned in the main text (see Methods), we ran a nested ANOVA with the log-transformed numbers of interactions under different behavioural classes as the dependent variable to check the effect of calf sex. As before, we could only test the effect of sex on infant calves due to sample size constraints. We found that the effect of calf sex was not significant (Table 1 below).

Supplementary Material 10, Table 1. Results of the ANOVA on the log number of different behavioural classes of calf-initiated interactions towards the three conspecific categories of females using 5 males and 5 female infant calves.

Effect	Effect (F/R)	*SS*	*df*	*MS*	*F*	*P*
Calf ID(calf sex)	Random	7.013	8	0.877	2.106	**0.043**
Calf sex	Fixed	0.458	1	0.458	0.522	0.490
Behavioural-class	Fixed	27.479	2	13.740	17.371	**<0.001**
Conspecific category	Fixed	39.014	2	19.507	33.393	**<0.001**
Calf ID(calf sex)*Behavioural-class	Random	12.655	16	0.791	1.900	**0.030**
Calf ID(calf sex)*Conspecific category	Random	9.347	16	0.584	1.403	0.158
Calf sex*Behavioural-class	Fixed	0.483	2	0.242	0.305	0.741
Calf sex*Conspecific category	Fixed	0.791	2	0.395	0.677	0.522
Behavioural-class*Conspecific category	Fixed	14.876	4	3.719	9.170	**<0.001**
Calf ID(calf sex)*Behavioural class*Conspecific category	Random	12.979	32	0.406	0.974	0.517
Calf sex*Behavioural-class*Conspecific category	Fixed	1.132	4	0.283	0.698	0.599
Error	_	37.472	90	0.416	_	_

Note: Inferences should not be drawn about Calf ID or interactions with this factor as each calf was sampled in only two focals.

Supplementary Material 11. Behavioural classes of calf-initiated non-suckling interactions.

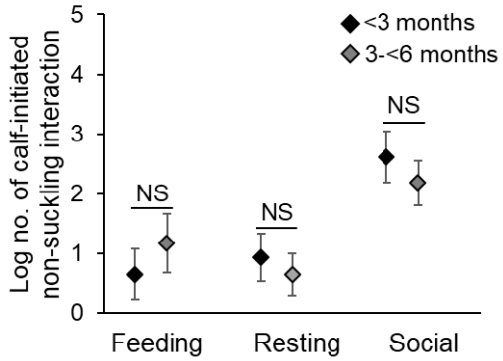
Of the calf-initiated interactions, there were a total of 539 feeding interactions (Mother: 328, Escort: 198, Other F: 13) for a total of 92.83 minutes (Mother: 63.15 minutes, Escort: 27.88 minutes, Other F: 1.80 minutes), 89 resting interactions (Mother: 36, Escort: 50, Other F: 3) for a total of 198.28 minutes (Mother: 80.48 minutes, Escort: 113.45 minutes, Other F: 4.35 minutes), and 556 social interactions (Mother: 199, Escort: 329, Other F: 28) for a total of 106.88 minutes (Mother: 34.52 minutes, Escort: 70.35 minutes, Other F: 2.02 minutes).

Of the 539 feeding interactions, 390 were suckling interactions, and a majority of them was with mothers (Supplementary Material 7). As mentioned in the main text (see Methods), we performed a nested ANOVA with only calf-initiated non-suckling interactions of the three behavioural classes with conspecific females and found that the pattern of results was the same as that of all calf-initiated interactions (see Table 2 and Figure 6 in the main text and Table 1 and Figure 1 below). Here again, newborn calves initiated similar numbers of interactions as infant calves towards conspecific females under the three behavioural classes (Table 1, Figure 1 below). Tukey's HSD tests involving feeding interactions showed a different pattern of results from that seen in the analysis using all calf-initiated interactions. Calves initiated similar numbers of feeding and social interactions (95% CI around difference between means for behavioural class: 0.310; Tukey's HSD: $P>0.05$, Table 2) towards conspecific females when all the calf-initiated interactions were considered. However, this comparison became significant when only calf-initiated non-suckling interactions were considered (95% CI around difference between means for behavioural class: 0.342; Tukey's HSD: $P<0.05$), as a majority of the calf-initiated feeding interactions were suckling interactions (see Supplementary Material 7). So, calves initiated a greater number of social interactions than non-suckling feeding interactions towards conspecific females (Figure 6b). Similarly, calves initiated a greater number of feeding interactions towards their mothers than towards other females (95% CI around difference between means for behavioural class x conspecific category: 0.502; $P<0.05$, Figure 6a). However, this comparison became non-significant when only calf-initiated non-suckling feeding interactions were considered (95% CI around difference between means for behavioural class: 0.452; $P>0.05$, Figure 6b), as a majority of the suckling interactions of calves were with their mothers (see Supplementary Material 7).

Supplementary Material 11, Table 1. Results of the ANOVA on the log number of non-suckling calf-initiated interactions towards the three conspecific categories of females under different behavioural classes. Significant *P* values are marked in bold.

