Calf Development, Calf-Conspecific Interactions, and the Effect of Calves on Female Social Structure in the Kabini Asian Elephant Population, Southern India

A thesis submitted for the degree of

Doctor of Philosophy

by

T. Revathe

Evolutionary and Organismal Biology Unit
Jawaharlal Nehru Centre for Advanced Scientific Research,
Bengaluru 560064, India.

July 2022

CERTIFICATE

This is to certify that the work presented in this thesis titled “**Calf Development, Calf-Conspecific Interactions, and the Effect of Calves on Female Social Structure in the Kabini Asian Elephant Population, Southern India**” has been carried out by Ms. T. Revathe under my supervision at the Evolutionary and Organismal Biology Unit, Jawaharlal Nehru Centre for Advanced Scientific Research, Bengaluru, India, and that the results in this thesis have not previously formed the basis for the award of any other degree, diploma, or fellowship.

TNC Vidya

Date: 15-July-2022

Prof. T.N.C. Vidya

DECLARATION

I declare that the matter presented in my thesis titled “**Calf Development, Calf-Conspecific Interactions, and the Effect of Calves on Female Social Structure in the Kabini Asian Elephant Population, Southern India**” is the result of studies carried out by me at the Evolutionary and Organismal Biology Unit of the Jawaharlal Nehru Centre for Advanced Scientific Research, Bengaluru, India, under the supervision of Prof. T.N.C. Vidya, and that this work has not been submitted elsewhere for any other degree.

In keeping with the general practice of reporting scientific observations, due acknowledgement has been made wherever the work described has been based on the findings of other investigators. Any omission, which might have occurred by oversight, is regretted.

Revathe T

Place: Bengaluru T. Revathe

Date: 15-July-2022

To my mother and Kevin

ACKNOWLEDGEMENTS

It is almost unbelievable that my 7-year PhD journey is coming to an end. Here I will attempt my very best to acknowledge every single person who paved the way for and who has helped me through this significant time in my life.

I would first like to acknowledge my guide Dr. TNC Vidya for trusting and giving me this extraordinary opportunity. I cannot begin to express in words how her decision to choose me as a PhD student – even though I had no idea about ecology and evolution, has shaped me and my life. I remember the day when I first joined her lab as a project assistant with no prior field experience. I was scared that I might not be able to do a good job – especially because during my first day in the field I couldn’t even tell apart juvenile and subadult elephants, but I leaned on my interests to carry on. From that very first day, Dr. Vidya has taught me everything I know about field work, animal behaviour, about how rigorous one has to be in one’s thought process, in collecting and analyzing data, and in one’s communication. She has been an inspiration in the scientific field, and I wish to learn and grow more with time and pass on what has been taught to me and to create such tremendous opportunities for the future generation of students.

I also thank Dr. Vidya for offering me the field work opportunity, which was one of the very best things to have ever happened in my life. To have gotten the chance to be in forest and observe elephants and other wonderful wildlife for 3.5 years is without a doubt one of the most cherished parts of my life.

I thank Dr. Vidya specifically for understanding my health condition and accommodating my needs, without which I wouldn’t be here today and submitting this thesis. I truly wish for every student who deal with chronic health conditions to get a supportive mentor who brings out the best in their students; it can make all the difference in the world for us. I also thank her for being a source of support when I was going through personal problems. I have grown both in my personal and academic life because of the immense effort she has put in guiding me throughout my time as a project assistant and then as a PhD student. I thank her for believing in me and making me believe in myself during many difficult situations.

I thank Dr. TNC Vidya and Prof. Amitabh Joshi for the exceptional PhD coursework. They have made me think about the importance – and the art, I would say, of teaching. I will truly miss attending their classes. I will miss the way Dr. Vidya makes us think and come up with hypotheses and predictions and the ways to test them during the *Animal Behaviour* class sessions. It's a joy to realise one's own potential through such teaching methods. Though I will miss my time as a PhD student taking coursework, I look forward to engaging in teaching and discussions with my own students some day.

I thank my Graduate Student Advisory Committee (GSAC) members: Prof. Amitabh Joshi and Prof. Mewa Singh. Their encouragements and questions during GSAC presentations were very helpful. I specifically thank Prof. Amitabh Joshi for writing to me about my progress after my GSAC meetings. His feedbacks have helped me assess myself and have shown me how much I have grown with time.

I thank Prof. Kavita Isvaran for being a supportive external during my comprehensive examination and for helping me out with GLMM analysis in R. I also thank her for the Advanced Statistics Workshop that she handled at IISc in January 2020, which made it possible for me to understand GLMM and write my own codes without much difficulty for chapter 2 analysis. I thank Prof. Amitabh Joshi for helping me out with ANOVA and post hoc tests for chapter 4. I thank Dr. Vidya for clarifying all my statistics-related doubts, even when I write so many long emails with so many questions.

I acknowledge my senior colleagues: Dr. Nandini, Dr. Keerthipriya, and Dr. Hansraj. Apart from my guide, all three of my seniors provided immense support and guidance, and for that I am truly thankful. Nandini was the first student to explain to me, the kind of work being conducted in the lab when I joined as a project assistant. It was a joy to share peaceful mornings with her in the lab talking about every possible topic one could think of. I thank her for being patient while teaching me elephant identification and for showing me how careful one must be in that process. I used to call her from the field panicking about seeing more than 30 elephants at a time because I didn't know any of them in the beginning. She would try to calm me down and tell me that it was only a matter of practice. I have tried to guide people who have joined after me in the same way when they had doubts about their potential to identify elephants. I hope I have been of some help to them.

I thank Keerthi for listening to me and discussing with me whenever I had some ideas about my work and encouraging me to pursue them. She also helped me with estimating the ages of calves and juveniles. I thank her for introducing me to politics and making me think deeply about various things. Tea-time discussions with her and Anuj were very enjoyable. I thank her for helping me out during multiple health emergencies. I also thank Keerthi for introducing me to Whiney, who was a big source of comfort and joy in the field station.

I thank Hansraj for teaching me field roads and making sure I was doing okay in field when I first joined as a project assistant. He also introduced me to many field staff, which made me comfortable in my subsequent communications with them. Our field work periods significantly overlapped, and it was delightful to sit outside the field station with Dopey on days when we had time and chat about what happened in field, which elephants we saw, etc. Hansraj, I still remember the connection you had with Kencha and how you used to tease Whiney and Dopey. It was a treat to witness such events. I also thank Hansraj for providing guidance with data analysis.

I thank Nandini and Hansraj for collecting data when I was sick and couldn't go to the field.

I have worked with many students in the field: Chiti, Aamir, Awani, and Ankana, and it was good to have them there. My most memorable days in field station were with Chiti when she had visited the field during 2014 December. I can still hear our loud laughter in a pitch-dark field station. It was so much fun to follow around dragonflies with you to photograph them, Chiti. It also gives me much happiness that you were the first person to write about my chapter 3 (also my first paper as a PhD student) as a science communication article. It was wonderful to have worked with Aamir and Awani, even though it was only for a short period of time. I shared my last season in the field with Ankana, and it was nice to learn about birds and insects from her. I particularly remember learning to spot cicada from her, which was fun.

I thank Athira for being supportive during difficult times and making sure that I was doing okay. It is almost unbelievable that it was only a couple of years ago that we both were in the institute amongst 25 other students dealing with the pandemic news. It's hard to imagine how things would have been if you were not here, Athira. I am glad to have you as a friend, and I hope we continue as good friends no matter where we are.

I thank all my past and current lab members for creating a healthy work environment and for looking after one another.

I thank the trackers with whom I worked in the field: Krishna, Shankar, and Ranga. They taught me Kannada and made sure of my safety in the field, especially when we walked inside the forest for sample collection. I am glad to have known them, to have worked with them, and to have shared a period of my life with them. I thank Pramod, who drove the jeep during my fieldwork, for making sure of everyone's safety while driving. It gives immense happiness when the people I have worked with in the field call me to talk about how the focal calves are doing, who has a new calf, which elephants they saw, etc. During the gut-wrenching drought year of 2017, Krishna, Shankar, and Pramod had been exceptionally helpful in looking for dead elephants and helping forest department staff. Though it was a very difficult field season – mainly emotionally, I am glad I had them as support. They took a lot of initiative when it came to collecting tissue samples (with proper permits) from dead elephants, especially when the areas were inaccessible. I thank all of them for teaching me about the plants they knew. It was also great to learn about their ancestors from them.

I thank Karnataka Forest Department and the Conservators and DCFs of Nagarahole and Bandipur National Parks and Tiger Reserves for permits, without which this thesis work would not have been possible. I am thankful to all the forest department staff for being so welcoming and accompanying us for important sample collection. I am thankful to the staff of DB Kuppe range for trusting me in my work and appreciating our team's help. They have been a tremendous source of encouragement during my entire fieldwork, and I am extremely happy to have known every single one of them. I thank Mr. Appaji, Mr. Vinu, Mr. Raju, Mr. Giri Gowda, Mr. Basavraj, Mr. Ashok Pujari, Mr. Keerthi, Mr. Nagaraj, Mr. Virbadhra, Mr. Praveen, Somanna, Somesh anna, and Krishnanna for their help during my field work. I thank Kari anna for accompanying me on the day of elephant census in 2017 and teaching me a lot about forest and telling me stories about his time as a watcher. I thank Mr. Pooviah for help with permits. I thank the various forest rangers especially Mr. Vinay, Mr. Satish, Mr. Madhusudhan, Mr. Saran Basappa. All of them have helped out so many times in the field. This list is by no means exhaustive, and I truly regret missing out anyone's name.

I thank Krishnanna and his wife and Latha akka for making us food during my field work. I specifically thank Latha akka for trying her best to pack breakfast and lunch on time before we left for field in the morning.

I thank JNCASR for my PhD fellowship and for the extension they provided in view of the pandemic. I thank JNCASR for offering an affordable, safe, and comfortable stay throughout my time as a PhD student. I am also thankful to JNCASR for all their institutional support.

I thank the housekeeping staff for their support in the hostel, especially during the pandemic.

The last 7 years have been an exceptionally difficult time for me because of my health condition, mainly because there aren't (m)any supportive and knowledgeable gynecologists who take women's health seriously. The online PCOS community has been so helpful because of whom I am at a much better place today of managing the symptoms of this long-term health condition. I have no words to express how supportive, non-judgmental, and inclusive the community is, who invest so much time and energy in figuring out ways to make the life of people with PCOS better. I am so grateful to every one of them for doing everything they can to make our lives better. To live with chronic fatigue and inflammation, hormonal imbalance, mood swings, and menorrhagia – to list a few of the symptoms – is by no means fun, to put it mildly. So, above all, I want to thank myself for never giving up and for fighting my way through the worst of days. I have, very often, searched for people with PCOS who have made it as a faculty. I hardly found anyone, but I would like to believe that they are out there. And I want to mark that here I am, a woman with PCOS, submitting her PhD thesis after 7 years of work. I want to tell the fellow people dealing with PCOS that it is possible to achieve our goals. I hope the coming years will be better for women's healthcare.

Family, Friends, Partner, and Animals

Firstly, I acknowledge my mother for being an extraordinary source of support. I am who I am because of her. From my childhood, she has done everything possible in her power to bring out the best in me. She has protected me and taught me all the good values I know. She is one of the kindest persons I have ever known in my life, and she has been my friend and my mentor. She has believed in me and supported me during crucial times. I am glad to have reached here and to have made her happy through this achievement. I dedicate my thesis to my mother.

I thank my sister for supporting me and encouraging me during difficult times. I thank my maternal grandparents for being so exceptional in supporting me. I am grateful to them for believing in my dreams and helping me achieve it through constant support.

I thank Ovee and Partha for being good friends, and I cherish the days I shared with them in Bengaluru.

There are two people in my life whom I cannot thank enough: my friend, Chaitu and my partner, Sooraj. To this date, I don’t understand how I got to know and share my life with such extraordinary people, but I am truly thankful for that.

Chaitu and I share more than a decade of friendship. We have held each other’s hands during the happiest and darkest of moments. I take great pride in being your friend, Chaitu. I thank you for the uncountable times and ways in which you have helped, protected, encouraged, and stood for me. You have always brought out the best in me, and I am grateful to have shared my college days with you and my PhD days with you in the same city. I cannot imagine being here without your friendship.

I thank my partner for being exceptionally kind and loving. Without your immense and constant support, I would not have survived the pandemic, especially when my health was at the worst state, Sooraj. I thank you for seeing my dreams and goals as your own and doing everything possible to help me reach them. I thank you for constantly believing in me, for supporting me through the worst of days, for standing by me through everything, and for your unwavering love. I am so glad to have you in my life and cannot wait to see where life takes us.

Finally, I thank all the animals that have accepted me into their life: Kevin, Whiney, Dopey, Kencha, and Bushy. All the days spent with them were the best. I dedicate my thesis also to my baby brother, Kevin. Words aren’t enough to express my love for him. I thank all the wonderful and extraordinary elephants I got the opportunity to observe and collect data on. I can never forget any of them.

Contents

THESIS ABSTRACT

Group-living is widespread among vertebrates and is expected to provide benefits such as decreased predation, enhanced feeding success, and higher survival of young ones (for example, Holekamp *et al.* 1997, Clutton-Brock *et al.* 1999, Packer *et al.* 1990). In large mammals, in which adults have few natural predators and grouping is likely to increase feeding competition, higher survival of young ones may be an important benefit of group living. Better survival of young ones through decreased predation or infanticide may result from increased group size, active guarding of young, or increased vigilance (Lee 1987, Packer *et al.* 2001, Santema and Clutton-Brock 2013). Better survival and improved well-being of young ones may also result from better care because of the participation of individuals apart from the mother in rearing offspring (Moehlman 1979, Clutton-Brock *et al.* 2001, Meehan *et al.* 2016). The arrival, therefore, of young ones may have considerable effects on social structure and behaviour of social mammals, especially those that show fission-fusion dynamics, in which groups or subgroups can split or rejoin flexibly to change group size and composition in response to fluctuating ecological and social environments (Aureli *et al.* 2008). Such species may show regrouping, increasing group sizes and/or forming new associations in the presence of young ones, and increased sociality and cooperation, possibly because of the need for cooperative offspring care (see Lee 1987, Wells *et al.* 1987, Gero *et al.* 2013, Holmes *et al.* 2016, Marealle *et al.* 2020). Thus, studying the effect of young ones on adult grouping patterns and sociality would help us understand the extent to which social structure is shaped by their presence and associations with them.

In this thesis, I attempted to understand the importance of young ones in female Asian elephant (*Elephas maximus*) society, collecting field data from Nagarahole and Bandipur National Parks and Tiger Reserves (Kabini elephant population) in southern India. Asian elephants are long-lived (Sukumar 2003), organised into matrilineal clans of mostly related females (Vidya and Sukumar 2005, Shetty 2016, Nandini *et al.* 2018), have a long period of dependency of young ones (Lahdenperä *et al.* 2016), and likely have a relatively low lifetime reproductive success. Thus, young ones are very valuable, and it has been suggested that cooperative care may be the *raison d'être* for female sociality in the Asian elephant (Gadgil and Nair 1984, Gadgil *et al.* 1985). I examined how the presence of calves (<1 year of age)

affected female group sizes and associations, studied the development of various behaviours in calves and how calves interacted with various conspecific females, and then examined allomothering (care by non-mother females) and some reasons for such care. The thesis is organised as a set of manuscripts.

In chapter 1, the ***General Introduction***, I give a brief introduction to the study system and questions. The thesis has four data chapters (chapters 2-5).

In chapter 2, titled ***Effect of calves and young juveniles on female group sizes and associations in an Asian elephant population in southern India***, I examined the effect of calves (<1 year of age) on female grouping patterns and associations using field data collected from 2009-2018. Female Asian elephants show fission-fusion dynamics (de Silva *et al.* 2011, Nandini *et al.* 2017, 2018), but group sizes and social structure were not found to vary much seasonally in the study population, in which a constraint on group sizes was also found (Nandini *et al.* 2017). However, I found that female group sizes (and the numbers of young adult and subadult females in groups) increased in the presence of calves and young juveniles (1-<2 years of age). I then compared female associations and certain network statistics between the presence and absence of calves and found that the number of adult female associates, the strength of female associations, and the clustering coefficient also increased in the presence of calves. Females were also more directly connected to one another in calf presence than in their absence. Thus, fission-fusion dynamics allowed for female sociality to increase in calf presence, perhaps to facilitate the protection of calves against predation and/or allomaternal care, despite potential feeding costs that may be involved.

The changes in group size, especially of young females who might provide care, led me to look at allomaternal care in the study population. However, since there was no previous work on calf behaviours, which would be required to study calf-conspecific interactions, I examined the development of various behaviours in calves. This is described in chapter 3, titled ***Development of motor control and behaviour in Asian elephants in the Kabini elephant population, southern India***. Here, I studied the ontogeny of trunk motor control, trunk lateralisation, and various behaviours, using field data that I collected from 2016-2018 on individually identified wild elephant calves and juveniles. I found that although calves are precocial and capable of locomotion soon after birth, their trunk motor skills developed gradually. However, lateralisation in trunk usage existed from a young age, suggesting that trunk laterality is not a developmental marker in Asian elephants. As adeptness in trunk motor skills developed only when calves were older, behaviours that required trunk usage, such as foraging, also developed gradually. Young calves spent most of their time resting; as a result, synchrony between mothers and offspring in behaviours was high only after about a year of birth. Thus, calves are slow maturing, and calves of all ages, especially young calves (<6 months of age) are highly dependent on their mothers for nutrition and support, making this period crucial for calf development and survival.

I went on to carry out a quantitative study of calf-female interactions. Although allomothering had been previously reported in captive, semi-captive, and wild Asian elephant populations (McKay 1973, Gadgil and Nair 1984, Rapaport and Haight 1987, Schulte 2000, Vidya 2014), there was hardly any detailed, quantitative data available from the wild. Therefore, I used calf-conspecific female (subadult and adult females) behavioural data collected from 2016-2018 on 20 unique calves (<6 months old) to identify allomothers and to understand the nature of calf-female interactions. This is described in chapter 4, titled ***Proximity and behavioural interactions between calves and female conspecifics in the Kabini Asian elephant population, southern India***. I compared the proximity and behavioural interactions during focal observations between calves and three categories of adult females: mothers, escorts (females that showed coordinated movement with the calf), and other females. As expected based on their precociality, calves were responsible for more changes in proximity than conspecifics, and were responsible for initiating and terminating a majority of the interactions with conspecific females. Almost by definition, calves were in closer proximity to escorts than other females were. However, I found that females who were escorts in focals showed affiliative and helpful behaviours towards calves, comparable to mothers and unlike other females, and could, therefore, be considered allomothers in those focals. Calves even had closer interactions with escorts than mothers in some contexts, although only mothers provided milk. Thus, escorts acted as allomothers and could be important in calves' lives, providing care during the developmental period of calves.

Finally, to understand the potential benefits of allomothering, in chapter 5, titled ***Possible functions of allomaternal care in the Kabini Asian elephant population, southern India***, I tested three functional hypotheses using behavioural data on 30 unique calves (<6 months) and group size data on 10 female clans collected from 2016-2018. I found that young, nulliparous females were primarily the allomothers and carried out a higher frequency of allomothering than expected, consistent with the learning to mother hypothesis. Whether the mothering skills learnt though allomothering make allomothers better mothers needs to be examined in the future. In accordance with the mother-benefit hypothesis, I found that calves with an allomother spent a higher proportion of their time away from and had fewer social interactions with their mothers than calves without an allomother. Whether this leads to enhanced foraging freedom for mothers needs to be studied by comparing the change in feeding rates of the mother in the presence and absence of an allomother for their calves. Calves with an allomother had the advantage of being close to, interacting with, and receiving support from their allomothers, but calves without an allomother were close only to their mothers. Frequent social interactions between calves and their allomothers may help in the integration of calves into the society and also help in the learning and development of social and foraging skills. I also found that female group sizes were larger not just in calf presence than in their absence, but additionally, in the presence than the absence of allomothers. Thus, calves could also experience increased group size benefits in the presence of an allomother, which along with social benefits, lend support to the infant-benefit hypothesis. Whether these advantages result in improved social skills and survival of calves need to be examined in the future.

In chapter 6, ***General Discussion***, I provide a short discussion of the results of this thesis. This thesis demonstrates a probable link between cooperative offspring care and female social structure in Asian elephants, and shows how fission-fusion dynamics may facilitate such care. It also opens several avenues for future research.

References

1. Aureli F, Schaffner CM, Boesch C, Bearder SK, Call J, Chapman CA, Connor R, Di Fiore A, Dunbar RIM, Henzi SP, Holekamp K, Korstjens AH, Layton R, Lee P, Lehmann J, Manson JH, Ramos-Fernández G, Strier KB and van Schaik CP (2008). Fission-fusion dynamics. *Current Anthropology* 49: 627-654.
2. Clutton-Brock TH, Gaynor D, McIlrath GM, Maccoll AD, Kansky R, Chadwick P, Manser M, Skinner JD and Brotherton PN (1999). Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. *Journal of Animal Ecology* 68: 672-683.
3. Clutton-Brock TH, Russell AF, Sharpe LL, Brotherton PN, McIlrath GM, White S and

Cameron EZ (2001). Effects of helpers on juvenile development and survival in meerkats. *Science* 293: 2446-2449.

4. de Silva S, Ranjeewa AD and Kryazhimskiy S (2011). The dynamics of social networks among female Asian elephants. *BMC Ecology* 11: 1-6.
5. Gadgil M and Nair VP (1984). Observations on the social behaviour of free ranging groups of tame Asiatic elephants (*Elephas maximus* Linn). *Proceedings of the Indian Academy of Sciences (Animal science)* 93: 225-233.
6. Gadgil M, Hegde M, Joshi NV and Gadgil S (1985). On the communication of well-being. *Proceedings of the Indian Academy of Sciences (Animal Sciences)* 94: 575-586.
7. Gero S, Gordon J and Whitehead H (2013). Calves as social hubs: dynamics of the social network within sperm whale units. *Proceedings of the Royal Society B: Biological Sciences* 280: 20131113.
8. Holekamp KE, Smale L, Berg R and Cooper SM (1997). Hunting rates and hunting success in the spotted hyena (*Crocuta crocuta*). *Journal of Zoology* 242: 1-5.
9. Holmes SM, Gordon AD, Louis EE and Johnson SE (2016). Fission-fusion dynamics in black-and-white ruffed lemurs may facilitate both feeding strategies and communal care of infants in a spatially and temporally variable environment. *Behavioural Ecology and Sociobiology* 70: 1949-1960.
10. Lahdenperä M, Mar KU and Lummaa V (2016). Short-term and delayed effects of mother death on calf mortality in Asian elephants. *Behavioural Ecology* 27: 166-174.
11. Lee PC (1987). Allomothering among African elephants. *Animal Behaviour* 35: 278–291.
12. Marealle WN, Holmern T and Røskaft E (2020). Factors Affecting Group Size and Vigilance Behaviour of Maasai Giraffe (Giraffa camelopardalis tippelskirchi) on the Serengeti-Ngorongoro Ecosystem, Tanzania. *East African Journal of Environment and Natural Resources* 2: 14-23.
13. McKay GM (1973). Behaviour and ecology of the Asiatic elephant in southeastern Ceylon. *Smithsonian Contributions to Zoology* 125: 1-113.
14. Meehan CL, Helfrecht C and Malcom CD (2016). Implications of lengthy development and maternal life history: allomaternal investment, peer relationships, and social networks. In: Meehan CL and Crittenden AN (eds.), *Childhood: Origins, Evolution, and Emplications*, pp. 199-220. University of New Mexico Press, NM, United States.
15. Moehlman PD (1979). Jackal helpers and pup survival. *Nature* 277: 382-383.
16. Nandini S, Keerthipriya P and Vidya TNC (2017). Seasonal variation in female Asian elephant social structure in Nagarahole-Bandipur, southern India. *Animal Behaviour* 134:

135-145.

17. Nandini S, Keerthipriya P and Vidya TNC (2018). Group size differences may mask underlying similarities in social structure: a comparison of female elephant societies. *Behavioural Ecology* 29: 145-159.
18. Packer C, Scheel D and Pusey AE (1990). Why lions form groups: Food is not enough. *American Naturalist* 136: 1-19.
19. Packer C, Pusey AE and Eberly LE (2001). Egalitarianism in female African lions. *Science* 293: 690-693.
20. Rapaport L and Haight J (1987). Some observations regarding allomaternal caretaking among captive Asian elephants (Elephas maximus). *Journal of Mammalogy* 68: 438-442.
21. Santema P and Clutton-Brock T (2013). Meerkat helpers increase sentinel behaviour and bipedal vigilance in the presence of pups. *Animal Behaviour* 85: 655-661.
22. Schulte BA (2000). Social structure and helping behaviour in captive elephants. *Zoo Biology* 19: 447–459.
23. Sukumar R (2003). *The Living Elephants: Evolutionary Ecology, Behaviour, and Conservation.* Oxford University Press, New York.
24. Vidya TNC (2014). Novel behaviour shown by an Asian elephant in the context of allomothering. *Acta Ethologica* 17: 123–127.
25. Wells RS, Scott MD and Irvine AB (1987). The social structure of free-ranging bottlenose dolphins. In Genoways HH (eds.), *Current Mammalogy*, pp. 247-305. Springer, Boston, MA.

CHAPTER 1

General Introduction

Introduction

In this thesis, I describe my work on calf development, the effect of calves and young juveniles on female social structure, and the nature and functions of allomaternal care, that I conducted on Asian elephants in Nagarahole and Bandipur National Parks and Tiger Reserves in southern India. In this chapter, I give a brief introduction to cooperative offspring care and group formation in animal societies, the study system, and the thesis objectives and broad outline of the thesis.

Group formation and offspring care in animal societies

The opposing nature of the benefits of group-living, such as enhanced feeding success (Rubenstein 1978, Ward and Zahavi 1973, Kruuk 1972, Gittleman 1989), decreased predation rate (Hamilton 1971, Alexander 1974, Gittleman 1989), safety against male harassment (Nurmi *et al.* 2018), opportunities for infant care and safety against infanticide (Packer *et al.* 1990, Jennions and MacDonald 1994, König 1997, Kerth and König 1999, Rendell *et al.* 2019), territorial defence (Packer *et al.* 1990, Packer *et al.* 2001), and information transfer (Kerth *et al.* 2006), and the costs of group-living, such as increased within-group competition for resources and decreased food intake (Jarman 1974), predation risk (Jarman 1974, Clutton-Brock and Harvey 1977), and disease transmission (Nunn *et al.* 2008), is thought to shape grouping patterns in animals. Enhanced care of infants is likely to be a primary benefit of group living in large mammals that do not have much adult predation and in which increasing group size leads to high feeding competition. Non-maternal care by females is often reported in species that show many of the following characteristics (see Riedman 1982): females live in highly social matrilineal societies and have a long gestation period, and offspring have a long period of postnatal development with a prolonged period of nutritional and social dependence on the mother, leading to high maternal investment, long interbirth intervals, and limited lifetime reproductive output. Therefore, while the need for cooperative resource defense is considered to be the primary evolutionary force behind female bonded societies in many primates (see Wrangham 1980), the need for cooperative offspring care, including protection against predation or infanticide, has been suggested to be either the primary or an additional important force behind the development of female-based social organization and the formation of long-term social bonds in some taxa that show the above mentioned traits (for example, Cetacea (sperm whales): Arnbom and Whitehead 1989, Whitehead *et al.* 1991, Whitehead 1996, Gero *et al.* 2013, Rendell *et al.* 2019; Proboscidea (Asian and African savannah elephants): Gadgil and Nair 1984, Lee 1987). The presence of dependent offspring is thought to contribute to keeping female groups cohesive (Gadgil and Nair 1984) and bringing about cooperation amongst females (Lee 1987).

Offspring care influencing female grouping patterns

The presence of dependent offspring may have considerable effects on social structure in group-living species that show fission-fusion dynamics, in which groups can split and rejoin in response to spatio-temporally varying ecological and social factors (Aureli *et al.* 2008). Apart from ecological factors, the presence of dependent offspring has been found to affect fission-fusion dynamics in some studies (Wells *et al.* 1987, Packer *et al.* 1990, Baird and Dill 1996, Kerth and König 1999, van Schaik 1999, Lehmann and Boesch 2004, Smith *et al.* 2008, Holmes *et al.* 2016, Bond *et al.* 2019). This may take various forms. Fission-fusion dynamics facilitate group size adjustments in the presence of vulnerable young offspring as a response to infanticide risk, causing coalescence in lions (Caraco and Wolf 1975, Packer *et al.* 1990) and forcing female howler monkeys to emigrate from the natal group once they reach a certain size (Crockett and Janson 2000). Group size adjustments may also be a response to predation (Wells *et al.* 1987), or to create opportunities for socialisation amongst young ones (van Schaik 1999), or to enhance opportunities for allomaternal care (Baird and Dill 1996, Holmes *et al.* 2016). Thus, in species that show cooperative rearing of offspring, fission-fusion dynamics may act as a mechanism to enhance offspring growth and survival, while also keeping the costs of within-group feeding competition low in the absence of young offspring. These studies are primarily on primates and cetaceans.

Offspring social interactions and care in animal societies

The importance of social partners in the proper development of young ones of social species has been known since the 1960s (Harlow 1965, 1971). As the development of social relationships is an important part of ontogeny, young and female interactions have been studied in many social species in the successive decades since Harlow's experiments (for e.g., Hinde and Atkinson 1970, Lee 1987, O'Brien and Robinson 1991, Mann and Smuts 1999, Lee and Moss 2011, Hill and Campbell 2014, Dunayer and Berman 2018). Such social interactions are usually heterogeneous in nature (Rowell *et al.* 1964). Apart from social interactions being important for the development of normal social behaviour, young-conspecific interactions are also important in species in which developing young ones have to socially learn complex foraging techniques to attain foraging independence (for e.g., Lee and Moss 1999, van Schaik *et al.* 2003).

Female social structure and the costs of interacting with group members are thought to influence maternal permissiveness and the nature of young-conspecific interactions (McKenna 1979, Maestripieri 1994), with the latter being either primarily positive or negative (Nicolson 1987). Primarily positive young-female interactions are considered as allomaternal care or allomothering (Nicolson 1987), where allomothering is a set of caretaking behaviours shown by females other than the biological mother towards young ones (Hrdy 1976, Whitehead 1996); such females are referred to as allomothers. Allomaternal care is thought to evolve under certain conditions (in primates): availability of female caretakers, low probability of group members harming young offspring of others, weak dominance relationships amongst females – making the retrieval of young ones from allomothers by mothers possible, and females showing sustained interest in taking care of young offspring of others (McKenna 1979).

Depending on the degree of development at birth, it is thought that either the young ones or the females take primary responsibility in maintaining proximity and initiating interactions, with females taking the initiative in altricial species and young ones taking the initiative in precocial species (Hill and Campbell 2014). As allomothers may incur fitness consequences through showing costly caretaking behaviours (see Rapaport and Haight 1987), it is likely that such form of care will be less frequent than maternal care. Additionally, several factors are known to influence who shows and receives allomaternal care, thus not all females in a social unit may indiscriminately care for a young one (reviewed in Nicolson 1987).

Functions of allomaternal care

Females may show allomaternal care for a variety of reasons, and it can be broadly divided into three categories: direct fitness benefits, indirect fitness benefits, and non-adaptive hypotheses (reviewed in Riedman 1982, Nicolson 1987, Chism 2000, Ross and MacLarnon 2000). Through allomaternal care, young, nulliparous females may learn important mothering skills before the birth of one's offspring (i.e., learning to mother hypothesis; Lancaster 1971, Hrdy 1976, Quiatt 1979) to increase the survival of their firstborn (Tardif *et al.* 1984, Fairbanks 1990, Stone *et al.* 2010), or subordinate females may increase their social status through acting as allomothers for the offspring of higher-ranking females (i.e., alliance formation or the status benefits hypothesis; Deag and Crook 1971, Deag 1974, Hrdy 1976, de

Waal 1990). In both cases, females increase their direct fitness benefits. Females living in societies with repeated interactions amongst members of the social unit may also reap direct benefits through reciprocally caring for each other's young ones (Riedman 1982, Chism 2000). Females of species living in societies with kin-based associations may have the opportunity to selectively help raise the offspring of related females to increase one's indirect fitness benefits through either benefitting the mother by allowing her foraging freedom (i.e., mother-benefit hypothesis; Hrdy 1976, Nicolson 1987, Ross and MacLarnon 2000) or benefiting the related offspring by improving its growth and survival (i.e., infant-benefit hypothesis; Hrdy 1976, Nicolson 1987, Ross and MacLarnon 2000). Through allomaternal care, later adoption, where necessary, may also become possible (Hrdy 1976).

Allomaternal care may also be shown for non-adaptive reasons. If high maternal responsiveness leads to better development and survival of one's offspring, selection for maternal care and strong mother-offspring bonding are expected. Females then may be predisposed to show allomaternal care as a by-product or a side-effect of this selection pressure (i.e., by-product hypothesis; Quiatt 1979, Silk 1999, Silk *et al.* 2003). Under this hypothesis, young-female interactions are not expected to be aggressive (Silk *et al.* 2003). Finally, it has been proposed that cooperative behaviour, having arisen in a lineage, may simply persist if there is no selection against it (Edwards and Naeem 1993). However, if alloparenting is costly, it is unlikely to persist through phylogenetic inertia.

Study species: the Asian elephant

The Asian elephant (*Elephas maximus*) – an umbrella (Shrader-Frechette and McCoy 1993) and keystone (Bond 1993) species, is one of the three extant elephant species of the Order Proboscidea (the other two being the African savannah elephant, *Loxodonta africana*, and African forest elephant, *Loxodonta cyclotis*). The Asian elephant is classified as endangered according to the 2019 IUCN Red List (Williams *et al.* 2020). The global population size of the species may be about 48,000-51,000, although estimates for many countries are guesses, but India almost certainly harbours over 60% of the global wild population of Asian elephants (Williams *et al.* 2020). Southern India, followed by northeastern India, has the largest populations, with the Brahmagiri-Nilgiris-Eastern Ghats landscape in southern India having the single largest population, with over 8000 elephants (Baskaran 2013).

Male and female Asian elephants differ in their morphology, dispersal patterns, and reproductive and social behaviours. With a polygynous mating system, there is pronounced sexual size dimorphism, with males being much larger than females (see Sukumar 2003). Males (although not all males) carry tusks but not females (see Sukumar 2003). Females live in matrilineal societies, while males start to disperse away from their natal clans around 10 years of age (Sukumar 1989, Desai and Johnsingh 1995). Males only form infrequent, temporary associations with females thereafter (Keerthipriya *et al.* 2021), and males do not take part in parental care (Gadgil and Nair 1984). Adult males (over 15 years of age) come into musth, which is a period of heightened sexual activity, however, elephants breed throughout the year, and musth is not synchronous across all the males in a population (Jainudeen *et al.* 1972, see Sukumar 2003, Keerthipriya *et al.* 2020). The mean age of first conception of females is about 10 years (de Silva *et al.* 2013), although males reproduce later. Females give birth to single young, or, very rarely, twins, who are precocial in nature (Gadgil and Nair 1984, Nair 1989, Sukumar 2003). Adult Asian elephants do not have natural predators; however, tigers are reported to prey upon dependent young offspring (Williams 1950, Sukumar 2003, personal observations).

As mentioned above, females live in a matrilineal society, and the most inclusive level of social organisation is the clan (Nandini *et al.* 2018). Fission-fusion dynamics (within clans) allow females to have longer-term associates apart from the immediate ones in their groups at a given point in time (de Silva *et al.* 2011, Nandini *et al.* 2017, 2018). Group sizes in the Asian elephant populations studied have been smaller than those in African savannah elephant populations, and more fluid groupings (individual-based to flexible-nested multilevel society in Asian elephants compared to flexible-nested to strict nested multilevel society in African savannah elephants) have been found in the former (de Silva and Wittemyer 2012, Nandini *et al.* 2018). Weaker dominance than in the African savannah elephant was found in the Uda Walawe Asian elephant population (de Silva *et al.* 2017), but a high frequency of between-clan dominance and a lower frequency and weaker expression of within-clan dominance were found in the Kabini Asian elephant population (Shetty 2016, Gautam 2019, Gautam and Vidya 2019). Females within clans were also found to be mostly, but not always, related in the Kabini population, with first- and second-order relatives often being the closest associates (Shetty 2016). Females cooperate for resource defense and offspring care (Gadgil and Nair 1984, see Vidya and Sukumar 2005), and cooperative offspring care is thought be a central component of female Asian elephant societies (Gadgil and Nair 1984, see Schulte 2000). Allomothering has been reported in captive (Gadgil and Nair 1984, Rapaport and Haight

1987) and wild Asian elephants (Jayantha *et al.* 2009, Vidya 2014), but has not been studied in detail in the wild.

The current study was carried out in Nagarahole and Bandipur National Parks and Tiger Reserves (centred around the Kabini reservoir and referred to here as the Kabini elephant population), which are part of the Nilgiris-Eastern Ghats landscape in southern India. A long-term elephant monitoring project was established here in 2009 (the *Kabini Elephant Project;* see Vidya *et al.* 2014, Keerthipriya and Vidya 2021).

Objectives of the study and thesis outline

This thesis is divided into six chapters, including this Introduction and the Conclusion. Chapters 2-5 are data chapters, which are written in manuscript format. Chapter 3 is already published.

As a previous study on the study population found that females maintained extended associations despite an apparent group size constraint (an average group size of 2 regardless of clan size, Nandini *et al.* 2017), I wanted to examine if cooperative offspring care (i.e., calf protection against predation and allomaternal care) is one of the possible reasons for maintaining such associations. Therefore, in Chapter 2, I first studied the effect of the presence of calves and young ones (<2 years old) on female group size, group size experienced, and female associations and social networks using the long-term data collected from 2009-2018.

To understand the link between fission fusion dynamics and cooperative offspring care, I then wanted to study the nature, frequency, and functions of allomothering in the study population. Before studying allomothering in the Kabini population of Asian elephants, in Chapter 3, I studied ontogeny of trunk lateralization, trunk motor skills, and various social and non-social behaviours in calves and juveniles to understand the crucial period of calf development, as such a detailed study has not been carried out in any wild Asian elephant population (in India), except one study on the semi-captive Asian elephants (development of non-social behaviour; Nair 1989) and one on the Uda Walawe population of Asian elephants in Sri Lanka (Webber 2017). In Chapter 4, I then studied calf-conspecific females interactions using calves less than six months of age to understand the nature of allomaternal care in the study population. As mentioned above, apart from the nature of allomaternal care, the functional significance of allomothering has also not been studied in detail in any Asian elephant population. Therefore, in Chapter 5, I tested three direct and indirect benefits hypotheses, namely learning to mother, mother-benefit, and infant-benefit hypotheses, of allomothering using calves less than 6 months of age to understand the possible functions of allomothering in the Kabini Asian elephants. In Chapter 6, I briefly summarise and discuss the findings from the data chapters and suggest planned future works to understand the role of fission-fusion dynamics in facilitating cooperative offspring care and the consequences of allomothering in the Asian elephant.

References

1. Alexander RD (1974). The evolution of social behaviour. *Annual Review of Ecology and Systematics* 5: 325-383.
2. Arnbom T and Whitehead H (1989). Observations on the composition and behaviour of groups of female sperm whales near the Galapagos Islands. *Canadian Journal of Zoology* 67: 1-7.
3. Aureli F, Schaffner CM, Boesch C, Bearder SK, Call J, Chapman CA, Connor R, di Fiore A, Dunbar RIM, Henzi SP, Holekamp K, Korstjens AH, Layton R, Lee P, Lehmann J, Manson JH, Ramos-Fernández G, Strier KB and van Schaik CP (2008). Fission-fusion dynamics: new research frameworks. *Current Anthropology* 49: 627-654.
4. Baird RW and Dill LM (1996). Ecological and social determinants of group size in transient killer whales. *Behavioural Ecology* 7: 408-416.
5. Baskaran N (2013) An overview of Asian elephants in the Western Ghats, southern India: Implications for the conservation of Western Ghats ecology. *Journal of Threatened Taxa* 5: 4854-4870.
6. Bond ML, Lee DE, Ozgul A and König B (2019). Fission–fusion dynamics of a megaherbivore are driven by ecological, anthropogenic, temporal, and social factors. *Oecologia* 191: 335-347.
7. Bond WJ (1993). Keystone species. In: Schulze ED, Mooney HA (eds.), *Ecosystem Function and Biodiversity*, pp. 237-253. Springer-Verlag, Berlin.
8. Caraco T and Wolf LL (1975). Ecological determinants of group sizes of foraging lions. *The American Naturalist* 109: 343-352.
9. Chism J (2000). Allocare patterns among cercopithecines. *Folia Primatologica* 71: 55-66.

10. Clutton-Brock TH and Harvey PH (1977). Primate ecology and social organization. *Journal of Zoology* 183: 1-39.
11. Crockett CM and Janson C H (2000). Infanticide in red howlers: female group size, male composition, and a possible link to folivory. In van Schaik CP and Janson CH (eds.), *Infanticide by Males and its Implications*, pp. 75-98. Cambridge University Press, Cambridge.
12. de Silva S, Ranjeewa A and Kryazhimskiy S (2011). The dynamics of social networks among female Asian elephants. *BMC Ecology* 11: 17.
13. de Silva S and Wittemyer G (2012). A comparison of social organization in Asian elephants and African savannah elephants. *International Journal of Primatology* 33: 1125-1141.
14. de Silva S, Webber CE, Weerathunga US, Pushpakumara TV, Weerakoon DK and George Wittemyer (2013). Demographic variables for wild Asian elephants using longitudinal observations. *PLoS One* 8: e82788.
15. de Silva S, Schmid V and Wittemyer G (2017). Fission–fusion processes weaken dominance networks of female Asian elephants in a productive habitat. *Behavioural Ecology* 28: 243-252.
16. de Waal F (1990). Do rhesus mothers suggest friends to their offspring? *Primates* 31: 597-600.
17. Deag JM (1974). *A Study of the Social Behaviour and Ecology of the Wild Barbary Macaque Macaca sylvanus L.* Ph.D. thesis, University of Bristol, England.
18. Deag JM and Crook JH (1971). Social behaviour and ‘agonistic buffering’ in the wild Barbary macaque *Macaca sylvana L. Folia Primatologica* 15: 183-200.
19. Desai AA and Johnsingh AJT (1995). Social organization and reproductive strategy of the male Asian elephant (*Elephas maximus*). In Daniel JC and Datye H (eds.) *A Week with Elephants*, pp. 532-532. Bombay Natural History Society and Oxford University Press, Bombay.
20. Dunayer ES and Berman CM (2018). Infant handling among primates. *International Journal of Comparative Psychology* 31.
21. Edwards SV and Naeem S (1993). The phylogenetic component of cooperative breeding in perching birds. *The American Naturalist* 141: 754-789.
22. Fairbanks LA (1990). Reciprocal benefits of allomothering for female vervet monkeys. *Animal Behaviour* 40: 553-562.
23. Gadgil M and Nair PV (1984). Observations on the social behaviour of free ranging

groups of tame Asiatic elephant (*Elephas maximus* Linn). *Proceedings of the Indian Academy of Sciences (Animal Sciences)* 93: 225-233.

24. Gautam H (2019). *Resource Availability, Within-clan and Between-Clan Agonistic Interactions, and Dominance Relationships amongst Female Asian Elephants in Nagarahole National Park, Southern India*. Ph.D. thesis, Jawaharlal Nehru Centre for Advanced Scientific Research, Bengaluru.
25. Gautam H and Vidya TNC (2019). A test of the socioecological model in female Asian elephants: the effects of food abundance, food distribution, and competitor density on within-clan and between-clan contests. *bioRxiv* 754515. https://doi.org/10.1101/754515.
26. Gero S, Gordon J and Whitehead H (2013). Calves as social hubs: dynamics of the social network within sperm whale units. *Proceedings of the Royal Society B: Biological Sciences* 280: 20131113.
27. Gittleman JL (1989). Carnivore group living: comparative trends. In: *Carnivore Behaviour, Ecology, and Evolution*. pp. 183-207. Springer, Boston, MA.
28. Hamilton WD (1971). Geometry for the selfish herd. *Journal of Theoretical Biology* 31: 295-311.
29. Harlow HF and Suomi SJ (1971). Social recovery by isolation-reared monkeys. *Proceedings of the National Academy of Sciences* 68: 1534-1538.
30. Harlow HF, Dodsworth RO and Harlow MK (1965). Total social isolation in monkeys. *Proceedings of the National Academy of Sciences* 54: 90-97.
31. Hill HM and Campbell C (2014). The frequency and nature of allocare by a group of belugas (*Delphinapterus leucas*) in human care. *International Journal of Comparative Psychology* 27: 501-514.
32. Hinde RA and Atkinson S (1970). Assessing the roles of social partners in maintaining mutual proximity, as exemplified by mother-infant relations in rhesus monkeys. *Animal Behaviour* 1: 169-176.
33. Holmes SM, Gordon AD, Louis EE and Johnson SE (2016). Fission-fusion dynamics in black-and-white ruffed lemurs may facilitate both feeding strategies and communal care of infants in a spatially and temporally variable environment. *Behavioural Ecology and Sociobiology* 70: 1949-1960.
34. Hrdy SB (1976). Care and exploitation of nonhuman primate infants by conspecifics other than the mother. *Advances in the Study of Behaviour* 6: 101-158.
35. Jainudeen MR, McKay GM and Eisenberg JF (1972). Observations on musth in the domesticated Asiatic elephant (*Elephas maximus*). *Mammalia* 36: 247-261.

36. Jarman P (1974). The social organisation of antelope in relation to their ecology. *Behaviour* 48: 215-267.
37. Jayantha D, Dayawansa PN, Padmalal UK and Ratnasooriya WD (2009). Social relationships of wild juvenile Asian elephants *Elephas maximus* in the Udawalawa National Park, Sri Lanka. *Journal of Threatened Taxa* 26: 211-214.
38. Jennions MD and Macdonald DW (1994). Cooperative breeding in mammals. *Trends in Ecology and Evolution* 9: 89-93.
39. Keerthipriya P and Vidya TNC. (2021). Kabini Elephant Project: a long-term programme for understanding Asian elephant behaviour and ecology. *Trumpet* 2: 14-21.
40. Keerthipriya P, Nandini S and Vidya TN (2021). Effects of male age and female presence on male associations in a large, polygynous mammal in southern India: the Asian elephant. *Frontiers in Ecology and Evolution* 9: 616666.
41. Keerthipriya P, Nandini S, Gautam H, Revathe T and Vidya TN (2020). Musth and its effects on male–male and male–female associations in Asian elephants. *Journal of Mammalogy* 101: 259-270.
42. Kerth G and König B (1999). Fission, fusion and nonrandom associations in female Bechstein's bats (*Myotis bechsteinii*). *Behaviour* 136: 1187-1202.
43. Kerth G, Ebert C and Schmidtke C (2006). Group decision making in fission–fusion societies: evidence from two-field experiments in Bechstein's bats. *Proceedings of the Royal Society* B 273: 2785-2790.
44. König B (1997). Cooperative care of young in mammals. *Naturwissenschaften* 84: 95-104.
45. Kruuk H (1972). *The Spotted Hyena: A Study of Predation and Social Behaviour*. University of Chicago Press, Chicago.
46. Lancaster JB (1971). Play mothering: the relations between juvenile females and young infants among free-ranging vervet monkeys (*Cercopithecus aethiops*). *Folia Primatologica* 15: 161-182.
47. Lee PC (1987). Allomothering among African elephants. *Animal Behaviour* 35: 278-291.
48. Lee PC and Moss CJ (1999). The social context for learning and behavioural development among wild African elephants. In Box HO and Gibson KR (eds.), *Mammalian Social Learning: Comparative and Ecological Perspectives*, pp. 102-125. Cambridge University Press, Cambridge.
49. Lee PC and Moss CJ (2011). Calf development and maternal rearing strategies. In: Moss CJ, Croze H and Lee PC (eds.), *The Amboseli Elephants: A Long-Term Perspective on a*

Long-Lived Mammal, pp 224-237. University of Chicago Press, Chicago.

50. Lehmann J and Boesch C (2004). To fission or to fusion: effects of community size on wild chimpanzee (*Pan troglodytes verus*) social organisation. *Behavioural Ecology and Sociobiology* 56: 207-216.
51. Maestripieri D (1994). Social structure, infant handling, and mothering styles in group-living Old World monkeys. *International Journal of Primatology* 15: 531-553.
52. Mann J and Smuts BB (1999) Behavioural development in wild bottlenose dolphin newborns (*Tursiops* sp.). *Behaviour* 136: 529-566.
53. McKenna JJ (1979). The evolution of allomothering behaviour among colobine monkeys: function and opportunism in evolution. *American Anthropologist* 81: 818-840.
54. Nair PV (1989). Development of nonsocial behaviour in the Asiatic elephant. *Ethology* 82: 46-60.
55. Nandini S, Keerthipriya P and Vidya TNC (2017). Seasonal variation in female Asian elephant social structure in Nagarahole-Bandipur, southern India. *Animal Behaviour* 134: 135-145.
56. Nandini S, Keerthipriya P and Vidya TNC (2018). Group size differences may mask underlying similarities in social structure: a comparison of female elephant societies. *Behavioural Ecology* 29: 145-159.
57. Nicolson NA (1987). Infants, mothers, and other females. In Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW and Struhsaker TT (eds.), *Primate Societies*, pp. 330-342. University of Chicago Press, Chicago.
58. Nunn CL, Thrall PH, Stewart K and Harcourt AH (2008). Emerging infectious diseases and animal social systems. *Evolutionary Ecology* 22: 519-543.
59. Nurmi NO, Hohmann G, Goldstone LG, Deschner T and Schülke O (2018). The "tolerant chimpanzee"—towards the costs and benefits of sociality in female bonobos. *Behavioural Ecology* 29: 1325-1339.
60. O'Brien TG and Robinson JG (1991). Allomaternal care by female wedge-capped capuchin monkeys: effects of age, rank and relatedness. *Behaviour* 119: 30-50.
61. Packer C, Pusey AE and Eberly LE (2001). Egalitarianism in female African lions. *Science* 293: 690-693.
62. Packer C, Scheel D and Pusey AE (1990). Why lions form groups: food is not enough. *American Naturalist* 136: 1-19.
63. Quiatt D (1979). Aunts and mothers: adaptive implications of allomaternal behaviour of nonhuman primates. *American Anthropologist* 81: 310-319.

64. Rapaport L and Haight J (1987). Some observations regarding allomaternal caretaking among captive Asian elephants (*Elephas maximus*). *Journal of Mammalogy*. 68: 438-442.
65. Rendell L, Cantor M, Gero S, Whitehead H and Mann J (2019). Causes and consequences of female centrality in cetacean societies. *Philosophical Transactions of the Royal Society B: Biological Sciences* 374: 20180066.
66. Riedman ML (1982). The evolution of alloparental care and adoption in mammals and birds. *Quarterly Review of Biology* 57: 405-435.
67. Ross C and MacLarnon A (2000). The evolution of non-maternal care in anthropoid primates: a test of the hypotheses. *Folia Primatologica* 71: 93-113.
68. Rowell TE, Hinde RA and Spencer-Booth Y (1964). "Aunt"-Infant interaction in captive rhesus monkeys. *Animal Behaviour* 12: 219-226.
69. Rubenstein DI (1978). On predation, competition, and the advantages of group living. In: Bateson PPG and Klopfer PH (eds.), *Social Behaviour*, pp. 205-231. Springer, Boston, MA.
70. Schulte BA (2000). Social structure and helping behaviour in captive elephants. *Zoo Biology* 19: 447-459.
71. Shetty NR (2016). *Social Structure, Genetic Relatedness, and Dominance Relationships in Female Asian Elephants in Nagarahole and Bandipur National Parks, Southern India.* Ph.D. thesis, Jawaharlal Nehru Centre for Advanced Scientific Research, Bengaluru.
72. Shrader-Frechette KS and McCoy (1993). *Method in Ecology. Strategies for Conservation.* Cambridge University Press, Cambridge.
73. Silk JB (1999). Why are infants so attractive to others? The form and function of infant handling in bonnet macaques. *Animal Behaviour* 57: 1021-1032.
74. Silk JB, Rendall D, Cheney DL and Seyfarth RM (2003). Natal attraction in adult female baboons (*Papio cynocephalus ursinus*) in the Moremi Reserve, Botswana. *Ethology* 109: 627-644.
75. Smith JE, Kolowski JM, Graham KE, Dawes SE and Holekamp KE (2008). Social and ecological determinants of fission–fusion dynamics in the spotted hyaena. *Animal Behaviour* 76: 619-36.
76. Stone AI, Mathieu D, Griffin L and Bales KL (2010). Alloparenting experience affects future parental behaviour and reproductive success in prairie voles (*Microtus ochrogaster*). *Behavioural processes* 83: 8-15.
77. Sukumar R (1989) *The Asian Elephant: Ecology and Management.* Cambridge University Press, Cambridge.

78. Sukumar R (2003). *The Living Elephants: Evolutionary Ecology, Behaviour, and Conservation.* Oxford University Press, New York.
79. Tardif SD, Richter CB and Carson RL (1984). Effects of sibling-rearing experience on future reproductive success in two species of Callitrichidae. *American Journal of Primatology* 6: 377-380.
80. van Schaik CP (1999). The socioecology of fission-fusion sociality in orangutans. *Primates* 40: 69-86.
81. van Schaik CP, Ancrenaz M, Borgen G, Galdikas B, Knott CD, Singleton I, Suzuki A, Utami SS and Merrill M (2003). Orangutan cultures and the evolution of material culture. *Science* 299: 102-105.
82. Vidya TNC and Sukumar R (2005). Social and reproductive behaviour in elephants. *Current Science* 10: 1200-1207.
83. Vidya TNC (2014). Novel behaviour shown by an Asian elephant in the context of allomothering. *Acta Ethologica* 17: 123-127.
84. Vidya TNC, Prasad D and Ghosh A (2014). Individual identification in Asian elephants. *Gajah* 40: 3-17.
85. Ward P and Zahavi A (1973). The importance of certain assemblages of birds as “information-centres” for food-finding. *Ibis* 115: 517-534.
86. Webber CE (2017). *A Comparison of Behavioural Development of Elephant Calves in Captivity and in the Wild: Implications for Welfare*. Ph.D. thesis, University of Stirling.
87. Wells RS, Scott MD and Irvine AB (1987). In: Genoways HH (eds.), The social structure of free-ranging bottlenose dolphins. In *Current Mammalogy*, pp. 247-305. Springer, Boston, MA.
88. Whitehead H (1996). Babysitting, dive synchrony, and indications of alloparental care in sperm whales. *Behavioural Ecology and Sociobiology* 38: 237-244.
89. Whitehead H, Waters S and Lyrholm T (1991). Social organization of female sperm whales and their offspring: constant companions and casual acquaintances. *Behavioural Ecology and Sociobiology* 29: 385-389.
90. Williams C, Tiwari SK, Goswami VR, de Silva S, Kumar A, Baskaran N, Yoganand K, Menon V (2020) *Elephas maximus*. The IUCN Red List of Threatened Species 2020: e.T7140A45818198.
91. Williams JH (1950). *Elephant Bill.* Doubleday, New York.
92. Wrangham RW (1980). An ecological model of female-bonded primate groups. *Behaviour* 75: 262-300.

CHAPTER 2

Effect of Calves and Young Juveniles on Female Group Sizes and Associations in an Asian Elephant Population in Southern India

Title: Effect of calves and young juveniles on female group sizes and associations in an Asian elephant population in southern India

Authors: T. Revathe, S. Nandini[1†], P. Keerthipriya[2†], Hansraj Gautam[3†], and T.N.C. Vidya[*]

Affiliation: Evolutionary and Organismal Biology Unit, Jawaharlal Nehru Centre for Advanced Scientific Research (JNCASR), Bengaluru 560064, India.
[1] Present address: Azim Premji Foundation, Doddakannelli, Sarjapur Road, Bengaluru, India.
[2] Present address: 1500 W Plum Street, Fort Collins, CO 80521, USA.
[3] Present address: National Centre for Biological Sciences, Bengaluru, India.
[†] Equal contributors.

[*] Corresponding author.
Email: tncvidya@jncasr.ac.in; ORCID iD: 0000-0002-7143-9008.

Manuscript to be posted on bioRxiv shortly.

Author contributions:

T.N.C. Vidya and T. Revathe conceived this study. TR collected field data during June 2014–June 2018, HG primarily during 2013-2016, PK during 2011–2014, SN during 2010–2013, and TNCV helped during 2009–2010. TR carried out the analyses. TR primarily and TNCV wrote the manuscript, and all the authors read and finalised it.

Abstract

Fission-fusion dynamics allow for group sizes and compositions to change in response to varying ecological, social, and demographic factors. We examined how one such factor - the presence of young ones - might affect group size and associations in female Asian elephants, which show fission-fusion dynamics. A previous finding of constraints on female group size suggested that there might not be an increase in group size, whereas high density of tiger, which can prey upon young ones, suggested a benefit to increased group size. We collected field data on group sizes, experienced group sizes (typical group sizes experienced by individuals), and associations between females, in the presence and absence of young ones, from 2009-2018 in Nagarahole and Bandipur National Parks (Kabini elephant population), southern India. Group sizes and experienced group sizes of adult females were higher in the presence of young ones (both calves less than a year old, and including young juveniles, 1-<2 years old). The number of subadult females and, to a smaller extent, the number of young adult females, who could be potential allomothers, were significantly higher when there was a calf or young juvenile in the sighting, whereas the number of males associating with female groups did not change significantly in most analyses. A comparison of social network measures showed that adult female associations became closer and stronger in the presence of calves. Thus, female group sizes and sociality were higher in the presence of calves than in their absence. Larger group size and greater sociality may increase protection from predation and/or allomothering to young offspring.

Keywords

Social organisation, fission-fusion dynamics, female group size, group size experienced, association networks, allomothering, calf, Kabini Asian elephant population.

Introduction

Group-living is widespread among animals and is expected when the benefits of group-living, such as enhanced feeding success (due to territorial defense, cooperative food capture, information transfer, or learning of foraging skills; for example, Kruuk 1972, Rubenstein 1978, Wrangham 1980, Marzluff *et al.* 1996, Weinrich *et al.* 1992), decreased predation (for example, Clutton-Brock *et al.* 1999), and increased infant care and survival (for example, Packer *et al.* 2001, Gero *et al.* 2013), outweigh the costs of group-living, such as increased within-group competition and disease transmission (for example, Jarman 1974, Nunn *et al.* 2008, VanderWaal *et al.* 2014). Since the ecological and social factors that affect grouping may vary spatiotemporally, fission-fusion dynamics are thought to have evolved in some species as a response to this variability. One of the frequently varying ecological factors is food resource availability, which is expected to affect grouping through increased within-group competition and travelling time (for example, van Schaik *et al.* 1983, Wrangham *et al.* 1993, Chapman *et al.* 1995). Thus, species that show fission-fusion dynamics periodically adjust their group sizes and compositions, often in response to food resources/competition (for example, Kummer 1971 and Asensio *et al.* 2009 in primates, Smith *et al.* 2008 in spotted hyaena, Wittemyer *et al.* 2005 in African savannah elephant); groups fission into subgroups when resources are scarce, and subgroups fuse into larger groups when resources are abundant in order to obtain benefits of sociality. However, apart from ecological factors, temporal factors such as time of day (Bond *et al.* 2019 in giraffe), demographic factors such as community size (Lehmann and Boesch 2004 in chimpanzee), and social factors such as infanticide risk, competition over reproductively active females, the sex of individuals in the group, and the presence of young ones (Packer *et al.* 1990, Kerth and König 1999, Crockett and Janson 2000, Holmes *et al.* 2016, Aguilar-Melo *et al.* 2020) may also affect group size and fission-fusion dynamics. Understanding the effects of these various ecological and social factors in shaping animal societies, including fission-fusion societies, has long been central to many studies of vertebrate social systems and organisation (Crook and Gartlan 1966, Kummer 1978, Nishida 1968, Jarman 1974, Wrangham 1980, van Schaik and van Hooff 1983, Chapman *et al.* 1995, Sterck *et al.* 1997, Wittemyer *et al.* 2005, Smith *et al.* 2008).

Female Asian elephants show fission-fusion dynamics (Sukumar 1989, de Silva *et al.* 2011, Nandini *et al.* 2018), with the most inclusive social unit termed the clan and the set of individuals seen together in the field termed a group (Nandini *et al.* 2018; a group is usually a subset of the clan and not the entire clan due to fission-fusion dynamics). Females are philopatric, whereas males disperse from their natal clans when they are about 10 years old, and thereafter form only temporary associations with females (Desai and Johnsingh 1995, Keerthipriya *et al.* 2021). Thus, females are usually, although not always, related within clans and groups (Vidya and Sukumar 2005, Nandini 2016), and intense agonistic interactions have been observed between clans in at least one population (Gautam and Vidya 2019, Kabini elephant population in southern India). Unlike the case of the African savannah elephant (Western and Lindsay 1984, Wittemyer *et al.* 2005), seasonal differences in group size and association measures were not found in the Kabini Asian elephant population after accounting for clan identity, despite strong seasonality in habitat and space use (Nandini *et al.* 2017; similar analyses have not been published from any other population). Moreover, there was indication of a constraint on group size, with average group sizes not differing across clans of different sizes (which would have different numbers of available females for association; Nandini *et al.* 2017). Thus, resource availability within the forest during the dry and wet seasons did not seem to affect group size or social structure. However, associations were not fixed, and fission-fusion dynamics allowed for meeting clan-mates while keeping the average group size small (Nandini *et al.* 2017), pointing to extended associations in the clan being beneficial.

Since Asian elephants show a long period of calf dependency on the mother (Revathe *et al.* 2020), and since calves may be preyed upon by tigers (Williams 1950, Eisenberg 1980, Sukumar 2003), one of the benefits of extended female associations may be allomothering, wherein females other than the biological mother take care of young ones (for example, Whitehead 1996, Gero *et al.* 2009, in sperm whales, Lee 1987, Lee and Moss 2011 in African savannah elephants, Gadgil and Nair 1984, Nair 1989, Vidya 2014 in Asian elephant). The need for such alloparental care may have been evolutionarily important for the development of female sociality, and the presence of calves may keep female groups cohesive in elephants and other species (see Gadgil and Nair 1984, Lee 1987, Whitehead *et al.* 1991, Whitehead 1996, Gero *et al.* 2013, Holmes *et al.* 2016, Rendell *et al.* 2019). An increase in female group size and/or association strength in the presence of young, dependent offspring has been seen in some species (African lions: Packer *et al.* 1990, Bottlenose dolphins: Wells *et al.* 1987, Bearzi *et al.* 1997, Campbell *et al.* 2002, Maasai giraffe: Marealle *et al.* 2020, Lemurs: Holmes *et al.* 2016, Transient killer whales: Baird and Dill 1996, Sperm whales: Gero *et al.* 2009, Gero *et al.* 2013, Degus: Wey *et al.* 2013), and the sociality of females may positively affect infant survival (Silk *et al.* 2003, McFarland *et al.* 2017). Thus, we wanted to examine the effect of the presence of young ones on female group size and associations in a wild Asian elephant population showing fission-fusion dynamics, and addressed the specific questions below. We considered young ones to include calves, which were defined as being less than a year old, and young juveniles, which were 1–<2 years old.

a) Is there a difference between group sizes in the presence and absence of calves or young ones?

We expected that there might be no difference in female group sizes in the presence and absence of calves due to constraints on group size (Nandini *et al.* 2017) and the possibly high energetic demand of lactation. However, it was also possible that there might be temporary increases in group size in the presence of calves, despite average group sizes being small overall, due to possible anti-predatory benefits in high tiger density habitat (see pp. 73-98, Jhala *et al.* 2008). An increase in group size, if present, could occur through the addition of females of any age, or females that were young or did not have their own dependent offspring and might actively help by allomothering. We did not expect the number of adult and subadult males associating with female groups to change. If there were increases in group sizes in the presence of calves, we wanted to see if this persisted in the presence of all young ones (calves and young juveniles). Young juveniles were not likely to have as high a mortality rate as calves, but they could also be preyed upon by tigers.

b) Are the group sizes experienced by adult females different in the presence and absence of calves/young ones in the group?

In populations with high variance in group size, a majority of the individuals experience groups larger than the average. Therefore, Jarman (1974; also see Jovani and Mavor 2011) suggested that typical group size – i.e., the group size that an average animal experiences or finds itself in – would be a better measure of animal grouping tendencies rather than group size itself. We examined whether the experienced group sizes experienced by adult females varied in the presence and absence of calves/young ones. We used experienced group size (typical group size) in addition to group size because many clans showed individual-based fission-fusion dynamics, in which individual females could decide to join or leave a group (Nandini *et al.* 2018); thus, it was possible for females to be variously represented in the presence and absence of young ones, even when the clan itself was observed to similar extents in both cases.

c) Does the presence of calves affect adult female associations?

Female elephants might change their associations in the presence of calves due to benefits to themselves or the calves or both. While the adults do not face predation risk inside protected areas, associations with certain individuals (who might provide allomaternal care and allow the mother freedom to forage) might help alleviate nutritional stress during lactation. We expected adult female associations to change in the presence of calves. An increase in the number of associations would be expected if the group size increased in the presence of calves. However, even in the absence of group size changes, individual-based fission-fusion dynamics could allow for certain females to take the place of others, resulting in different associations.

Methods

Field data collection

We carried out field data collection on Asian elephants in Nagarahole National Park and Tiger Reserve (11.85304°-12.26089° N, 76.00075°-76.27996° E) and Bandipur National Park and Tiger Reserve (11.59234°-11.94884° N, 76.20850°- 76.86904° E) in southern India (Figure 1). The parks mainly comprise dry and moist deciduous forests, and they are separated by the Kabini reservoir on the River Kabini. There is a dry (beginning mid-December to mid-June) and a wet season (see Nandini *et al.* 2017 for more details), with the receding backwaters of the reservoir forming a grassland that attracts elephants and other herbivores during the dry season. The elephant population here has been studied since 2009, and hundreds of elephants have been identified (Kabini Elephant Project: see Vidya *et al.* 2014). We carried out fieldwork from 2009-2018, between about 6:15 AM and 5:45-6:45 PM (depending on daylight and field permits), sampling fixed routes in the forest and backwaters in a stratified manner (greater sampling in the backwaters; see Nandini *et al.* 2017 for more details).

We identified female elephant groups as aggregations of one or more adult females (at least 10 years old) within 50-100 m of one another that showed coordinated movement and behaviours (Nandini *et al.* 2018). Adult females could be accompanied by subadults (subadult females: 5–<10 years old, subadult males: 5–<15 years old), juveniles (1–<5 years old), and calves (<1 year old) of both sexes. Rarely, one or more subadult females (possibly accompanied by other age-sex classes) without any adult female formed female groups.

Animals were aged based on shoulder height, body length and bulk among others (see Sukumar 1989, Vidya *et al.* 2014), with rough (5- or 10-year intervals) age-classes being used for animals born before 2000. Individuals were identified based on a combination of natural physical characteristics such as ear shape, length, nicks, holes, and tears on ears, back shape, tail length and hair brush shape, and, in the case of males, tusk length, shape, and symmetry (see Vidya *et al.* 2014). All the individuals in a group were considered to be associating with one another. Adult (at least 15 years old) and old subadult (10-15 years old) males were considered to associate with a female group if they fed within about 10 m of the group or interacted with the group (Keerthipriya *et al.* 2021).

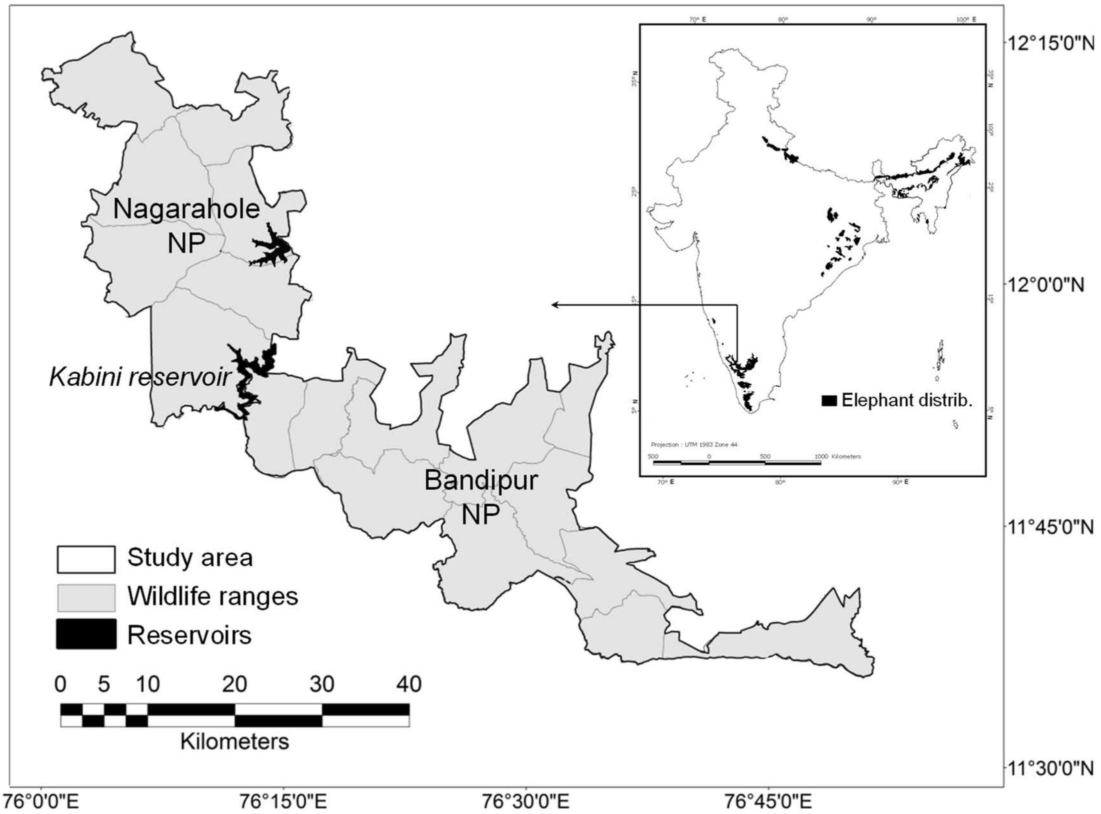


Figure 1. Map showing the location of Nagarahole and Bandipur National Parks and the Kabini reservoir between them. Inset: Map of India with the approximate distribution of elephants (based on Vidya *et al.* 2005).

Data analysis

We used sighting data on female groups and mixed-sex groups (old subadult and adult males associating with female groups) collected from 2009-2018 to calculate group sizes, experienced group sizes, and female associations. The dataset of independent sightings (sightings that were separated by at least 2.5 hours; see Nandini *et al.* 2018) that had all the individuals age-sex classified were split into three year-sets – 2009-2012, 2013-2015, and 2016-2018 – to minimise the potential effects of demographic changes on group sizes and association patterns. A single analysis on pooled data from 2009-2018 was not performed as that would assume that all the individuals were present at all times. We could also not use year-set as a random factor in such a pooled analysis as all the clans, as well as females of a clan, were not sighted across all three year-sets. A nested design could not be used either as some females within each clan were sighted in more than one year-set.

Clans were identified through modularity-based community detection (Louvain method – Blondel *et al.* 2008) in association networks (see Nandini *et al.* 2018). Within each year-set, only those clans that were sighted at least five times each in the presence and absence of calves were retained for analysis (see Supplementary Material 1 for details of clans). We carried out the analyses to look at the effect of calves (<1 year) and to look at the effect of all the young ones up to 2 years of age.

Group sizes in the presence and absence of calves

For each female group sighting (henceforth, sighting), we first calculated the 1) total group size of all the individuals present in the sighting, 2) group size excluding males ≥10 years of age, and 3) number of adult females. In order to look at the numbers of females who could potentially be allomothers, we calculated the 4) number of adult females without a calf, 5) number of adult females without a calf or a young juvenile, 6) number of young adult females (≥10 to <15 years), and 7) number of subadult females (≥5 to <10 years). While the movement of some subadult females might not be independent of their mothers, it was possible that others could be part of groups without their mothers. We also calculated the number of males that were at least 10 years old (and would have, therefore, begun the process of dispersal and would be able to associate with different groups) in each sighting. We found that several of the variables above were correlated amongst themselves. Therefore, for the analyses, we used the number of adult females, number of young adult females, number of subadult females, and the number of males ≥10 years of age (which had correlation coefficients less than 0.7; $R^2<0.50$; Supplementary Material 2).

As none of these variables was normally distributed, we used generalized linear mixed-effects models to compare group sizes in the presence (at least one calf per sighting) and absence of calves. When analysing the number of adult females, since all the sightings contained at least one adult female and there was overdispersion, we used a Zero-Truncated Negative Binomial Model (ZTNBM). The other variables could have values of zero in a sighting; therefore, depending on whether there was overdispersion or not in the variable for the year-set being analysed, we used either a Negative Binomial Model (NBM) or a Poisson Model, respectively. We used the log link for all the models.

Calf presence or absence was a fixed factor and clan identity was a random factor. We included the interaction between the two factors for the full model F. To assess the significance of the random effects, we ran two reduced models $R1$ and $R2$: the first without the interaction term, and the second without either the interaction term or clan identity, so that log-likelihood tests could be used to test for significance. We determined the significance of the interaction term by comparing $-2(\log L_F - L_{R1})$ to χ^2 [$\alpha=0.05$, $df=df_F - df_{R1}$], and the significance of clan identity by comparing $-2(\log L_{R1} - L_{R2})$ to the χ^2 [$\alpha=0.05$, $df=df_{R1} - df_{R2}$] (Bolker *et al.* 2021).

While all the clans would have adult females, it was possible for a clan not to have any young adult female or subadult female during a particular year-set. Therefore, for analyses of young adult females and subadult females, we included only those clans that had at least one young adult female or subadult female, respectively, during at least 50% of calf-present and calf-absent periods in the year-set.

Group sizes in the presence and absence of young ones

The same analyses as above were carried out on female group sightings to examine the effect of the presence of young ones (calves as well as young juveniles <2 years of age) on the different measures of group size. The same clans used to examine the effect of calf presence on group sizes were used here.

Group sizes experienced by adult females in the presence and absence of calves

Using the same sightings as those used for the group size analyses above, we calculated the group sizes experienced by each adult female in each sighting as the numbers of individuals of the kinds specified below in its sighting (group) (Jarman 1974): 1) the number of adult females (including the focal adult female), and, since we were interested in the classes of individuals who could potentially provide allomothering, 2) the number of young adult females (excluding the focal adult female if she was a young adult), and 3) the number of subadult females. (Other variables explored were correlated amongst themselves.) We used only those adult females who were sighted at least 5 times each in the presence and absence of calves (calf presence and absence here refers to the status of the sighting, irrespective of whose calf it was) for this analysis. We used generalized linear mixed-effects models to compare the group sizes experienced by adult females in the presence and absence of calves. We used calf presence/absence as a fixed factor and female identity nested within clan identity as a random factor, and included the interaction between the two. We determined the significance of the random effects following the procedure explained for the group size analysis above. As before, the number of adult females experienced could not contain zeroes as all the sightings had at least one adult female. Therefore, depending on whether this variable was over-dispersed or not within a year-set, we used a ZTNBM or a Zero-Truncated Poisson Model (ZTP), respectively. The other variables could have values of zero and, depending on whether they were overdispersed or not, we used a NBM or a Poisson model, respectively. We used a log link for all the models.

Group sizes experienced by adult females in the presence and absence of young ones

We carried out the same analyses as above to examine the effect of both calf and young juvenile presence on the different measures of group sizes experienced by adult females.

All the group size and experienced group size analyses were run in R (version 4.1.1) using the package 'glmmTMB' (Magnusson *et al.* 2017). As there was no function available to calculate R^2 for zero-truncated models, we squared the Spearman's rank order correlation r between the fitted values of the model and the observed values to obtain R^2. 95% CI of Spearman's r was computed by bootstrapping (n=1000 replicates) using the R package 'RVAideMemoire' (Hervé 2022).

Adult female associations and social networks in the presence and absence of calves

We calculated association indices (AIs) between adult females separately for sightings with and without calves in each year-set. The females used for the analysis were seen at least five times each in calf absence and calf presence (not necessarily their own calf) within each year-set. Association index (AI) was calculated as the simple ratio index, the ratio of the number of times two individuals were seen together to the total number of times they were seen (see

Ginsberg and Young 1992). We calculated the average AI and kurtosis (‘tailedness’ of a distribution in relation to its mean, compared to that of a normal distribution) of AI in calf presence and absence, and compared each statistic between calf presence and calf absence using sampled randomisation tests (Sokal and Rohlf 1981, pp. 791-794). We performed 10,000 permutations of the data by randomly marking sightings as either calf present (permuted ‘calf-present’ dataset) or calf absent (permuted ‘calf-absent’ dataset), and inferred statistical significance if the observed difference in average AI (or kurtosis of AI) between calf presence and absence was higher than 95% of the differences from the permuted data.

We also calculated the following three network statistics – degree, path length, and clustering coefficient – and tested if they were different between calf presence and absence using sampled randomisation tests. Degree is the number of direct associates of an individual; path length is the smallest number of edges joining two nodes (i.e., the smallest number of connections from one adult female to another); and clustering coefficient measures the proportion of a focal individual’s direct associates who are also direct associates of one another (Whitehead 2008). These calculations and the randomisation tests were carried out using MATLAB R2015b (The MathWorks, Inc, 1984-2015, www.mathworks.com). Association networks of females in the presence and absence of calves were constructed in Gephi 0.8.2 (Bastian *et al.* 2002).

Results

We observed 16 clans at least five times each in the presence and absence of calves from 2009-2018. Of these clans, four clans were seen in only one year-set, five clans were seen in two year-sets, and the remaining seven clans were seen in all three year-sets (see Supplementary Material 1).

Group sizes in the presence and absence of calves

There was a significant effect of calf presence/absence on the numbers of adult and young adult females in all three year-sets (Table 1), with the numbers being significantly higher in calf presence than in calf absence (average numbers of adult females per group in the three year-sets: 3.77-4.45 in calf presence, 2.25-2.40 in calf absence; average numbers of young adult females per group in the three year-sets: 0.76-1.27 in calf presence, 0.46-0.71 in calf absence; Figure 2, Supplementary Material 3). Clan identity and its interaction with calf presence/absence also significantly affected the number of adult and young adult females (Table 1, Supplementary Material 4, Figure 3a,c,e). There was a significant effect of calf presence/absence on the numbers of subadult females in the first two year-sets, with their numbers being higher in the presence than absence of calves, but the effect was not significant in the 2016-2018 year-set (average numbers of subadult females per group in the three year-sets: 0.91-2.01 in calf presence, 0.40-0.93 in calf absence; Table 2, Figure 2). However, a significant effect of clan and its interaction with calf presence/absence on the number of subadult females was found in all three year-sets (Table 2, Supplementary Material 4, Figure 3b,d,f). There was no significant effect of calf presence/absence and only an effect of clan identity on the number of males in female groups (Table 2, Supplementary Material 4, Figure 3b,d,f).

Clan size itself increased across the three year-sets in many clans (see Supplementary Material 1), and an associated increase in the average numbers of adult females in the presence of calves and young ones was observed; the highest average number each of adult females, young adult females, and subadult females was observed in the year-set that had the highest total number of each of them (Supplementary Material 1, 3). However, an increase in the total numbers of adult, young adult, and subadult females in clans did not lead to an increase in their average numbers in the absence of calves or young ones to the same extent as in their presence. The absolute increase in the numbers of young adult and subadult females in calf presence, although significant, was smaller than the increase in the number of all adult females taken together, possibly because they were fewer in number (Supplementary Material 1). To check if this demographic effect might have been partly responsible for the lower R^2s observed in the GLMMs of the numbers of young adult and subadult females, we repeated the analyses with only those clans in which the numbers of young adult females and the numbers of subadult females were greater than or equal to the numbers of calves (year-sets 2013-2015 and 2016-2018 used; insufficient data for 2009-2012). We found that while the R^2s for the numbers of young adult females increased (2013-2015: 0.24 from 0.16; 2016-2018: 0.19 from 0.13), those for the numbers of subadult females decreased (2013-2015: 0.20 from 0.33; 2016-2018: 0.14 from 0.28). Moreover, the R^2s from the GLMMs on the numbers of young adult females and the numbers of young adult females experienced (see below) were lower than those from the GLMMs on the numbers of subadult females and the numbers of subadult females experienced even in the year-set (2016-2018) when the number of subadult females was smaller than the number of young adult females (Supplementary Material 1, 4).

Group sizes in the presence and absence of young ones (individuals <2 years old)

Almost all the results from the GLMMs to examine the effect of the presence of young ones (<2 years) on group sizes mirrored the results from the GLMMs to examine the effect of the presence of calves on group sizes (Tables 1, 2, Supplementary Material 4). The numbers of adult, young adult, and subadult females were significantly higher in the presence than in the absence of young ones in all the three year-sets (Figure 2, Supplementary Material 3). The R^2s of the models examining the effect of young ones (calves and young juveniles) on group sizes were higher than those examining the effect of only calves (Tables 1, 2, Supplementary Material 4). The R^2s of the models explaining the effect of young ones on the numbers of adult females (0.22-0.38 for the three year-sets) and subadult females (0.14-0.37) were moderate, while R^2s of the models examining the effect of young ones on the numbers of young adult females were low (0.06-0.17). Surprisingly there was a significant effect of young one presence on the number of males in the 2009-2012 year-set (Table 2, Supplementary Material 4), with the number of males being slightly higher in young one presence (Supplementary Material 3), but this was not significant in the other two year-sets, in keeping with the results of the GLMMs examining the effect of calf presence on the number of males.

Table 1. Results of the full GLMMs to examine the effects of Calf presence/absence (P/A in table) (fixed effect; SE of the estimates shown for this and the intercept), Clan identity, and Clan x Calf presence/absence (random effects, for which SDs are given) on the numbers of adult and young adult females. Significant *P* values are in bold. Asterisks mark significant random effects compared with reduced models (Supplementary Material 4). R^2 of the best models are shown. The last column has the results of the GLMMs to examine the effect of young ones (<2 years) for comparison; +: same significance pattern as the current GLMMs; sig: significant, ns: not significant (see Supplementary Material 4).

Dependent variable	Estimate	*SE* of estimate / SD	1.96 *SE*	95% CI of estimate		*z*	*P*	<2 y
				Lower	Upper			
No. of adult females: 2009-2012 *(Calf P: 434, Calf A:1270 sightings), R^2=0.17*								
Intercept	0.147	0.131	0.256	-0.110	0.403	1.122	0.262	sig
Calf P/A (P)	1.052	0.146	0.287	0.765	1.338	7.192	**<0.001**	**+**
Clan		0.195					*	+
Clan x Calf P/A		0.243					*	+
No. of adult females: 2013-2015 *(Calf P: 403, Calf A:1336 sightings), R^2=0.17*								
Intercept	0.442	0.122	0.239	0.203	0.680	3.628	**<0.001**	**+**
Calf P/A (P)	0.840	0.147	0.288	0.551	1.128	5.712	**<0.001**	**+**
Clan		0.192					*	+
Clan x Calf P/A		0.290					*	+
No. of adult females: 2016-2018 *(Calf P: 694, Calf A:1364 sightings), R^2=0.27*								
Intercept	0.158	0.119	0.234	-0.076	0.392	1.325	0.185	+
Calf P/A (P)	1.137	0.146	0.287	0.850	1.423	7.775	**<0.001**	**+**
Clan		0.122					*	+
Clan x Calf P/A		0.287					*	+
No. of young adult females: 2009-2012 *(Calf P: 349, Calf A:1120 sightings), R^2=0.05*								
Intercept	-1.070	0.168	0.328	-1.398	-0.741	-6.386	**<0.001**	**+**
Calf P/A (P)	0.595	0.153	0.300	0.295	0.895	3.889	**<0.001**	**+**
Clan		0.224					*	+
Clan x Calf P/A		0.385					*	ns
No. of young adult females: 2013-2015 *(Calf P: 364, Calf A:1274 sightings), R^2=0.16*								
Intercept	-0.922	0.225	0.441	-1.363	-0.480	-4.093	**<0.001**	**+**
Calf P/A (P)	0.641	0.232	0.455	0.186	1.097	2.762	**0.006**	**+**
Clan		0.456					*	+
Clan x Calf P/A		0.502					*	+
No. of young adult females: 2016-2018 *(Calf P: 667, Calf A:1288 sightings), R^2=0.13*								
Intercept	-0.611	0.170	0.334	-0.944	-0.277	-3.588	**<0.001**	**+**
Calf P/A (P)	0.479	0.182	0.356	0.123	0.835	2.634	**0.008**	**+**
Clan		0.368					*	+
Clan x Calf P/A		0.375					*	+

Table 2. Results of the full GLMMs to examine the effects of Calf presence/absence (P/A in table) (fixed effect; SE of the estimates shown for this and the intercept), Clan identity, and Clan x Calf presence/absence (random effects, for which SDs are given) on the numbers of subadult females and old subadult and adult males. Significant *P* values are in bold. Asterisks mark significant random effects based on reduced models (see Supplementary Material 4). The last column has the results of the GLMMs to examine the effect of young ones (<2 years) for comparison; +: same significance pattern as the current GLMMs; sig: significant, ns: not significant (details in Supplementary Material 4).

Dependent variable	Estimate	*SE* of estimate / SD	1.96 *SE*	95% CI of estimate		*z*	*P*	<2 y
				Lower	Upper			
No. of subadult females: 2009-2012 *(Calf P: 434, Calf A:1270 sightings), R^2=0.09*								
Intercept	-0.843	0.143	0.281	-1.124	-0.562	-5.887	**<0.001**	**+**
Calf P/A (P)	0.699	0.118	0.231	0.468	0.929	5.929	**<0.001**	**+**
Clan		0.187					*	+
Clan x Calf P/A		0.377					*	+
No. of subadult females: 2013-2015 *(Calf P: 382, Calf A:1237 sightings), R^2=0.33*								
Intercept	-0.515	0.208	0.408	-0.923	-0.107	-2.474	**0.013**	**+**
Calf P/A (P)	0.600	0.210	0.411	0.190	1.011	2.866	**0.004**	**+**
Clan		0.465					*	+
Clan x Calf P/A		0.401					*	+
No. of subadult females: 2016-2018 *(Calf P: 596, Calf A:1273 sightings), R^2=0.28*								
Intercept	-1.339	0.363	0.712	-2.051	-0.627	-3.684	**<0.001**	**+**
Calf P/A (P)	0.653	0.351	0.687	-0.035	1.340	1.861	0.063	sig
Clan		0.692					*	+
Clan x Calf P/A		0.795					*	+
No. of males ≥10 yrs: 2009-2012 *(Calf P: 434, Calf A:1270 sightings), R^2=0.02*								
Intercept	-1.848	0.173	0.339	-2.187	-1.508	-10.670	**<0.001**	**+**
Calf P/A (P)	0.328	0.182	0.356	-0.027	0.684	1.810	0.070	sig
Clan		0.259					*	+
Clan x Calf P/A		0.336					NS	+
No. of males ≥10 yrs: 2013-2015 *(Calf P: 403, Calf A:1336 sightings), R^2=0.01*								
Intercept	-1.912	0.180	0.352	-2.264	-1.559	-10.630	**<0.001**	**+**
Calf P/A (P)	0.094	0.225	0.440	-0.346	0.535	0.420	0.674	+
Clan		0.409					*	+
Clan x Calf P/A		0.187					NS	sig
No. of males ≥10 yrs: 2016-2018 *(Calf P: 694, Calf A:1364 sightings), R^2=0.03*								
Intercept	-1.478	0.146	0.287	-1.764	-1.191	-10.096	**<0.001**	**+**
Calf P/A (P)	-0.006	0.182	0.356	-0.362	0.350	-0.036	0.972	+
Clan		0.318					*	+
Clan x Calf P/A		0.279					*	ns

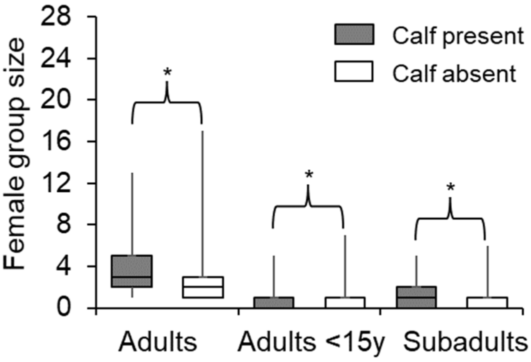
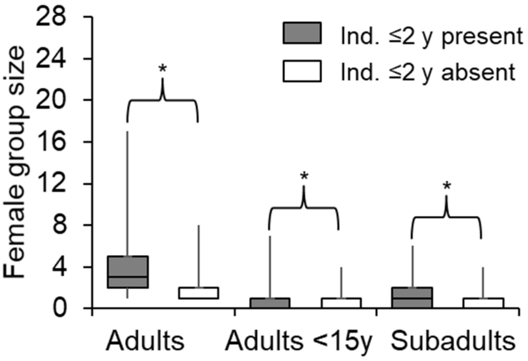
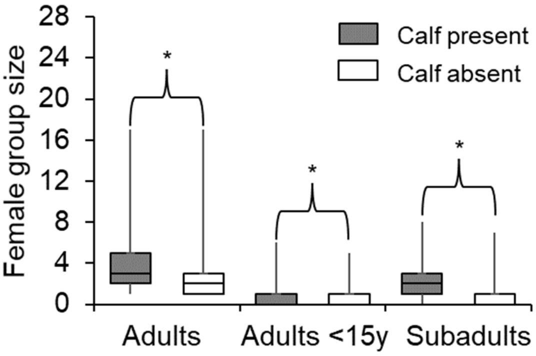
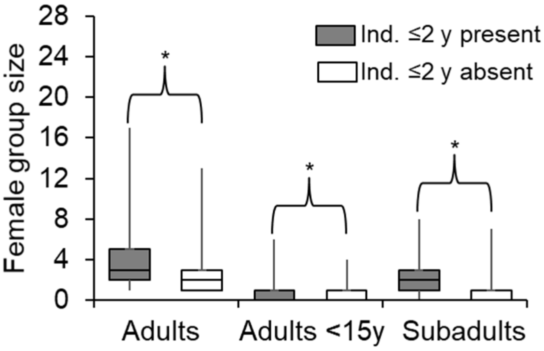
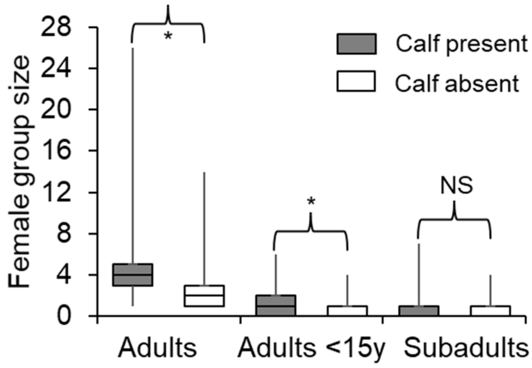
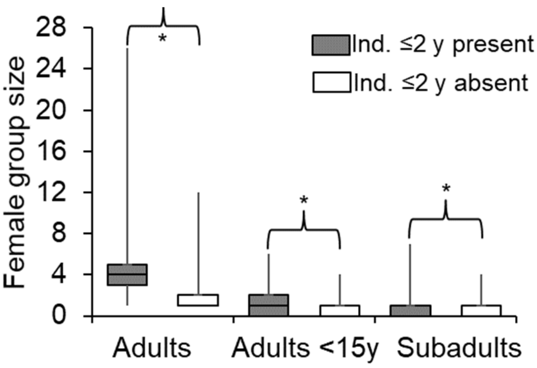
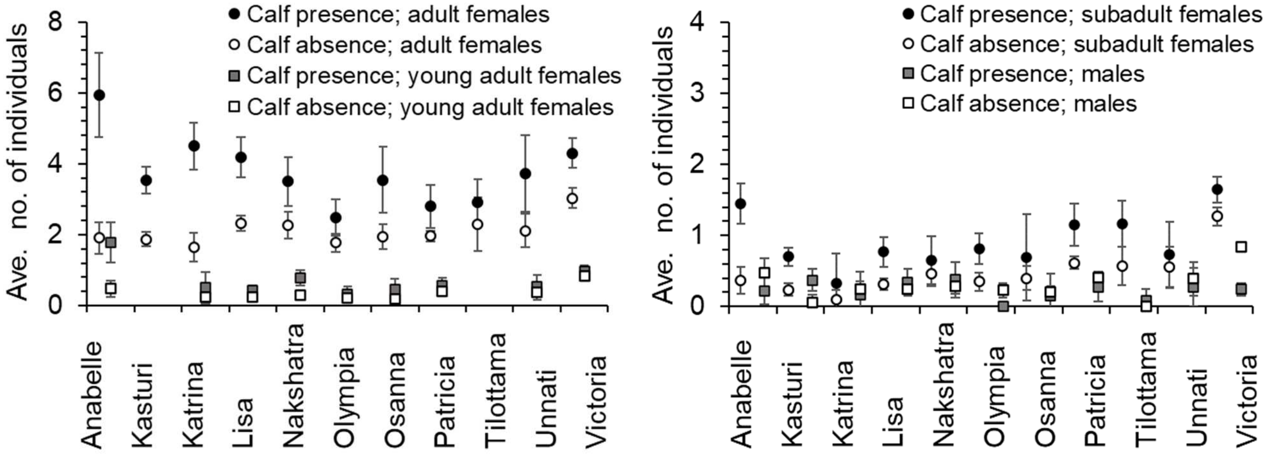
Year	Calf present/absent	Young one (<2 years) present/absent
2009- 2012		
2013- 2015		
2016- 2018		

Figure 2. Numbers of adult, young adult, and subadult females, in sightings with and without calves, and with and without young ones, in the three year-sets. Boxes show the 25th percentile, median, and 75th percentile, and bars indicate the minimum and maximum. Significant differences are marked with asterisks.