Effect	Effect (F/R)	*SS*	*df*	*MS*	*F*	*P*
Age-class	Fixed	0.283	1	0.283	0.434	0.518
Calf ID(Age-class)	Random	11.717	18	0.651	1.872	**0.021**
Behavioural-class	Fixed	53.409	2	26.704	22.801	**<0.001**
Conspecific category	Fixed	43.610	2	21.805	31.139	**<0.001**
Behavioural-class* Conspecific category	Fixed	11.796	4	2.949	7.385	**<0.001**
Age-class*Behavioural-class	Fixed	3.639	2	1.820	1.554	0.225
Age-class*Conspecific category	Fixed	0.390	2	0.195	0.278	0.759
Age-class*Behavioural-class*Conspecific category	Fixed	2.857	4	0.714	1.789	0.140
Calf ID(Age-class)*Behavioural-class	Random	42.162	36	1.171	3.368	**<0.001**
Calf ID(Age-class)*Conspecific category	Random	25.209	36	0.700	2.013	**0.002**
Calf ID(Age-class)*Behavioural-class*Conspecific category	Random	28.749	72	0.399	1.148	0.232
Error	_	62.601	180	0.348	_	_

Note: Inferences should not be drawn about Calf ID or interactions with this factor as each calf was sampled in only two focals.



	Feeding		Resting		Social	
Average ± 95% CI no. of interactions	2.2 ± 1.87	5.3 ± 4.84	2.8 ± 2.28	1.7 ± 1.22	17.1 ± 5.38	10.7 ± 4.19

Supplementary Material 11, Figure 1. Log numbers of calf-initiated non-suckling interactions of the three behavioural classes by newborn and infant calves towards conspecific females. Error bars are 95% CI. NS indicates lack of statistical significance.

Supplementary Material 12. Termination of calf-initiated interactions.

All interactions

Supplementary Material 12, Table 1. Results of the nested ANOVA on the logit proportion of calf-initiated interactions towards mothers and escorts that were terminated by these females. The asterisks in the *P* values column indicate significance in the ANOVA on the logit proportion of calf-initiated non-suckling interactions (see Supplementary Material 12, Table 2) for comparison.

Effect	Effect (F/R)	*SS*	*df*	*MS*	*F*	*P*
Calf ID(Age-class)	Random	1.121	14	0.080	1.387	0.216*
Age-class	Fixed	0.236	1	0.236	2.953	0.108
Conspecific category	Fixed	0.036	1	0.036	1.314	0.271
Age-class*Conspecific category	Fixed	0.012	1	0.012	0.440	0.518
Calf ID(Age-class)*Conspecific category	Random	0.388	14	0.028	0.480	0.927
Error	_	1.848	32	0.058	_	_

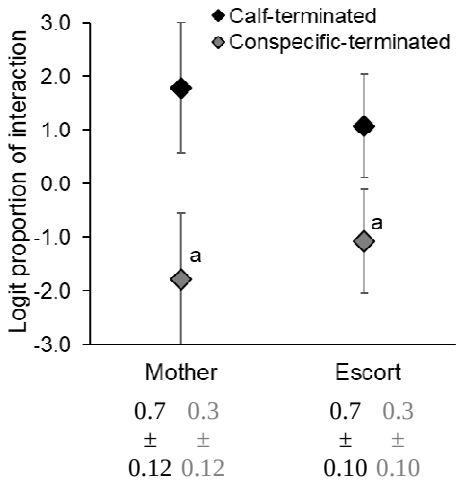
Non-suckling interactions

Of the 794 calf-initiated non-suckling interactions with mothers, escorts, and other females, calves terminated 563 interactions, and conspecifics terminated 231. There was no difference between newborn and infant calves in the logit proportions of their non-suckling interactions terminated by their mothers and escorts (Table 1 below). Mothers and escorts terminated similar proportions of calf-initiated non-suckling interactions (Table 1, Figure 1 below). There were insufficient data to examine the effect of calf sex on terminations.

Supplementary Material 12, Table 2. Results of the nested ANOVA on the logit proportion of calf-initiated non-suckling interactions towards mothers and escorts that were terminated by these conspecific females. Significant *P* values are marked in bold.

Effect	Effect (F/R)	SS	df	MS	F	P
Calf ID(Age-class)	Random	156.403	12	13.034	2.986	**0.008**
Age-class	Fixed	50.021	1	50.021	3.838	0.074
Conspecific category	Fixed	7.087	1	7.087	0.831	0.380
Age-class*Conspecific category	Fixed	4.301	1	4.301	0.504	0.491
Calf ID(Age-class)*Conspecific category	Random	102.316	12	8.526	1.954	0.071
Error	_	122.205	28	4.364	_	_

Note: Inferences should not be drawn about Calf ID or interactions with this factor as each calf was sampled in only two focals.