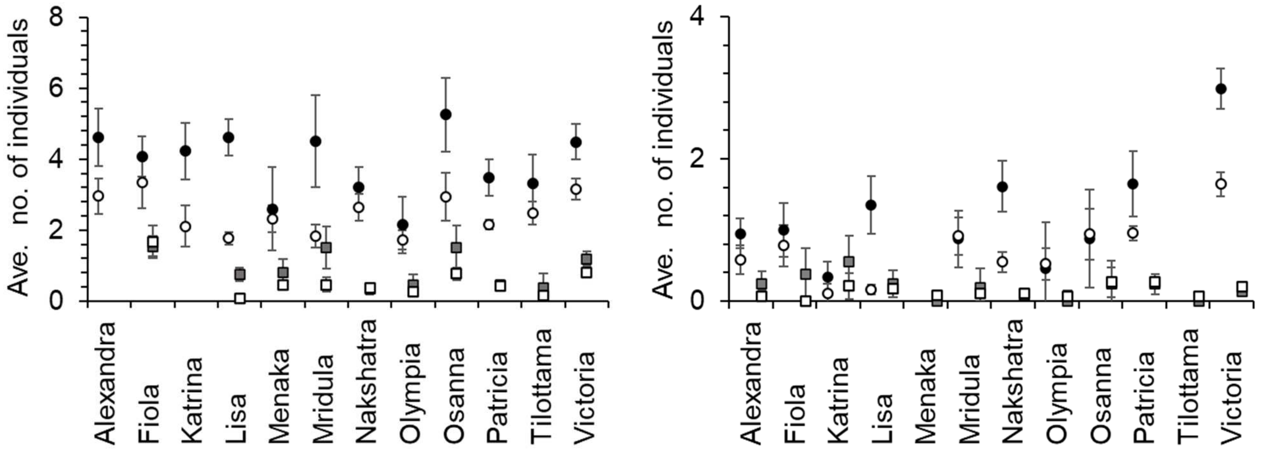
a. 2009-2012: adult and young adult females

b. 2009-2012: subadult females and males



c. 2013-2015: adult and young adult females

d. 2013-2015: subadult females and males



e. 2016-2018: adult and young adult females

f. 2016-2018: subadult females and males

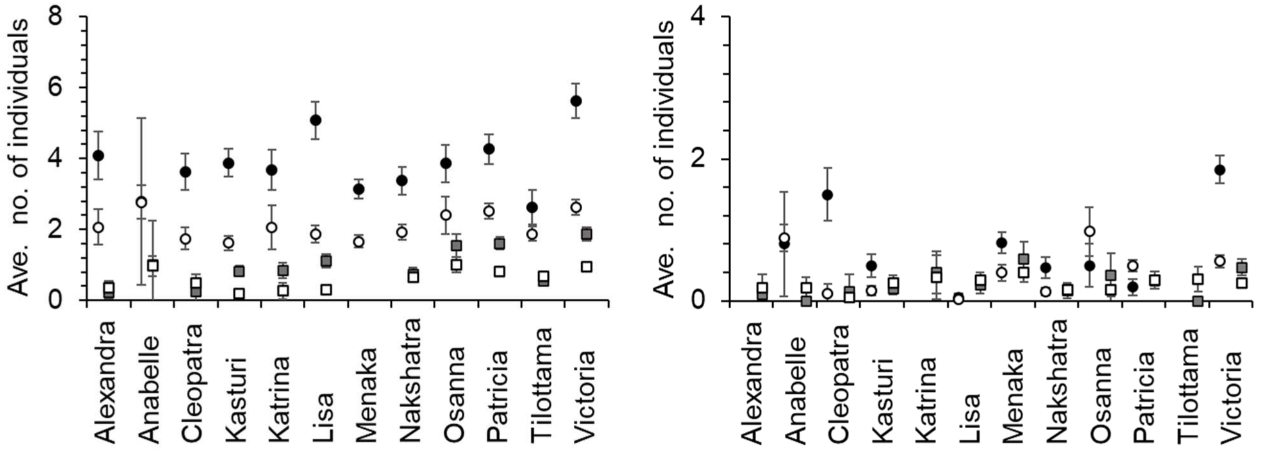


Figure 3. Average group sizes in terms of numbers of adult (circles) and young adult (squares) females (a,c,e), and subadult females (circles) and males ≥10 years of age (squares) (b,d,f) in

calf presence (black/grey) and absence (white). Data from 11 (clan size range: 4-30 adult females), 12 (clan size range: 6-38 adult females), and 12 (clan size range: 6-48 adult females) focal clans during 2009-2012, 2013-2015, and 2016-2018, respectively, are shown. Error bars are 1.96 SE.

Group sizes experienced by adult females in the presence and absence of calves/young ones

In all three year-sets, there was a significant effect of calf presence/absence in the sighting on the numbers of adult females, young adult females, and subadult females experienced by adult females (Table 3); their numbers were significantly higher in the presence than in the absence of calves (average numbers of adult females experienced per group by adult females in the three year-sets: 5.09-6.21 in calf presence, 3.62-4.21 in calf absence; average numbers of young adult females experienced per group by adult females in the three year-sets: 0.94-1.58 in calf presence, 0.76-0.94 in calf absence; average numbers of subadult females experienced per group by adult females in the three year-sets: 1.35-2.69 in calf presence, 0.56-1.79 in calf absence Figure 4, Supplementary Material 3), as seen in the analyses of group sizes. There were also significant interaction effects of adult females nested within clans with calf presence/absence, as well as clan with calf presence/absence, on the numbers of adult, young adult, and subadult females experienced (Table 3, Supplementary Material 5). Experienced group sizes were better explained by the models with calf presence/absence than group sizes were; the R^2s of the models explaining the effect of calves on the numbers of adult females experienced ranged from 0.28-0.40 for the three year-sets, that explaining the effect of calves on the numbers of young adult females experienced, from 0.14-0.36, and that explaining the effect of calves on the numbers of subadult females experienced, from 0.39-0.56 (Tables 1-3, Supplementary Material 5).

Results of the experienced group size analyses to examine the effect of the presence of young ones (all individuals <2 years old) showed identical patterns of significance to those of the analyses (above) to examine the effect of the presence of calves, but had higher effect sizes (Table 3, Supplementary Material 5).

Table 3. Results of the full GLMMs for the numbers of adult, young adult, and subadult females experienced by adult females in the presence and absence of calves. R^2 for the best models are shown. Intercept and calf presence/absence (P/A in table) are fixed factors for which SE is given. Significant *P* values are marked in bold. Clan//AF_ID and Clan are random effects for which SD is given. Clan//AF_ID indicates that AF_ID is nested within clan. Asterisks mark significant random effects compared to reduced models (see Supplementary Material 5). The last column has the results of the GLMMs to examine the effect of young ones for comparison; +: same significance pattern as the current GLMMs; sig: significant, ns: not significant (see Supplementary Material 5).

Dependent variable	Estimate	*SE* of estimate / SD	1.96 *SE*	95% CI of estimate		*z*	*P*	<2 y
				Lower	Upper			
No. of adult females experienced: 2009-2012 *(Calf P: 1389 sightings, Calf A: 2325 sightings), R^2=0.28*								
Intercept	1.000	0.104	0.204	0.796	1.204	9.617	**<0.001**	**+**
Calf P/A	0.504	0.080	0.156	0.348	0.660	6.337	**<0.001**	**+**
Clan//AF_ID: Intercept		0.295					_	
Clan//AF_ID: Calf P/A(P)		0.222					*	+
Clan: Intercept		0.283					_	
Clan: Calf P/A (P)		0.189					*	+
No. of adult females experienced: 2013-2015 *(Calf P: 1413 sig., Calf A: 1791 sig.), R^2=0.34*								
Intercept	1.114	0.112	0.219	0.895	1.333	9.965	**<0.001**	**+**
Calf P/A	0.475	0.103	0.202	0.273	0.677	4.601	**<0.001**	**+**
Clan//AF_ID: Intercept		0.174					_	
Clan//AF_ID: Calf P/A(P)		0.198					*	+
Clan: Intercept		0.338					_	
Clan: Calf P/A (P)		0.293					*	+
No. of adult females experienced: 2016-2018 *(Calf P: 2573 sig., Calf A: 2462 sig.), R^2=0.40*								
Intercept	0.754	0.144	0.281	0.472	1.035	5.251	**<0.001**	**+**
Calf P/A	0.758	0.098	0.191	0.567	0.950	7.770	**<0.001**	**+**
Clan//AF_ID: Intercept		0.384					_	
Clan//AF_ID: Calf P/A(P)		0.322					*	+
Clan: Intercept		0.406					_	
Clan: Calf P/A (P)		0.224					*	+
No. of young adult females experienced: 2009-2012 *(Calf P: 1131 sightings, Calf A: 2057 sightings), R^2=0.14*								
Intercept	-0.900	0.226	0.443	-1.343	-0.457	-3.479	**0.001**	**+**
Calf P/A	0.538	0.144	0.282	0.256	0.820	3.574	**<0.001**	**+**
Clan//AF_ID: Intercept		0.462					_	
Clan//AF_ID: Calf P/A(P)		0.324					*	+
Clan: Intercept		0.571					_	
Clan: Calf P/A (P)		0.289					*	+

Dependent variable	Estimate	*SE* of estimate / SD	1.96 *SE*	95% CI of estimate		*z*	*P*	
No. of young adult females experienced: 2013-2015 *(Calf P: 1292 sightings, Calf A: 1654 sightings), R^2=0.36*								
Intercept	-0.964	0.289	0.567	-1.531	-0.397	-3.334	**0.001**	**+**
Calf P/A	0.781	0.244	0.479	0.302	1.260	3.195	**0.001**	**+**
Clan//AF_ID: Intercept		0.276					_	
Clan//AF_ID: Calf P/A(P)		0.498					*	+
Clan: Intercept		0.831					_	
Clan: Calf P/A (P)		0.645					*	+
No. of young adult females experienced: 2016-2018 *(Calf P: 2511 sightings, Calf A: 2347 sightings), R^2=0.17*								
Intercept	-0.736	0.192	0.376	-1.112	-0.361	-3.844	**<0.001**	**+**
Calf P/A	0.582	0.157	0.308	0.274	0.890	3.709	**<0.001**	**+**
Clan//AF_ID: Intercept		0.561					_	
Clan//AF_ID: Calf P/A(P)		0.387					*	+
Clan: Intercept		0.494					_	
Clan: Calf P/A (P)		0.366					*	+
No. of subadult females experienced: 2009-2012 *(Calf P: 1389 sightings, Calf A: 2325 sightings), R^2=0.39*								
Intercept	-0.443	0.169	0.331	-0.774	-0.112	-2.625	**0.009**	**+**
Calf P/A	0.559	0.091	0.179	0.380	0.738	6.126	**<0.001**	**+**
Clan//AF_ID: Intercept		0.491					_	
Clan//AF_ID: Calf P/A(P)		0.327					*	+
Clan: Intercept		0.470					_	
Clan: Calf P/A (P)		0.205					*	+
No. of subadult females experienced: 2013-2015 *(Calf P: 1358 sightings, Calf A: 1648 sightings), R^2=0.54*								
Intercept	-0.252	0.324	0.636	-0.888	0.384	-0.777	0.437	+
Calf P/A	0.500	0.233	0.456	0.044	0.955	2.149	**0.032**	**+**
Clan//AF_ID: Intercept		0.284					_	
Clan//AF_ID: Calf P/A(P)		0.207					*	+
Clan: Intercept		0.937					_	
Clan: Calf P/A (P)		0.637					*	+
No. of subadult females experienced: 2016-2018 *(Calf P: 2416 sightings, Calf A: 2341 sightings), R^2=0.56*								
Intercept	-1.537	0.455	0.891	-2.428	-0.647	-3.382	**0.001**	**+**
Calf P/A	0.859	0.335	0.656	0.202	1.515	2.565	**0.010**	**+**
Clan//AF_ID: Intercept		0.614					_	
Clan//AF_ID: Calf P/A(P)		0.760					*	+
Clan: Intercept		1.263					_	
Clan: Calf P/A (P)		0.836					*	+

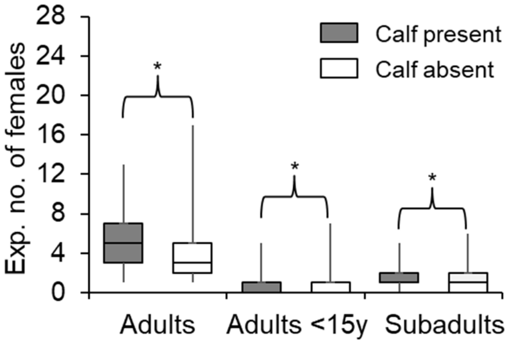
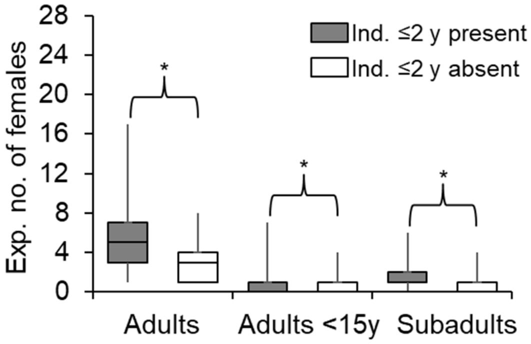
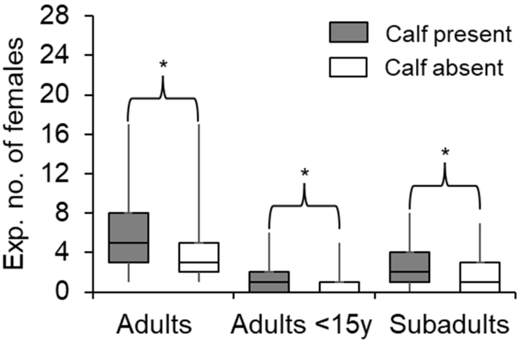
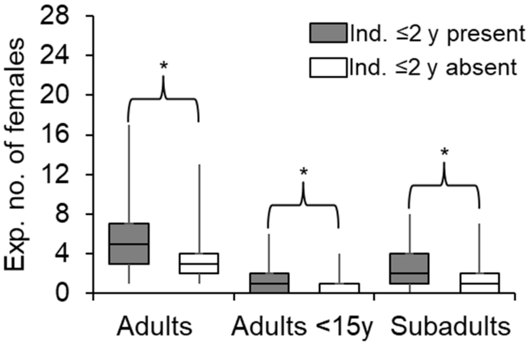
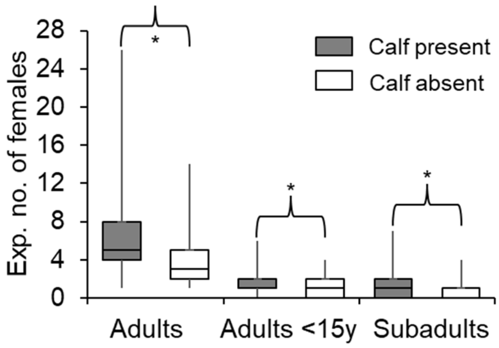
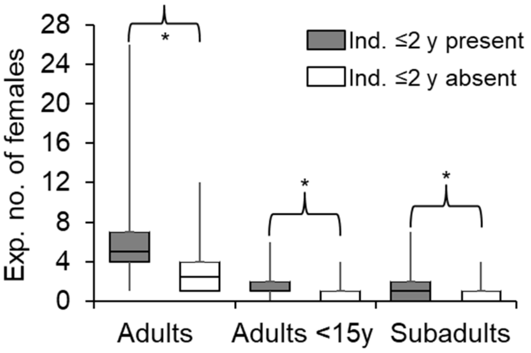
Year	Calf present/absent	Individuals <2 years present/absent
2009- 2012		
2013- 2015		
2016- 2018		

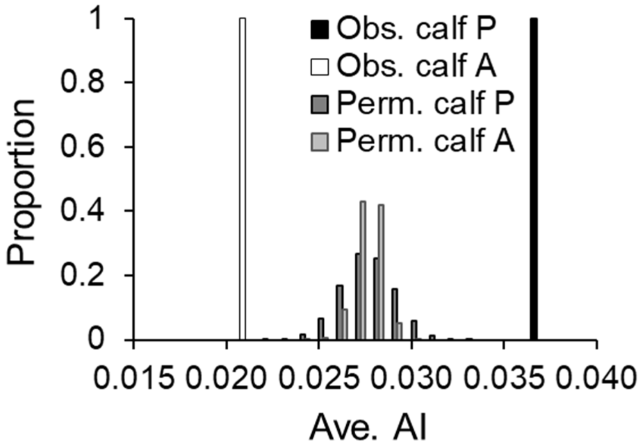
Figure 4. Boxplots with experienced group sizes: the numbers of adult, young adult, and subadult females experienced by adult females in the presence and absence of calves and young ones (individuals <2 years old) in their sightings. Minimum, 25th percentile, median, 75th percentile, and maximum are shown. Significant differences are marked with asterisks.

Comparison of female associations in the presence and absence of calves

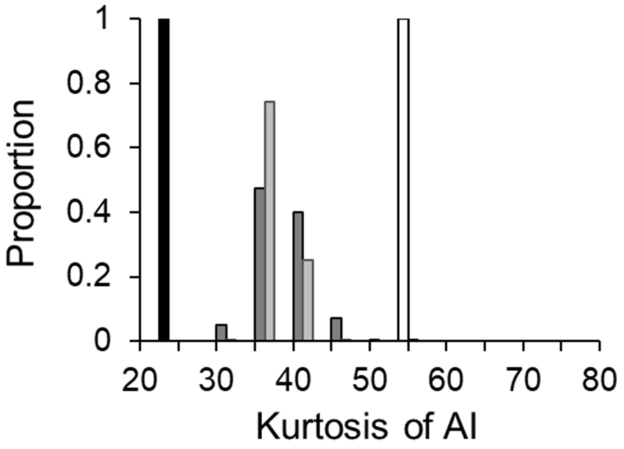
AI distributions in the presence and absence of calves were highly skewed (see Supplementary Material 6) as expected because females associate with others within their clans and very rarely across clans (Nandini *et al.* 2018; percentage of non-zero AIs in calf presence: 12.0%, 13.6%, 14.1%, in calf absence: 10.1%, 12.0%, 9.2%, for the year-sets 2009-2012, 2013-2015, and 2016-2018, respectively). The average AI between adult females was significantly higher in calf presence than in calf absence in all three year-sets, based on sampled randomization tests, and the kurtosis of AI was significantly lower in calf presence than in calf absence (Figure 5, Supplementary Material 6). There was a greater number of higher AI values in the presence than in the absence of calves (Supplementary Material 6).

We constructed association networks using 92 unique adult females (that were sighted at least five times each in the absence and presence of calves) from 10 clans, 80 adult females from 11 clans, and 100 adult females from 12 clans for the year-sets 2009-2012, 2013-2015, and 2016-2018, respectively (Figure 6). The average degree was significantly higher in the presence than in the absence of calves in all three year-sets (calf presence: 11.2-15.0, calf absence: 10.0-10.5), as was the average clustering coefficient (Figure 5, Supplementary Material 6). The SD of degree was significantly higher in the presence than in the absence of calves in the 2013-2015 and 2016-2018 year-sets, but not significantly different in 2009-2012 (Figure 5, Supplementary Material 6). Average path length was significantly lower in the presence than in the absence of calves in 2009-2012 and 2013-2015, but not in 2016-2018 (Figure 5, Supplementary Material 6).

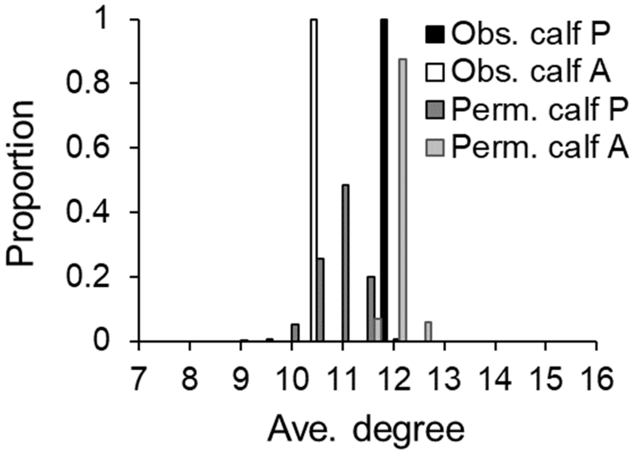
2013-2015: Average AI



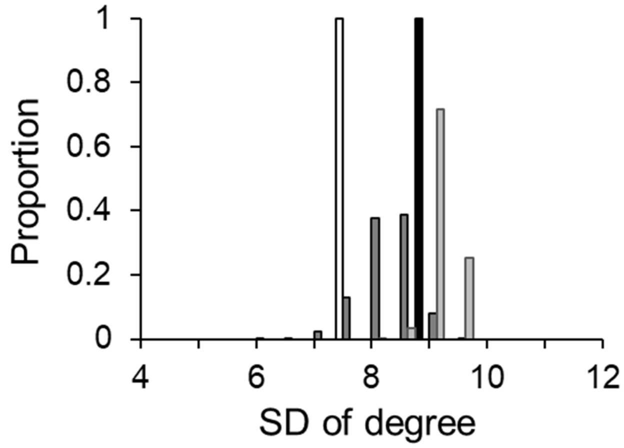
2013-2015: Kurtosis of AI



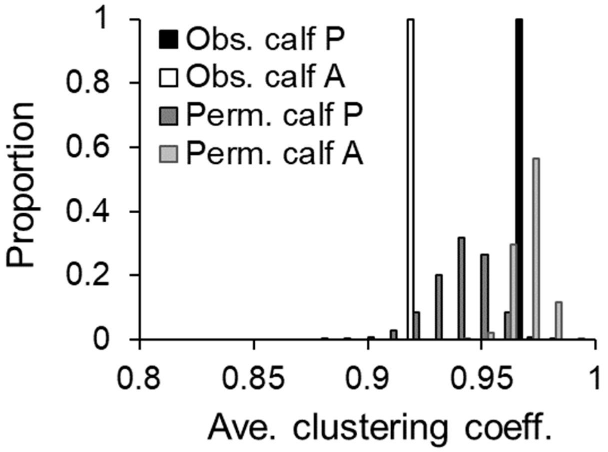
2013-2015: Average degree



2013-2015: SD of degree



2013-2015: Average clustering coefficient



2013-2015: Average path length

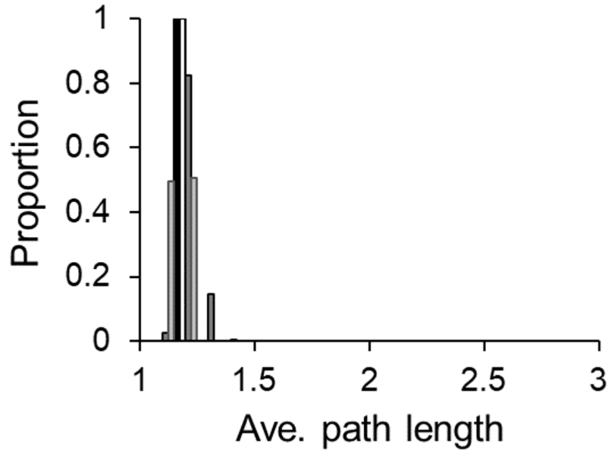


Figure 5. Frequency distributions of average AI, kurtosis of AI, average degree, SD of degree, average clustering coefficient, and average path length from 10,000 permuted ‘calf-present’ and ‘calf-absent’ datasets, and the observed values of each variable in the presence and absence of calves, for the 2013-2015 year-set (see Supplementary Material 6 for the other year-sets).

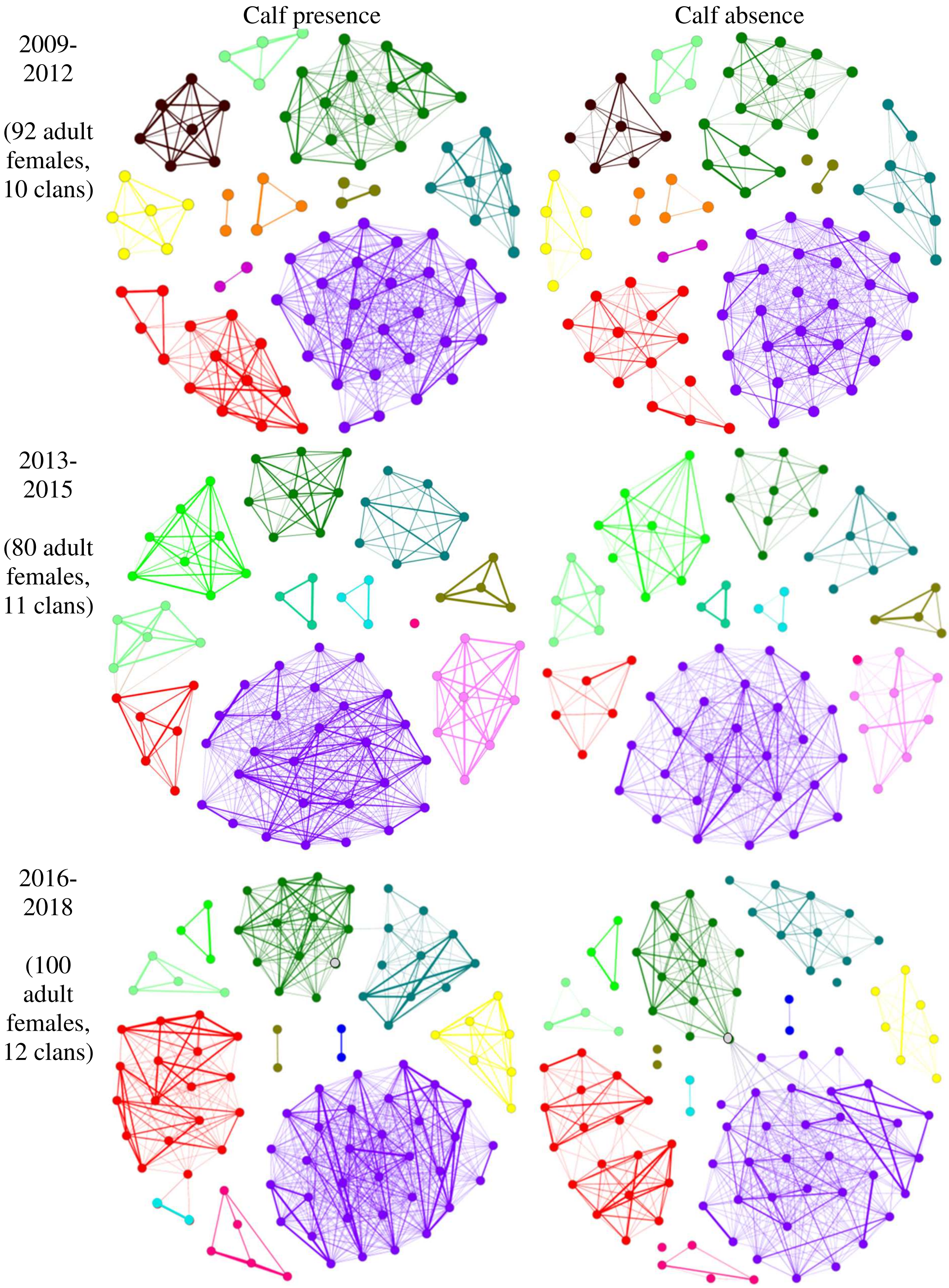


Figure 6. Association networks of adult females (seen at least five times each in calf presence and absence in a year-set) in the presence and absence of calves constructed using the Fruchterman Reingold layout (Fruchterman and Reingold 1991) in Gephi. Each node represents an adult female and the colours represent distinct clans, initially detected as

modularity classes. The edges between each pair of nodes represent non-zero AI and are weighted by AI values. Connections between clans were observed 5 times in calf presence (between Patricia's and Tilottama's clans) and once (resulting in a few connections) in calf absence (between Menaka's and Mridula's clans) in 2013-2015. In the year-set 2016-2018, the connections observed across two clans (Victoria's and Lisa's) in calf absence was a result of a young adult female who lost her clanmates and began to associate with both these clans (see Keerthipriya and Vidya 2021). The connections observed between the two sets of clans in calf presence (in 2016-2018) was a result of two young adult females from two different clans (Nakshatra's and Lisa's) associating with two females with young calves from two other clans (Merissa's and Patricia's, respectively).

Discussion

Individuals living in fission-fusion societies have the advantage of flexibly changing their group size and composition in response to the costs associated with intra-group feeding competition, while maximising the benefits of sociality (for example, Asensio *et al.* 2009, Sueur *et al.* 2011, Holmes *et al.* 2016). In the first such study of the kind, we examined whether the presence of calves or young ones affects the sociality of adult females in the Asian elephant, which shows fission-fusion dynamics. While it had previously been suggested that fission-fusion dynamics in the Kabini elephant population might allow for extended beneficial associations amongst clan-mates while maintaining small group sizes (Nandini *et al.* 2017, 2018), we found that females actually increased their group sizes and associations in the presence of young, which may decrease predation risk to calves or facilitate cooperative offspring care. We discuss the results below.

Comparison of group sizes/experienced group sizes in the presence and absence of calves/young ones

We found that female group sizes changed in the presence of calves (<1 year old): the numbers of adult, young adult, and subadult females, but not the number of males, were higher in the presence than in the absence of calves. On an average, there were roughly 1.5-2 (across the year-sets; see Supplementary Material 3) additional adult females in the presence of calves. This increase was also seen when the effect of all the young ones (calves and young juveniles 1-<2 years old) was considered, with the number of additional adult females being roughly

1.8-2.4 in the presence of young ones. Thus, apart from calf presence, higher group sizes of adult females were observed in the presence of young juveniles (1-2 years old) also than in their absence. Unfortunately, formal group size analysis with the four different combinations of calf and young juvenile presence and absence could not be carried out as all the combinations were not observed in most clans. However, when sightings from different clans were combined, the average number of adult females was similar in the presence of a single calf or a single young juvenile, and it was higher when there was more than one calf, or a calf and a young juvenile, than when there was a single calf or young juvenile (Supplementary Material 7).

Previously, McKay (1973) had reported on Asian elephants in Sri Lanka that groups with calves had females apart from the mother, and that large groups (15 or more individuals), which were seen only occasionally, always had calves and juveniles. Being an early study, no further analysis was done on this aspect. Larger group sizes in the presence of young offspring have also been found in some other species that show fission-fusion dynamics (Bottlenose dolphins: Campbell *et al.* 2002, Bearzi *et al.* 1997, Wells *et al.* 1987; Orangutans: van Schaik 1999, Ruffed lemurs: Holmes *et al.* 2016; Warthogs: White *et al.* 2010). However, with the exception of van Schaik’s (1999) study, it was not known if the increase in group size was additionally due to an interaction between the season and offspring presence. In the Kabini elephant population, there was no consistent group size variation within clans across seasons (Nandini *et al.* 2017), although group size may also be affected by other factors such as habitat (grassland versus dry or moist deciduous forest) through differences in the availability and distribution of resources.

The extents to which the numbers of young adult females and subadult females differed between the presence and absence of calves were smaller (smaller effect size, R^2) than the extents to which adult females differed between the presence and absence of calves. However, an examination of clan demography showed that the poorer fit in the former case was not solely due to the relative numbers of the different age-classes of females to calves in the clan. While young adult females contributed to a small extent to the larger group sizes and larger experienced group sizes in the presence of young ones, older adult females and subadult females contributed to larger group sizes to a greater extent. Changes in the numbers of adult females could have arisen from fission-fusion dynamics, but the greater number of subadult females might be at least partly be a demographic effect. Asian elephants have a long interbirth interval, which varies between 2.5-8 years in the wild (Gal Oya, Sri Lanka: 2.5-8 years, McKay 1973; Lahugala, Sri Lanka: 2.5-4 years, McKay 1973; Wasgamuwa, Sri Lanka: 4 years, Sukumar 2003; Uda Walawe, Sri Lanka: 6 years, de Silva *et al.* 2013; Nilgiris, India: 4.5 years, Sukumar 2003; BRT, India: 4.7 years, Sukumar 1989), but is often a minimum of 4 years due to around 21 months of gestation and around 24 months of anestrus period because of lactation (Sukumar 2003). Therefore, a calf, and even more likely a young juvenile, will often be a subadult by the time its mother has her next calf, resulting in subadults and calves in the same groups if the subadult does not move away from the mother.

While the number of old subadult and adult males (≥10 years old) did not differ between the presence and absence of calves, it was significantly higher in the presence than in the absence of young ones (<2 years old) in the 2009-2012 (full and reduced models) and 2016-2018 (reduced models) year-sets (Supplementary Material 4). It is possible that this was due to the larger number of females present (which were also present in the presence of calves though), along with female reproductive status. In dolphins, the proportions of adult males in calf groups were found to be less than expected as mothers avoided associating with males (Gibson and Mann 2008).

The patterns found based on analyses of experienced group sizes were similar to those found based on group sizes, but with higher R^2s. Due to the absence of data, we could not compare the experienced group sizes in our study with those from any other elephant population. In transient killer whales, experienced group size ('typical group size') was found to increase with the number of calves and young juveniles in the group (Baird and Dill 1996). It is also important in the future to examine the group sizes experienced by mother and non-mother adult females separately in order to understand if females behave differently in terms of grouping patterns in the presence of their own versus others' calves.

Potential costs and benefits of increased group size

As mentioned earlier, a previous study showed that there was a constraint on female group size in the Kabini elephant population, with the average group sizes (numbers of adult females per group) remaining somewhat similar even in clans of large sizes (which had more females available with whom to associate) (Nandini *et al.* 2017). High rates of agonism have also been reported from this population, with group size having an effect on within-clan agonism (Gautam and Vidya 2019). Subsequently, constraints on male group size were also found

(Keerthipriya *et al.* 2021). Thus, the larger group sizes and experienced group sizes in the presence of calves and young juveniles are likely to be costly, and it would be interesting to examine feeding rates of group members, as well as group spread, in the different scenarios.

Large group sizes may provide protection against predation, opportunities for allomaternal care, and socialization of young ones (for associations later in life). Calf mortality is high in the study population (from preliminary data, Kabini Elephant Project), and young, dependent offspring (<2 years of age) in elephants have high mortality rates in general (African savannah elephants: Lee 1987, Moss 2001, Lee and Moss 2011, captive Asian elephants: Eisenberg 1980, Sukumar *et al.* 1997, Mar *et al.* 2012), with the mortality rate decreasing with age. African savannah elephant calves face a risk of predation by lions (Wittemyer *et al.* 2005) and Asian elephant calves, predation by tigers (Williams 1950, Eisenberg 1980, personal observation). Since group sizes in our study were higher in the presence than absence of both calves and young juveniles, it would be interesting to find out until what offspring age the larger group sizes persist. Mortality rate was found to stabilize only around 5 years of age in semi-captive Asian elephants in southern India (Sukumar *et al.* 1997), but the relative contributions of predation and disease to mortality are not known. The larger group sizes in the presence of calves or young ones may be tied to the risk of predation, with the number of adult females in groups decreasing with increasing offspring age as seen in dolphins (Wells *et al.* 1987, Gibson and Mann 2008).

Larger group sizes in the presence of young may also arise from the presence of allomothers, although whether the group size increases because of the addition of an allomother or whether one of the females after the group size increasing (probably to reduce predation risk) becomes an allomother is not known. We found the increase in group size to occur through an increase in the number of subadult and young adult females, as well as older adult females. Since the former two categories do not usually have dependent offspring of their own, they might show allomaternal care (see section below). As mentioned above, the number of subadult females might be higher partly because of demographic factors, while the number of adult females would change due to fission-fusion dynamics. Larger group sizes in the presence of young may also arise from mothers preferring to associate together, as seen in some other species (Bechstein’s bat: Kerth and König 1999, mountain goats: Godde *et al.* 2015), due to increased energetic requirements of lactation. Possible assortative grouping based on reproductive status will be examined in the future.

Comparison of female social networks in the presence and absence of calves

The larger group sizes in calf presence than absence led to higher sociality, with significantly higher average AI, degree, and clustering coefficient (although the difference in values of clustering coefficient was small), and lower path length. The higher average AI in calf presence than absence in all the year-sets, pointing to stronger associations in calf presence, occurred through certain females within clans associating more strongly in calf presence than in calf absence (the SD of AI was higher in calf presence; data not shown). While the kurtosis of AI was greater than 3 (that of a normal distribution) in both the presence and absence of calves, indicating that extreme values were more likely than in a normal distribution, there were a larger number of high AI values in the presence of calves. Whether the top associates of adult females change in the presence and absence of calves remains to be seen.

Adult females associated with a greater number of other adult females in calf presence, as found by the higher average degree in calf presence than in calf absence. On average, adult females associated with 1-2 additional adult females in calf presence in the first two year-sets. This was higher (~5 adult females) in the 2016-2018 year-set because of one clan (Victoria) that had a larger number of adult females in that year-set (Supplementary Material 1). Recalculating the average degree without this clan gave a difference of about 1.8 between the average degree in calf presence and absence. The SD of degree was also significantly higher in calf presence than absence (except in 2009-2012, again due to Victoria's clan; see Supplementary Material 6). Thus, certain adult females were associating with a greater number of other adult females in the presence than absence of calves. The exact changes in associations that take place remain to be examined. Whether the greater number of direct connections between clan-mates (shorter path length) in the presence of calves translates to benefits through information transfer also remains to be seen. We have also not compared the network statistics of individual females here. Examining the network statistics of mothers and other females before and after the birth of calves would be the next step in understanding how calves affect female sociality. Mothers and calves were found to be central to the social network, and calves were found to be central to female relationships, in sperm whales (Gero *et al.* 2013).

Benefits of increased associations in the presence of dependent young

While increased group size itself can offer benefits in terms of reduced predation risk, associations amongst female elephants may be useful in cooperative offspring care (McKay

1973, Eisenberg 1980, Gadgil and Nair 1984, Lee 1987, Rapaport and Haight 1987, Schulte 2000, Lee and Moss 2011, Vidya 2014). Lee (1987) classified African savannah elephant females that were 5-15 years old as allomothers as they remained close to, assisted, and protected calves at times of distress. Early social interactions are important for later social competence in elephants (Lee and Moss 2014); thus, frequent interactions along with close proximity to their mothers and allomothers might be beneficial in terms of accelerating the learning process of foraging, survival, and other skills. Allomothering may also simultaneously increase the time spent foraging by mothers and improve the likelihood of calf survival, as seen in some species (for example, Lee 1987, Stanford 1992, Holmes *et al.* 2016, Raboin *et al.* 2021). As mentioned above, we do not know if the increase in group size results from allomother(s) joining the group, or whether additional females joining the group subsequently carry out low-cost allomothering. Whether the allomother chooses the mother or vice versa and which females mothers choose to associate with would be interesting to examine.

We found that CVs of female groups sizes were consistently smaller in young offspring presence than those in their absence in most of the clans across the three year-sets (not shown) – i.e., group sizes were less variable in young offspring presence than in their absence. It remains to be seen if this difference is significant and if there is a difference in the extent of variation in individual membership in a group between offspring presence and absence. A study on ruffed lemurs found that subgroups were more cohesive in the presence of highly dependent infants (Baden *et al.* 2016). Another function of increasing group size and associations could also be to enhance familiarisation amongst age cohorts and enhance opportunities for socialization (see van Schaik 1999).

In summary, in the Kabini Asian elephant population, we find changes in female social structure via fission-fusion dynamics, with females forming larger groups, having stronger connections, and meeting more clan-mates in the presence of young than in their absence. These changes may promote the survival of vulnerable offspring through associations with allomothers and/or other clanmates, which remains to be studied. Thus, apart from ecological factors (Nandini *et al.* 2018, Gautam and Vidya 2019), social factors – specifically, the presence of calves and young juveniles – seem to affect female sociality, and fission-fusion dynamics facilitates an increase in female sociality.

Acknowledgements

This work was funded by Department of Science and Technology's (Government of India) Ramanujan Fellowship (to TNCV) under Grant No. SR/S2/RJN-25/2007 (dated 09/06/2008), Council of Scientific and Industrial Research (CSIR), Government of India, under Grant No. 37(1375)/09/EMR-II and No. 37(1613)/13/EMR-II, National Geographic Society, USA, under Grant #8719-09 and #9378-13, and JNCASR. TR, SN, and HG were supported by Ph.D. fellowships from JNCASR, which also provided logistical support for the work. PK was supported by a Ph.D. fellowship from CSIR (No. 09/733(0152)/2011-EMR-I). The funders had no role in the study design, data collection, or preparation of the manuscript. This work is part of the Ph.D. thesis of TR.

We thank the offices of the PCCF(WL), Karnataka Forest Department, and of the Conservators and Deputy Conservators of Forests of Bandipur and Nagarahole National Parks and Tiger Reserves for field permits. We also thank various officials, from the PCCF(WL) and APCCF(WL), to the CFs, DCFs, ACFs and Range Forest Officers, to the staff of Nagarahole and Bandipur National Parks for their support over the years. We thank our field trackers Gunda, Rajesh, Krishna, Shankar, and Ranga, drivers Binu, Althaf, and Pramod, and others for field assistance. Deepika Prasad and Arjun Ghosh helped with initial data collection. We thank Kavita Isvaran for advice on GLMs.

References

1. Aguilar-Melo AR, Calmé S, Pinacho-Guendulain B, Smith-Aguilar SE and Ramos-Fernández G (2020). Ecological and social determinants of association and proximity patterns in the fission–fusion society of spider monkeys (*Ateles geoffroyi*). *American Journal of Primatology* 82: e23077.
2. Asensio N, Korstjens AH and Aureli F (2009). Fissioning minimizes ranging costs in spider monkeys: a multiple-level approach. *Behavioural Ecology and Sociobiology* 63: 649-659.
3. Baden AL, Webster TH and Kamilar JM (2016). Resource seasonality and reproduction predict fission–fusion dynamics in black-and-white ruffed lemurs (*Varecia variegata*). *American Journal of Primatology* 78: 256-279.
4. Baird RW and Dill LM (1996). Ecological and social determinants of group size in

transient killer whales. *Behavioural Ecology* 7: 408-416.

5. Bastian M, Heymann S and Jacomy M (2009). Gephi: an open source software for exploring and manipulating networks. *Proceedings of the Third International ICWSM* 8: 361-362.
6. Bearzi G, Notarbartolo-DI-Sciara G and Politi E (1997). Social ecology of bottlenose dolphins in the Kvarnerić (northern Adriatic Sea). *Marine Mammal Science* 13: 650-668.
7. Blondel VD, Guillaume JL, Lambiotte R and Lefebvre E (2008). Fast unfolding of communities in large networks. *Journal of Statistical Mechanics* 10: P10008.
8. Bolker B and others (2021). https://bbolker.github.io/mixedmodels-misc/glmmFAQ.html #testing-significance-of-random-effects
9. Bond ML, Lee DE, Ozgul A and König B (2019). Fission–fusion dynamics of a megaherbivore are driven by ecological, anthropogenic, temporal, and social factors. *Oecologia* 191: 335-347.
10. Campbell GS, Bilgre BA and Defran RH (2002). Bottlenose dolphins (*Tursiops truncatus*) in Tuneffe Atoll, Belize: occurrence, site fidelity, group size, and abundance. *Aquatic Mammals* 28: 170-180.
11. Chapman CA, Chapman LJ and Wrangham RW (1995). Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behavioural Ecology and Sociobiology* 36: 59-70.
12. Clutton-Brock TH, Gaynor D, McIlrath GM, Maccoll ADC, Kansky R, Chadwick P, Manser M, Skinner JD and Brotherton PNM (1999). Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. *Journal of Animal Ecology* 68: 672-683.
13. Crockett CM and Janson C H (2000). Infanticide in red howlers: Female group size, male composition, and a possible link to folivory. In: van Schaik CP and Janson CH (eds.), *Infanticide by Males and its Implications*, pp. 75-98. Cambridge University Press, Cambridge.
14. Crook JH and Gartlan JS (1966). Evolution of primate societies. *Nature* 210: 1200-1203.
15. de Silva S, Ranjeewa AD and Kryazhimskiy S (2011). The dynamics of social networks among female Asian elephants. *BMC Ecology* 11: 1-6.
16. de Silva S, Webber CE, Weerathunga US, Pushpakumara TV, Weerakoon DK and Wittemyer G (2013). Demographic variables for wild Asian elephants using longitudinal observations. *PLoS One* 8: e82788.
17. Desai AA and Johnsingh AJT (1995). Social organization and reproductive strategy of the male Asian elephant (*Elephas maximus*). In: Daniel JC and Datye H (eds.), *A Week with*

Elephants, pp. 532-532. Bombay Natural History Society, Bombay.

18. Eisenberg JF (1980). Ecology and behaviour of the Asian elephant. *Elephant* 1: 5.
19. Fairbanks LA (1990). Reciprocal benefits of allomothering for female vervet monkeys. *Animal Behaviour* 40: 553-562.
20. Gadgil M and Nair VP (1984). Observations on the social behaviour of free ranging groups of tame Asiatic elephants (*Elephas maximus* Linn). *Proceedings of the Indian Academy of Sciences (Animal sciences)* 93: 225-233.
21. Gautam H (2019). *Resource Availability, Within-clan and Between-Clan Agonistic Interactions, and Dominance Relationships amongst Female Asian Elephants in Nagarahole National Park, Southern India*. Ph.D. thesis, Jawaharlal Nehru Centre for Advanced Scientific Research, Bengaluru.
22. Gautam H and Vidya TNC (2019). A test of the socioecological model in female Asian elephants: the effects of food abundance, food distribution, and competitor density on within-clan and between-clan contests. *bioRxiv* 754515. https://doi.org/10.1101/754515.
23. Gero S, Engelhaupt D, Rendell L and Whitehead H (2009) Who cares? Between-group variation in alloparental caregiving in sperm whales. *Behavioural Ecology* 20: 838-843.
24. Gero S, Gordon J, and Whitehead H (2013). Calves as social hubs: dynamics of the social network within sperm whale units. *Proceedings of the Royal Society B: Biological Sciences* 280: 20131113.
25. Gibson QA and Mann J (2008). The size, composition and function of wild bottlenose dolphin (*Tursiops sp.*) mother–calf groups in Shark Bay, Australia. *Animal Behaviour* 76: 389-405.
26. Ginsberg JR and Young TP (1992). Measuring association between individuals or groups in behavioural studies. *Animal Behaviour* 44: 377-379.
27. Godde S, Côté SD and Réale D (2015). Female mountain goats, *Oreamnos americanus*, associate according to kinship and reproductive status. *Animal Behaviour* 108: 101-107.
28. Hervé M (2022). Package ‘RVAideMemoire’. https://cran.r-project.org/web/packages/RVAideMemoire/RVAideMemoire.pdf
29. Holmes SM, Gordon AD, Louis EE and Johnson SE (2016). Fission-fusion dynamics in black-and-white ruffed lemurs may facilitate both feeding strategies and communal care of infants in a spatially and temporally variable environment. *Behavioural Ecology and Sociobiology* 70: 1949-1960.
30. Jarman P (1974). The social organisation of antelope in relation to their ecology. *Behaviour* 48: 215-267.

31. Jhala YV, Gopal R and Qureshi Q (eds.) (2008). Status of tigers, co-predators and prey in India. Report. National Tiger Conservation Authority and Wildlife Institute of India. TR08/001.
32. Jovani R and Mavor R (2011). Group size versus individual group size frequency distributions: a nontrivial distinction. *Animal Behaviour* 82: 1027-1036.
33. Keerthipriya P and Vidya TNC. (2021). Kabini Elephant Project: a long-term programme for understanding Asian elephant behaviour and ecology. *Trumpet* 2: 14-21.
34. Keerthipriya P, Nandini S and Vidya TN (2021). Effects of male age and female presence on male associations in a large, polygynous mammal in southern India: The Asian elephant. *Frontiers in Ecology and Evolution* 9: 616666.
35. Kerth G and König B (1999). Fission, fusion and nonrandom associations in female Bechstein's bats (*Myotis bechsteinii*). *Behaviour* 136: 1187-1202.
36. Kruuk H (1972). *The Spotted Hyena: A Study of Predation and Social Behaviour*. University of Chicago Press, Chicago.
37. Kummer H (1971). Immediate causes of primate social structures. *Proceedings of the Third International Congress of Primatology* 3: 1-11.
38. Kummer H (1978). On the value of social relationships to nonhuman primates: a heuristic scheme. *Social Science Information* 17: 687-705.
39. Lee PC (1987). Allomothering among African elephants. *Animal Behaviour* 35: 278-291.
40. Lee PC and Moss CJ (2011). Calf development and maternal rearing strategies. In: Moss CJ, Croze H and Lee PC (eds.), *The Amboseli Elephants: A Long-Term Perspective on a Long-Lived Mammal,* pp 224-237. University of Chicago Press, Chicago.
41. Lee PC and Moss CJ (2014). African elephant play, competence and social complexity. *Animal Behaviour and Cognition* 1: 144-156.
42. Lehmann J and Boesch C (2004). To fission or to fusion: effects of community size on wild chimpanzee (*Pan troglodytes verus*) social organisation. *Behavioural Ecology and Sociobiology* 56: 207-216.
43. Magnusson A, Skaug H, Nielsen A, Berg C, Kristensen K, Maechler M, van Bentham K, Bolker B, Brooks M and Brooks MM (2017). Package 'glmmTMB'. R Package Version 0.2.0.
44. Mar KU, Lahdenperä M and Lummaa V (2012). Causes and correlates of calf mortality in captive Asian elephants (*Elephas maximus*). *PLoS One* 7: e32335.
45. Marealle WN, Holmern T and Røskaft E (2020). Factors affecting group size and vigilance behaviour of Maasai Giraffe (*Giraffa camelopardalis tippelskirchi*) on the

Serengeti-Ngorongoro ecosystem, Tanzania. *East African Journal of Environment and Natural Resources* 2: 14-23.

46. Marzluff JM, Heinrich B and Marzluff CS (1996). Raven roosts are mobile information centres. *Animal Behaviour* 51: 89-103.
47. McFarland R, Murphy D, Lusseau D, Henzi SP, Parker JL, Pollet TV and Barrett L (2017). The 'strength of weak ties' among female baboons: fitness-related benefits of social bonds. *Animal Behaviour* 126: 101-106.
48. McKay GM (1973). Behaviour and ecology of the Asiatic elephant in southeastern Ceylon. *Smithsonian Contributions to Zoology* 125: 1-113.
49. Moss CJ (2001). The demography of an African elephant (*Loxodonta africana*) population in Amboseli, Kenya. *Journal of Zoology* 255: 145-156.
50. Nair PV (1989). Development of nonsocial behaviour in the Asiatic elephant. *Ethology* 82: 46-60.
51. Nandini S (2016). *Social Structure, Genetic Relatedness, and Dominance Relationships in Female Asian Elephants in Nagarahole and Bandipur National Parks, Southern India*. Ph.D. thesis, JNCASR.
52. Nandini S, Keerthipriya P and Vidya TNC (2017). Seasonal variation in female Asian elephant social structure in Nagarahole-Bandipur, southern India. *Animal Behaviour* 134: 135-145.
53. Nandini S, Keerthipriya P and Vidya TNC (2018). Group size differences may mask underlying similarities in social structure: a comparison of female elephant societies. *Behavioural Ecology* 29: 145-159.
54. Nishida T (1968). The social group of wild chimpanzees in the Mahali mountains. *Primates* 9: 167-224.
55. Nunn CL, Thrall PH, Stewart K and Harcourt AH (2008). Emerging infectious diseases and animal social systems. *Evolutionary Ecology* 22: 519-543.
56. Packer C, Pusey AE and Eberly LE (2001). Egalitarianism in female African lions. *Science* 293: 690-693.
57. Packer C, Scheel D and Pusey AE (1990). Why lions form groups: food is not enough. *American Naturalist* 136: 1-19.
58. Raboin DL, Baden AL and Rothman JM (2021). Maternal feeding benefits of allomaternal care in black-and-white colobus (*Colobus guereza*). *American Journal of Primatology* 83: e23327.
59. Rapaport L and Haight J (1987). Some observations regarding allomaternal caretaking

among captive Asian elephants (*Elephas maximus*). *Journal of Mammalogy* 68: 438-442.

60. Rendell L, Cantor M, Gero S, Whitehead H and Mann J (2019). Causes and consequences of female centrality in cetacean societies. *Philosophical Transactions of the Royal Society B: Biological Sciences* 374: 20180066.
61. Revathe T, Anvitha S and Vidya TNC (2020). Development of motor control and behaviour in Asian elephants in the Kabini elephant population, southern India. *International Journal of Developmental Biology* 64: 377-392.
62. Rubenstein DI (1978). On predation, competition, and the advantages of group living. In: Bateson PPG and Klopfer PH (eds.), *Social Behaviour*: *Perspectives in Ethology*, Vol. 3, pp. 205-231. Springer, Boston.
63. Schulte BA (2000). Social structure and helping behaviour in captive elephants. *Zoo Biology* 19: 447-459.
64. Silk JB, Alberts SC and Altmann J (2003). Social bonds of female baboons enhance infant survival. *Science* 302: 1231-1234.
65. Smith JE, Kolowski JM, Graham KE, Dawes SE and Holekamp KE (2008). Social and ecological determinants of fission–fusion dynamics in the spotted hyaena. *Animal Behaviour* 76: 619-36.
66. Sokal RR and Rohlf FJ (1981). *Biometry: The Principles and Practice of Statistics in Biological Research*, (second edition). WH Feeman and Company, San Francisco.
67. Southwell CJ (1984). Variability in grouping in the eastern grey kangaroo, *Macropus giganteus* II. Dynamics of group formation. *Wildlife Research* 11: 437-449.
68. Stanford CB (1992). Costs and benefits of allomothering in wild capped langurs (*Presbytis pileata*). *Behavioural Ecology and Sociobiology* 30: 29-34.
69. Sterck EHM, Watts DP and van Schaik CP (1997). The evolution of female social relationships in nonhuman primates. *Behavioural Ecology and Sociobiology* 41: 291-309.
70. Sueur C, King AJ, Conradt L, Kerth G, Lusseau D, Mettke-Hofmann C, Schaffner CM, Williams L, Zinner D and Aureli F (2011). Collective decision-making and fission–fusion dynamics: a conceptual framework. *Oikos* 120: 1608-1617.
71. Sukumar R (1989). *The Asian Elephant: Ecology and Management*. Cambridge University Press, Cambridge.
72. Sukumar R (2003). *The Living Elephants: Evolutionary Ecology, Behaviour, and Conservation.* Oxford University Press, Oxford.
73. Sukumar R, Krishnamurthy V, Wemmer C and Rodden M (1997). Demography of captive Asian elephants (*Elephas maximus*) in southern India. *Zoo Biology* 16: 263-272.

74. Terborgh J and Janson CH (1986). The socioecology of primate groups. *Annual Reviews of Ecology and Systematics* 17: 111-136.
75. van Schaik CP (1999). The socioecology of fission-fusion sociality in orangutans. *Primates* 40: 69-86.
76. van Schaik CP, van Noordwijk MA, de Boer RJ and den Tonkelaar I (1983). The effect of group size on time budgets and social behaviour in wild long-tailed macaques (*Macaca fascicularis*). *Behavioural Ecology and Sociobiology* 13: 173-181.
77. VanderWaal KL, Atwill ER, Isbell LA and McCowan B (2014). Linking social and pathogen transmission networks using microbial genetics in giraffe (*Giraffa camelopardalis*). *Journal of Animal Ecology* 83: 406-414.
78. Vidya TNC (2014). Novel behaviour shown by an Asian elephant in the context of allomothering. *Acta Ethologica* 17: 123-127.
79. Vidya TNC and Sukumar R (2005). Social organization of the Asian elephant (*Elephas maximus*) in southern India inferred from microsatellite DNA. *Journal of Ethology* 23: 205-210.
80. Vidya TNC, Fernando P, Melnick DJ and Sukumar R (2005). Molecular genetic structure and conservation of Asian elephant (*Elephas maximus*) populations across India. *Animal Conservation* 8: 377-388.
81. Weinrich MT, Schilling MR and Belt CR (1992). Evidence for acquisition of a novel feeding behaviour: lobtail feeding in humpback whales, *Megaptera novaeangliae*. *Animal Behaviour* 44: 1059-1072.
82. Wells RS, Scott MD and Irvine AB (1987). The social structure of free-ranging bottlenose dolphins. In: Genoways HH (eds.), *Current Mammalogy*, pp. 247-305. Springer, Boston.
83. Western D and Lindsay WK (1984). Seasonal herd dynamics of a savanna elephant population. *African Journal of Ecology* 22: 229-244.
84. Wey TW, Burger JR, Ebensperger LA and Hayes LD (2013). Reproductive correlates of social network variation in plurally breeding degus (*Octodon degus*). *Animal Behaviour* 85: 1407-1414.
85. White AM, Cameron EZ and Peacock MM (2010). Grouping patterns in warthogs, *Phacochoerus africanus*: is communal care of young enough to explain sociality? *Behaviour* 147: 1-18.
86. Whitehead H (1996). Babysitting, dive synchrony, and indications of alloparental care in sperm whales. *Behavioural Ecology and Sociobiology* 38: 237-244.
87. Whitehead H (2008). *Analyzing Animal Societies: Quantitative Methods for Vertebrate*

Social Analysis. University of Chicago Press, Chicago.

88. Whitehead H, Waters S and Lyrholm T (1991). Social organization of female sperm whales and their offspring: constant companions and casual acquaintances. *Behavioural Ecology and Sociobiology* 29: 385-389.
89. Williams JH (1950). *Elephant Bill*. Doubleday, New York.
90. Wittemyer G, Douglas-Hamilton I and Getz WM (2005) The socio-ecology of elephants: analysis of the processes creating multi-tiered social structures. *Animal Behaviou*r 69: 1357-1371.
91. Wrangham RW (1980). An ecological model of female-bonded primate groups. *Behaviour* 75: 262-300.
92. Wrangham RW, Gittleman JL, Chapman CA (1993). Constraints on group size in primates and carnivores: population density and day-range as assays of exploitation competition. *Behavioural Ecology and Sociobiology* 32: 199-209.

Supplementary Material

Supplementary Material 1. Details of the clans sampled and used for analyses.

Supplementary Material 1, Table 1. The IDs of clans that were seen at least five times each in calf presence and absence within each year-set, the total number of days and the duration for which they were seen, and the number of sightings for each year-set are shown. All these clans were used for analyses of group size, and most of them (see Table 4 of this Supplementary Material) for experienced group size and female associations. If a focal clan was not seen at least five times each in calf presence and absence within a year-set, the number of sightings is not shown. Asterisks indicate that there was a calf in the clan during that year-set, but the clan was not seen at least five time with the calf (in the remaining cases, there was no calf during that period). The numbers of days on which the clans used for analyses (below) were sighted were 396 during 2009–2012, 392 during 2013–2015, and 333 during 2016–2018.

		2009-2012			2013-2015			2016-2018		
Clan name	Calf status	No. of sighting days	No. of independent sightings	Sighting duration (hours)	No. of sighting days	No. of independent sightings	Sighting duration (hours)	No. of sighting days	No. of independent sightings	Sighting duration (hours)
Alexandra	P	*	*	*	14	21	19.78	23	32	20.88
	A	-	-	-	33	43	16.90	21	27	7.07
Anabelle	P	11	18	12.67	*	*	*	5	5	1.02
	A	35	46	17.68	-	-	-	48	70	22.87
Cleopatra	P	-	-	-	*	*	*	7	8	2.02
	A	-	-	-	-	-	-	18	20	6.50
Fiola	P	*	*	*	7	13	9.08	-	-	-
	A	-	-	-	8	9	2.63	-	-	-
Kasturi	P	60	73	48.87	*	*	*	60	97	55.92
	A	88	136	73.28	-	-	-	57	101	64.28
Katrina	P	6	6	3.75	17	18	10.12	16	25	17.32
	A	16	20	17.68	16	19	11.07	12	15	5.45
Lisa	P	39	47	25.78	30	37	21.33	52	74	50.30
	A	119	172	90.47	105	174	73.93	104	163	56.58

Clan name	Calf status	2009-2012 No. of sighting days	2009-2012 No. of inde-pendent sightings	2009-2012 Sighting duration (hours)	2013-2015 No. of sighting days	2013-2015 No. of inde-pendent sightings	2013-2015 Sighting duration (hours)	2016-2018 No. of sighting days	2016-2018 No. of inde-pendent sightings	2016-2018 Sighting duration (hours)
Menaka	P	*	*	*	5	5	2.00	18	27	26.45
	A	-	-	-	43	51	31.07	48	76	28.13
Mridula	P	*	*	*	12	16	12.07	*	*	*
	A	-	-	-	29	35	18.72	-	-	-
Nakshatra	P	29	32	19.03	31	36	16.33	37	56	32.03
	A	58	74	31.78	61	82	34.47	93	135	48.97
Olympia	P	30	33	15.53	13	13	7.57	*	*	*
	A	57	66	28.92	52	67	34.17	-	-	-
Osanna	P	10	13	10.37	5	8	6.53	13	22	7.42
	A	39	60	41.12	20	34	12.07	27	40	15.67
Patricia	P	45	54	30.73	23	46	39.63	65	93	61.22
	A	195	348	176.82	233	477	214.02	174	351	140.58
Tilottama	P	10	12	5.83	12	16	11.05	34	41	31.05
	A	13	14	10.52	40	48	16.62	35	49	14.32
Unnati	P	11	11	9.20	-	-	-	-	-	-
	A	14	18	7.78	-	-	-	-	-	-
Victoria	P	72	135	75.73	84	174	92.88	74	214	136.13
	A	123	316	167.43	115	297	145.48	123	317	125.75

Supplementary Material 1, Table 2. Numbers of adult females (AF), young adult females, subadult females (SAF), and calves, in the datasets from 2009–2012, 2013–2015, and 2016–2018 used for group size analyses.

	2009-2012				2013-2015				2016-2018			
Clan name	AF	Young AF	SAF	Calf	AF	Young AF	SAF	Calf	AF	Young AF	SAF	Calf
Alexandra	-	-	-	-	11	0	2	7	13	2	0	2
Anabelle	11	3	3	6	-	-	-	-	16	5	4	2
Cleopatra	-	-	-	-	-	-	-	-	8	1	1	1
Fiola	-	-	-	-	9	4	1	1	-	-	-	-
Kasturi	7	0	1	3	-	-	-	-	9	1	3	4
Katrina	17	3	3	2	19	2	1	3	20	3	2	4
Lisa	16	2	4	11	18	2	3	4	20	3	3	4
Menaka	-	-	-	-	10	1	2	3	10	0	3	2
Mridula	-	-	-	-	9	3	2	3	-	-	-	-
Nakshatra	16	4	2	9	16	2	5	7	19	3	2	4
Olympia	25	4	6	6	29	5	6	7	-	-	-	-
Osanna	20	3	4	9	22	3	5	2	27	7	3	2
Patricia	21	5	5	7	22	2	10	3	31	10	4	8
Tilottama	4	0	2	3	6	2	0	1	6	1	0	2
Unnati	14	2	1	6	-	-	-	-	-	-	-	-
Victoria	30	6	13	15	38	8	16	12	48	15	13	13
Total	181	32	44	77	209	34	53	53	227	51	38	48

Supplementary Material 1, Table 3. The number of days and the duration for which different clans were seen in the presence and absence of young ones (including calves and young juveniles <2 years old). All these clans were used for group size analyses and most (see Table 4 in this Supplementary Material) for experienced group size analyses.

		2009-2012			2013-2015			2016-2018		
Clan name	Ind. <2y status	No. of sighting days	No. of inde-pendent sightings	Sighting duration (hours)	No. of sighting days	No. of inde-pendent sightings	Sighting duration (hours)	No. of sighting days	No. of inde-pendent sightings	Sighting duration (hours)
Alexandra	P	-	-	-	25	33	22.82	30	42	24.98
	A	-	-	-	26	31	13.87	14	17	2.97
Anabelle	P	23	33	18.78	-	-	-	6	6	1.13
	A	26	31	11.57	-	-	-	47	69	22.75
Cleopatra	P	-	-	-	-	-	-	8	9	2.10
	A	-	-	-	-	-	-	17	19	6.42
Fiola	P	-	-	-	12	18	11.23	-	-	-
	A	-	-	-	3	4	0.48	-	-	-
Kasturi	P	77	102	63.63	-	-	-	73	121	68.32
	A	73	107	58.55	-	-	-	49	77	51.88
Katrina	P	9	9	8.75	21	25	12.62	19	31	19.78
	A	13	17	12.68	11	12	8.57	7	9	2.98
Lisa	P	61	71	48.73	31	38	22.50	63	94	62.78
	A	105	148	67.53	104	173	72.77	94	143	44.10
Menaka	P	-	-	-	7	7	2.62	20	31	28.50
	A	-	-	-	42	49	30.45	46	72	26.08
Mridula	P	-	-	-	14	19	12.52	-	-	-
	A	-	-	-	28	32	18.27	-	-	-
Nakshatra	P	38	42	21.47	50	65	33.65	39	58	33.90
	A	51	64	29.35	43	53	17.15	92	133	47.10
Olympia	P	36	41	18.02	17	19	10.97	-	-	-
	A	54	58	26.43	48	61	30.77	-	-	-
Osanna	P	19	23	18.82	5	8	6.53	13	22	7.42
	A	35	50	32.67	20	34	12.07	27	40	15.67

		2009-2012			2013-2015			2016-2018		
Clan name	Ind. <2y status	No. of sighting days	No. of inde-pendent sightings	Sighting duration (hours)	No. of sighting days	No. of inde-pendent sightings	Sighting duration (hours)	No. of sighting days	No. of inde-pendent sightings	Sighting duration (hours)
Patricia	P	56	68	40.88	31	63	46.23	108	165	92.33
	A	192	334	166.67	230	460	207.42	155	279	109.47
Tilottama	P	14	17	8.77	35	44	19.65	37	44	32.38
	A	9	9	7.58	20	20	8.02	33	46	12.98
Unnati	P	16	19	14.18	-	-	-	-	-	-
	A	8	10	2.80	-	-	-	-	-	-
Victoria	P	120	270	152.32	115	267	147.08	94	247	149.25
	A	94	181	90.85	97	204	91.28	116	284	112.63

Supplementary Material 1, Table 4. Numbers of unique females in each of the 10, 11, and 11 focal clans, during 2009-2012, 2013-2015, and 2016-2018, respectively (shown in three rows), used for experienced group size analysis, and the total numbers of sightings of these females (numbers of sightings of each female added up) in the presence and absence of calves and young ones.

Clan name	No. of unique females	Total no. of sightings of females in calf P	Total no. of sightings of females in calf A	Total no. of sightings of females in ind. <2 y P	Total no. of sightings of females in ind. <2 y A
Alexandra	-	-	-	-	-
	8	90	112	137	65
	3	32	29	50	11
Anabelle	7	75	73	122	26
	-	-	-	-	-
	-	-	-	-	-
Cleopatra	-	-	-	-	-
	-	-	-	-	-
	2	14	20	14	20
Fiola	-	-	-	-	-
	3	33	22	47	8
	-	-	-	-	-
Kasturi	6	223	236	304	155
	-	-	-	-	-
	7	349	148	398	99
Katrina	-	-	-	-	-
	3	31	25	40	16
	2	29	13	34	8
Lisa	15	189	372	267	294
	8	142	211	149	204
	12	375	305	459	221
Menaka	-	-	-	-	-
	1	5	24	7	22
	5	62	115	66	111
Mridula	-	-	-	-	-
	8	72	64	78	58
	-	-	-	-	-
Nakshatra	8	91	124	104	111
	7	100	126	167	59
	11	155	223	155	223
Olympia	5	45	54	56	43
	-	-	-	-	-
	-	-	-	-	-

Clan name	No. of unique females	Total no. of sightings of females in calf P	Total no. of sightings of females in calf A	Total no. of sightings of females in ind. <2 y P	Total no. of sightings of females in ind. <2 y A
Osanna	3	18	26	25	19
	4	27	37	27	37
	2	18	24	18	24
Patricia	14	139	514	194	459
	6	139	229	172	196
	18	378	697	722	353
Tilottama	4	35	32	55	12
	5	50	119	127	42
	4	96	88	103	81
Unnati	2	11	19	18	12
	-	-	-	-	-
	-	-	-	-	-
Victoria	28	563	875	1076	362
	27	724	822	1117	429
	33	1065	800	1207	658

* Females from 12 focal clans used for analyses of associations from the 2016-2018 year-set, but only 11 were used here in analyses of experienced group size because one clan (Peggy) had only one adult female surviving (who associated with two different clans; see Keerthipriya and Vidya 2021), and clan was used as a factor in the analyses of experienced group size.

Supplementary Material 2. Correlations between group size variables.

Supplementary Material 2, Table 1. Spearman rank-order correlations between group size variables for each of the three year-sets one below the other; *r* values > 0.7 are marked in bold.

Variable	Total group size	Group size excluding males >=10 y old	No. of adult females	No. of adult females without a calf	No. of adult females without a calf or juvenile <2 y old	No. of males >=10 y old	No. of adult females 10-15 y old	No. of subadult females
Total group size	-	**0.989** **0.989** **0.985**	**0.901** **0.894** **0.928**	**0.805** **0.839** **0.828**	**0.717** **0.796** **0.811**	0.344 0.237 0.370	0.536 0.526 0.648	0.667 **0.723** 0.532
Group size excl. males >=10 y old	**0.989** **0.989** **0.985**	-	**0.909** **0.895** **0.938**	**0.810** **0.837** **0.833**	**0.721** **0.791** **0.815**	0.232 0.115 0.237	0.531 0.528 0.656	0.679 **0.737** 0.541
No. of adult females	**0.901** **0.894** **0.928**	**0.909** **0.895** **0.938**	-	**0.932** **0.965** **0.932**	**0.875** **0.941** **0.923**	0.227 0.163 0.250	0.612 0.643 **0.730**	0.482 0.490 0.370
No. of adult females without a calf	**0.805** **0.839** **0.828**	**0.810** **0.837** **0.833**	**0.932** **0.965** **0.932**	-	**0.932** **0.971** **0.984**	0.224 0.180 0.254	0.579 0.624 **0.712**	0.424 0.467 0.311
No. of adult females without a calf or juv. <2 y old	**0.717** **0.796** **0.811**	**0.721** **0.791** **0.815**	**0.875** **0.941** **0.923**	**0.932** **0.971** **0.984**	-	0.202 0.194 0.256	0.552 0.603 **0.721**	0.331 0.428 0.300
No. of males >=10 y old	0.344 0.237 0.370	0.232 0.115 0.237	0.227 0.163 0.250	0.224 0.180 0.254	0.202 0.194 0.256	-	0.213 0.100 0.192	0.146 0.051 0.136
No. of adult females 10-15 y old	0.536 0.526 0.648	0.531 0.528 0.656	0.612 0.643 **0.730**	0.579 0.624 **0.712**	0.552 0.603 **0.721**	0.213 0.100 0.192	-	0.311 0.311 0.232
No. of subadult females	0.667 **0.723** 0.532	0.679 **0.737** 0.541	0.482 0.490 0.370	0.424 0.467 0.311	0.331 0.428 0.300	0.146 0.051 0.136	0.311 0.311 0.232	-

Supplementary Material 3. Group sizes and experienced group sizes.

Supplementary Material 3, Table 1. Average (1.96 SE) group sizes and average numbers of adult, young adult, and subadult females experienced by adult females in the presence and absence of calves (<1 year old).

Group size measure	2009-2012		2013-2015		2016-2018	
	Calf P	Calf A	Calf P	Calf A	Calf P	Calf A
Group size						
No. of adult females	3.77 (0.208)	2.28 (0.099)	4.12 (0.258)	2.40 (0.099)	4.45 (0.200)	2.25 (0.093)
No. of young adult females	0.76 (0.093)	0.47 (0.047)	0.94 (0.115)	0.46 (0.041)	1.27 (0.087)	0.71 (0.049)
No. of subadult females	1.10 (0.094)	0.64 (0.050)	2.01 (0.181)	0.93 (0.066)	0.91 (0.099)	0.40 (0.038)
No. of males ≥10 years old	0.26 (0.056)	0.20 (0.028)	0.18 (0.043)	0.20 (0.026)	0.30 (0.048)	0.26 (0.032)
Group size experienced by adult females						
No. of adult females experienced	5.09 (0.134)	3.83 (0.115)	5.91 (0.177)	4.21 (0.136)	6.21 (0.144)	3.62 (0.098)
No. of young adult females experienced	0.94 (0.060)	0.78 (0.051)	1.34 (0.075)	0.76 (0.051)	1.58 (0.055)	0.94 (0.041)
No. of subadult females experienced	1.39 (0.059)	1.11 (0.050)	2.69 (0.113)	1.79 (0.082)	1.35 (0.065)	0.56 (0.033)

Supplementary Material 3, Table 2. Average (1.96 SE) group sizes and average numbers of adult, young adult, and subadult females experienced by adult females in the presence and absence of young ones (<2 years old).

Group size measure	2009-2012		2013-2015		2016-2018	
	Ind. <2 P	Ind. <2 A	Ind. <2 P	Ind. <2 A	Ind. <2 P	Ind. <2 A
Group size						
No. of adult females	3.74 (0.175)	1.91 (0.081)	4.06 (0.207)	2.12 (0.090)	4.39 (0.175)	1.97 (0.081)
No. of young adult females	0.84 (0.082)	0.35 (0.040)	0.96 (0.091)	0.37 (0.038)	1.27 (0.077)	0.61 (0.048)
No. of subadult females	1.19 (0.079)	0.46 (0.044)	1.98 (0.140)	0.77 (0.064)	0.86 (0.084)	0.36 (0.038)
No. of males ≥10 years old	0.29 (0.046)	0.16 (0.028)	0.17 (0.033)	0.20 (0.029)	0.33 (0.045)	0.23 (0.031)
Group size experienced by adult females						
No. of adult females experienced	5.27 (0.123)	2.86 (0.086)	5.80 (0.146)	3.44 (0.136)	6.09 (0.123)	2.91 (0.089)
No. of young adult females experienced	1.06 (0.056)	0.45 (0.038)	1.33 (0.060)	0.45 (0.047)	1.57 (0.047)	0.70 (0.041)
No. of subadult females experienced	1.55 (0.052)	0.71 (0.045)	2.66 (0.089)	1.36 (0.092)	1.23 (0.055)	0.48 (0.036)

Supplementary Material 4. Results of group size analyses.

Supplementary Material 4, Table 1. Results of the full and the two reduced GLMMs for the numbers of adult and young adult females in Calf presence/absence (P/A in table). Significant *P* values of model comparisons are marked in bold, which indicates that a particular reduced model is significantly different from the model that is above it in the table.

Variable	Model parameters		Model	AIC	*R* 95% *CI*	R^2	*P*
	Fixed effect	Random effect					
No. of adult females 2009-2012	Calf P/A	Clan, Clan x Calf P/A	ZTNBM	5713.2	0.41 (0.37 - 0.45)	0.17	_
	Calf P/A	Clan	ZTNBM	5727.7	0.40 (0.35 - 0.43)	0.16	**<0.001**
	Calf P/A	_	ZTNBM	5795.3	0.36 (0.31 - 0.40)	0.13	**<0.001**
No. of adult females 2013-2015	Calf P/A	Clan, Clan x Calf P/A	ZTNBM	6069.0	0.42 (0.38 - 0.46)	0.17	_
	Calf P/A	Clan	ZTNBM	6096.2	0.39 (0.34 - 0.42)	0.15	**<0.001**
	Calf P/A	_	ZTNBM	6138.0	0.35 (0.31 - 0.39)	0.12	**<0.001**
No. of adult females 2016-2018	Calf P/A	Clan, Clan x Calf P/A	ZTNBM	7245.1	0.52 (0.49 - 0.56)	0.27	_
	Calf P/A	Clan	ZTNBM	7264.9	0.51 (0.48 - 0.54)	0.26	**<0.001**
	Calf P/A	_	ZTNBM	7341.8	0.50 (0.46 - 0.53)	0.25	**<0.001**
No. of young adult females 2009-2012	Calf P/A	Clan, Clan x Calf P/A	Poisson	2771.7	_	0.05	_
	Calf P/A	Clan	Poisson	2778.4	_	0.04	**0.003**
	Calf P/A	_	Poisson	2903.7	_	0.01	**<0.001**
No. of young adult females 2013-2015	Calf P/A	Clan, Clan x Calf P/A	Poisson	3107.5	_	0.16	_
	Calf P/A	Clan	Poisson	3131.6	_	0.10	**<0.001**
	Calf P/A	_	Poisson	3309.9	_	0.02	**<0.001**
No. of young adult females 2016-2018	Calf P/A	Clan, Clan x Calf P/A	Poisson	4616.2	_	0.13	_
	Calf P/A	Clan	Poisson	4639.7	_	0.11	**<0.001**
	Calf P/A	_	Poisson	4859.7	_	0.04	**<0.001**

Supplementary Material 4, Table 2. Results of the full and the two reduced GLMMs for the numbers of subadult females and males at least 10 years old in Calf presence/absence (P/A in table). Significant *P* values of model comparisons are marked in bold, which indicates that a particular reduced model is significantly different from the model that is above it in the table. Since the reduced model for male number was not different from the full model, the results of the reduced one are shown at the end (Table 2a).

Variable	Model parameters		Model	AIC	R^2	*P*
	Fixed effect	Random effect				
No. of subadult females 2009-2012	Calf P/A	Clan, Clan x Calf P/A	Poisson	3673.3	0.09	_
	Calf P/A	Clan	Poisson	3684.5	0.06	**<0.001**
	Calf P/A	_	Poisson	3957.9	0.02	**<0.001**
No. of subadult females 2013-2015	Calf P/A	Clan, Clan x Calf P/A	NBM	4365.2	0.33	_
	Calf P/A	Clan	NBM	4384.6	0.28	**<0.001**
	Calf P/A	_	NBM	4713.4	0.03	**<0.001**
No. of subadult females 2016-2018	Calf P/A	Clan, Clan x Calf P/A	Poisson	3260.2	0.28	_
	Calf P/A	Clan	Poisson	3367.3	0.24	**<0.001**
	Calf P/A	_	Poisson	3815.4	0.03	**<0.001**
No. of males ≥10 yrs 2009-2012	Calf P/A	Clan, Clan x Calf P/A	NBM	1913.8	0.02	_
	Calf P/A	Clan	NBM	1914.1	0.02	0.1257
	Calf P/A	_	NBM	1929.7	0	**<0.001**
No. of males ≥10 yrs 2013-2015	Calf P/A	Clan, Clan x Calf P/A	NBM	1822.7	0.01	_
	Calf P/A	Clan	NBM	1821.2	0.01	**0.462**
	Calf P/A	_	NBM	1835.9	0	**<0.001**
No. of males ≥10 yrs 2016-2018	Calf P/A	Clan, Clan x Calf P/A	NBM	2682.1	0.03	_
	Calf P/A	Clan	NBM	2684.2	0.02	**0.042**
	Calf P/A	_	NBM	2703.7	0	**<0.001**

Table 2a.

Dependent variable	Estimate	*SE* of estimate	1.96 *SE*	95% CI of estimate		*z*	*P*
				Lower	Upper		
No. of males >=10 years (2009-2012) ~ Calf P/A + (1|Clan)							
Intercept	-1.812	0.165	0.323	-2.135	-1.489	-11.003	**<0.001**
Calf P/A (P)	0.229	0.127	0.248	-0.019	0.477	1.808	0.071
Clan		0.361					

Supplementary Material 4, Table 3. Results of the full GLMMs for the number of adult females and the number of young adult females for the three year-sets. Intercept and Ind. <2y presence/absence (P/A in table) are fixed effects (for which SE of the estimate is calculated), whereas Clan and Clan x Ind. <2y presence/absence are random effects (for which SD is given). Significant *P* values are marked in bold. Asterisks mark significant random effects based on comparison with reduced models (next table).

Dependent variable	Estimate	*SE* of estimate / SD	1.96 *SE*	95% CI of estimate		*z*	*P*
				Lower	Upper		
No. of adult females: 2009-2012 *(Ind. <2y P: 695 sightings, Ind. <2y A: 1009 sightings)*							
Intercept	0.245	0.092	0.181	0.064	0.426	2.659	**0.008**
Ind. <2y P/A (P)	0.948	0.121	0.237	0.711	1.185	7.832	**<0.001**
Clan		0.000					*
Clan x Ind. <2y P/A		0.242					*
No. of adult females: 2013-2015 *(Ind. <2y P: 606 sightings, Ind. <2y A: 1133 sightings)*							
Intercept	0.234	0.115	0.224	0.009	0.458	2.042	**0.041**
Ind. <2y P/A (P)	1.027	0.129	0.252	0.775	1.279	7.992	**<0.001**
Clan		0.172					*
Clan x Ind. <2y P/A		0.222					*
No. of adult females: 2016-2018 *(Ind. <2y P: 870 sightings, Ind. <2y A: 1188 sightings)*							
Intercept	0.000	0.137	0.269	-0.268	0.269	0.001	0.999
Ind. <2y P/A (P)	1.241	0.176	0.346	0.896	1.587	7.035	**<0.001**
Clan		0.000					*
Clan x C_J A/P		0.369					*
No. of young adult females: 2009-2012 *(Ind. <2y P: 576 sightings, Ind. <2y A: 893 sightings)*							
Intercept	-1.333	0.171	0.336	-1.668	-0.997	-7.774	**<0.001**
Ind. <2y P/A (P)	0.877	0.172	0.337	0.539	1.214	5.093	**<0.001**
Clan		0.319					*
Clan x Ind. <2y P/A		0.255					NS
No. of young adult females: 2013-2015 *(Ind. <2y P: 548 sightings, Ind. <2y A: 1090 sightings)*							
Intercept	-1.067	0.232	0.455	-1.522	-0.612	-4.593	**<0.001**
Ind. <2y P/A (P)	0.756	0.265	0.520	0.236	1.275	2.851	**0.004**
Clan		0.424					*
Clan x Ind. <2y P/A		0.532					*
No. of young adult females: 2016-2018 *(Ind. <2y P: 839 sightings, Ind. <2y A: 1116 sightings)*							
Intercept	-0.727	0.183	0.358	-1.085	-0.369	-3.977	**<0.001**
Ind. <2y P/A (P)	0.567	0.206	0.403	0.164	0.969	2.757	**0.006**
Clan		0.357					*
Clan x Ind. <2y P/A		0.422					*

Supplementary Material 4, Table 4. Results of the full and the two reduced GLMMs for the numbers of adult and young adult females in young one (individuals <2 years) presence/absence (P/A in table). Significant *P* values of model comparisons are marked in bold, which indicates that a particular reduced model is significantly different from the model that is above it in the table.

Variable	Model parameters		Model	AIC	*R* 95% *CI*	R^2	*P*
	Fixed effect	Random effect					
No. of adult females 2009-2012	Ind. <2y P/A	Clan, Clan x Ind. <2y P/A	ZTP	5714.1	0.50 (0.46 - 0.53)	0.25	–
	Ind. <2y P/A	Clan	ZTP	5734.2	0.48 (0.44 - 0.51)	0.23	**<0.001**
	Ind. <2y P/A	_	ZTP	5791.9	0.48 (0.44 - 0.51)	0.23	**<0.001**
No. of adult females 2013-2015	Ind. <2y P/A	Clan, Clan x Ind. <2y P/A	ZTNBM	5949.4	0.47 (0.43 - 0.50)	0.22	–
	Ind. <2y P/A	Clan	ZTNBM	5958.3	0.43 (0.39 - 0.47)	0.19	**<0.001**
	Ind. <2y P/A	_	ZTNBM	5979.1	0.45 (0.41 - 0.49)	0.20	**<0.001**
No. of adult females 2016-2018	Ind. <2y P/A	Clan, Clan x Ind. <2y P/A	ZTNBM	6982.0	0.61 (0.58 - 0.64)	0.38	–
	Ind. <2y P/A	Clan	ZTNBM	7029.6	0.59 (0.56 - 0.61)	0.34	**<0.001**
	Ind. <2y P/A	_	ZTNBM	7123.6	0.57 (0.54 - 0.60)	0.33	**<0.001**
No. of young adult females 2009-2012	Ind. <2y P/A	Clan, Clan x Ind. <2y P/A	Poisson	2713.0	_	0.06	_
	Ind. <2y P/A	Clan	Poisson	2714.7	_	0.05	0.053
	Ind. <2y P/A	_	Poisson	2793.3	_	0.04	**<0.001**
No. of young adult females 2013-2015	Ind. <2y P/A	Clan, Clan x Ind. <2y P/A	Poisson	3009.8	_	0.17	_
	Ind. <2y P/A	Clan	Poisson	3056.7	_	0.12	**<0.001**
	Ind. <2y P/A	_	Poisson	3200.7	_	0.05	**<0.001**
No. of young adult females 2016-2018	Ind. <2y P/A	Clan, Clan x Ind. <2y P/A	Poisson	4478.5	_	0.14	_
	Ind. <2y P/A	Clan	Poisson	4540.7	_	0.14	**<0.001**
	Ind. <2y P/A	_	Poisson	4775.4	_	0.06	**<0.001**

Supplementary Material 4, Table 5. Results of the full GLMMs for the number of subadult females and the numbers of old subadult and adult males for the three year-sets. Intercept and Ind. <2y presence/absence (P/A in table) are fixed effects (for which SE of the estimate is calculated), whereas Clan and Clan x Ind. <2y presence/absence are random effects (for which SD is given). Significant *P* values are marked in bold. Asterisks mark significant random effects based on comparison with reduced models (see next table).

Dependent variable	Estimate	*SE* of estimate / SD	1.96 *SE*	95% CI of estimate		*z*	*P*
				Lower	Upper		
No. of subadult females: 2009-2012 *(Ind. <2y P: 695 sightings, Ind. <2y A: 1009 sightings)*							
Intercept	-1.195	0.188	0.369	-1.564	-0.827	-6.355	**<0.001**
Ind. <2y P/A (P)	1.011	0.213	0.417	0.594	1.428	4.748	**<0.001**
Clan		0.307					*
Clan x Ind. <2y P/A		0.419					*
No. of subadult females: 2013-2015 *(Ind. <2y P: 555 sightings, Ind. <2y A: 1064 sightings)*							
Intercept	-0.683	0.211	0.414	-1.098	-0.269	-3.232	**0.001**
Ind. <2y P/A (P)	0.787	0.217	0.426	0.360	1.213	3.618	**<0.001**
Clan		0.437					*
Clan x Ind. <2y P/A		0.414					*
No. of subadult females: 2016-2018 *(Ind. <2y P: 753 sightings, Ind. <2y A: 1116 sightings)*							
Intercept	-1.602	0.413	0.809	-2.412	-0.793	-3.880	**<0.001**
Ind. <2y P/A (P)	0.987	0.395	0.773	0.214	1.760	2.502	**0.012**
Clan		0.884					*
Clan x Ind. <2y P/A		0.768					*
No. of males ≥10 years: 2009-2012 *(Ind. <2y P: 695 sightings, Ind. <2y A: 1009 sightings)*							
Intercept	-1.976	0.201	0.393	-2.369	-1.583	-9.855	**<0.001**
Ind. <2y P/A (P)	0.511	0.226	0.443	0.069	0.954	2.265	**0.024**
Clan		0.340					*
Clan x Ind. <2y P/A		0.130					NS
No. of males ≥10 years: 2013-2015 *(Ind. <2y P: 606 sightings, Ind. <2y A: 1133 sightings)*							
Intercept	-1.858	0.170	0.333	-2.191	-1.525	-10.942	**<0.001**
Ind. <2y P/A (P)	-0.040	0.138	0.270	-0.310	0.231	-0.287	0.774
Clan		0.439					*
Clan x Ind. <2y P/A		0.000					*
No. of males ≥10 years: 2016-2018 *(Ind. <2y P: 870 sightings, Ind. <2y A: 1188 sightings)*							
Intercept	-1.579	0.152	0.298	-1.877	-1.281	-10.387	**<0.001**
Ind. <2y P/A (P)	0.226	0.171	0.336	-0.110	0.561	1.316	0.188
Clan		0.298					*
Clan x Ind. <2y P/A		0.273					NS

Supplementary Material 4, Table 6. Results of the full and the two reduced GLMMs for the numbers of subadult females and males at least 10 years old in young one (individuals <2 years) presence/absence (P/A in table). Significant *P* values of model comparisons are marked in bold, which indicates that a particular reduced model is significantly different from the model that is above it in the table. Since a reduced model was not different from the full model in two cases, the results of those two reduced models are shown at the end (Table 6a).