Supplementary Material 12, Figure 1. Logit proportions of calf-initiated non-suckling interactions towards their mothers and escorts that were terminated by the calves and by the conspecific females. Error bars are 95% CI. Letters above the data points indicate pattern of statistical significance. Proportions of calf-initiated non-suckling interactions terminated by calves and conspecific females are written below the graph (average ± 95% CI).

Supplementary Material 13. Types of responses from conspecific females for calf-initiated interactions.

All interactions

Supplementary Material 13, Table 1. Results of the ANOVA on the logit proportions of all calf-initiated interactions towards mothers and escorts that elicited a positive or a neutral response. Significant *P* values are marked in bold. The asterisks in the *P* values column indicate significance in the ANOVA on the log numbers of calf-initiated non-suckling interactions (see Supplementary Material 13, Table 2) for comparison.

Effect	Effect (F/R)	*SS*	*df*	*MS*	*F*	*P*
Calf ID(Age-class)	Random	17.477	14	1.248	0.241	0.997
Age class	Fixed	1.363	1	1.363	1.092	0.314
Response type	Fixed	766.890	1	766.890	43.888	**<0.001***
Conspecific category	Fixed	0.002	1	0.002	0.002	0.966
Calf ID(Age-class)*Response type	Random	244.635	14	17.474	3.374	**<0.001***
Calf ID(Age-class)*Conspecific category	Random	13.358	14	0.954	0.184	0.999
Age class*Response type	Fixed	76.427	1	76.427	4.374	0.055
Age class*Conspecific category	Fixed	0.273	1	0.273	0.286	0.601
Response type*Conspecific category	Fixed	6.574	1	6.574	1.117	0.298
Age class*Response type*Conspecific category	Fixed	1.882	1	1.882	0.320	0.581
Calf ID(Age-class)*Response type*Conspecific category	Random	82.386	14	5.885	1.136	0.345
Error	_	331.429	64	5.179	_	_

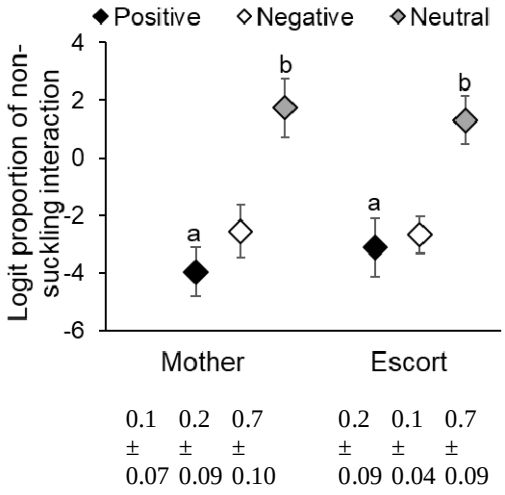
Non-suckling interactions

After removing the suckling interactions, of the 756 calf-initiated interactions towards mothers and escorts (Supplementary Material 7), there was a positive or a negative response for 174 of the interactions. Similar to the analysis using the full data, we found that there was a significant effect of response type and the interaction between calf ID and response type (Table 2 below, Figure 1 below). None of the other effects was significant.

Supplementary Material 13, Table 2. Results of the ANOVA on the logit proportions of non-suckling calf-initiated interactions towards mothers and escorts that elicited a positive or a neutral response. Significant *P* values are marked in bold.

Effect	Effect (F/R)	*SS*	*df*	*MS*	*F*	*P*
Calf ID(Age-class)	Random	41.365	12	3.447	0.600	0.833
Age class	Fixed	9.395	1	9.395	2.726	0.125
Response type	Fixed	784.004	1	784.004	40.673	**<0.001**
Conspecific category	Fixed	1.993	1	1.993	0.888	0.365
Calf ID(Age-class)*Response type	Random	231.309	12	19.276	3.355	**0.001**
Calf ID(Age-class)*Conspecific category	Random	26.932	12	2.244	0.391	0.961
Age class*Response type	Fixed	74.367	1	74.367	3.858	0.073
Age class*Conspecific category	Fixed	3.073	1	3.073	1.369	0.265
Response type*Conspecific category	Fixed	10.609	1	10.609	1.136	0.294
Age class*Response type*Conspecific category	Fixed	1.880	1	1.880	0.201	0.662
Calf ID(Age-class)*Response type*Conspecific category	Random	112.050	12	9.338	1.625	0.111
Error	_	321.774	56	5.746	_	_

Note: Inferences should not be drawn about Calf ID or interactions with this factor as each calf was sampled in only two focals.



Supplementary Material 13, Figure 1. Logit proportions of calf-initiated non-suckling interactions towards mothers and escorts that elicited a positive, neutral, and negative

responses from the conspecific females. Error bars are 95% CI. Letters above the data points indicate patterns of statistical significance (a<b). Proportions of calf-initiated non-suckling interactions that elicited a positive, neutral, and negative responses from the conspecific females are written below the graph (average ± 95% CI).

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