Variable	Model parameters		Model	AIC	R^2	*P*
	Fixed effect	Random effect				
No. of subadult females 2009-2012	Ind. <2y P/A	Clan, Clan x Ind. <2y P/A	Poisson	3546.5	0.14	_
	Ind. <2y P/A	Clan	Poisson	3557.3	0.08	**<0.001**
	Ind. <2y P/A	_	Poisson	3762.7	0.08	**<0.001**
No. of subadult females 2013-2015	Ind. <2y P/A	Clan, Clan x Ind. <2y P/A	NBM	4281.1	0.32	_
	Ind. <2y P/A	Clan	NBM	4298.6	0.29	**<0.001**
	Ind. <2y P/A	_	NBM	4598.5	0.05	**<0.001**
No. of subadult females 2016-2018	Ind. <2y P/A	Clan, Clan x Ind. <2y P/A	Poisson	3241.7	0.37	_
	Ind. <2y P/A	Clan	Poisson	3323.6	0.25	**<0.001**
	Ind. <2y P/A	_	Poisson	3790.8	0.04	**<0.001**
No. of males ≥10 y 2009-2012	Ind. <2y P/A	Clan, Clan x Ind. <2y P/A	NBM	1902.2	0.02	_
	Ind. <2y P/A	Clan	NBM	1900.2	0.02	0.979
	Ind. <2y P/A	_	NBM	1910.7	0	**<0.001**
No. of males ≥10 y 2013-2015	Ind. <2y P/A	Clan, Clan x Ind. <2y P/A	NBM	1823.2	0.01	_
	Ind. <2y P/A	Clan	NBM	1821.2	0.01	**<0.001**
	Ind. <2y P/A	_	NBM	1834.1	0	**<0.001**
No. of males ≥10 y 2016-2018	Ind. <2y P/A	Clan, Clan x Ind. <2y P/A	NBM	2674.3	0.03	_
	Ind. <2y P/A	Clan	NBM	2675.0	0.02	0.102
	Ind. <2y P/A	_	NBM	2692.9	0	**<0.001**

Table 6a.

Dependent variable	Estimate	*SE* of estimate	1.96 *SE*	95% CI of estimate		*z*	*P*
				Lower	Upper		
No. of males >=10 years (2009-2012) ~ Ind.<=2y P/A + (1|Clan)							
Intercept	-1.973	0.165	0.323	-2.297	-1.650	-11.970	**<0.001**
Ind.<=2y P/A (P)	0.506	0.123	0.241	0.266	0.747	4.123	**<0.001**
Clan		0.361					
No. of males >=10 years (2016-2018) ~ Ind.<=2y P/A + (1|Clan)							
Intercept	-1.620	0.135	0.265	-1.885	-1.355	-11.978	**<0.001**
Ind. <2y P/A (P)	0.340	0.096	0.189	0.151	0.529	3.522	**<0.001**
Clan		0.349					

Supplementary Material 5. Results of experienced group size analyses.

Supplementary Material 5, Table 1. Results of the full and the two reduced GLMMs for the numbers of adult, young adult, and subadult females experienced by adult females. Significant *P* values of model comparisons are marked in bold, which indicates that a particular reduced model is significantly different from the model that is above it in the table. Here, (1|Clan//AF_ID) represents the random factor AF_ID nested within clan (this would be (1|Clan/AF_ID) in *R* notation but a double slash is used here to avoid confusion with Calf P/A), and (Calf P/A | Clan//AF_ID) represents the interaction between the random factor AF_ID nested within clan and the fixed factor Calf presence/absence (P/A in table).

Variable	Model parameters		Model	AIC	*R* 95% *CI*	R^2	*P*
	Fixed effect	Random effect					
No. of adult females experienced 2009-2012	Calf P/A	(Calf P/A | Clan//AF_ID)	ZTNBM	15916.7	0.53 (0.51 - 0.56)	0.28	_
	Calf P/A	(1 | Clan//AF_ID)	ZTNBM	16011.6	0.50 (0.48 - 0.53)	0.25	**<0.001**
	Calf P/A	_	ZTNBM	16566.3	0.29 (0.26 - 0.31)	0.08	**<0.001**
No. of adult females experienced 2013-2015	Calf P/A	(Calf P/A | Clan//AF_ID)	ZTNBM	14474.1	0.58 (0.55 - 0.61)	0.34	_
	Calf P/A	(1 | Clan//AF_ID)	ZTNBM	14560.0	0.54 (0.51 - 0.57)	0.29	**<0.001**
	Calf P/A	_	ZTNBM	15234.0	0.29 (0.26 - 0.32)	0.08	**<0.001**
No. of adult females experienced 2016-2018	Calf P/A	(Calf P/A | Clan//AF_ID)	ZTNBM	22359.3	0.63 (0.61 - 0.65)	0.40	_
	Calf P/A	(1 | Clan//AF_ID)	ZTNBM	22624.0	0.59 (0.57 - 0.61)	0.35	**<0.001**
	Calf P/A	_	ZTNBM	23508.1	0.43 (0.41 - 0.45)	0.18	**<0.001**
No. of young adult females experienced 2009-2012	Calf P/A	(Calf P/A | Clan//AF_ID)	Poisson	7386.0	_	0.14	_
	Calf P/A	(1 | Clan//AF_ID)	Poisson	7440.8	_	0.13	**<0.001**
	Calf P/A	_	Poisson	8204.5	_	0	**<0.001**
No. of young adult females experienced 2013-2015	Calf P/A	(Calf P/A | Clan//AF_ID)	Poisson	6922.7	_	0.36	_
	Calf P/A	(1 | Clan//AF_ID)	Poisson	7126.4	_	0.20	**<0.001**
	Calf P/A	_	Poisson	8228.7	_	0.05	**<0.001**

Variable	Fixed effect	Random effect	Model	AIC	*R* 95% *CI*	R^2	*P*
No. of young adult females experienced 2016-2018	Calf P/A	(Calf P/A | Clan//AF_ID)	Poisson	12975.4	_	0.17	_
	Calf P/A	(1 | Clan//AF_ID)	Poisson	13148.1	_	0.17	**<0.001**
	Calf P/A	_	Poisson	14309.0	_	0.06	**<0.001**
No. of subadult females experienced 2009-2012	Calf P/A	(Calf P/A | Clan//AF_ID)	Poisson	9669.6	_	0.39	_
	Calf P/A	(1 | Clan//AF_ID)	Poisson	9747.8	_	0.14	**<0.001**
	Calf P/A	_	Poisson	10783.0	_	0.01	**<0.001**
No. of subadult females experienced 2013-2015	Calf P/A	(Calf P/A | Clan//AF_ID)	Poisson	10160.9	_	0.54	_
	Calf P/A	(1 | Clan//AF_ID)	Poisson	10310.9	_	0.35	**<0.001**
	Calf P/A	_	Poisson	11928.0	_	0.07	**<0.001**
No. of subadult females experienced 2016-2018	Calf P/A	(Calf P/A | Clan//AF_ID)	Poisson	9850.7	_	0.56	_
	Calf P/A	(1 | Clan//AF_ID)	Poisson	10329.6	_	0.38	**<0.001**
	Calf P/A	_	Poisson	13290.0	_	0.10	**<0.001**

Supplementary Material 5, Table 2. Results of the full GLMMs for the numbers of adult, young adult, and subadult females experienced by adult females in young one (individuals <2 years old) presence and absence in all three year-sets. Intercept and Ind. <2y presence/absence (P/A in table) are fixed factors for which SE is given. Significant *P* values are marked in bold. Clan//AF_ID and Clan are random effects for which SD is given. Clan//AF_ID indicates that AF_ID is nested within clan (this would be Clan/AF_ID in *R* notation but a double slash is used here to avoid confusion with P/A). Asterisks mark significant random effects based on comparison with reduced models (see the next table).

Dependent variable	Estimate	*SE* of estimate / SD	1.96 *SE*	95% CI of estimate		*z*	*P*
				Lower	Upper		
No. of adult females experienced: 2009-2012 *(Ind. <2y P: 2221 sightings, Ind. <2y A: 1493 sightings)*							
Intercept	0.588	0.183	0.359	0.228	0.947	3.205	**0.001**
Ind. <2y P/A	0.877	0.186	0.365	0.512	1.241	4.710	**<0.001**
Clan//AF_ID: Intercept		0.322					-
Clan//AF_ID: Ind. <2y P/A (P)		0.305					*
Clan: Intercept		0.510					-
Clan: Ind. <2y P/A (P)		0.516					*
No. of adult females experienced: 2013-2015 *(Ind. <2y P: 2068 sightings, Ind. <2y A: 1136 sightings)*							
Intercept	0.990	0.102	0.199	0.791	1.189	9.743	**<0.001**
Ind. <2y P/A	0.555	0.100	0.196	0.358	0.751	5.537	**<0.001**
Clan//AF_ID: Intercept		0.305					-
Clan//AF_ID: Ind. <2y P/A (P)		0.236					*
Clan: Intercept		0.265					-
Clan: Ind. <2y P/A (P)		0.265					*
No. of adult females experienced: 2016-2018 *(Ind. <2y P: 3226 sightings, Ind. <2y A: 1809 sightings)*							
Intercept	0.557	0.129	0.253	0.304	0.810	4.323	**<0.001**
Ind. <2y P/A	0.946	0.099	0.195	0.751	1.141	9.515	**<0.001**
Clan//AF_ID: Intercept		0.454					-
Clan//AF_ID: Ind. <2y P/A (P)		0.413					*
Clan: Intercept		0.314					-
Clan: Ind. <2y P/A (P)		0.178					*

Dependent variable	Estimate	*SE* of estimate / SD	1.96 *SE*	95% CI of estimate		*z*	*P*
No. of young adult females experienced: 2009-2012 *(Ind. <2y P: 1963 sightings, Ind. <2y A:1326 sightings)*							
Intercept	-1.193	0.159	0.312	-1.506	-0.881	-7.487	**<0.001**
Ind. <2y P/A	0.818	0.140	0.274	0.544	1.092	5.844	**<0.001**
Clan//AF_ID: Intercept		0.667					-
Clan//AF_ID: Ind. <2y P/A (P)		0.576					*
Clan: Intercept		0.311					-
Clan: Ind. <2y P/A (P)		0.229					*
No. of young adult females experienced: 2013-2015 *(Ind. <2y P: 1891 sightings, Ind. <2y A: 1055 sightings)*							
Intercept	-1.118	0.286	0.560	-1.678	-0.558	-3.912	**<0.001**
Ind. <2y P/A	0.877	0.281	0.552	0.325	1.428	3.117	**0.002**
Clan//AF_ID: Intercept		0.446					-
Clan//AF_ID: Ind. <2y P/A (P)		0.245					*
Clan: Intercept		0.786					-
Clan: Ind. <2y P/A (P)		0.775					*
No. of young adult females experienced: 2016-2018 *(Ind. <2y P: 3160 sightings, Ind. <2y A:1698 sightings)*							
Intercept	-0.940	0.175	0.344	-1.283	-0.596	-5.361	**<0.001**
Ind. <2y P/A	0.794	0.149	0.292	0.502	1.086	5.332	**<0.001**
Clan//AF_ID: Intercept		0.651					-
Clan//AF_ID: Ind. <2y P/A (P)		0.545					*
Clan: Intercept		0.384					-
Clan: Ind. <2y P/A (P)		0.265					*
No. of subadult females experienced: 2009-2012 *(Ind. <2y P: 2221 sightings, Ind. <2y A: 1493 sightings)*							
Intercept	-0.952	0.254	0.499	-1.451	-0.454	-3.743	**<0.001**
Ind. <2y P/A	1.010	0.258	0.505	0.505	1.515	3.921	**<0.001**
Clan//AF_ID: Intercept		0.614					-
Clan//AF_ID: Ind. <2y P/A (P)		0.415					*
Clan: Intercept		0.680					-
Clan: Ind. <2y P/A (P)		0.705					*
No. of subadult females experienced: 2013-2015 *(Ind. <2y P: 1934 sightings, Ind. <2y A: 1072 sightings)*							
Intercept	-0.545	0.380	0.745	-1.290	0.200	-1.435	0.151
Ind. <2y P/A	0.753	0.300	0.589	0.164	1.342	2.507	**0.012**
Clan//AF_ID: Intercept		0.393					-
Clan//AF_ID: Ind. <2y P/A (P)		0.351					*
Clan: Intercept		1.075					-
Clan: Ind. <2y P/A (P)		0.810					*

Dependent variable	Estimate	*SE* of estimate / SD	1.96 *SE*	95% CI of estimate		*z*	*P*
No. of subadult females experienced: 2016-2018 *(Ind. <2y P: 3039 sightings, Ind. <2y A: 1718 sightings)*							
Intercept	-2.127	0.682	1.338	-3.464	-0.789	-3.117	**0.002**
Ind. <2y P/A	1.553	0.469	0.919	0.634	2.473	3.312	**0.001**
Clan//AF_ID: Intercept		0.697					-
Clan//AF_ID: Ind. <2y P/A (P)		0.599					*
Clan: Intercept		1.863					-
Clan: Ind. <2y P/A (P)		1.175					*

Supplementary Material 5, Table 3. Results of the full and the two reduced GLMMs for the numbers of adult, young adult, and subadult females experienced by adult females in young one (individuals <2 years) presence/absence. Significant *P* values of model comparisons are marked in bold, which indicates that a particular reduced model is significantly different from the model that is above it in the table. Here, (1 | Clan//AF_ID) represents the random factor AF_ID nested within clan and (Ind. <2y P/A | Clan//AF_ID) represents the interaction between the random factor AF_ID nested within clan and the fixed factor Ind. <2y presence/absence (P/A in table).

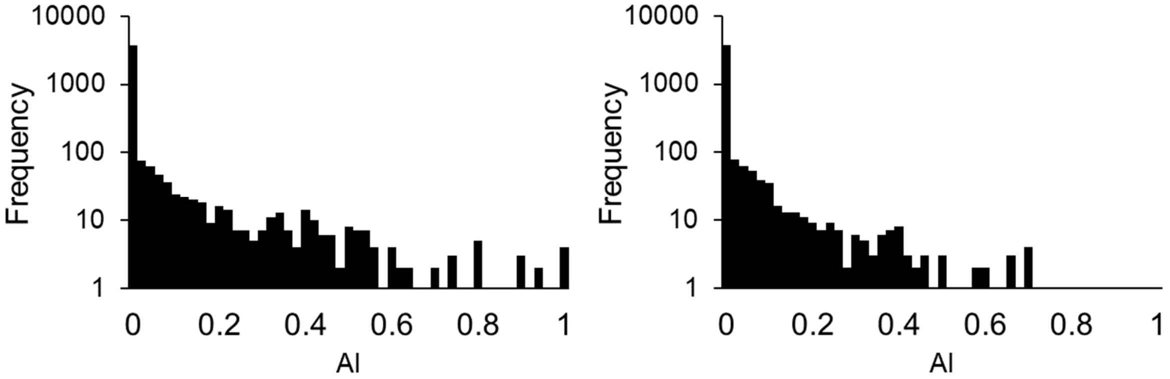
Variable	Model parameters		Model	AIC	*R*	R^2	*P*
	Fixed effect	Random effect			95% *CI*		
No. of adult females experienced 2009-2012	Ind. <2y P/A	(Ind. <2y P/A | Clan//AF_ID)	ZTNBM	15408.6	0.61 (0.58 - 0.63)	0.37	–
	Ind. <2y P/A	(1 | Clan//AF_ID)	ZTNBM	15515.9	0.58 (0.56 - 0.60)	0.34	**<0.001**
	Ind. <2y P/A	_	ZTNBM	15976.1	0.45 (0.42 - 0.48)	0.20	**<0.001**
No. of adult females experienced 2013-2015	Ind. <2y P/A	(Ind. <2y P/A | Clan//AF_ID)	ZTNBM	14232.0	0.63 (0.60 - 0.65)	0.39	–
	Ind. <2y P/A	(1 | Clan//AF_ID)	ZTNBM	14301.1	0.60 (0.57 - 0.62)	0.35	**<0.001**
	Ind. <2y P/A	_	ZTNBM	14999.2	0.39 (0.36 - 0.42)	0.15	**<0.001**
No. of adult females experienced 2016-2018	Ind. <2y P/A	(Ind. <2y P/A | Clan//AF_ID)	ZTNBM	21934.7	0.67 (0.65 - 0.68)	0.44	–
	Ind. <2y P/A	(1 | Clan//AF_ID)	ZTNBM	22095.2	0.64 (0.63 - 0.66)	0.42	**<0.001**
	Ind. <2y P/A	_	ZTNBM	22936.1	0.54 (0.52 - 0.56)	0.29	**<0.001**
No. of young adult females experienced 2009-2012	Ind. <2y P/A	(Ind. <2y P/A | Clan//AF_ID)	Poisson	7145.1	_	0.10	_
	Ind. <2y P/A	(1 | Clan//AF_ID)	Poisson	7189.6	_	0.16	**<0.001**
	Ind. <2y P/A	_	Poisson	7781.6	_	0.09	**<0.001**
No. of young adult females experienced 2013-2015	Ind. <2y P/A	(Ind. <2y P/A | Clan//AF_ID)	Poisson	6818.0	_	0.30	_
	Ind. <2y P/A	(1 | Clan//AF_ID)	Poisson	6868.6	_	0.25	**<0.001**
	Ind. <2y P/A	_	Poisson	7891.1	_	0.14	**<0.001**

Variable	Fixed effect	Random effect	Model	AIC	R 95% *CI*	R^2	P
No. of young adult females experienced 2016-2018	Ind. <2y P/A	(Ind. <2y P/A | Clan//AF_ID)	Poisson	12790.0	_	0.15	_
	Ind. <2y P/A	(1 | Clan//AF_ID)	Poisson	12890.7	_	0.18	**<0.001**
	Ind. <2y P/A	_	Poisson	13986.0	_	0.11	**<0.001**
No. of subadult females experienced 2009-2012	Ind. <2y P/A	(Ind. <2y P/A | Clan//AF_ID)	Poisson	9332.4	_	0.41	_
	Ind. <2y P/A	(1 | Clan//AF_ID)	Poisson	9439.3	_	0.17	**<0.001**
	Ind. <2y P/A	_	Poisson	10273.0	_	0.11	**<0.001**
No. of subadult females experienced 2013-2015	Ind. <2y P/A	(Ind. <2y P/A | Clan//AF_ID)	Poisson	10003.9	_	0.56	_
	Ind. <2y P/A	(1 | Clan//AF_ID)	Poisson	10207.6	_	0.36	**<0.001**
	Ind. <2y P/A	_	Poisson	11638.0	_	0.15	**<0.001**
No. of subadult females experienced 2016-2018	Ind. <2y P/A	(Ind. <2y P/A | Clan//AF_ID)	Poisson	9943.6	_	0.96	_
	Ind. <2y P/A	(1 | Clan//AF_ID)	Poisson	10191.8	_	0.40	**<0.001**
	Ind. <2y P/A	_	Poisson	13361.0	_	0.10	**<0.001**

Supplementary Material 6. Associations between adult females in the presence and absence of calves.

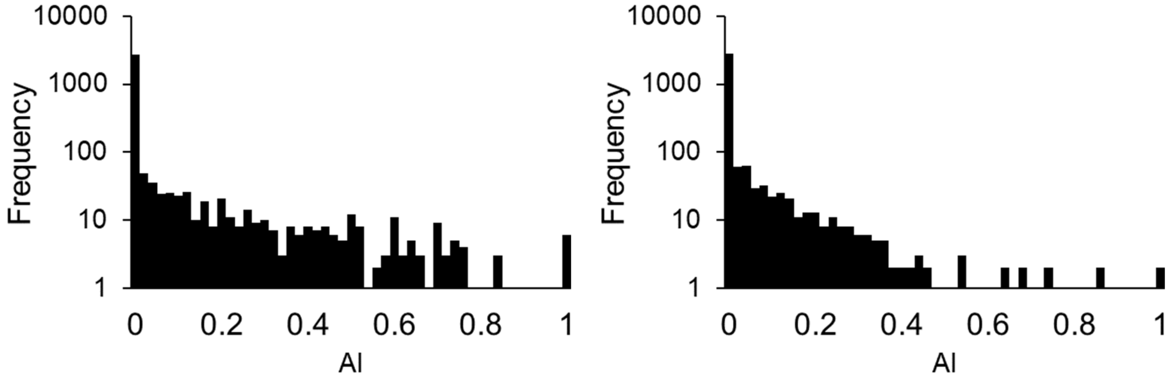
a. 2009-2012: Calf presence

b. 2009-2012: Calf absence



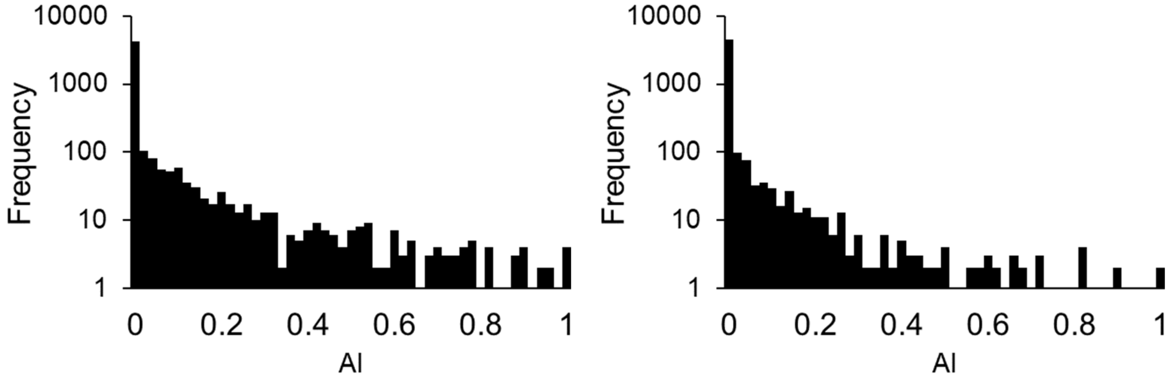
c. 2013-2015: Calf presence

d. 2013-2015: Calf absence



e. 2016-2018: Calf presence

f. 2016-2018: Calf absence



Supplementary Material 6, Figure 1. AI distributions based on the sightings of 92 unique adult females in a) calf presence and b) calf absence during the year-set 2009-2012, 80 unique adult females in c) calf presence and d) calf absence during the year-set 2013-2015, and 100 unique adult females in e) calf presence and f) calf absence during the year-set 2016-2018.

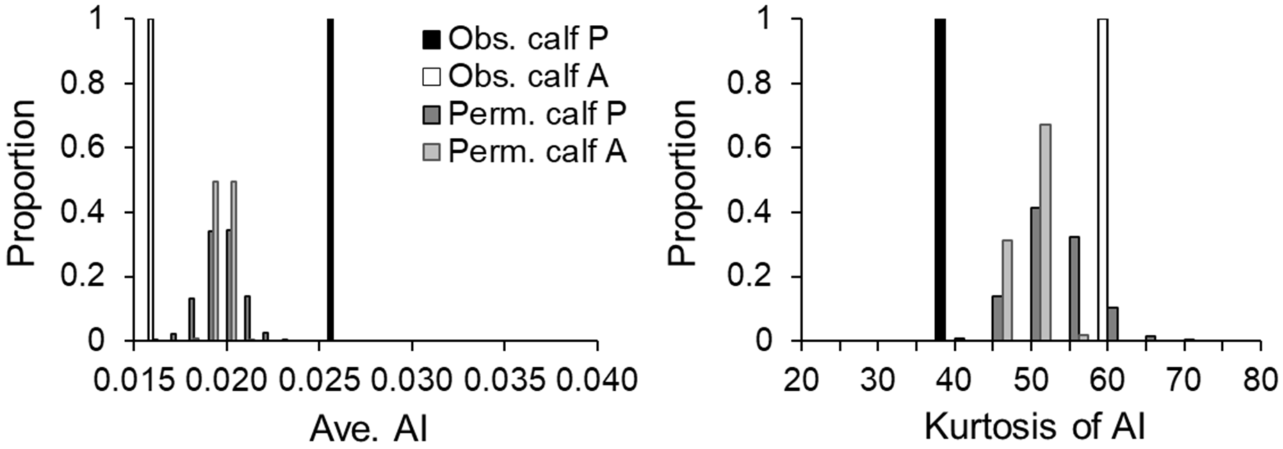
Supplementary Material 6, Table 1. Average (SD) AI, kurtosis of AI, and network statistics in the presence and absence of calves, and averages of these statistics from sampled randomization tests with 10,000 randomizations. The analyses were carried out using sightings of 92, 80, and 100 unique adult females sighted at least five times each in calf presence and calf absence during 2009-2012, 2013-2015, and 2016-2018, respectively. Significant *P* values are shown in bold. The permuted SD values are average SD values (averaged across 10,000 randomised datasets).

Year	Category	Average AI (SD)	Kurtosis of AI	Average degree (SD)	Average clustering coefficient (SD)	Average path length (SD)
2009-2012	Calf presence observed	0.026 (0.1013)	36.64	11.2 (7.66)	0.90 (0.092)	0.09 (0.123)
	Calf absence observed	0.016 (0.0693)	57.22	10.4 (7.93)	0.89 (0.111)	1.31 (0.551)
	Calf presence permuted	0.019 (0.0807)	49.63	9.8 (7.10)	0.88 (0.123)	1.32 (0.515)
	Calf absence permuted	0.019 (0.0773)	45.93	12.1 (8.77)	0.93 (0.086)	1.15 (0.372)
	P value	**<0.001**	**<0.001**	**<0.001**	**0.005**	**<0.001**
2013-2015	Calf presence observed	0.036 (0.1248)	23.19	11.6 (8.76)	0.96 (0.072)	1.11 (0.319)
	Calf absence observed	0.020 (0.0810)	53.34	10.0 (7.40)	0.91 (0.100)	1.20 (0.400)
	Calf presence permuted	0.027 (0.0976)	35.02	10.7 (7.93)	0.93 (0.084)	1.16 (0.367)
	Calf absence permuted	0.027 (0.0950)	33.93	11.8 (8.87)	0.96 (0.061)	1.09 (0.290)
	P value	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
2016-2018	Calf presence observed	0.030 (0.1106)	33.73	15.0 (10.22)	0.93 (0.092)	1.41 (0.713)
	Calf absence observed	0.015 (0.0740)	71.37	10.5 (7.53)	0.85 (0.143)	1.84 (0.799)
	Calf presence permuted	0.023 (0.0881)	43.62	13.1 (9.08)	0.89 (0.127)	2.30 (1.309)
	Calf absence permuted	0.023 (0.0869)	43.13	14.6 (10.02)	0.91 (0.111)	2.36 (1.403)
	P value	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.272

Supplementary Material 6, Table 2. Average and SD of AI and average network statistics based on sightings of 64 unique adult females (excluding Victoria's clan) that were observed at least five times each in calf presence and calf absence during the year-set 2009-2012, and averages of these statistics based on the sampled randomization test with 10,000 randomizations. Significant *P* values are shown in bold. Please note that calf presence and calf absence permuted SD values are average SD values (averaged across 10,000 randomised datasets).

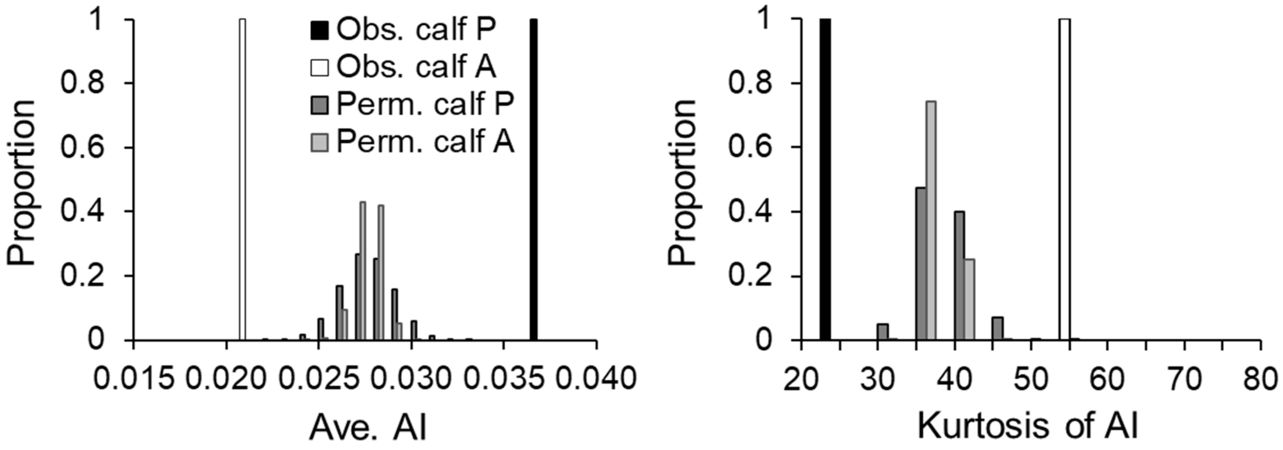
Category	Average AI (SD)	Kurtosis of AI	Average degree (SD)	Average clustering coefficient (SD)	Average path length (SD)
Calf presence observed	0.035 (0.1282)	25.00	6.8 (3.61)	0.93 (0.098)	1.22 (0.448)
Calf absence observed	0.018 (0.0820)	46.13	5.6 (2.85)	0.91 (0.127)	1.44 (0.680)
Calf presence permuted	0.024 (0.0982)	38.431	5.7 (3.07)	0.92 (0.124)	1.33 (0.559)
Calf absence permuted	0.024 (0.0940)	34.84	6.7 (3.58)	0.93 (0.101)	1.22 (0.438)
P value	**<0.001**	**<0.001**	**<0.001**	**0.118**	**<0.001**

The SD of degree was not significantly different between calf presence and absence in 2009-2012, but it was significantly different in the rest of the two year-sets. During 2009-2012, two central adult females (Victoria and Imperia) died in the largest focal clan (Victoria). As a result of this, associations amongst adult females of this clan were more fragmented than when those two females were alive (field observation). Many calves were born after the death of these females; thus, many female sightings of this clan in calf presence were recorded after the death of these females. So, we speculated that when females of other clans, on an average, had higher degree in calf presence than absence, the degree of adult females of Victoria's clan decreased because of clan being more fragmented now. To check this, we reran sampled randomisation tests for the year-set 2009-2012 without sightings from Victoria's clan. We found that SD of degree was significantly higher in calf presence than in absence (Table above) as seen in the rest of the year-sets, confirming the speculation that fragmentation of a clan due to the death of central females caused the lack of significant difference in SD of degree.



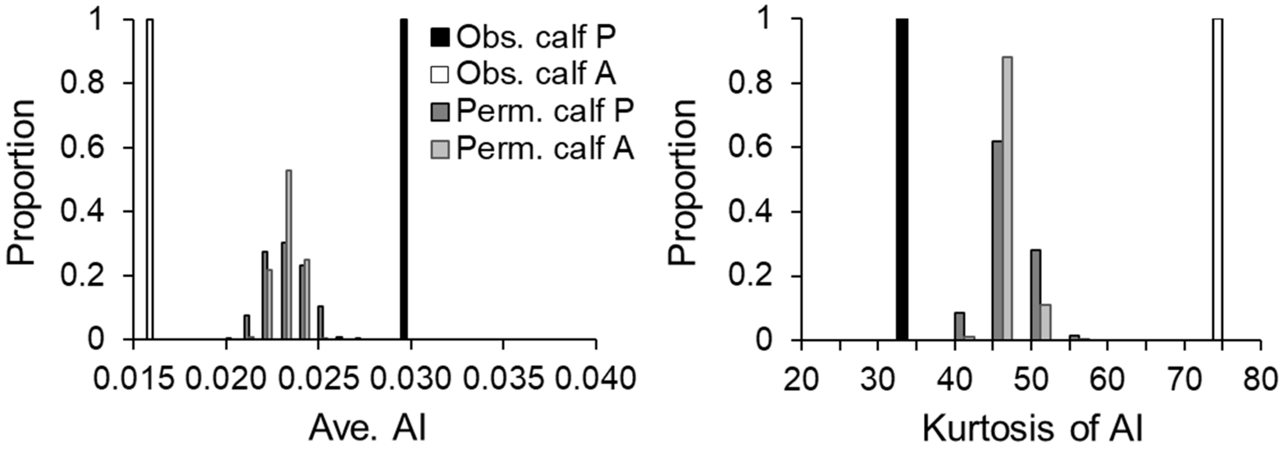
2009-2012: Average AI

2009-2012: Kurtosis of AI



2013-2015: Average AI

2013-2015: Kurtosis of AI

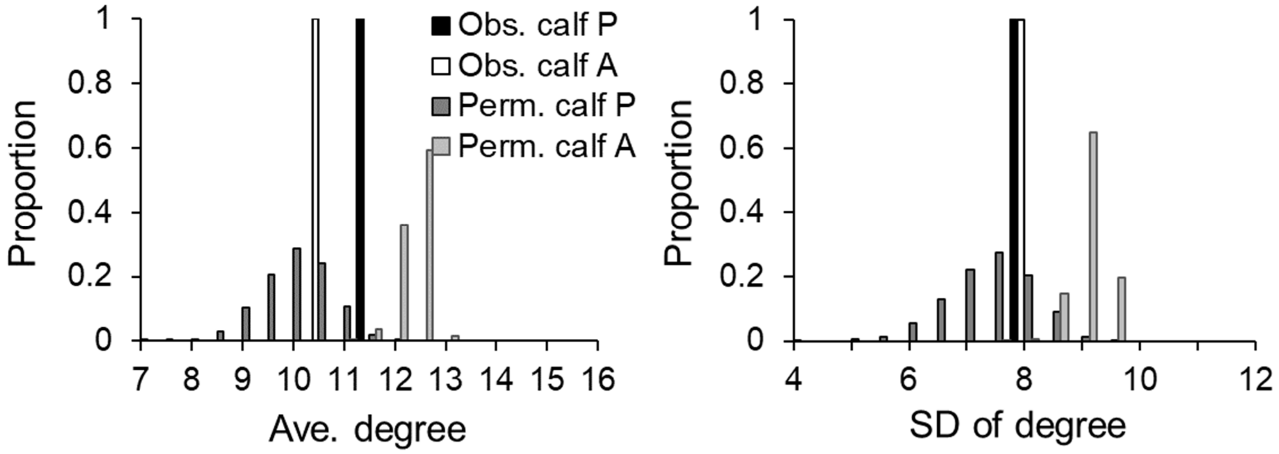


2016-2018: Average AI

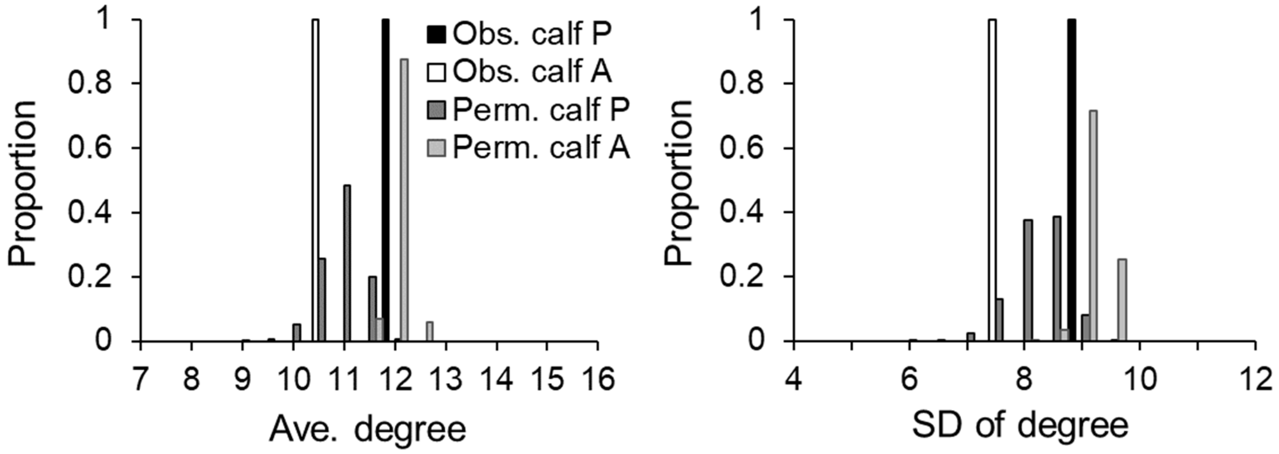
2016-2018: Kurtosis of AI

Supplementary Material 6, Figure 2. Distributions of average AI and kurtosis of AI of permuted ‘calf-present’ and ‘calf-absent’ datasets, and the observed average AI and observed kurtosis of AI in the presence and absence of calves for the three year-sets.

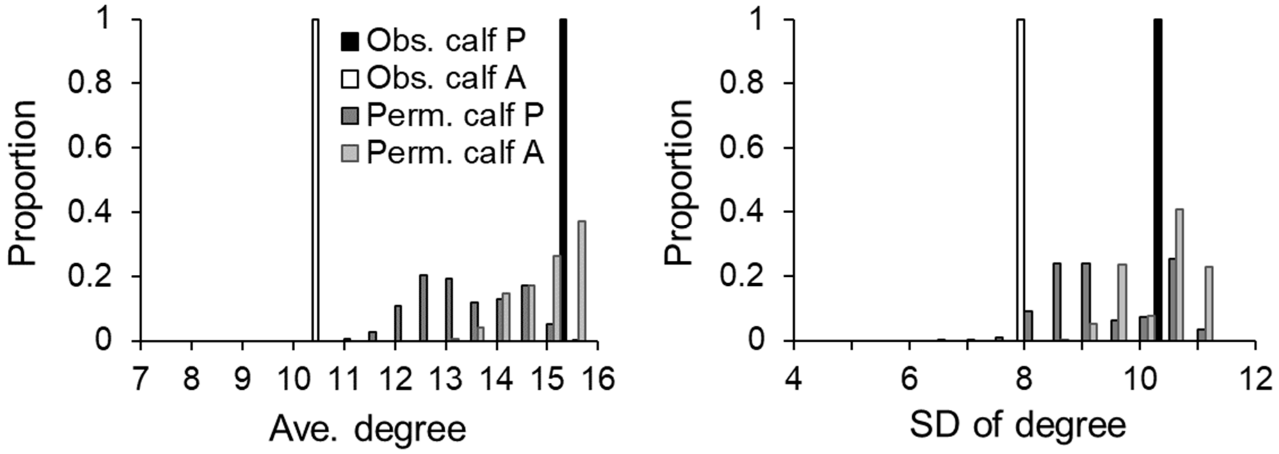
2009-2012: Average degree 2009-2012: SD of degree



2013-2015: Average degree 2013-2015: SD of degree



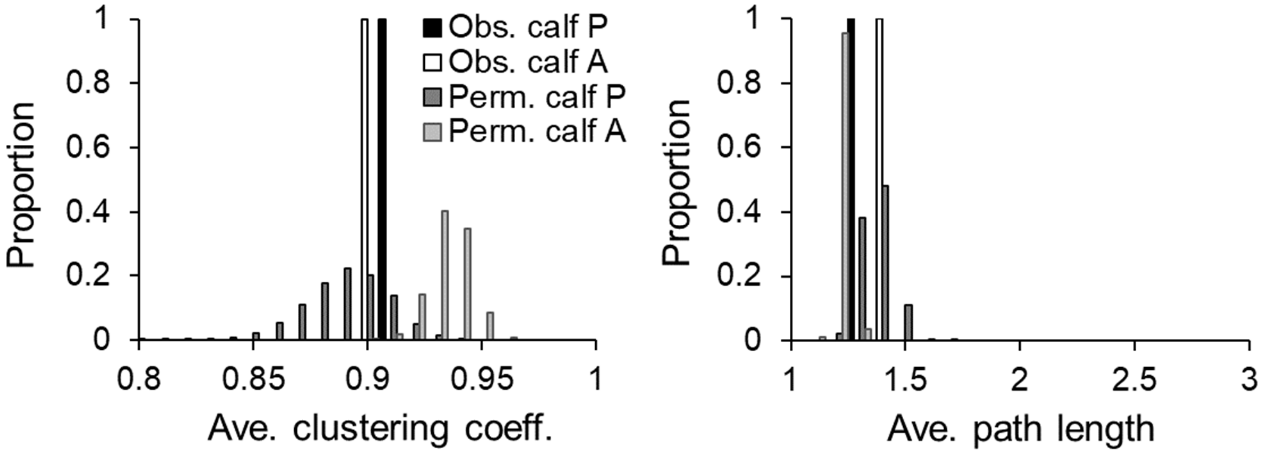
2016-2018: Average degree 2016-2018: SD of degree



Supplementary Material 6, Figure 3. Distributions of average degree and SD of degree of permuted ‘calf-present’ and ‘calf-absent’ datasets, and the observed values in the presence and absence of calves for the three year-sets.

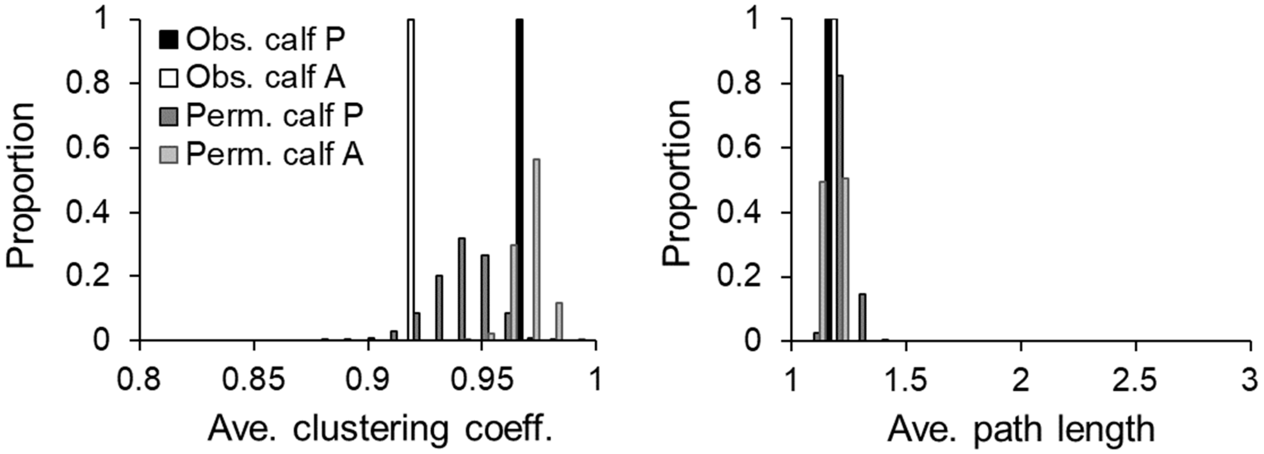
2009-2012: Average clustering coefficient

2009-2012: Average path length



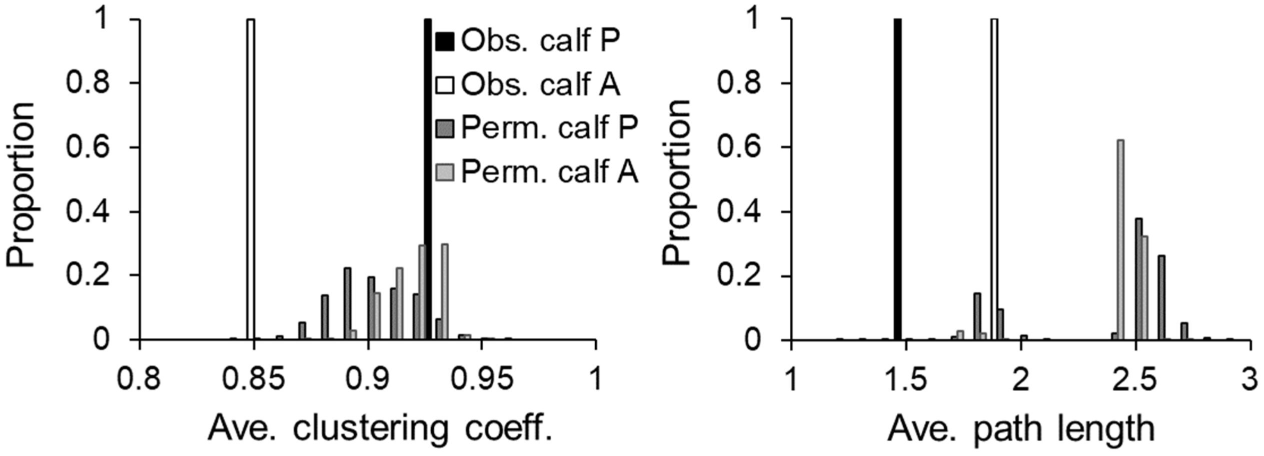
2013-2015: Average clustering coefficient

2013-2015: Average path length



2016-2018: Average clustering coefficient

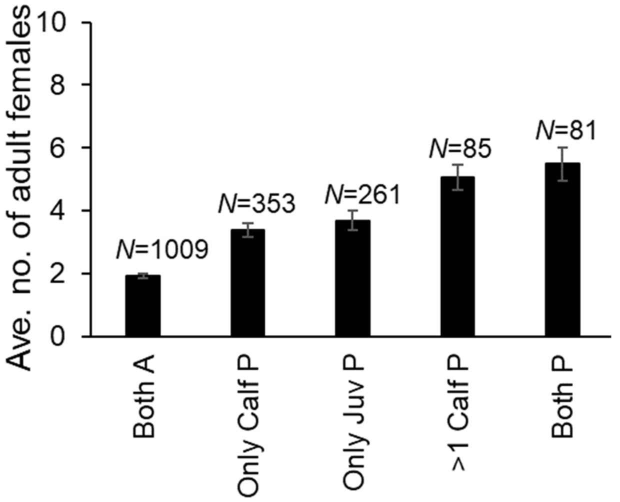
2016-2018: Average path length



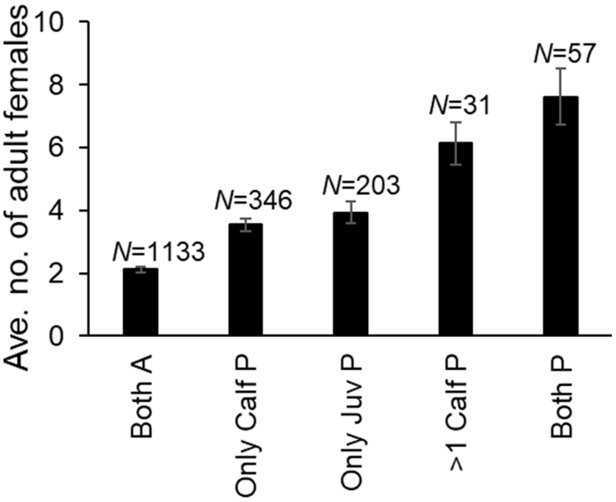
Supplementary Material 6, Figure 4. Distributions of average clustering coefficient and average path length permuted ‘calf-present’ and ‘calf-absent’ datasets, and the observed values in the presence and absence of calves for the three year-sets.

Supplementary Material 7. Average number of adult females in the presence and absence of combinations of calves and young juveniles.

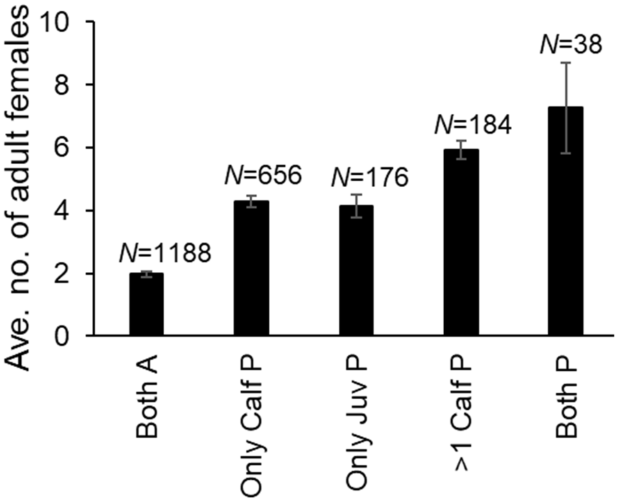
2009-2012



2013-2015



2016-2018



Supplementary Material 7, Figure 1. Average numbers of adult females in calf and young juvenile (1-<2 years old) absence (both A), only calf presence (Only Calf P), only young juvenile presence (Only Juv P), more than one calf presence and young juvenile absence (>1 Calf P), and both calf and young juvenile presence (both P) within each year-set. Since most clans did not have all the combinations of calf and young juvenile presence and absence (10 sightings or more under each category: only 3 clans in 2009-2012, and 1 clan each in 2013-2015 and 2016-2018), this was not analysed in an ANOVA framework and only the trends are shown here. Data from all the clans are combined here. *N* above each bar indicates number of independent female group sightings. Error bars are 95% CI.

CHAPTER 3

Development of Motor Control and Behaviour in Asian Elephants in the Kabini Elephant Population, Southern India

Title: Development of motor control and behaviour in Asian elephants in the Kabini elephant population, southern India

Authors: T. Revathe, S. Anvitha, and T.N.C. Vidya*

Affiliation: Evolutionary and Organismal Biology Unit, Jawaharlal Nehru Centre for Advanced Scientific Research (JNCASR), Bengaluru 560064, India.

* Corresponding author.
Email: T.N.C. Vidya: tncvidya@jncasr.ac.in; ORCID iD for T.N.C. Vidya: 0000-0002-7143-9008.

Based on published paper:

T. Revathe, S. Anvitha, T.N.C. Vidya (2020). Development of motor control and behaviour in Asian elephants in the Kabini elephant population, southern India. *International Journal of Developmental Biology* 64: 367-382.

Author contributions:

T. Revathe and T.N.C. Vidya conceived this study. TR collected field data and carried out behavioural scoring and data analysis. SA helped with scoring and analysis. TR primarily and TNCV wrote the manuscript, and all the authors read and finalised it.

Abstract

Although neonates of precocial mammals are capable of locomotory, sensory, nutritional, and thermoregulatory independence to some extent soon after birth, they attain their adult body mass more slowly than altricial mammals, allowing for an extended period of learning or perfecting skills to an adult-like degree. Asian elephants are precocial but are nutritionally dependent on the mother for at least two years and are long-lived and social. We wanted to examine the ontogeny of trunk motor control and various behaviours in Asian elephant calves and see whether the former develops faster than the latter since limb motor control is achieved soon after birth. We collected field data on trunk use, lateralisation, and behaviours from individually identified, free-ranging elephants in southern India and examined how they were affected by age and other factors. Unlike limb motor control, we found trunk motor skills and behaviours to develop gradually with age. Trunk lateralisation occurred very early on, was not highly dependent on trunk motor skills, and is probably not a developmental marker in Asian elephants. Adult-like behaviours that required low trunk usage emerged within 3 months, while some feeding behaviours, emerged later. Calves spent less time resting and more time feeding as they grew and their activity budgets resembled those of adults only after a year; hence, mother-offspring behavioural synchrony was low for young calves and increased with age. Behavioural development and trunk motor control in Asian elephants are both gradual processes, taking about a year to mature.

Keywords

Asian elephant, ontogeny of behaviour, ethogram, calf behaviour, development of motor skills, precocial, trunk laterality, postnatal development, synchrony, Kabini Elephant Project.

Introduction

Young ones of all mammalian species go through a period of, often co-occurring, anatomical, physiological, and behavioural development. The study of the ontogeny of behaviour examines when and how rudimentary forms of various behaviours of young ones become elaborated and perfected, although since the nutritional and social requirements of immatures may be different from those of mature individuals, not all behaviours shown by young ones are necessarily primitive; specific behaviours may be lost or gained depending on changes in ecology of the animals as they grow (Scott *et al.* 1974, Barrett and Bateson 1978, Bateson 1981, Hinde and Bateson 1984, Bateson 1987, Holekamp and Smale 1998, Bateson 2017). Two modal developmental types are found amongst mammals: precociality and altriciality. Neonates of precocial mammals are capable of locomotion soon after birth, are either entirely nutritionally independent or may forage independently of the parents while continuing to be nursed, and show sensory and thermoregulatory independence (Derrickson 1992). Neonates of altricial mammals are born helpless, often with eyes closed and devoid of hair, lacking locomotor abilities, and hence require extensive parental investment for food provisioning and thermoregulation (Derrickson 1992, Scheiber *et al.* 2017). Although precocial mammals are heavier at birth, born after a relatively longer gestation period than altricial mammals, they attain their adult body mass more slowly than the latter (Derrickson 1992). Hence, such neonates may have a prolonged period of dependency on the mother (Kleiman 1972, Poirier and Smith 1974, Derrickson 1992) resulting in increased time for socialisation between the mother-offspring pair (Washburn and Hamburg 1965, Kleiman 1972, Derrickson 1988) and increased opportunity for social learning and exploration while being defended by the mother and others in the group (Washburn and Hamburg 1965, Poirier and Smith 1974, Joffe 1997). Therefore, such precocial mammals, while possibly becoming adept in motor tasks fairly quickly after birth, may show more gradual and longer-term changes in behaviour (Kruuk 1972, Pratt and Anderson 1979, Nair 1989, Holekamp and Smale 1998, Mendonca *et al.* 2016).

The order Proboscidea (within the clade Afrotheria) has been classified as precocial by Derrickson (1992), who used four axes of developmental categories – locomotory, nutritional, sensory, and thermoregulation – to carry out such classification. Newborn elephant calves can stand up, with some assistance, within a few minutes or hours after birth (Sharma and Krishnamurthy 1984, Nair 1989, Sukumar 2003), although proper limb coordination may develop only by around one month of age (Nair 1989, Sukumar 2003). Calves also show sensory and thermoregulatory independence. However, a calf is completely dependent on its mother for nutrition during the first three months of life (Nair 1989, Sukumar 2003, Webber 2017). The only published papers on Asian elephant calf development in India were based on work carried out on semi-captive elephants held by the Forest Department (Gadgil and Nair 1984, Sharma and Krishnamurthy 1984, Nair 1989). Nair (1989) found that calves were gradually trying to pluck grass from the second month onwards and were feeding on short blades of grass from the end of the fourth month, although their primary source of nutrition remained their mother's milk. A recent study on the early social behaviour of a captive Asian elephant calf at the Rosamond Gifford Zoo, USA found that the calf showed sucking behaviour soon after birth and adult-like feeding behaviour had not developed till at least four months of age, although the calf was observed to manipulate objects like leaves and taste them (Petraccione *et al.* 2017). African elephant calves become nutritionally self-sufficient only at 2 years of age, consuming mother's milk to a small extent even beyond 3 years of age (Lee and Moss 1986, Lee and Moss 2011). Similarly, in a study conducted on semi-captive elephants of the Myanmar Timber Enterprise, it was found that calves were usually weaned between the ages of 4 and 5 years or sooner depending on the inter-birth interval (Mar *et al.* 2012). Since elephants are long-lived (see Sukumar 2003) and possibly learn various behaviours, motor tasks such as those involving walking probably develop faster than various behaviours. However, elephants also perform motor tasks with their trunk in addition to their limbs, and as the trunk is not required for immediate movement (nor is it used immediately after it is born – Nair 1989), it is possible that motor tasks using the trunk also develop gradually over a period of time. We, therefore, wanted to examine the development of trunk motor control and various behaviours in wild Asian elephant calves.

The trunk is very important for feeding, drinking, smelling, dusting, and use in social interactions. Behavioural lateralisation is thought to improve an animal's performance in foraging, predation, cognitive tasks and fear responses (Rogers 2002), and strong trunk lateralisation has previously been observed in individual adult Asian elephants (Martin and Niemitz 2003, Keerthipriya *et al.* 2015, Giljov *et al.* 2018). Trunk lateralisation was previously observed in juveniles also (Keerthipriya *et al.* 2015, Giljov *et al.* 2018) and even one two-month-old calf had shown strong trunk side preference (Keerthipriya *et al.* 2015). However, because of the small number of calves (less than one year old) sampled previously, the ontogeny of trunk lateralisation was not known. Owing to the novelty of feeding on vegetation, the possible practice required for using the trunk, and the possible lack of trunk strength at a young age, side preference in trunk movement could be expected to gradually develop from birth until the time calves feed primarily on grass. In the study of a single captive Asian elephant calf, the calf was able to perform an increasing number of complex and physically well-developed behaviours with age, suggesting that the expression of such skillful behaviours might be linked to physical maturity (Petraccione *et al.* 2017). However, it was also possible that, due to their precocial nature, maturation of trunk motor skills might occur early on and be manifest as early lateralisation of the trunk (as seen in the single two-month-old calf – Keerthipriya *et al.* 2015). Therefore, we wanted to examine the use of the trunk and development of side biases in trunk movement (see Figure 1) with age in young elephants.

As mentioned above, since neonates of precocial mammals that have a long period of dependency on the mother may have a longer time for the development of various behaviours, we also wanted to examine the development of different kinds of behaviours (see Figure 2) in this precocial but long-lived species with complex behaviours, in order to find out when adult-like behaviours emerged, whether there were differences in this timing based on behavioural categories (see Supplementary Material 1), and to examine the extent of synchrony in behaviours between calves of different ages and their mothers. Synchronisation of activities can be costly when there are individuals with varying demands in a group, and this may lead to segregation between group members (Conradt 1998). However, segregation is not an option in the case of young ones that are dependent on the mother, leading to increased pressure for faster development of similar behaviours in the young as in adults and, hence, synchrony of behaviours.

We collected data on wild, individually identified elephants from Nagarahole and Bandipur National Parks and Tiger Reserves, referred to here as the Kabini elephant population, from December 2015-2017, in order to examine the development of trunk use and behaviours.

Methods

Field data collection

The data used in this study were collected from December 2015 to December 2017. Field work was conducted in Nagarahole National Park and Tiger Reserve (11.85304°-12.26089°

N, 76.00075°-76.27996° E) and Bandipur National Park and Tiger Reserve (11.59234°-11.94884° N, 76.20850°- 76.86904° E) in southern India. Nagarahole and Bandipur National Parks primarily comprise dry and moist deciduous forests and are separated by the Kabini reservoir. During the dry season (mid-December to mid-June), as water recedes, abundant fresh grass becomes available and it results in a large congregation of herbivores around the backwaters (Vidya *et al.* 2014). Most of the behavioural data was collected from around the backwaters because of good visibility. The Kabini Elephant Project has recorded hundreds of individually identified elephants and this population (called the Kabini elephant population henceforth) has been studied since 2009 (Vidya *et al.* 2014). Field work was typically carried out from ~6 AM to ~7 PM during the dry season and from ~6 AM to ~6 PM during the wet season. Elephant groups were observed from a distance of over 40 m to avoid any disturbance to their natural activity. When elephants were sighted, they were age-sex classified and individually identified. Animals were aged based on shoulder height, body length and bulk. They were categorised into broad age categories as calf (<1 year), juvenile (1-<5 years), subadult (5-<10 years in the case of females and 5-<15 years in the case of males), or adult (>= 10 or 15 years, for females and males, respectively). Birth records for identified females were maintained from 2009 and the date and place of birth (if known) and the sex of calves were recorded. Thus, by 2015, more accurate ages were known for calves and juveniles (based on when the mother was sighted last without a calf and when she first appeared with the calf), as they were born after the beginning of the Kabini Elephant Project, while adults were placed into 10-year age classes. Asian elephants are sexually dimorphic and were sexed based on genitalia. Photos, videos, and/or sketches of the elephant's ears, tail, tail hair, back shape, wounds and warts (if any), and tusks (in the case of males) or tushes were used to identify individuals (see Vidya *et al.* 2014).

Female elephants in the population are socially organised into clans, which are the most inclusive level of social structure (Nandini *et al.* 2018). However, entire clans are rarely seen together. Instead, subsets of females from the clan form small groups, which may change in composition through fission-fusion dynamics (Nandini *et al.* 2017). We identified a female group as a set of females showing coordinated movement and behaviour, and usually within 50-100 m of one another. The location of the group was recorded using a GPS and behavioural observations were carried out when the group was undisturbed and in clear sight. We carried out scan sampling (Altmann 1974) at half-hour intervals and wrote down the behaviour shown by each individual in the group during each "instantaneous" scan. In the intervals between the scans, we carried out focal animal sampling (Altmann 1974) for 20 minutes, during which we recorded the activities of individually identified calves or juveniles in the group using a SONY handycam (HDR-PJ540E).

Behaviour scoring and data analyses

We used the focal videos recorded in the field to score for trunk use and various behaviours.

Trunk use and side preference

We scored for trunk use of individually identified calves and juveniles during 5 minutes (± 3 seconds) of focal videos on a given day. While it was theoretically possible to use the entire focal video to score for various behaviours, only parts of the video when the trunk tip was clearly visible could be used for scoring trunk use (as the orientation of the trunk tip was sometimes not visible even in the short grass). During this period, we noted 1) the numbers of times the focal individual used the trunk in clockwise and anticlockwise directions to pluck, gather, or grab vegetation or other objects successfully, 2) the numbers of times the focal individual attempted to move the trunk in clockwise and anticlockwise direction but did not successfully pluck vegetation or other objects, and 3) the number of times the focal individual touched the ground straight, without curling the tip of the trunk (see Figure 1). Additionally, 4) the number of times vegetation or other objects were placed on the right or left side of the mouth (Figure 1) and 5) and the number of times the individual touched the right or left side of its body were noted. Whenever the trunk movement, placement of grass or other objects and body touch was not clearly visible it was considered to be an unresolved movement/placement/body touch and not considered for analysis.

Figure 1. Calves/juveniles showing different trunk movements: a) and b): trunk movements used to pluck and gather vegetation successfully in a) a clockwise direction and b) an anticlockwise direction; c) and d): unsuccessful attempted trunk movements to pluck/gather vegetation in c) a clockwise direction and d) an anticlockwise direction; e) calf using its trunk to touch the ground straight, without curling the tip; f) and g): trunk used to place vegetation inside the mouth f) through the right side and g) through the left side; h) and i): trunk used to touch the body on the h) right side and i) left side.

The direction of side preference was measured using the lateral bias index (Bard *et al.* 1990), calculated as $(R-L)/(R+L)$, where R was the number of trunk movements towards the right (or clockwise) and L was the number of trunk movement towards the left (or anti-clockwise). Positive values of the index, therefore, indicated a right side bias and negative values, a left side bias. Binomial tests were used to check for statistically significant side bias (clockwise/anticlockwise) in trunk movement while plucking and gathering vegetation or other objects successfully and unsuccessfully, for preference in the placement of vegetation or other objects on the right or left side of the mouth, and for preference in the side of the body touched. The absolute value of the lateral bias index indicates the strength of lateralisation, with 0 indicating no side bias and 1 indicating strong side bias.

Since our dataset included repeated observations on the same individuals within and across age classes, we carried out repeated measures ANOVAs on the variable examined for lateralisation (such as logit proportion of clockwise successful or unsuccessful trunk movement, logit proportion of right side trunk placement in the mouth, etc.) by the same individuals, across days but within the same age class. We used four age classes for this purpose: <3 months old, 3-6 months, 6-12 months, and >12 months. We also used sex and age class as categorical factors in the ANOVA. If there was little variability across days sampled within the same age class, one sample from each individual during that age class could be used to construct the distributions of lateral bias index or strength, without biasing this due to multiple sampling of some individuals. We found consistency in direction overall within individuals sampled on different days within an age class even at young ages and, therefore, created subsets of the different datasets (successful trunk movement, unsuccessful trunk movement, straight trunk touch, trunk placement in the mouth, and body touch) with each individual being represented only once in a particular age class. If an individual was sampled more than once in the same age class, only the first sampling instance was included.

We used mixed-effects models to statistically examine the effect of age class on the strengths of different types of trunk lateralisation (successful and unsuccessful trunk use, mouth placement, and body touch) and proportions of unsuccessful trunk use (calculated by dividing the number of clockwise and anticlockwise unsuccessful trunk movements by the total number of clockwise and anticlockwise successful and unsuccessful trunk movements) and straight trunk touches (calculated by dividing the number of straight touches by the total number of trunk movements, including straight touches and clockwise and anticlockwise successful and unsuccessful trunk movements). In these models, which were run using Statistica 7 (StatSoft, Inc. 2004), age class (<3 months, 3-6 months, 6-12 months and greater than 12 months) was the fixed factor and individual identity of the calf/juvenile was a random factor. We logit transformed the dependent variables because they were highly non-normal, but the results remained similar when the analyses were performed on the untransformed data also. We expected trunk side preferences to increase with age in the context of feeding but not in the context of body touches.

Behaviour data: activity budget, behaviour duration, and age

While the various behaviours seen during the scans (at 30-minute intervals) had been written down in the field, video footage of focal animal sampling was scored for various behaviours (see Supplementary Material 1). Focal animal scoring was carried out on a second-by-second basis to obtain fine-scale details about the behaviours displayed. Various behaviours were identified and described based on these focal videos (see Supplementary Material 1). These behaviours were classified based on their nature as feeding, resting, grooming, or social (including exploratory behaviours and play) behavioural classes.

Figure 2. Calves and juveniles of different age classes showing various behaviours. Feeding-related behaviours: a) taking grass from a conspecific, b) trying to locating the nipple in the wrong direction, c) sucking from a non-mother conspecific, d) chewing on grass, and, e) (calf on the left) drinking water using the mouth directly and (juvenile on the right) using the trunk to drink water; grooming-related behaviours: f) spraying dust/grass onto itself, g) rolling in grass; resting-related behaviour: h) trying to sit down; social interaction, play, and exploration related behaviours: i) climbing on a conspecific, j) placing trunk tip in the mouth of a conspecific, k) smelling dung, l) checking a conspecific (see Supplementary Material 1 for more behaviour descriptions and photos).

The behaviours of all identified individuals noted during scan sampling were used to construct activity budgets for different age classes of individuals. Since scan sampling sampled all individuals in the group, we could compare calves with adults using this data. We then used the focal animal sampling data on calves to examine the proportion of the focal duration that calves of different age-classes spent displaying behaviours belonging to the different behavioural classes. This was done by running a General Linear Model (GLM) on the logit proportion of time spent in various behaviours, with age-class and behavioural class of calf action as fixed factors and calf identity as a random factor. The three age classes used were <3 months, 3-6 months, and 6-12 months. We further wanted to check if there was any difference in the proportion of time spent in different behavioural classes within the first three months after birth. Hence, we also divided calves into four age classes: <1 month, 1-2 months, 2-3 months, and >3 months and repeated the GLM. Since focal animal sampling of calves was carried out on a second-by-second basis, we also examined the duration of various behaviours shown and used a GLM to find out whether age-class and behavioural class (fixed factors) or calf identity (random factor) affected behaviour duration.

Behaviour data: behavioural stages and age

We also classified behaviours based on the skill of execution and broad timing of behaviour as calf-specific, adult-like, preparatory adult behaviour (if it was an incipient stage of an adult-like behaviour but not executed with much skill), or preparatory calf behaviour (if it was an incipient stage of a calf-specific behaviour but not executed with much skill) (see Supplementary Material 1). We wanted to examine when adult-like behavioural expression develops. We, therefore, calculated the proportions of time spent by calves in showing preparatory, calf-specific, preparatory calf, and adult-like behaviours under the four behavioural classes mentioned above and ran GLMs using age class and behavioural class as fixed factors and calf identity as a random factor. We used the age classes <3 months, 3-6 months, and 6-12 months, but also additionally used <1 month, 1-2 months, 2-3 months, and >3 months for this analysis.

Behavioural synchrony between mother and calf

We calculated the behavioural-class synchrony between calves/juveniles and their mothers, with synchrony being 1 if the calf/juvenile and its mother showed behaviours belonging to the same behavioural class during a particular scan, and synchrony being 0 if they showed behaviours belonging to different behavioural classes during that scan. We ran generalized linear mixed-effects models with synchrony as a binomial dependent variable, age of the calf/juvenile and behavioural class as fixed factors, and identities of the calf/juvenile and mother as random factors. The analysis was carried out using the *fitglme* function in MATLAB R2011a, with a logit link function. ΔAIC values were calculated as the difference between the AIC of the best model (i.e. the model with the smallest AIC value) and the AIC of each of the other models, in order to find out whether there were multiple 'best' models (if the ΔAIC values were less than 2).

Results

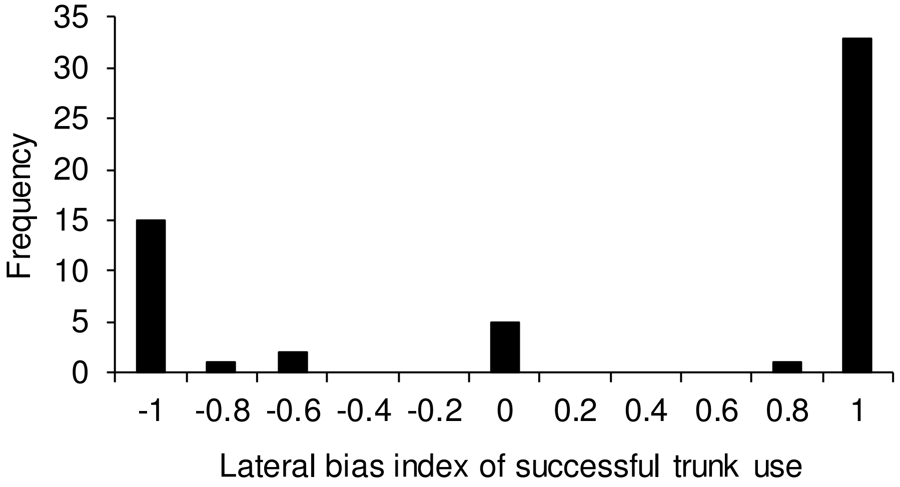
Trunk motor control and lateralisation

We obtained data on trunk use from focal animal sampling, by video-recording calves (<1 year old) or juveniles (1-<5 years old) and scoring the videos (see Methods). A total of 30 calves and juveniles, consisting of 16 females and 14 males, from 9 different clans, and ranging in age from <1-29 months, were sampled for examining trunk lateralisation of different kinds during 101 focal sessions for a total duration of 505.45 min (see Supplementary Material 2). Data were collected on 1) the numbers of times the focal individual used the trunk in clockwise and anticlockwise directions to pluck, gather, or grab vegetation or other objects successfully, 2) the numbers of times the focal individual attempted to move the trunk in clockwise and anticlockwise direction but did not successfully pluck vegetation or other objects, 3) the number of times the focal individual touched the ground straight, without curling the tip of the trunk, 4) the number of times vegetation or other objects were placed on the right or left side of the mouth, and 5) and the number of times the individual touched the right or left side of its body (see Figure 1), and the direction of side preference was measured using the lateral bias index (Bard *et al.* 1990; see Methods). The strength of lateralisation was obtained as the absolute value of the lateral bias index (see Methods). We expected trunk side preferences to increase with age when the trunk was used in the context of feeding but not in the context of body touches.

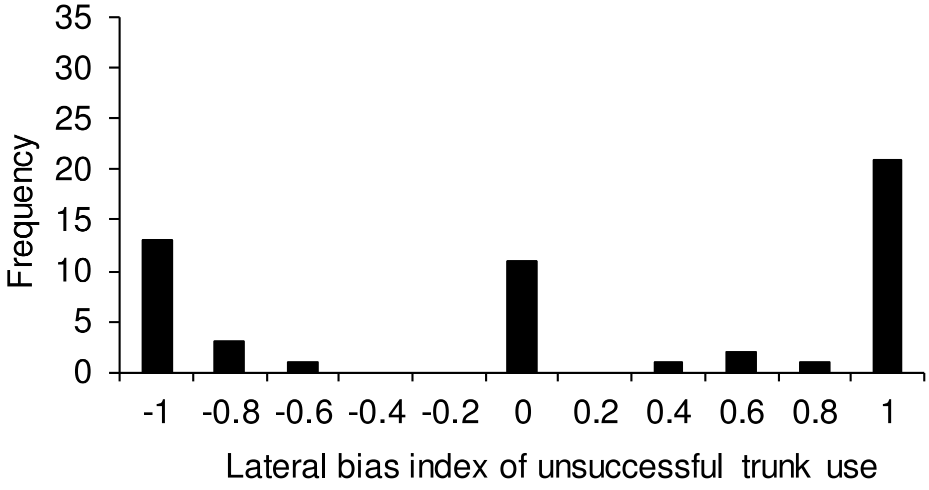
Since these datasets included repeated observations on the same individuals within age classes, we carried out repeated measures ANOVAs on the logit proportion of clockwise (successful or unsuccessful) trunk movement by the same individuals, across days but within the same age class (using sex and age class as categorical factors), and found that these did not change across the repeat samples (see Supplementary Material 3). The same was true when repeated measures ANOVAs were carried out on the logit proportions of right side trunk placement in mouth, and right side body touch, and was only of borderline significance when straight trunk movement was examined (see Supplementary Material 3). Thus, there was consistency within individuals sampled within an age class. We, therefore, carried out the subsequent analyses using subsets of the different datasets (successful trunk movement, unsuccessful trunk movement, straight trunk touch, trunk placement in the mouth, and body touch), in which each individual was represented only once in a particular age class (<3, 3-6, 6-12, and >12 months; see Methods).

We found overall significant side preference in successful trunk use in 87 of the 94 sessions in which successful trunk use was observed (92.6%; 52 out of 57 (91.2%) sessions with each individual being represented only once in an age class; significance based on binomial tests, $P<0.05$). Significant side preference was lower when there was unsuccessful trunk use, with significant side preference observed in 55 out of 79 such sessions (69.6%; 42 out of 53 (79.2%) sessions with each individual being represented only once in an age class; significance based on binomial tests, $P<0.05$). Significant side preference in mouth placement was seen only in 41 out of 85 sessions (48.2%; 20 out of 52 (38.5%) sessions with each individual being represented only once in an age class) and significant side preference in body touch was seen only in 26 out of 89 sessions (29.2%; 13 out of 55 (23.6%) sessions with each individual being represented only once in an age class). Thus, the lateral bias index of trunk use was different from zero in most of the cases, while the lateral bias index of trunk placement in the mouth and body touch were largely zero (Figure 3). The average (across 53 sessions with each individual being represented only once in an age class) proportion of straight trunk touches with no directionality was 27.8%.

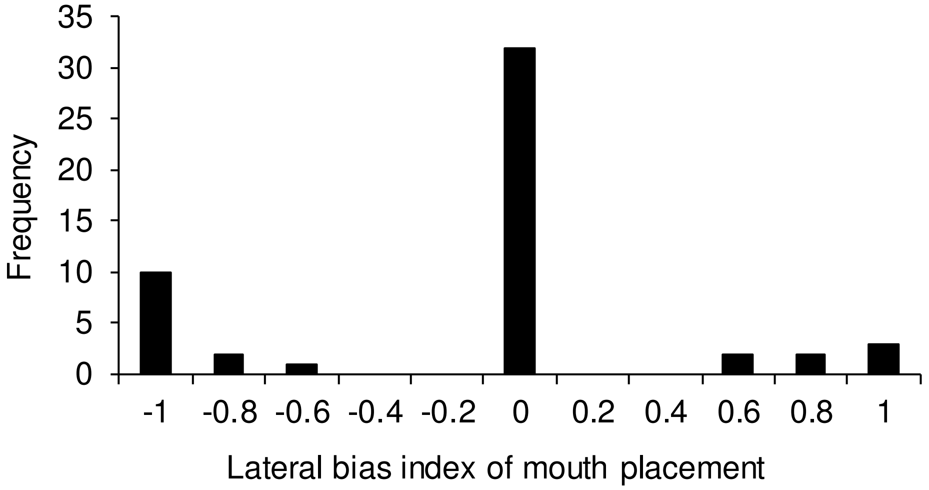
a.


Frequency
35
30
25
20
15
10
5
0
-1
-0.8
-0.6
-0.4
-0.2
0
0.2
0.4
0.6
0.8
1
Lateral bias index of successful trunk use

b.


Frequency
35
30
25
20
15
10
5
0
-1
-0.8
-0.6
-0.4
-0.2
0
0.2
0.4
0.6
0.8
1
Lateral bias index of unsuccessful trunk use

c.


Frequency
35
30
25
20
15
10
5
0
-1
-0.8
-0.6
-0.4
-0.2
0
0.2
0.4
0.6
0.8
1
Lateral bias index of mouth placement

d.

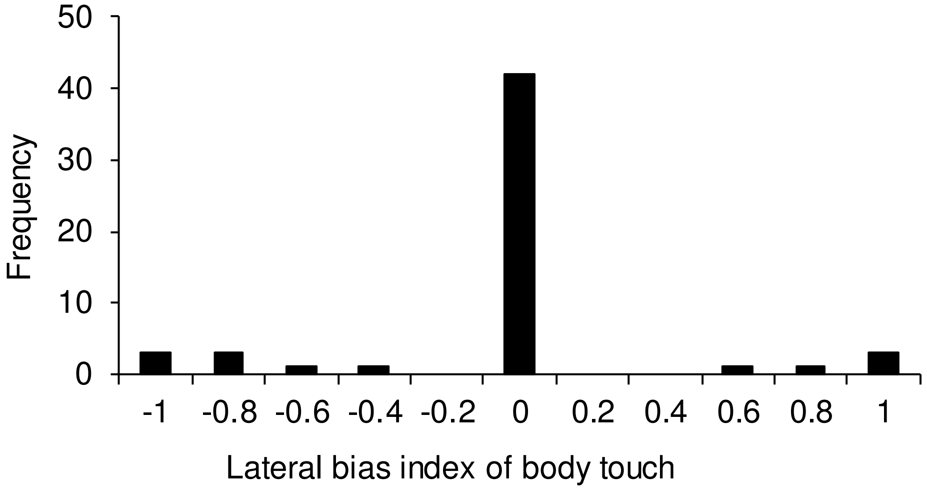


Figure 3. Lateral bias index distributions of a) successful trunk use, b) unsuccessful trunk use, c) mouth placement, and d) body touch. These distributions are based on a combination of different age classes of calves/juveniles but using only one session scored per calf/juvenile in a particular age class.

Visual inspection of the lateral bias index based on successful trunk use across age classes showed the greatest proportion of unlateralised individuals in the <3 months age class (Figure 4). The proportion of unlateralised individuals decreased across age classes until all individuals over 12 months of age were completely lateralised in successful trunk use. A similar pattern was seen in unsuccessful trunk use, but individuals over 12 months of age also showed a lateral bias index of zero in this category (Figure 4). However, this must be read along with the finding that the total proportion of unsuccessful trunk use itself decreased with age (Figure 5). The frequency distribution of the proportion of straight touches shifted towards the left with increasing age class, with older individuals showing a smaller proportion of straight touches (Figure 4, 5).

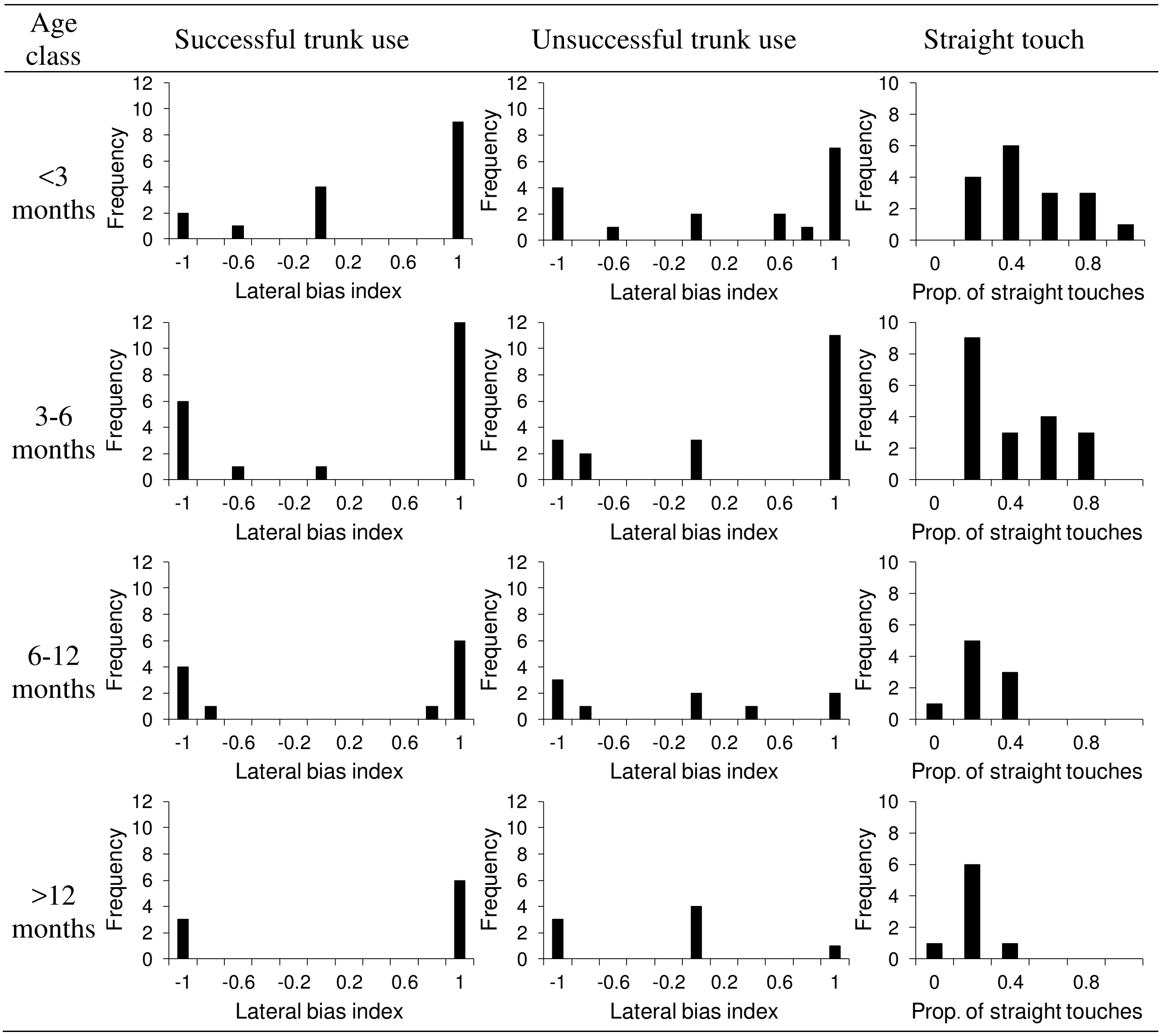


Figure 4. Frequency distributions of lateral bias indices calculated from successful and unsuccessful trunk use and of the proportion of straight touches, for individuals of different age classes. Individuals that did not exhibit significant lateral bias have been shown to have lateral bias index value of zero.

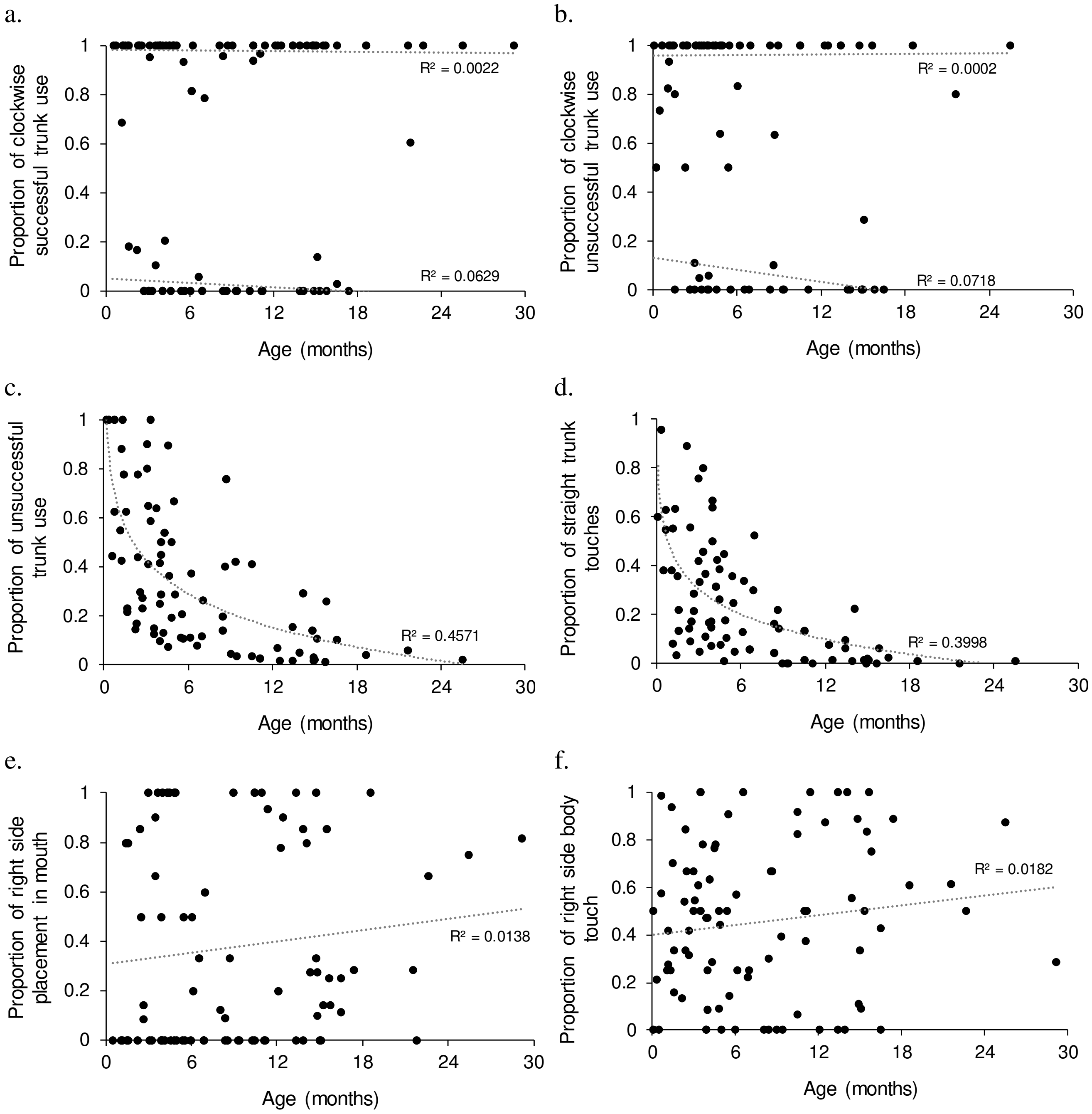


Figure 5. Proportions of a) clockwise successful trunk use, b) clockwise unsuccessful trunk use, c) unsuccessful trunk use (calculated as the ratio of unsuccessful - clockwise and anticlockwise - movements divided by the total number of unsuccessful and successful trunk movements), d) straight trunk touches (calculated as the ratio of the number of straight trunk touches divided by the total number of trunk movements, including straight touches, successful, and unsuccessful movements), e) right side placement of the trunk in the mouth, and f) right side body touch using the trunk, with increasing age. Regression lines (logarithmic regressions in the case of c and d) are shown along with R^2 values. Regression lines are drawn separately for the clockwise and anticlockwise movements in panels a and b.

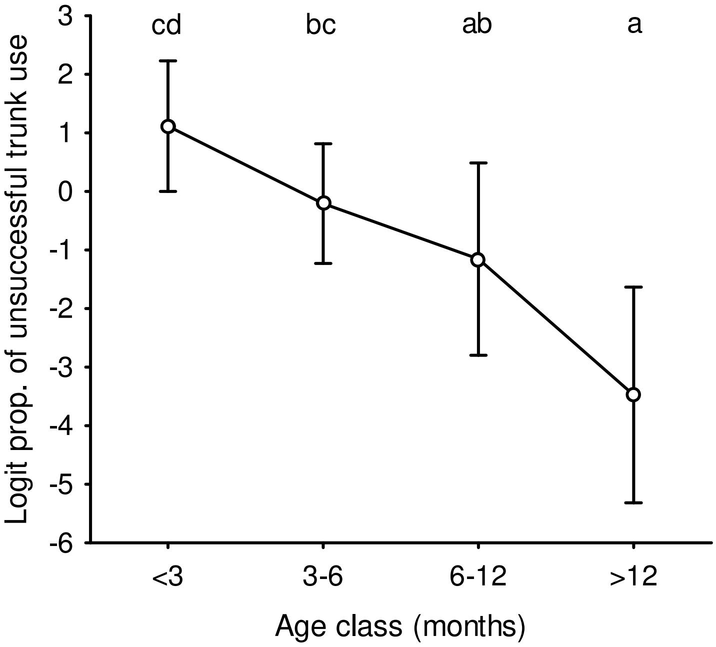
We used mixed-effects models (with age class as the fixed factor and individual identity as random factor) to statistically examine the effect of age class on the strengths of lateralisation (the absolute values of the lateral bias index) and proportion of straight trunk touches. Although we could see a small trend with age class in lateral bias indices of successful and unsuccessful trunk use, there was no effect of age class on the logit strengths of lateralisation in successful or unsuccessful trunk use, in mouth placement, or in body touches (Table 1), probably because many of the calves less than 3 months old already showed significant lateralisation (Figure 4). There was an effect of individual identity on the lateralisation in successful trunk use but not on the other dependent variables.

However, there was a significant effect of age class on the logit proportions of unsuccessful trunk movements (although this had a borderline non-significant adjusted whole model R^2) and straight trunk touches, with decreasing proportions of both with increasing age (see Table 1, Figure 6). *Post hoc* Tukey's HSD tests showed the same patterns of differences across age classes in both variables. The logit proportions of unsuccessful trunk movements and straight trunk touches of <3-month-old and 3-6-month-old calves were significantly higher than those of >12-month-old juveniles (Tukey's HSD tests: logit proportion of unsuccessful trunk movements: <3-month-old and >12-month old calves/juveniles: P<0.001; 3-6-month-old and >12-month old calves/juveniles: P=0.025; logit proportion of straight trunk touches: <3-month-old and >12-month old calves/juveniles: P<0.001; 3-6-month-old and >12-month old calves/juveniles: P=0.002). The logit proportions of unsuccessful trunk movements and straight trunk touches of <3-month-old calves were also significantly higher than those of 6-12-month-old calves (logit proportion of unsuccessful trunk movements: P=0.011; logit proportion of straight trunk touches: P=0.015), but those of <3-month-old and 3-6 month-old calves were not significantly different from each other (logit proportion of unsuccessful trunk movements: P=0.073; logit proportion of straight trunk touches P=0.412). The logit proportions of unsuccessful trunk movements and straight trunk touches of 3-6-month old calves and 6-12-month-old calves, and 6-12-month-old calves and >12-month-old juveniles were also not significantly different from each other (Tukey's HSD tests: logit proportion of unsuccessful trunk movements: 3-6-month old and 6-12-month-old calves: P=0.523; 6-12-month-old and >12-month-old calves/juveniles: P=0.433; logit proportion of straight trunk touches: 3-6-month old and 6-12-month-old calves: P=0.192; 6-12-month-old and >12-month-old calves/juveniles: P=0.292; Figure 6).

Table 1. Results of mixed-effects models to test the effects of age class and individual identity on the logit strengths of different types of lateralisations and on the logit proportion of straight trunk touches. Significant *P* values are shown in bold.

Effect	Effect type	*SS*	*df*	*MS*	Den.Syn. Error *df*	Den.Syn. Error *MS*	*F*	*P*
Logit strength of lateralisation in successful trunk use (Mult. R^2=0.792, Adj. R^2=0.535, *P*=0.003)								
Intercept	Fixed	513.84	1	513.84	34.77	11.11	46.24	**<0.001**
Individual ID	Random	377.34	28	13.48	25.00	4.60	2.93	**0.004**
Age class	Fixed	23.52	3	7.84	25.00	4.60	1.70	0.192
Error		114.98	25	4.60				
Logit strength of lateralisation in unsuccessful trunk use (Mult. R^2=0.616, Adj. R^2=0.091, *P*=0.352)								
Intercept	Fixed	93.85	1	93.85	45.23	18.52	5.07	**0.029**
Individual ID	Random	524.35	27	19.42	22.00	16.75	1.16	0.365
Age class	Fixed	68.49	3	22.83	22.00	16.75	1.36	0.280
Error		368.57	22	16.75				
Logit proportion of unsuccessful trunk use (Mult. R^2=0.728, Adj. R^2=0.357, *P*=0.053)								
Intercept	Fixed	29.07	1	29.07	45.78	3.64	7.98	**0.007**
Individual ID	Random	101.38	27	3.75	22.00	3.42	1.10	0.416
Age class	Fixed	57.89	3	19.30	22.00	3.42	5.64	**0.005**
Error		75.26	22	3.42				
Logit proportion of straight trunk touches (Mult. R^2=0.773, Adj. R^2=0.463, *P*=0.015)								
Intercept	Fixed	118.84	1	118.84	41.81	2.03	58.68	**<0.001**
Individual ID	Random	62.51	27	2.32	22.00	1.46	1.59	0.135
Age class	Fixed	45.10	3	15.03	22.00	1.46	10.32	**<0.001**
Error		32.04	22	1.46				
Logit strength of lateralisation in mouth placement (Mult. R^2=0.489, Adj. R^2=-0.185, *P*=0.794)								
Intercept	Fixed	111.01	1	111.01	45.11	17.46	6.36	**0.015**
Individual ID	Random	391.29	26	15.05	22.00	25.78	0.58	0.905
Age class	Fixed	40.96	3	13.65	22.00	25.78	0.53	0.667
Error		567.09	22	25.78				
Logit strength of lateralisation in body touch (Mult. R^2=0.571, Adj. R^2=-0.006, *P*=0.519)								
Intercept	Fixed	567.75	1	567.75	46.43	12.70	44.72	**<0.001**
Individual ID	Random	358.02	28	12.79	23.00	12.49	1.02	0.482
Age class	Fixed	48.99	3	16.33	23.00	12.49	1.31	0.296
Error		287.20	23	12.49				

a.



b.

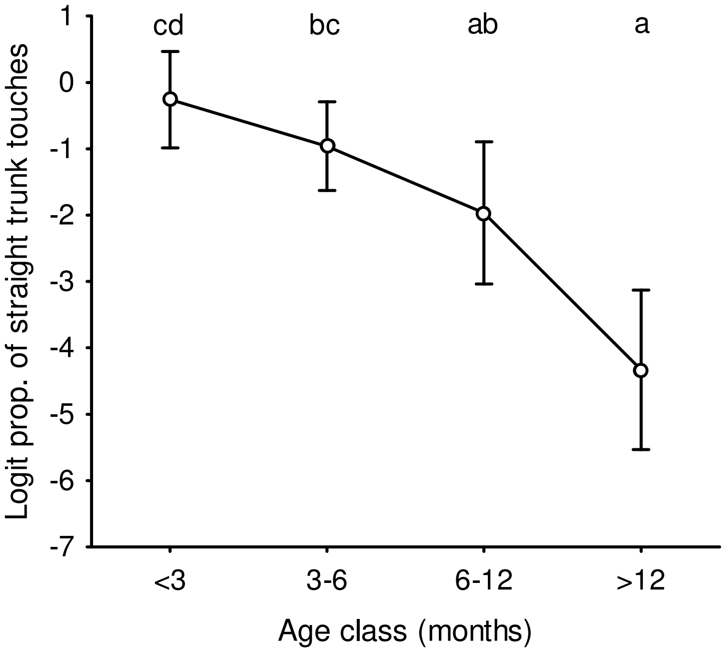


Figure 6. The logit proportion of a) unsuccessful trunk use (out of successful and unsuccessful trunk use) and b) straight trunk touches (out of successful and unsuccessful trunk movements and straight touches) shown by calves/juveniles of different age classes. Results of *post hoc* tests are shown as alphabets at the top of the graph: a<b<c<d and shared alphabets indicate non-significant comparisons. Error bars are 95% CI. The untransformed proportions corresponding to the four logit proportions in a) are 0.781, 0.413, 0.197, and 0.055, respectively, and in b) are 0.387, 0.249, 0.105, and 0.036, respectively.

We examined the correlation between the strength of side bias in successful trunk movements and the proportion of unsuccessful trunk movements and found a negative correlation (Pearson's R= -0.43, P<0.05, R^2=0.184, Spearman's R= -0.167, P>0.05, see Figure 7), but the value of the correlation was small. Similarly, we also found a small, negative correlation between the strength of side bias in successful trunk movements and the proportion of straight trunk touches, but only using parametric correlations (although the data were non-normal) (Pearson's R= -0.45, P<0.05, R^2=0.201, Spearman's R= -0.264, P>0.05, see Figure 7).

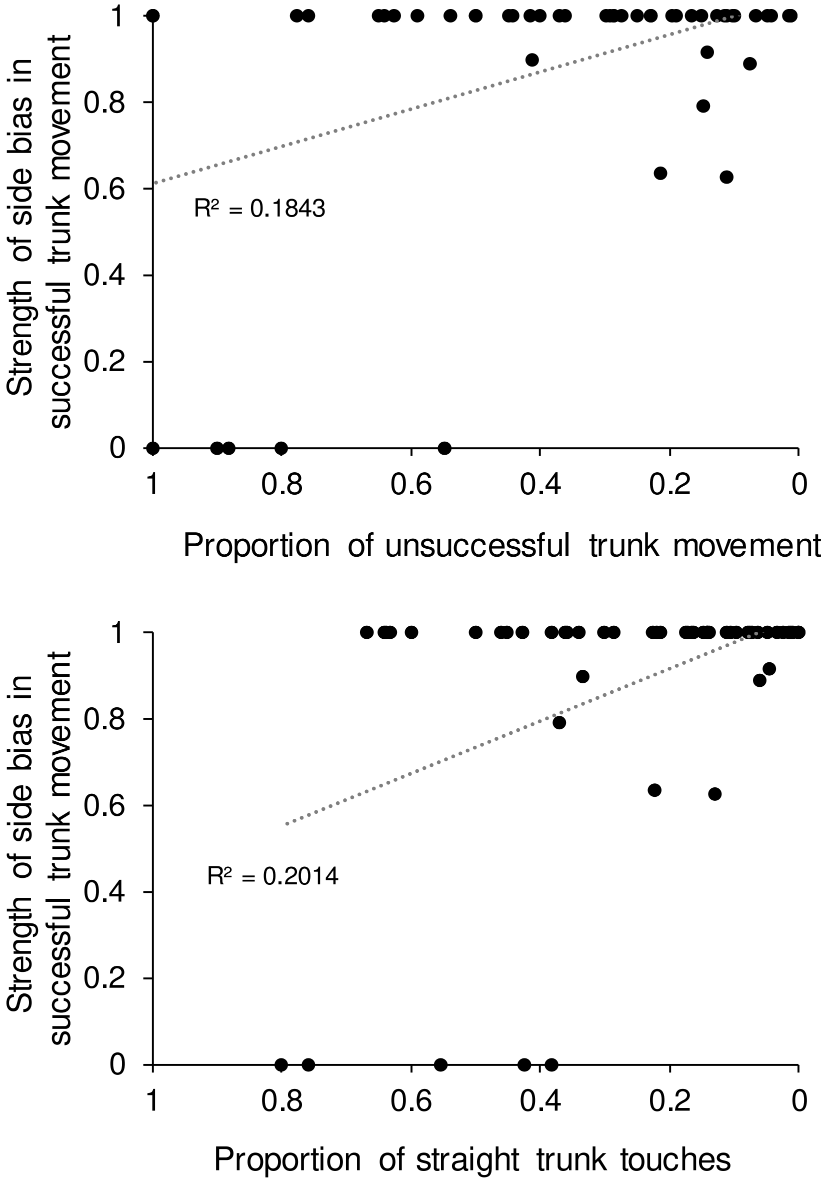


Figure 7. Strength of side preference in successful trunk movement and trunk motor ability in terms of a) proportion of unsuccessful trunk movement and b) proportion of straight trunk touches. The x-axes are reversed as the proportions decrease with increasing age.

Behaviour

Activity budget and age

Analyses on activity states were carried out on data collected through scan sampling (see Methods) from February to December 2016 (see Table 2 for sample sizes and age-sex classes sampled). Scan samples from 69 days, collected on 68 unique males and 168 unique females (236 in all), were used to analyse behavioural data. Focal samples on 30 unique calves, of which 16 were males and 14 were females, from 11 different clans, collected from January 2016 to November 2017, were used for fine-scale analyses of various calf behaviours. These calves were from 11 different clans (see Table 3 for sample sizes and age-sex classes sampled). We recorded a total of 81 different calf behaviours which were classified into four behavioural classes: a) feeding, b) grooming, c) resting, and d) social interaction, play and exploration related behaviours (see Supplementary Material 1).

We used scan sampling data to construct activity budgets for individuals of different age classes and found that the proportion of time (scans) individuals spent feeding increased with age until about 2 years of age, after which it was roughly the same (Figure 8). The proportion of time spent resting similarly decreased, being the maximum in calves below six months of age, followed by calves up to 1 year of age (Figure 8).

Table 2. Number of scan samples used to obtain data on behavioural states and the age class and sex of individuals sampled.

Age class (in years)	No. of scans for behaviour sampling		
	Scans on males	Scans on females	Total
<0.25	70	61	131
0.25-0.5	64	79	143
0.5-1	17	48	65
1-1.5	16	45	61
1.5-2	2	26	28
2-3	26	41	67
3-5	26	35	61
5-10	142	241	383
10-15	95	392	487
15-20	22	184	206
20-30	16	221	237
30-40	8	208	216
40-50	1	203	204
50-60	3	148	151
60-65	0	53	53
Total	508	1985	2493

Table 3. Number of focal sessions and focal duration of individuals of different age-sex classes.

Age class (months)	Number of focal sessions			Focal duration (in min)		
	Males	Females	Total	Males	Females	Total
<3	12	11	23	179.92	165.57	345.48
3-6	7	8	15	107.35	121.72	229.07
6-12	4	9	13	61.22	138.62	199.83

Figure 8. Proportion of scans during which individuals of different age classes showed different classes of behaviour. The trendline shown is for the proportion of scans spent in feeding behaviour and is a logarithmic fit given by the equation $y = 0.1866 \ln(x) + 0.4962$.

We used the focal animal sampling data on calves to examine behaviour at a fine scale (second-by-second data scoring). The second-by-second scoring of focal videos for a total duration of 774.38 min showed that the behaviours displayed by calves lasted for short durations (average ± 1.96 SE duration of a behaviour: 14.00 ± 1.25 seconds; number of behavioural actions scored: 3221) and thus changed rapidly. The minimum and maximum durations taken to complete a behaviour were 1 second and 600 seconds, respectively. The average (± 1.96 SE) duration of feeding behaviours was 21.7 (± 2.25) seconds, that of grooming behaviours was 8.5 (±1.61) seconds, that of resting behaviours was 17.8 (± 3.96) seconds, and that of social interactions, play and exploration behaviours was 6.2 (± 0.48) seconds.

Of the 3221 behavioural actions by calves that we observed, 71% of the behaviours lasted for less than or equal to 10 seconds. However, despite the short duration of calf actions, the proportion of scans (which are usually meant to recover relatively long ‘states’) spent in different behavioural classes were not very different from those based on focal sampling. The proportion of time spent on feeding-related behaviours was 0.48 based on the scans compared to 0.52 based on focal animal sampling, that spent on social interactions, play and exploration was 0.15 based on scans compared to 0.14 based on focal animal sampling, and that spent on grooming-related behaviours was 0.02 based on scans compared to 0.07 based on focal animal sampling. The proportion of time spent on resting-related behaviours seemed to be greater (average=0.35) based on scans than based on focal animal sampling (average=0.27). A GLM to examine the effects of age-class and behavioural class of calf action (fixed factors) and calf identity (random factor) on behaviour duration showed no significant effect of age-class ($F_{2,181}$=1.658, P=0.193), behavioural class of calf action ($F_{3,181}$=1.986, P=0.118) or interaction between age class and behavioural class of calf action ($F_{6,181}$=1.490, P=0.184) (see Supplementary Material 4).

We ran a General Linear Model (GLM) with age-class and behavioural class of calf action as fixed factors and calf identity as a random factor to find out how these affected calf behaviour. While there was no significant main effect of age class ($F_{2,199}$=0.278, P=0.758), there were significant effects of behavioural class ($F_{3,199}$=27.265, P<0.001) and interaction between age class and behavioural class ($F_{6,199}$=8.090, P<0.001) on the logit proportion of time spent in various behaviours. *Post hoc* Tukey's HSD tests showed that calves spent a significantly higher proportion of time in feeding related activities (average ± 1.96 SE proportion of time: 0.461 ± 0.082) than in grooming related activities (average ± 1.96 SE: 0.079 ± 0.030; P<0.001) and in social interactions, play, and exploration related activities (average ± 1.96 SE: 0.141 ± 0.032; P<0.001), but the time spent in feeding related activities was not significantly different from that spent in resting related activities (average ± 1.96 SE: 0.318 ± 0.080; P=0.402). *Post hoc* Tukey's HSD tests also showed that the logit proportion of time spent in feeding by <3-month-old calves (average ± 1.96 SE proportion of time: 0.292 ± 0.096) was significantly lower than that spent by 6-12-month-old calves (average ± 1.96 SE: 0.740 ± 0.130; P<0.001), but was not significantly different from that of 3-6-month-old calves (average ± 1.96 SE: 0.521 ± 0.146; P=0.340; see Figure 9). There was no significant difference in the logit proportion of time spent in feeding between 3-6-month-old and 6-12-month-old calves (P=0.860). The logit proportion of time spent resting by <3-month-old calves (average ± 1.96 SE proportion of time: 0.460 ± 0.119) was significantly higher than that spent by 6-12-month-old calves (average ± 1.96 SE: 0.101 ± 0.086; P<0.001) but was not significantly different from that of 3-6-month-old calves (average ± 1.96 SE: 0.252 ± 0.134; P=0.203), and there was no significant difference in the logit proportion of time spent in resting between 3-6-month-old and 6-12-month-old calves (*P*=0.870; see Figure 9). There was no significant difference between any of the age classes in the logit proportion of time spent in grooming and social interactions, play and exploration related activities.

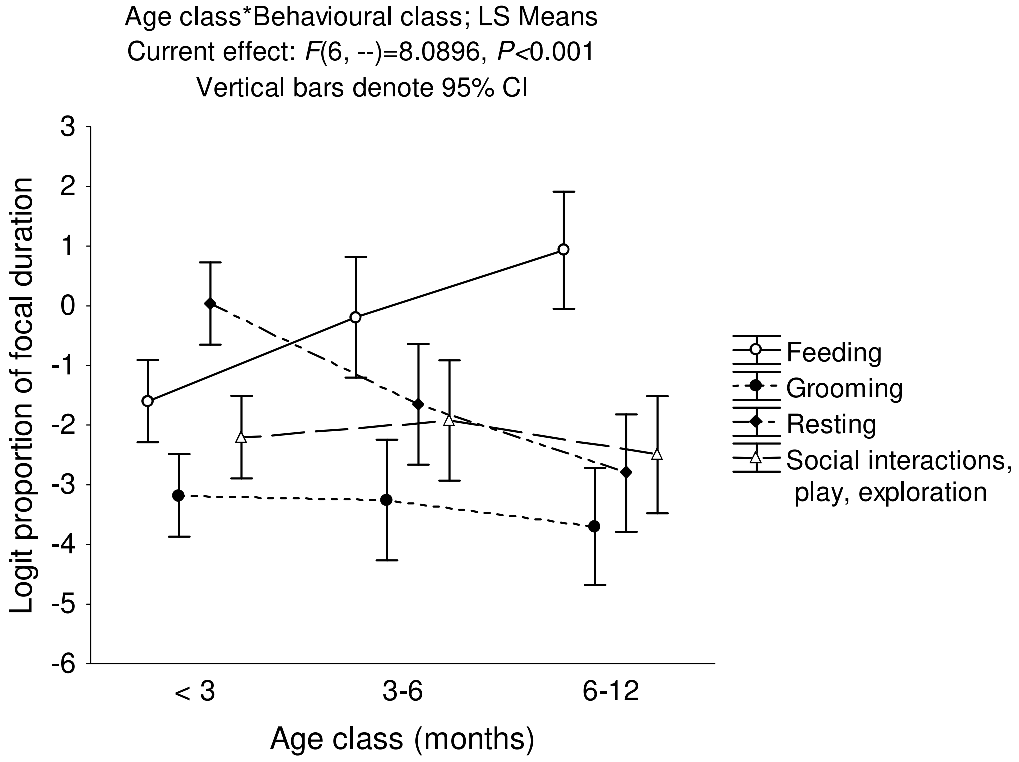


Figure 9. Proportion of focal duration spent in feeding, grooming, resting, and social interactions, play and exploration related behaviours by calves of different age classes. Error bars are 95% CI.

We further wanted to check if there was any difference in the proportion of time spent in different behavioural classes within the first three months after birth. Hence, we divided calves into four age classes: <1 month, 1-2 months, 2-3 months, and >3 months of age and carried out the GLM as described above. We found no significant main effect of age class again ($F_{3,195}$=0.148, *P*=0.931). Although there was a significant main effect of behavioural class ($F_{3,195}$=19.998, *P*<0.001) and a significant interaction effect between age class and behavioural class ($F_{9,195}$=4.704, *P*<0.001), Tukey's HSD tests did not show a significant difference between any pair of the age classes within 3 months of age for any of the behavioural classes.

Behavioural stages and age

Based on the level of competence of behavioural execution by a calf and when the behaviour was normally shown, we classified the 81 calf behaviours observed into four behavioural stages: a) preparatory calf behaviour, b) preparatory adult behaviour, c) calf-specific behaviour, and d) adult-like behaviour (see Methods, Supplementary Material 1). Preparatory calf behaviours were seen only in the context of feeding behaviours, and preparatory adult behaviours were seen in all behavioural classes except for grooming, which had only calf-specific (and only a single such behaviour, seen only once in the field) and adult-like behaviours (Figure 10).

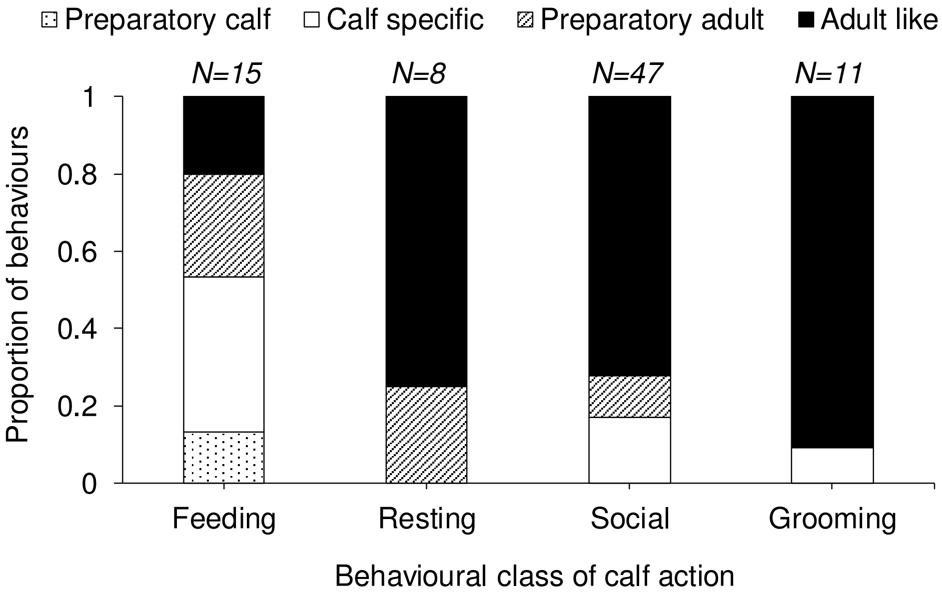
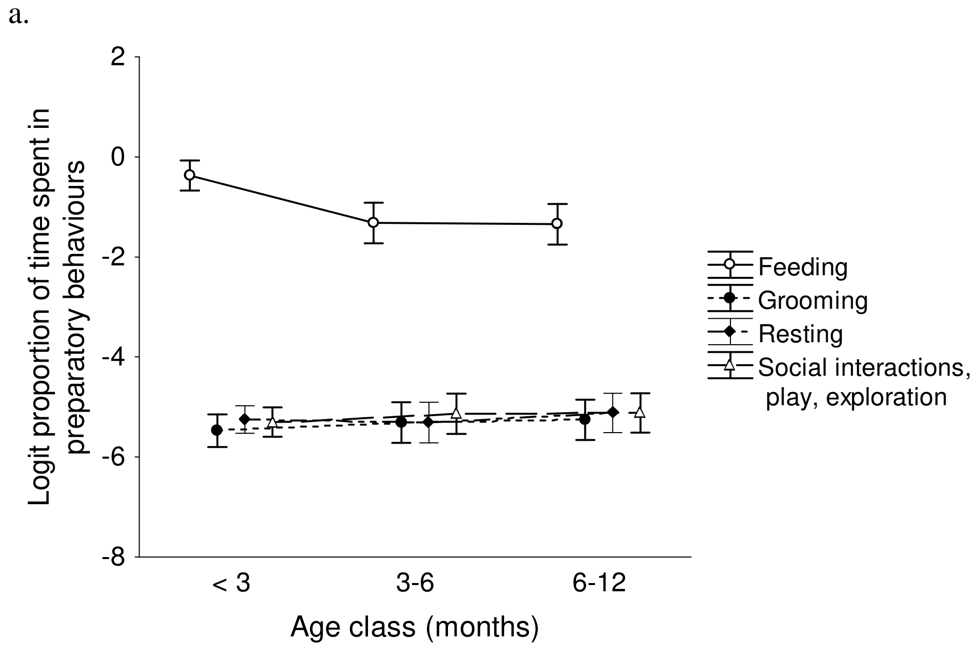


Figure 10. Proportion of unique calf behaviours belonging of different behavioural stages: a) preparatory calf behaviour, b) calf-specific behaviour, c) preparatory adult behaviour, and d) adult-like behaviour under different behavioural classes: 1) feeding, 2) resting, 3) social interaction, play and exploration, and 4) grooming related behaviours. *N* is the number of unique behaviours in that behavioural class.

We ran a GLM on the logit proportion of time spent by calves in showing preparatory behaviours (preparatory calf and preparatory adult combined as preparatory calf behaviour was seen only in the context of the initial sucking from the mother), using age class and behavioural class as fixed factors and calf identity as a random factor. Age class did not have a significant effect on the proportion of time spent by calves in showing preparatory behaviours ($F_{2,181}$=0.761, P=0.469), but there was a significant main effect of behavioural class ($F_{3,181}$=437.817, P<0.001) and a significant interaction effect between age class and behavioural class ($F_{6,181}$=3.977, P=0.001). The logit proportion of time spent in preparatory behaviours was higher in feeding-related behaviours (average ± 1.96 SE proportion of time: 0.543 ± 0.088) than in resting-related behaviours (average ± 1.96 SE proportion of time: 0.002 ± 0.002; P<0.001) or social interaction, play and exploration-related behaviours (average ± 1.96 SE proportion of time: 0.003 ± 0.003; P<0.001). There was no significant difference between the behavioural classes resting and social interactions, play and exploration in the proportion of time spent in preparatory behaviours. Calves <3 months of age showed a higher logit proportion of time in preparatory feeding behaviour (average ± 1.96 SE proportion of time: 0.741 ± 0.111) than calves 3-6 months of age (average ± 1.96 SE proportion of time: 0.400 ± 0.159; Tukey's HSD test, P<0.001) and calves 6-12 months of age (average ± 1.96 SE proportion of time: 0.346 ± 0.119; P<0.001, Figure 11). There was no significant difference in the time spent in preparatory feeding behaviour between calves of 3-6 and 6-12 months of age (P=1.000). There were also no significant differences across age classes in the logit proportions of time spent in preparatory behaviours under the grooming, resting, or social interactions categories (see Figure 11). GLM using the four age classes - <1 month, 1-2 months, 2-3 months, and > 3 months - showed significant effects of age class ($F_{3,177}$=5.033, P=0.002), behavioural class ($F_{3,177}$=461.583, P<0.001), and interaction of the two ($F_{9,177}$=4.117, P<0.001), but *post hoc* Tukey's HSD tests did not yield any significant difference in the logit proportions of time spent in preparatory behaviours of any behavioural class between any pair of the age classes within 3 months of age.



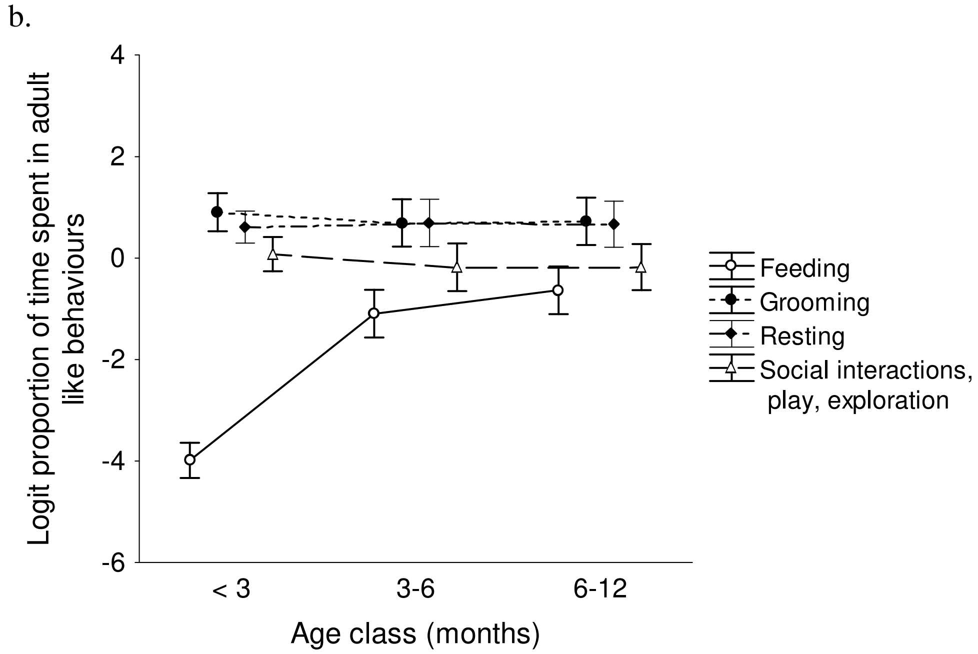


Figure 11. Logit proportion of time spent in a) preparatory behaviours and b) adult-like behaviours, under different behavioural classes by calves belonging to three age classes.

We ran a GLM on the logit proportion of time spent by calves in showing adult-like behaviours also, as with the one on preparatory behaviours above. There were significant effects of age class ($F_{2,181}$=11.213, P<0.001), behavioural class ($F_{3,181}$=110.696, P<0.001), and interaction between these two factors ($F_{6,181}$=26.016, P<0.001) on the logit proportion of time calves showed adult-like behaviours. The logit proportion of time spent in adult-like behaviours by calves <3 months of age (average ± 1.96 SE proportion of time: 0.716 ± 0.077) was significantly lower than that shown by calves 3-6 months of age (average ± 1.96 SE proportion of time: 0.826 ± 0.077; Tukey's HSD test: $P<0.001$) and 6-12 months of age (average ± 1.96 SE proportion of time: 0.857 ± 0.064; $P<0.001$), and the latter two age classes did not significantly differ from each other ($P=0.759$). The logit proportion of time spent in adult-like behaviours by calves under the behavioural class feeding (average ± 1.96 SE proportion of time: 0.333 ± 0.092) was significantly lower than those spent under grooming (average ± 1.96 SE proportion of time: 1.000 ± 0.00; $P<0.001$), resting (average ± 1.96 SE proportion of time: 0.987 ± 0.011; $P<0.001$), and social interaction, play and exploration behavioural classes (average ± 1.96 SE proportion of time: 0.800 ± 0.068; $P<0.001$). The logit proportion of time spent in adult-like behaviours by calves under the behavioural class grooming was significantly higher than that spent under social interactions, play, exploration ($P<0.001$) but was not significantly different from that under resting ($P=0.899$). The proportion of time spent in adult-like behaviours by calves under the behavioural class resting was higher than that spent under social interactions, play, exploration ($P<0.001$). The logit proportion of time spent in adult-like behaviours under the behavioural class feeding by calves under 3 months of age (average ± 1.96 SE proportion of time: 0.078 ± 0.074) was significantly lower than that by calves of 3-6 months of age (average ± 1.96 SE proportion of time: 0.516 ± 0.174; $P<0.001$) and 6-12 months of age (average ± 1.96 SE proportion of time: 0.591 ± 0.130; $P<0.001$), while there was no significant difference between calves of 3-6 and 6-12 months of age ($P=0.930$; see Figure 11). There was also no significant difference between the proportions of time spent in adult-like behaviours between any of the three age classes under each of the other behavioural classes (Figure 11).

Like the preparatory behaviours, we also looked at the logit proportion of time spent in adult-like behaviours by calves within 3 months of age. Although there were significant effects of age class ($F_{3,177}=7.776$, $P<0.001$), behavioural class ($F_{3,177}=206.966$, $P<0.001$), and interaction between these two factors ($F_{9,177}=18.592$, $P<0.001$) on the logit proportion of time spent in adult-like behaviours by calves, Tukey's HSD tests were not significant between any pair of the age classes within 3 months of age.

Behavioural synchrony

We calculated the behavioural-class synchrony between calves/juveniles and their mothers, with synchrony being 1 if the calf/juvenile and its mother showed behaviours belonging to the same behavioural class during a particular scan, and synchrony being 0 if they showed behaviours belonging to different behavioural classes. Based on generalized linear mixed-effects models with synchrony as a binomial dependent variable, age of the calf/juvenile, and behavioural class as fixed factors, and identities of the mother and calf/juvenile as random factors (see Methods), we found the best model explaining synchrony to include calf age and behavioural class (Table 4). However, there were also three other equally good models, whose ΔAIC with the best model was smaller than 2. These models included calf sex, calf identity, and mother identity, respectively, in addition to calf age and behavioural class (Tables 4,5). Synchrony between mother and calf/juvenile based on resting-related behaviours increased dramatically between the age of less than six months (almost no synchrony) to about 2 years (almost complete synchrony) (Figure 12). Synchrony in social interactions increased gradually throughout the period of being a calf and then juvenile. Synchrony in feeding was high throughout because elephants spend most of their waking hours in feeding-related activities. Grooming-related activities became less synchronised with increasing age of the offspring (Figure 12).

Table 4. Results of generalized linear mixed-effects models with synchrony in behavioural class between mother and offspring (“calf” in this table and the next includes calves and juveniles) as the binomial dependent variable, calf age and behavioural class as fixed factors, and identities of the calf/juvenile and mother as random factors.

Model	**No. of parameters**		**AIC**	**ΔAIC**	**Deviance**
	Fixed	**Random**			
Synchrony ~ 1 + Calf age + Behavioural class	2	_	249.94	0	239.94
Synchrony ~ 1 + Calf age + Behavioural class + Sex	3	_	250.62	0.68	238.62
Synchrony ~ 1 + Calf age + Behavioural class + (1 | Calf ID)	2	1	251.69	1.75	239.69
Synchrony ~ 1 + Calf age + Behavioural class + (1 | Mother ID)	2	1	251.7	1.76	239.7
Synchrony ~ 1 + Calf age + Behavioural class + Sex + (1 | Calf ID)	3	1	252.55	2.61	238.55

Model	**No. of parameters**		**AIC**	**ΔAIC**	**Deviance**
	Fixed	**Random**			
Synchrony ~ 1 + Calf age + Behavioural class + Sex + (1 | Mother ID)	3	1	252.62	2.68	238.62
Synchrony ~ 1 + Calf age + Behavioural class + (1 | Calf ID) + (1 | Mother ID)	2	2	253.69	3.75	239.69
Synchrony ~ 1 + Calf age + Behavioural class + Sex + (1 | Calf ID) + (1 | Mother ID)	3	2	254.55	4.61	238.55
Synchrony ~ 1 + Behavioural class	1	_	254.96	5.02	246.96
Synchrony ~ 1 + Behavioural class + Sex	2	_	255.45	5.51	245.45
Synchrony ~ 1 + Behavioural class + (1 | Calf ID)	1	1	256.24	6.3	246.24
Synchrony ~ 1 + Behavioural class + (1 | Mother ID)	1	1	256.32	6.38	246.32
Synchrony ~ 1 + Behavioural class + Sex + (1 | Calf ID)	2	1	257.14	7.2	245.14
Synchrony ~ 1 + Behavioural class + Sex + (1 | Mother ID)	2	1	257.45	7.51	245.45
Synchrony ~ 1 + Behavioural class + (1 | Calf ID) + (1 | Mother ID)	1	2	258.24	8.3	246.24
Synchrony ~ 1 + Behavioural class + Sex + (1 | Calf ID) + (1 | Mother ID)	2	2	259.14	9.2	245.14
Synchrony ~ 1 + Calf age + Sex + (1 | Calf ID)	2	1	534.67	284.73	526.67
Synchrony ~ 1 + Calf age + Sex + (1 | Mother ID)	2	1	534.67	284.73	526.67
Synchrony ~ 1 + Calf age + (1 | Calf ID)	1	1	534.89	284.95	528.89
Synchrony ~ 1 + Calf age + (1 | Mother ID)	1	1	535.07	285.13	529.07
Synchrony ~ 1 + Calf age + Sex + (1 | Calf ID) + (1 | Mother ID)	2	2	536.67	286.73	526.67
Synchrony ~ 1 + Calf age + (1 | Calf ID) + (1 | Mother ID)	1	2	536.89	286.95	528.89
Synchrony ~ 1 + Calf age + Sex	2	_	540.42	290.48	534.42
Synchrony ~ 1 + Calf age	1	_	544.7	294.76	540.7
Synchrony ~ 1 + Sex + (1 | Calf ID)	1	1	586.78	336.84	580.78
Synchrony ~ 1 + Sex + (1 | Calf ID) + (1 | Mother ID)	1	2	588.78	338.84	580.78
Synchrony ~ 1 + Sex + (1 | Mother ID)	1	1	590.53	340.59	584.53
Synchrony ~ 1 + Sex	1	_	690.6	440.66	686.6

Table 5. Parameter estimates and their confidence intervals and statistical significance from the best models to explain mother-offspring synchrony.

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
Model: *Synchrony ~ 1 + Calf age + Behavioural class*							
Fixed effects							
Intercept	-0.628	0.277	-2.268	510	0.024	-1.172	-0.084
Calf age	0.450	0.179	2.517	510	0.012	0.099	0.800
Behavioural class - Resting	-2.880	0.408	-7.057	510	<0.001	-3.681	-2.078
Behavioural class - Social interaction, play, exploration	-0.139	0.281	-0.494	510	0.622	-0.690	0.456
Behavioural class - Feeding	3.403	0.333	10.211	510	<0.001	2.748	0.456
Random effects							
Error	1.000						
Model: *Synchrony ~ 1 + Calf age + Behavioural class + Sex*							
Fixed effects							
Intercept	-0.663	0.279	-2.374	509	0.018	-1.211	-0.114
Calf age	0.439	0.176	2.493	509	0.013	0.093	0.785
Behavioural class - Resting	-2.851	0.408	-6.982	509	<0.001	-3.653	-2.049
Behavioural class - Social interaction, play, exploration	-0.133	0.281	-0.473	509	0.637	-0.685	0.420
Behavioural class - Feeding	3.407	0.334	10.208	509	<0.001	2.751	4.062
Sex	-0.200	0.175	-1.148	509	0.252	-0.544	0.142
Random effects							
Error	1.000						
Model: *Synchrony ~ 1 + Calf age + Behavioural class + (1 | Calf ID)*							
Fixed effects							
Intercept	-0.657	0.300	-2.187	510	0.029	-1.247	-0.669
Calf age	0.468	0.189	2.472	510	0.014	0.096	0.840
Behavioural class - Resting	-2.931	0.420	-6.986	510	<0.001	-3.755	-2.107
Behavioural class - Social interaction, play, exploration	-0.175	0.286	-0.611	510	0.54	-0.737	0.387
Behavioural class - Feeding	3.496	0.344	10.156	510	<0.001	2.820	4.173
Random effects							
Calf ID intercept	0.410			45 levels			
Error	1.000						

Effect	Estimate	SE	*t*	df	*P* value	95% CI	
Model: *Synchrony ~ 1 + Calf age + Behavioural class + (1 | Mother ID)*							
Fixed effects							
Intercept	-0.658	0.300	-2.192	510	0.029	-1.247	-0.680
Calf age	0.469	0.189	2.480	510	0.013	0.097	0.840
Behavioural class - Resting	-2.930	0.420	-6.986	510	<0.001	-3.754	-2.106
Behavioural class - Social interaction, play, exploration	-0.174	0.286	-0.609	510	0.543	-0.736	0.388
Behavioural class - Feeding	3.496	0.344	10.161	510	<0.001	2.820	4.172
Random effects							
Mother ID intercept	0.408			45 levels			
Error	1.000						

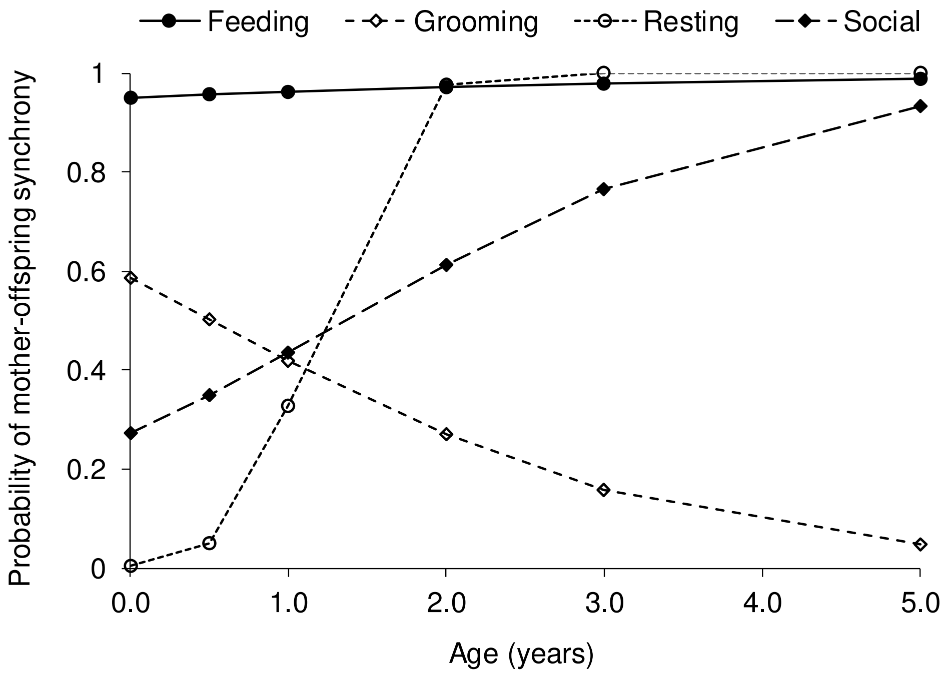


Figure 12. Curves showing the expected probabilities of mother-offspring behavioural synchrony with calves/juveniles of different ages. The curves were obtained using logistic regression equations (without calf or mother identity as a random factor). The probability of synchrony under feeding is represented by the equation $e^{(2.9556+(0.29158)*age)/(1+exp(2.9556+(0.29158)*age))}$, that under grooming is represented by the equation $e^{(0.34817+(-0.671809)*age)/(1+exp(0.34817+(-0.671809)*age))}$, and the probability of synchrony under resting is represented by the equation $e^{(-5.1188+(4.40502)*age)/(1+exp(-5.1188+(4.40502)*age))}$. The probability of synchrony under social interactions, play, and exploration is represented by the equation $e^{(-}$

0.98085+(0.720646)*age)/(1+exp(-0.98085+(0.720646)*age)).

Discussion

This is one of the first studies of the development of trunk motor control and behaviours in Asian elephant calves. We found that both trunk motor control and behaviours develop gradually over a period in this precocial species, but trunk lateralisation occurs early on (the last also observed by Keerthipriya *et al.* 2015). As mentioned in the Introduction, Asian elephant calves can walk within hours of being born, albeit unsteadily, but do not use their trunk immediately (Nair 1989). We found that there was an effect of age on trunk motor use, with the proportions of unsuccessful clockwise and anticlockwise trunk movements and straight trunk touches decreasing from <3 months of age to about a year of age. However, there was no statistically significant independent effect of age on trunk lateralisation itself, as it seemed to arise very early in development, and only individual identity contributed to explaining lateralisation in successful trunk use. Many of the calves less than 3 months old already showed significant lateralisation and all the calves over 6 months of age showed significant lateralisation when the trunk was used successfully. Moreover, calves showed trunk side preferences even when they could not use the trunk successfully. A correlation between trunk motor skills (seen as lowered proportions of unsuccessful trunk movements or straight trunk touches) and lateralisation (based on successful trunk movements) would be seen if practice using the trunk gave rise to lateralisation due to its possibly increased efficiency. Alhough we found a negative correlation between the strength of successful trunk movements and the proportion of unsuccessful trunk movements and between the strength of successful trunk movements and the proportion of straight trunk touches, the values of the correlations were low. Therefore, it appears that lateralisation is not highly dependent on adeptness in trunk use. Since the inability to use the trunk successfully did not prevent lateralisation, it is possible that trunk lateralisation itself is innate, while trunk motor skills develop with age, and trunk lateralisation is probably not a good chronological marker of development in Asian elephants. Thus, precociality does not hasten the use of the trunk although limbs are used early on and trunk lateralisation occurs early. Since altricial mammals such as chimpanzees, gorillas, and humans take several months to a few years to have set hand preferences (Ramsay 1980, Boesch 1991, Byrne and Bryne 1991), it had been suggested that trunk lateralisation may be correlated with precociality (Keerthipriya *et al.* 2015). Our results showing a lack of concordance between trunk motor ability and laterality now raise doubts about the hypothesis, although studies on other species will be required to test it.

Although precociality allows for early independent locomotion, we found that it took about one year - about the time it took for calves to approximate adult-like behavioural activity patterns - for trunk motor skills to be developed properly. This is consistent with the observations on a captive Asian elephant calf that showed increasingly fine motor skills from 2 to 17 weeks of age (Petraccione *et al.* 2017). Whereas both precocial and altricial species have the basic locomotor ability to perform alternating stepping limb movements soon after birth, the neuromuscular strength and coordination to support the body and actually walk soon after birth is present only in precocial species as these elements mature embryonically rather than postnatally as in altricial species (Muir 2000). It appears that similar neuromuscular strength and coordination required for trunk motor control develops only postnatally in elephants. This may result from phylogenetic inertia, in ontogeny, and it calls for an examination of the ontogeny of lateralisation in other related and unrelated species (such elephant shrews, which also belong to Afrotheria, and tapirs) that have elongated noses. Unlike the precociality in limb use, it is possible that in the ancestral state, when a modification of the upper lip evolved, the development of strength and coordination of the structure may have taken place postnatally rather than during the embryonic stages. Therefore, when the trunk evolved in elephants, its functional development, as a result of being constrained by its phylogeny, may have continued to occur postnatally. In fact, the upper lip and proboscis are not fused together during the early foetal ontogeny in the African savannah elephant (Fischer and Trautmann 1987). Phylogenetic inertia in ontogeny of lateralisation of the trunk may be examined by studying the development and laterality of the upper lip and nose of related species. Elephants do not have many close relatives, but elephant shrews, aardvarks, and hyraxes that also belong to the clade Afrotheria could possibly be studied. One could also study the ontogeny and lateralisation of the elongated noses of tapirs, which are not related to elephants, and relatives of tapirs such as horses, donkeys, and zebras (the tapirs also do not have close relatives).

Our results on the behaviours displayed by calves showed that various behaviours developed over a period of time, resulting in an approximation of adult-like behaviour at the age of about 1-2 years, although there were more subtle changes in activity budgets until the age of about 5-10 years. Behaviours that require trunk control, such as some feeding-related behaviours, developed gradually as trunk motor control also developed over several months, while adult-like behaviours were seen in the context of grooming and resting. In wild African savannah elephants and captive Asian elephants, some of the first behavioural elements to develop were those related to locomotion, resting, and sucking (Lee 1986, Nair 1989, Lee and Moss 2011) - these are behaviours that do not require trunk usage.

We found that young calves spent considerable time in practicing the preparatory steps to feeding. They spent time sniffing the grass, trying to hold and pluck it, investigating the grass collected by conspecifics, and, sometimes, sitting on the ground to nibble grass blades directly without using the trunk. Adult-like feeding behaviours were primarily shown by calves that were older than 3 months of age, and older calves (6-12 months) spent the highest proportion of time in expressing adult-like feeding patterns. Nair (1989) had examined the sequence of events involved in feeding and found that only the older calves (> 6 months) approximated an adult-like feeding sequence (hold-pull-place in mouth). However, although the proportion of adult-like behaviours and the time spent in feeding increased as the calves became older, the duration of feeding activities did not differ between the younger and older calves, suggesting that efficiency in feeding was not fully developed by 1 year of age and might take longer to reach an adult's level of competence. In captive Asian elephants, it was observed that the diversity of food species available to calves was much less than that available to juveniles and subadults, and some of the food species require substantial physical force to procure, which a calf is not capable of (Nair 1989). Thus, the skills required to perfect feeding behaviour might be practiced and elaborated beyond this period.

Most of the resting-related behaviours exhibited by calves resembled those of adults, although most of the calf resting bouts involved them lying down on the ground while subadults and adults usually rested standing up. During the initial few weeks after birth, calves were seen leaning on the mother to rest and were sliding down against her leg to rest on the ground. Most of the grooming and social interactions, play and exploration related behaviours shown by calves were also adult-like, except for certain grooming behaviours, such as spraying dust onto oneself, that requires control over the trunk. In African savannah elephants it was found that the social interaction rate and the kinds of responses to these interactions differed between calves and juveniles and between the sexes (Lee 1986, Lee and Moss 2011, Webber 2017). We did not examine the behaviours of juveniles of different sexes, but we did not find an effect of sex on trunk lateralisation and motor development in calves. We also examined the effect of sex on calf behaviour in our preliminary analyses but did not find an effect and pooled the data together to improve sample sizes. In Asian elephants, Webber (2017) also did not find an effect of sex on the time calves spent feeding, moving, or resting. We, however, found sex to be a factor in one of the best models explaining synchrony between mother and calf.

The proportion of time spent on resting-related behaviours decreased with age, with young calves showing the highest proportion of time spent resting, similar to that found in captive Asian elephant populations (Gadgil and Nair 1984, Nair 1989, Webber 2017) and in African savannah elephants (Lee 1986, Lee and Moss 2011, Webber 2017). Since elephants are megaherbivores and spend ~50%-~75% of their time feeding (McKay 1973, Sukumar 2003, Baskaran *et al.* 2010), resting by calves would be a cost to the mother, restricting movement required to find forage. The mother may sometimes be extremely restricted if she stands over a young calf to provide shade (as elephants can get dangerously over-heated). The activity budget hypothesis (Ruckstuhl 1998, Ruckstuhl and Neuhaus 2001), proposed initially in the context of sexual segregation, suggested that the degree of within group synchrony may be influenced by the differences in physiological demands between individuals arising from variations in reproductive stage, sex, or age. Since synchronisation of activities of a heterogeneous group would entail costs through individuals making compromises, such groups may segregate or fission along common lines.

The nutritional requirements of an elephant calf are different from that of the mother and there are substantial differences in the activity budgets of the calf and mother. In the case of bottlenose dolphins, which also have precocial motor skills and a long period (3-8 years) of nursing, calves, even newborns, can temporarily separate from their mothers and swim alone or with other conspecifics (Mann and Smuts 1999, see Gibson and Mann 2008). In harp seals, which are also precocial, females leave their pups after 2 days of birth and swim out to feed, returning to nurse the pups once in a while, spending only about 15% of their time with the pups (Kovacs 1987). The young ones of giraffes are “hiders”, remaining separated from the mother after birth except during nursing (Langman 1977). Since none of these is the case in the Asian elephant, the calf being dependent on the mother, behaviours that decrease synchrony may decrease rapidly with calf age if synchrony is expensive. We found that the proportion of time spent resting was significantly lower in calves older than 6 months of age than in calves below 3 months of age, and juveniles over 1 year of age were similar to adult females in their proportion of time spent resting. The proportion of time spent feeding increased with calf age but was not accompanied by a significant increase in the mother-offspring feeding synchrony because adult females spend most of their time feeding. Synchrony in social interactions between the mother-offspring pair increased with age although the proportion of time spent in these behaviours or the durations of these behaviours did not increase with age. It is not clear if calves or their mothers influence one another such that these behaviours coincide more frequently.

The pattern of a continuous increase or decrease in behaviours across age classes as we found in Asian elephant calves is not the only kind of behavioural ontogeny expected. The ontogeny of behaviour in young ones may be a smooth, gradual transition from imperfect or underdeveloped behavioural state to a range of completely developed adult behaviours (Klopfer 1988) or could vary in other ways. Bottlenose dolphin calves, which can socialise partly independently of their mother, have a peak in socialising during the first year, followed by a decline (Gibson and Mann 2008). The ontogeny of behaviour is marked by abrupt discontinuities as a result of the differences in the ecology and social environment between the young and the adult in the spotted hyena (Holekamp and Smale 1998). Spotted hyena neonates are precocial, with eyes open and a moderately advanced dentition (Kruuk 1972). They socialize exclusively with their mother and sibling (establishing a dominance relationship with the sibling) in the natal den in the first few weeks after birth, followed by socialising with others when transferred to the communal den (Frank *et al.* 1991, Holekamp and Smale 1998). Therefore, play and fighting behaviours may show abrupt changes although feeding behaviours develop gradually (Holekamp and Smale 1998). Orangutans showed more continuous change, with feeding, and social play behaviours increasing with age, but resting and non-social play decreasing with age (Mendonca *et al.* 2016).

Although we found trunk motor skills and behaviours to develop gradually over several months, they developed over a very short time relative to the lifespan (over 70 years, see Sukumar 2003) of the species, although individuals can continue to learn social behaviours as they grow into juveniles, subadults, and adults. They developed over a relatively short time compared to the time to weaning also, as elephants are seen to nurse for at least two years and the weaning is gradual (personal observations). Harp seal pups are highly precocious and weaned abruptly when they are just 12-15 days old, but remain predominantly immobile before that, mostly only shifting positions, and abruptly taking to the water to swim without any ‘teaching’ (Kovacs 1987). Orangutans have a prolonged period of dependence on the mother, being in continuous body contact for the first three months, being assisted with locomotion until they are about 3 years of age, and being suckled up to 7 years of age, due to their solitary lifestyle that necessitates that the young are ecologically competent before they are weaned (Noordwijk and van Schaik 2005). In social species like the Asian elephant, weaned juveniles can continue to receive information or protection from others in their clan. It would be interesting to examine the effect of interaction of precociality/altriciality and sociality on the ontogeny of behaviour.

Thus, we found that while elephant calves may be anatomically and physiologically well developed at birth, fine motor skills and some of the social and non-social behaviours develop over many months. With increase in control over motor skills, calves begin to show complex behaviours that require dexterity in trunk usage, and their behavioural repertoire begins to match that of an adult. The efficiency with which calves performed various behaviours like feeding also improved with age. We found that laterality in trunk usage and certain behaviours such as sucking, resting, and less complex grooming behaviours seemed to be innate as calves showed these from a very young age. As trunk motor control and trunk-limb coordination necessary to pluck and process grass take several months to develop, the prolonged period of offspring dependency on the mother can be highly crucial and beneficial in terms of nutritional support. This period might also be beneficial in view of defense against predators and development of important social skills, and can be examined in the future.

Acknowledgements

This work was funded by the Council of Scientific and Industrial Research, Government of India, under Grant No. 37(1613)/13/EMR-II and Jawaharlal Nehru Centre for Advanced Scientific Research (JNCASR). TR and SA were supported as students by JNCASR. This work is part of TR’s Ph.D. thesis. We thank the offices of the PCCF, Karnataka Forest Department, and of the Conservators of Forests of Nagarahole and Bandipur National Parks and Tiger Reserves for field permits. We also thank various officials from the PCCF and APCCF, to the Conservators of Forests and Range Forest Officers, to the staff of Nagarahole and Bandipur National Parks for their support. We thank Krishna, Shankar, Pramod and others for help in the field, and Hansraj Gautam for some videos.

References

1. Altmann J (1974). Observational study of behaviour: sampling methods. *Behaviour* 49: 3-4.
2. Bard KA, Hopkins WD and Fort CL (1990). Lateral bias in infant chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology* 104: 309-321.
3. Barrett P and Bateson P (1978). The development of play in cats. *Behaviour* 66: 106-120.
4. Bateson P (1981). Ontogeny of behaviour. *British Medical Bulletin* 37: 159-164.
5. Bateson P (1987). Biological approaches to the study of behavioural development. *International Journal of Behavioural Development* 10: 1-22.
6. Bateson P (2017). *Behaviour, Development and Evolution.* Open book publishers, Cambridge.
7. Boesch C (1991). Teaching among wild chimpanzees. *Animal Behaviour* 41: 530-532.
8. Conradt L (1998) Could asynchrony in activity between the sexes cause inter-sexual social segregation in ruminants? *Proceeding of the Royal Society of London B: Biological Sciences* 265: 1359-1363.
9. Derrickson EM (1988). The effect of experimental termination of lactation on subsequent growth in *Peromyscus leucopus*. *Canadian Journal of Zoology* 66: 2507-2512.
10. Derrickson EM (1992). Comparative reproductive strategies of altricial and precocial eutherian mammals. *Functional Ecology* 6: 57-65.
11. Fischer MS and Trautmann U (1987). Fetuses of African elephants (*Loxodonta africana*) in photographs. *Elephant* 2: 40-45.
12. Frank GL, Glickman FL and Licht P (1991). Fatal sibling aggression, precocial development, and androgens in neonatal Spotted hyenas. *Science* 252: 702-704.
13. Gadgil M and Nair PV (1984). Observations on the social behaviour of free ranging groups of tame Asiatic elephant (*Elephas maximus* Linn). *Proceedings of the Indian Academy of Sciences (Animal Sciences)* 93: 225-233.
14. Gibson QA and Mann J (2008). Early social development in wild bottlenose dolphins: sex differences, individual variation and maternal influence. *Animal Behaviour* 76: 375-387.
15. Giljov A, Karenina K and Malashichev Y (2018). Facing each other: mammal mothers and infants prefer the position favouring right hemisphere processing. *Biology Letters 14*: 20170707.
16. Hinde RA and Bateson P (1984). Discontinuities versus continuities in behavioural development and the neglect of process. *International Journal of Behavioural*

Development 7: 129-143.

17. Holekamp KE and Smale L (1998). Behavioural development in the spotted hyena. *BioScience* 12: 997-1005.
18. Joffe TH (1997). Social pressures have selected for an extended juvenile period in primates. *Journal of Human Evolution* 32: 593-605.
19. Keerthipriya P, Tewari R and Vidya T N C (2015). Lateralization in trunk and forefoot movements in a population of free-ranging Asian elephants (*Elephas maximus*). *Journal of Comparative Psychology 129*: 377.
20. Kleiman DG (1972). Maternal behaviour of the green acouchi (*Myoprocta pratti* Pocock), a South American caviomorph rodent. *Behaviour* 43: 48-84.
21. Klopfer P (1988). Metaphors for development: How important are experiences early in life? *Developmental Psychobiology* 21: 671-678.
22. Kovacs KM (1987). Maternal behaviour and early behavioural ontogeny of harp seals, *Phoca groenlandica*. *Animal Behaviour* 35: 844-855.
23. Kruuk H (1972). *The Spotted Hyena*. University of Chicago Press, Chicago.
24. Langman VA (1977). Cow-calf relationships in giraffe (*Giraffa camelopardalis giraffa*). *Zeitschrift für Tierpsychologie* 43: 264-286.
25. Lee PC (1986). Early social development among African elephant calves. *National Geographic Research* 2: 388-401.
26. Lee PC and Moss CJ (1986). Early maternal investment in male and female Asiatic elephant calves. *Behavioural Ecology and Sociobiology* 18: 353-361.
27. Lee PC and Moss CJ (2011). Calf development and maternal rearing strategies. In: Moss CJ, Croze H and Lee PC (eds.), *The Amboseli Elephants: A Long-Term Perspective on a Long-Lived Mammal,* pp 224-237. University of Chicago Press, Chicago.
28. Mann J and Smuts BB (1999) Behavioural development in wild bottlenose dolphin newborns (*Tursiops* sp.). *Behaviour* 136: 529-566.
29. Mar KU, Lahdenperä M and Lummaa V (2012). Causes and correlates of calf mortality in captive Asian elephants (*Elephas maximus*). *PLoS One* 7: e32335
30. Mckay GM (1973). Behaviour and ecology of the Asiatic elephant in southeastern Ceylon. *Smithsonian Contributions to Zoology* 125: 1-113.
31. Martin F and Niemitz C (2003). "Right-trunkers" and "left-trunkers": side preferences of trunk movements in wild Asian elephants (*Elephas maximus*). *Journal of Comparative Psychology* 117: 371.
32. Mendonca RS, Kanamori T, Kuze N, Hayashi M, Bernard H and Matsuzawa T

(2016). Development and behaviour of wild infant-juvenile East Bornean orangutans (*Pongo pygmaeus morio)* in Danum Valley. *Primates* 58: 211-224.

33. Muir GD (2000) Early ontogeny of locomotor behaviour: a comparison between altricial and precocial animals. *Brain Research Bulletin* 53: 719-726.
34. Nair PV (1989). Development of nonsocial behaviour in the Asiatic elephant. *Ethology* 82: 46-60.
35. Nandini S, Keerthipriya P and Vidya TNC (2017). Seasonal variation in female Asian elephant social structure in Nagarahole-Bandipur, southern India. *Animal Behaviour* 134: 135-145.
36. Nandini S, Keerthipriya P and Vidya TNC (2018). Group size differences may mask underlying similarities in social structure: a comparison of female elephant societies. *Behavioural Ecology* 1-15.
37. Petraccione J, Root-gutteridge H, Cusano DA and Parks DE (2017). Exploring the early social affiliations and behaviour of a captive Asian elephant (*Elephas maximus*) calf. *Journal of Zoo Aquarium Research* 5: 131-136.
38. Poirier FE and Smith EO (1974). Socializing functions of primate play. *American Zoologist* 14: 275-287.
39. Pratt DM and Anderson VH (1979). Cow-calf relationships and the social development of the calf in the Serengeti. *Zeitschrift für Tierpsychologie* 51: 233-251.
40. Ramsay D (1980). Onset of unimanual handedness in infants. *Infant Behaviour and Development* 3: 377-385.
41. Rogers LJ (2002). Lateralised brain function in anurans: comparison to lateralisation in other vertebrates. *Laterality 7*: 219-239.
42. Ruckstuhl KE (1998). Foraging behaviour and sexual segregation in bighorn sheep. *Animal Behaviour* 56: 99-106.
43. Ruckstuhl KE and Neuhaus P (2001). Behavioural synchrony in ibex groups: effects of age, sex and habitat. *Behaviour* 138: 1033-1046.
44. Scheiber IBR, Weiß BM, Kingma SA and Komdeur J (2017). The importance of the altricial – precocial spectrum for social complexity in mammals and birds – a review. *Frontiers in Zoology* 14: 3.
45. Scott JP, Stewart JM and de Ghett VJ (1974). Critical periods in the organization of systems. *Developmental Psychobiology* 7: 489-513.
46. Sharma R and Krishnamurthy KV (1984). Behaviour of a neonate elephant (*Elephas maximus*). *Applied Animal Behaviour Science* 13: 157-161.

47. Sukumar R (2003). *The Living Elephants: Evolutionary Ecology, Behaviour, and Conservation*. Oxford University Press, New York.
48. van Noordwijk M A and van Schaik C P (2005). Development of ecological competence in Sumatran orangutans. *American Journal of Physical Anthropology* 127: 79-94.
49. Vidya TNC, Prasad D and Ghosh A (2014). Individual identification in Asian elephants. *Gajah* 40: 3-17.
50. Washburn S and Hamburg D (1965). The implications of primate research. In: DeVore I, (ed.) *Primate behaviour: field studies of monkeys and apes*, pp. 607-623. Holt, Rinehart and Winston, New York.
51. Webber C E (2017). *A Comparison of Behavioural Development of Elephant Calves in Captivity and in the Wild: Implications for Welfare*. Ph.D. thesis, University of Sterling.

Supplementary Material

Supplementary Material 1. Details of various behaviours.

We present here, a list of various behaviours and their categorisation, and photos of different kinds of behaviours. We recorded a total of 85 different calf activities. We classified behaviours into four behavioural classes: a) feeding, b) grooming, c) resting, and d) social interaction, play, exploration related behaviours. Four out of these 85 activities were physiological (yawning, hiccupping, urinating, and defecating) and were not classified under any of the above-mentioned behavioural classes. Based on the level of competence of behavioural execution by a calf, the 81 behaviours were classified into four behavioural stages namely, a) preparatory calf behaviour, b) preparatory adult behaviour, c) calf-specific behaviour, and d) adult-like behaviour (Table 1 below).

Supplementary Material 1, Table 1. The names of behaviours, their descriptions, behavioural classes, and behavioural stages.

No.	Name of the behaviour/ activity	Behaviour code	Behaviour/activity description	Behavioural class	Behavioural stage
1	Attempt to feed	ATF	Attempt to feed on grass/browse but not successfully.	Feeding related	Preparatory adult behaviour
2	Coprophagy	COP	Eat elephant dung.	Feeding related	Calf-specific
3	Drink	DRK	Drink water using trunk to suck up water and deliver to mouth.	Feeding related	Adult-like
4	Drink with mouth	DRM	Use the mouth directly to drink from the water surface.	Feeding related	Preparatory adult behaviour
5	Feed	FED	Feed on grass/browse.	Feeding related	Adult-like

No.	Name of the behaviour	Behaviour code	Behaviour/activity description	Behavioural class	Behavioural stage
6	Walk-pluck	WSP	Sniff the ground for food or pluck grass while walking.	Feeding related	Adult-like
7	Investigate food	INV	Investigate a conspecific's food (in its mouth)/smell the grass that another individual is scraping off, but NOT take the other animal's food (which is TGC).	Feeding related	Preparatory adult behaviour
8	Push mammary gland	NPH	Push at a conspecific's (usually the mother's) mammary gland using the head.	Feeding related	Preparatory calf behaviour
9	Pull nipple	NPL	Pull at or holding a conspecific's (usually the mother's) nipple.	Feeding related	Preparatory calf behaviour
10	Search for nipple correctly	NPR	Try to locate a conspecific's (usually the mother's) nipple in the correct orientation, between the forelegs. This includes sniffing in the direction of a nipple also.	Feeding related	Preparatory calf behaviour
11	Search for nipple in the wrong direction	NPW	Try to locate a conspecific's (usually the mother's) nipple in the wrong direction, between the hind legs, or try to suck between the hind legs.	Feeding related	Preparatory calf behaviour
12	Allosuck	SUA	Suck on the mammary glands of an allomother.	Feeding related	Calf-specific
13	Suck from female	SUF	Suck on the mammary glands of a female conspecific other than the mother or allomother.	Feeding related	Calf-specific

No.	Name of the behaviour	Behaviour code	Behaviour/activity description	Behavioural class	Behavioural stage
14	Suck from mother	SUM	Suck on the mammary glands of the mother.	Feeding related	Calf-specific
15	Take grass from a conspecific	TGC	Take grass from a conspecific’s scraped-off grass pile.	Feeding related	Preparatory adult behaviour
16	Take grass from a spot	TGS	Pluck grass from the same spot where a conspecific (usually the mother or allomother) is already feeding.	Feeding related	Preparatory adult behaviour
17	Alert	ALR	Stand still on alert with the ears spread out.	Social interaction, play, exploration	Adult-like
18	Avoid	AVO	Turn away/walk away/run or stop fighting with other calves and move away when being approached by the other calf's mother or allomother.	Social interaction, play, exploration	Adult-like
19	Avoid and show back	AVB	Turn away and present the back (subordinate behaviour), including spreading legs or standing still to be checked.	Social interaction, play, exploration	Adult-like
20	Chase birds	CHB	Chase after or shoo away birds by lashing out with the trunk.	Social interaction, play, exploration	Adult-like
21	Chew	CHE	Try to chew or bite any body part of a conspecific but not in dominance.	Social interaction, play, exploration	Calf-specific
22	Chew trunk	CHT	Roll trunk and place in own mouth or chew trunk or suck on the trunk tip.	Social interaction, play, exploration	Calf-specific

No.	Name of the behaviour	Behaviour code	Behaviour/activity description	Behavioural class	Behavioural stage
23	Check	CHQ	Check a conspecific but not in dominance.	Social interaction, play, exploration	Adult-like
24	Extend trunk	EXT	Extend trunk towards a conspecific.	Social interaction, play, exploration	Adult-like
25	Head butt	HBT	Head butt another calf such that the two heads meet straight on and not one over the other (this is prolonged like the trunk wrestling of adults, but the trunks are not intertwined).	Social interaction, play, exploration	Adult-like
26	Hit with head	HIT	Raise head to place it on a (usually young) conspecific's head and then bring down the head on the other individual's head with some force.	Social interaction, play, exploration	Adult-like
27	Kick conspecific	KIC	Kick a conspecific.	Social interaction, play, exploration	Adult-like
28	Kick object	KIO	Kick an inanimate object or at birds.	Social interaction, play, exploration	Adult-like
29	Kick air	KKA	Kick out in the air.	Social interaction, play, exploration	Preparatory adult behaviour
30	Lash	LSH	Lash out with the trunk towards a conspecific or heterospecific.	Social interaction, play, exploration	Adult-like

No.	Name of the behaviour	Behaviour code	Behaviour/activity description	Behavioural class	Behavioural stage
31	Place	PLC	Place the trunk on an inanimate object on the ground to smell and investigate (this excludes smelling dung). This is different from play. Here, the object is not lifted off from the ground although the object may be touched or turned.	Social interaction, play, exploration	Adult-like
32	Play climb	PCL	Climb on or roll over a conspecific in play.	Social interaction, play, exploration	Calf-specific
33	Play mount	PLM	Mount another individual from behind in play.	Social interaction, play, exploration	Preparatory adult behaviour for males
34	Play with object	PLO	Play with grass, sticks (including biting sticks), or other objects.	Social interaction, play, exploration	Calf-specific
35	Raise head in play	PRH	Raise head and try to place on another individual (even if unsuccessfully) in play and not with force.	Social interaction, play, exploration	Preparatory adult behaviour
36	Pass	PTS	Pass from one side to the other of an adult or subadult through the space between that conspecific's trunk and forelegs or under the belly.	Social interaction, play, exploration	Calf-specific
37	Play with trunk	PWT	Play with one's own trunk (all trunk motions are included in this).	Social interaction, play, exploration	Calf-specific

No.	Name of the behaviour	Behaviour code	Behaviour/activity description	Behavioural class	Behavioural stage
38	Push	PSH	Push with head against any part of the body, other than the head, of another individual.	Social interaction, play, exploration	Adult-like
39	Roar	ROR	Produce a deep prolonged laryngeal call.	Social interaction, play, exploration	Adult-like
40	Rub	RUB	Rub against a conspecific and not in dominance.	Social interaction, play, exploration	Adult-like
41	Rumble	RUM	Emit a continuous resonant laryngeal call.	Social interaction, play, exploration	Adult-like
42	Run	RUN	Run (usually in the absence of social interaction).	Social interaction, play, exploration	Adult-like
43	Shake head	SHK	Shake head when disturbed or scared.	Social interaction, play, exploration	Adult-like
44	Shove	SHO	Use the body to shove against another individual's body.	Social interaction, play, exploration	Adult-like
45	Slide	SLD	Slide off an adult's or subadult's leg to eventually lie down.	Resting	Preparatory adult behaviour
46	Smell dung	SMD	Smell dung.	Social interaction, play, exploration	Adult-like
47	Sniff conspecific	SNF	Sniff near the genitals of a conspecific but without contact, and not in dominance.	Social interaction, play, exploration	Adult-like

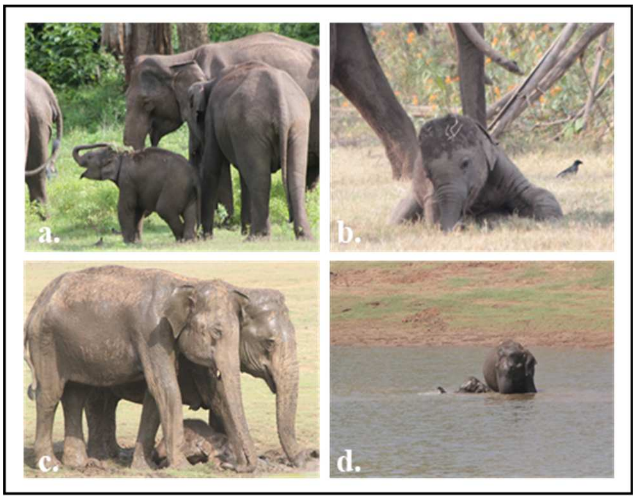
No.	Name of the behaviour	Behaviour code	Behaviour/activity description	Behavioural class	Behavioural stage
48	Sniff air	SNI	Sniff the air, including in the direction of a conspecific or heterospecific.	Social interaction, play, exploration	Adult-like
49	Walk-sniff	SNW	Raise trunk and sniff the air while walking.	Social interaction, play, exploration	Adult-like
50	Sniff oneself	SON	Sniff itself.	Social interaction, play, exploration	Adult-like
51	Turn towards call	TDC	Turn towards the direction of a call from a conspecific.	Social interaction, play, exploration	Adult-like
52	Trumpet	TMP	Emit a loud sound (usually ascending in frequency) through the trunk.	Social interaction, play, exploration	Adult-like
53	Touch	TOU	Use trunk to touch a conspecific on its head (but not the mouth which would be TRM) or body (but not genitals which would be CHK or CHQ), and not in dominance (dominance would be TCH).	Social interaction, play, exploration	Adult-like
54	Trunk in mouth	TRM	Place trunk tip in the mouth of a conspecific.	Social interaction, play, exploration	Adult-like
55	Trip	TRP	Fall down or trip while walking.	Social interaction, play, exploration	Preparatory adult behaviour
56	Twine trunk	TTW	Entwine trunk with that of a conspecific but not in dominance.	Social interaction, play, exploration	Adult-like

No.	Name of the behaviour	Behaviour code	Behaviour/activity description	Behavioural class	Behavioural stage
57	Walk	WLK	Walk but not in response to dominance.	Social interaction, play, exploration	Adult-like
58	Pick	PIC	Try to pick up an object (other than grass).	Social interaction, play, exploration	Preparatory adult behaviour
59	Hold	HLD	Hold an object in the trunk.	Social interaction, play, exploration	Adult-like
60	Circle	CRL	Walk around in a circle (spin around).	Social interaction, play, exploration	Calf-specific
61	Shift	SFT	Shift the body or trunk without moving away from the spot such that it ends physical contact with a conspecific.	Social interaction, play, exploration	Adult-like
62	Wait	WTG	Turn towards the direction of a conspecific and wait for it to follow or stop while walking and wait for a conspecific to join.	Social interaction, play, exploration	Adult-like
63	Being pushed	BPS	Being pushed by a conspecific. This code is used when the calf is not showing any behaviour of its own but is going through the interaction initiated by a conspecific.	Social interaction, play, exploration	Adult-like
64	Hiccup	HCU	Sudden jerking movement of a calf's head and trunk (appears involuntary) accompanied by a sound.	Physiological	Not applicable

No.	Name of the behaviour	Behaviour code	Behaviour/activity description	Behavioural class	Behavioural stage
65	Lean	LEN	Stand or sit leaning on a conspecific.	Resting	Preparatory adult behaviour
66	Lie down	LIE	Lie down on the ground.	Resting	Adult-like
67	Sit	SIT	Sit down with hindlegs bent and the rear resting on the ground.	Resting	Adult-like
68	Squat	SQT	Bend hindlegs and prepare to sit.	Resting	Adult-like
69	Stand	STD	Stand still relaxed.	Resting	Adult-like
70	Yawn	YAW	Slow opening of the mouth, followed by the mouth being in a wide-open posture for a brief time, and subsequent quick closure of the mouth.	Physiological	Not applicable
71	Stretch	SRT	Stretch body usually after getting up or before lying down.	Resting	Adult-like
72	Get up	GUP	Try to get up to sitting or standing position after lying down.	Resting	Adult-like
73	Bathe	BTH	Lie down in the water.	Grooming related	Adult-like
74	Defecate	DEF	Defaecate.	Physiological	Not applicable
75	Extract and spray	ESP	Use trunk to extract liquid from the pharyngeal pouch and spray it on oneself.	Grooming related	Adult-like
76	Switch flies	FLY	Keep away flies using the tail or trunk.	Grooming related	Adult-like
77	Roll	ROL	Roll in the mud or on grass.	Grooming related	Adult-like

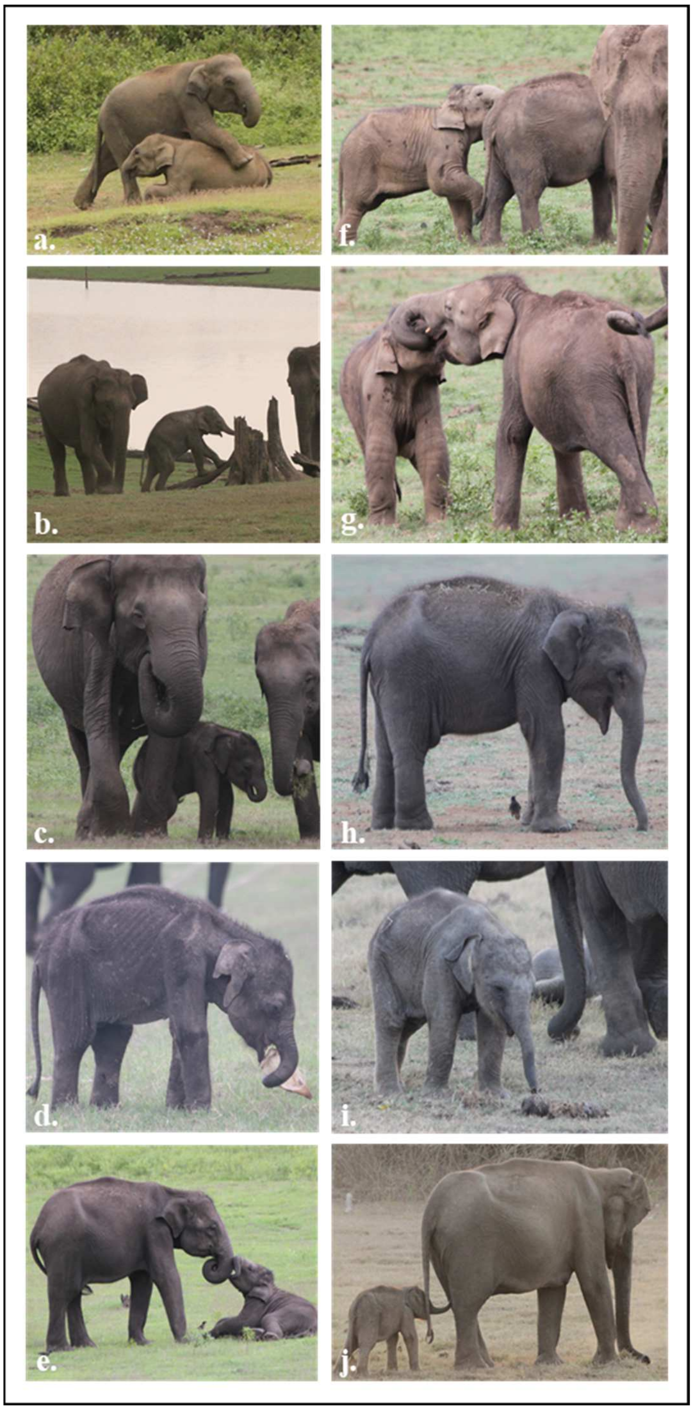
No.	Name of the behaviour	Behaviour code	Behaviour/activity description	Behavioural class	Behavioural stage
78	Scratch	SCR	Scratch itself with the trunk, leg or tail.	Grooming related	Adult-like
79	Scratch against	SIO	Scratch itself with an inanimate object or rub itself against a stump or tree.	Grooming related	Adult-like
80	Splash	SPL	Use trunk to splash water onto itself.	Grooming related	Adult-like
81	Spray	SPR	Spray dust onto itself using the trunk.	Grooming related	Adult-like
82	Splash urine	SPU	Splash a conspecific's urine onto itself.	Grooming related	Calf-specific
83	Beat tail	TLS	Beat tail against a stump or tree.	Grooming related	Adult-like
84	Touch itself	TWT	Use trunk to touch itself on any part of the body except inside mouth (which is CHE).	Grooming related	Adult-like
85	Urinate	URI	Urinate	Physiological	Not applicable

Supplementary Material 1, Figure 1. Calves and juveniles of different age classes showing feeding related behaviours belonging to four behavioural stages: a) investigate food in a conspecific's mouth and b) taking grass from a conspecific belong to preparatory adult behaviour; c) locating nipple in the correct direction and d) locating the nipple in the wrong direction belong to preparatory calf behaviour; e) coprophagy, f) sucking from a non-mother conspecific, g) holding the nipple, and h) sucking from the mother belong to calf-specific behaviours; and, i) plucking and collecting grass, j) chewing on grass, k) calf on the left drinking water using the mouth and l) drinking water using the trunk.



Supplementary Material 1, Figure 2. Adult-like grooming related behaviours shown by calves and juveniles: a) spraying dust/grass onto oneself, b) rolling in grass, c) wallowing in mud, and d) bathing.

Supplementary Material 1, Figure 3. Resting behaviours shown by calves can be categorized into two behavioural stages: a) leaning on a conspecific while resting belongs to preparatory adult behaviour; b) trying to sit down, c) sitting down, and d) lying belong to adult-like behavioural expression.



Supplementary Material 1, Figure 4. Social interactions (which includes play and explorative behaviours) of calves and juveniles belong to three behavioural stages: behaviours like a) climbing on a conspecific, b) investigating an inanimate object, c) chewing one's own trunk, d.) playing with an object, and, e) trying to bite/chew any part of a conspecific, belong to calf-specific category; f) raising one's head to place it on a conspecific belong to preparatory adult behaviour; and, behaviours like, g) placing trunk tip in the mouth of a conspecific, h) sniffing the ground, i) smelling dung, j) checking a conspecific, belong to adult-like behaviours.

Supplementary Material 2. Details of calves/juveniles sampled for observing trunk motor control and lateral bias.

The identities and age-sex categorisation of calves/juveniles sampled for observing lateralisation in trunk use are shown below (Table 1).

Supplementary Material 2, Table 1. The identities and age-sex categorisation of calves/juveniles sampled for observing lateralisation in trunk use and the time for which they were scored.

S.No.	Name	Sex	Age class (months)	Duration scored (sec)
1	Althea_2015_F	Female	>12	1200
2	Emerald_2016_F	Female	6-12	899
3	Genette_2017_F	Female	<3	600
4	Georgina_2017_F	Female	<3	600
5	Hannah_2016_F	Female	<3	300
	Hannah_2016_F		3-6	300
	Hannah_2016_F		6-12	301
6	Ilaena_2016_F	Female	<3	300
	Ilaena_2016_F		3-6	300
	Ilaena_2016_F		6-12	300
7	Ilsa_2016_F	Female	<3	602
	Ilsa_2016_F		3-6	302
	Ilsa_2016_F		6-12	300
8	Ketki_2016_F	Female	<3	300
	Ketki_2016_F		3-6	300
	Ketki_2016_F		6-12	600
9	Kokila_2015_F	Female	<3	300
	Kokila_2015_F		3-6	300
	Kokila_2015_F		6-12	300
	Kokila_2015_F		>12	300
10	Leena_2017_F	Female	<3	600
	Leena_2017_F		3-6	600
11	Linda_2016_F	Female	<3	300
	Linda_2016_F		6-12	903
	Linda_2016_F		>12	300
12	Lynn_2015_F	Female	6-12	901
	Lynn_2015_F		>12	900

S.No.	Name	Sex	Age class (months)	Duration scored (sec)
13	Marlene_2015_F	Female	3-6	300
	Marlene_2015_F		6-12	300
	Marlene_2015_F		>12	600
14	Salvia_2016_F	Female	<3	300
15	Suhrita_2016_F	Female	<3	303
	Suhrita_2016_F		3-6	300
16	Zarin_2015_F	Female	3-6	300
17	Alena_2017_M	Male	<3	300
	Alena_2017_M		3-6	600
18	Camila_2016_M	Male	<3	300
	Camila_2016_M		3-6	300
19	Jacintha_2015_M	Male	>12	2406
20	Kasturi_2018_M	Male	<3	600
21	Kausalya_2015_M	Male	3-6	597
	Kausalya_2015_M		6-12	904
	Kausalya_2015_M		>12	1500
22	Keerthana_2016_M	Male	6-12	600
23	Namrata_2017_M	Male	3-6	600
24	Narmada_2015_M	Male	3-6	300
	Narmada_2015_M		6-12	300
25	Sarayu_2016_M	Male	3-6	599
26	Serena_2016_M	Male	<3	300
	Serena_2016_M		3-6	300
	Serena_2016_M		>12	903
27	Suveera_2016_M	Male	<3	300
	Suveera_2016_M		3-6	300
28	Valerie_2016_M	Male	<3	602
	Valerie_2016_M		3-6	300
	Valerie_2016_M		>12	300
29	Vanessa_2015_M	Male	<3	303
	Vanessa_2015_M		3-6	600
30	Zerad_2015_M	Male	3-6	300
	Zerad_2015_M		6-12	302

Supplementary Material 3. Results of repeated measures ANOVAs to examine the effect of multiple sampling days of the same calves/juveniles within the same age class.

As explained in the main text, since our dataset included repeated observations on the same individuals within and across age classes, we carried out repeated measures ANOVAs on the variable examined for lateralisation (such as logit proportion of clockwise successful or unsuccessful trunk movement, logit proportion of right side trunk placement in the mouth, etc.) by the same individuals, across days but within the same age class (<3 months old, 3-6 months, 6-12 months, and >12 months). If there was no variability across days sampled within the same age class, one sample from each individual during that age class could be used to construct the distributions of lateral bias index or strength. Results from the different repeated measures ANOVAs are given in the tables below. There was no significant effect of day of sampling (for individuals in the same age class) on the logit proportions of clockwise successful and unsuccessful trunk movements, right side mouth placement, and right side body touch, and there was only borderline significance of day when the logit proportion of straight trunk movement was considered.

Supplementary Material 3, Table 1. Results of repeated measures ANOVAs on the logit proportion of clockwise successful trunk movement by the same individuals, across days but within the same age class. The analysis was carried out with sex and age class as categorical factors separately for want of adequate sample size to examine them in a combined manner.

Effect	*SS*	*df*	*MS*	*F*	*P*
Intercept	2.774	1	2.774	0.068	0.798
Sex	118.050	1	118.050	2.880	0.108
Error	696.763	17	40.986		
Day	2.486	1	2.486	1.343	0.262
Day x sex	0.357	1	0.357	0.193	0.666
Error	31.457	17	1.850		

Effect	*SS*	*df*	*MS*	*F*	*P*
Intercept	6.326	1	6.326	0.118	0.736
Age class	9.901	3	3.300	0.062	0.979
Error	804.911	15	53.661		
Day	4.931	1	4.931	3.066	0.100
Day x age class	7.689	3	2.563	1.593	0.233
Error	24.125	15	1.608		

Supplementary Material 3, Table 2. Results of repeated measures ANOVAs on the logit proportion of clockwise unsuccessful trunk movement by the same individuals, across days but within the same age class. Sex and age class were used as categorical factors. Significant results are marked in bold.

Effect	*SS*	*df*	*MS*	*F*	*P*
Intercept	**185.131**	**1**	**185.131**	**5.725**	**0.033**
Sex	70.991	1	70.991	2.195	0.162
Age class	100.515	3	33.505	1.036	0.409
Sex x Age class	124.719	3	41.573	1.286	0.321
Error	420.389	13	32.338		
Day	0.620	1	0.620	0.096	0.761
Day x sex	0.592	1	0.592	0.092	0.766
Day x age class	22.347	3	7.449	1.159	0.363
Day x sex x age class	41.034	3	13.678	2.128	0.146
Error	83.573	13	6.429		

Supplementary Material 3, Table 3. Results of repeated measures ANOVAs on the logit proportion of straight trunk movement by the same individuals, across days but within the same age class. Sex and age class were used as categorical factors. Significant results are marked in bold.

Effect	*SS*	*df*	*MS*	*F*	*P*
Intercept	**107.389**	**1**	**107.389**	**51.922**	**0.000**
Sex	0.137	1	0.137	0.066	0.801
Age class	**85.597**	**3**	**28.532**	**13.795**	**0.000**
Sex x Age class	9.501	3	3.167	1.531	0.253
Error	26.888	13	2.068		
Day	**7.877**	**1**	**7.877**	**4.919**	**0.045**
Day x sex	4.134	1	4.134	2.582	0.132
Day x age class	1.485	3	0.495	0.309	0.818
Day x sex x age class	16.227	3	5.409	3.378	0.051
Error	20.818	13	1.601		

Supplementary Material 3, Table 4. Results of repeated measures ANOVAs on the logit proportion of right side mouth placement by the same individuals, across days but within the same age class. The analysis was carried out with sex and age class as categorical factors separately for want of adequate sample size to examine them in a combined manner.

Effect	*SS*	*df*	*MS*	*F*	*P*
Intercept	53.590	1	53.590	2.199	0.160
Sex	81.157	1	81.157	3.331	0.089
Error	341.135	14	24.367		
Day	3.394	1	3.394	0.535	0.476
Day x sex	6.803	1	6.803	1.073	0.318
Error	88.739	14	6.339		

Effect	*SS*	*df*	*MS*	*F*	*P*
Intercept	34.326	1	34.326	1.062	0.322
Age class	2.113	2	1.056	0.033	0.968
Error	420.179	13	32.321		
Day	3.038	1	3.038	0.428	0.525
Day x age class	3.185	2	1.592	0.224	0.802
Error	92.357	13	7.104		

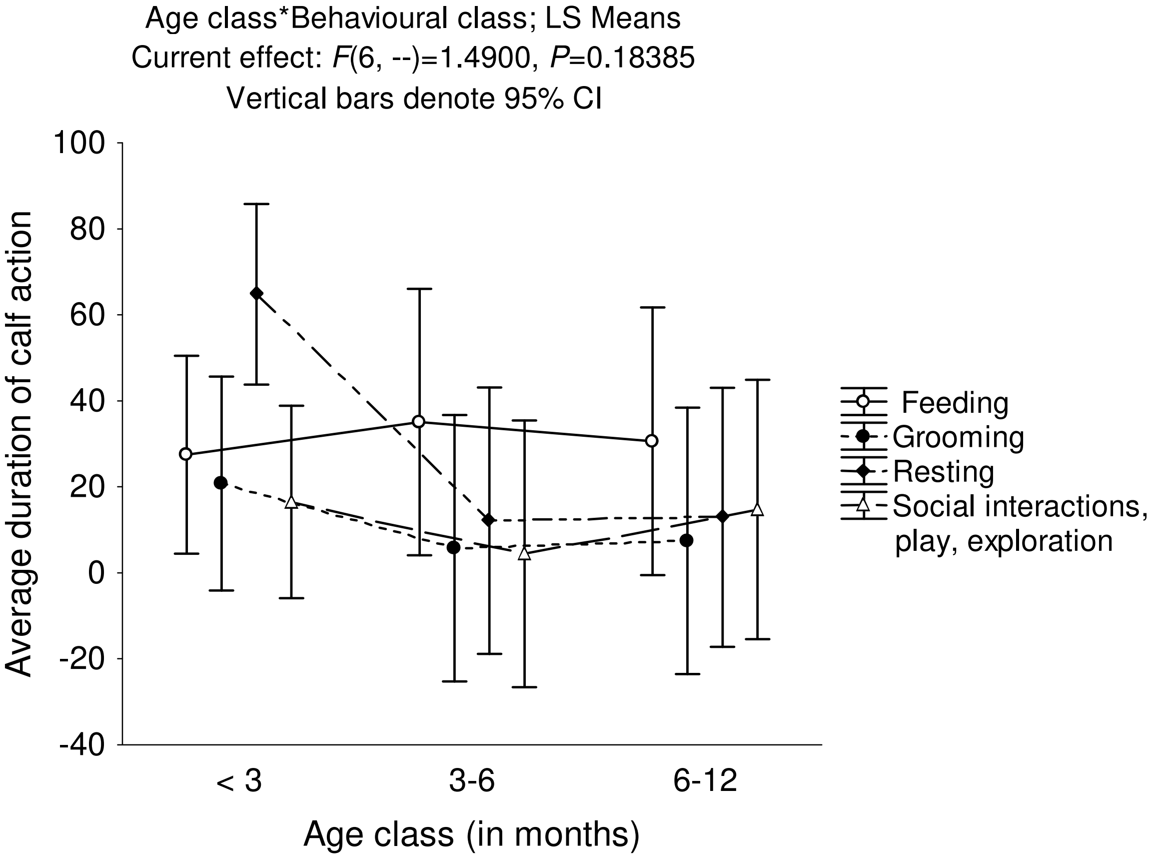
Supplementary Material 3, Table 5. Results of repeated measures ANOVAs on the logit proportion of right side body touch by the same individuals, across days but within the same age class. The analysis was carried out with sex and age class as categorical factors separately for want of adequate sample size to examine them in a combined manner.

Effect	*SS*	*df*	*MS*	*F*	*P*
Intercept	7.663	1	7.663	1.381	0.254
Sex	14.244	1	14.244	2.567	0.126
Error	105.445	19	5.550		
Day	3.646	1	3.646	0.375	0.547
Day x sex	4.648	1	4.648	0.478	0.498
Error	184.577	19	9.715		

Effect	*SS*	*df*	*MS*	*F*	*P*
Intercept	4.708	1	4.708	0.715	0.409
Age class	7.761	3	2.587	0.393	0.760
Error	111.929	17	6.584		
Day	5.087	1	5.087	0.458	0.507
Day x age class	0.566	3	0.189	0.017	0.997
Error	188.659	17	11.098		

Supplementary Material 4. Effect of age, behavioural class, and individual identity on behaviour duration.

As mentioned in the main text, we carried out a GLM to examine the effects of age-class and behavioural class of calf action (fixed factors) and calf identity (random factor) on behaviour duration. We found no significant effect of age-class ($F_{2,181}$=1.658, P=0.193), behavioural class of calf action ($F_{3,181}$=1.986, P=0.118) or interaction between age class and behavioural class of calf action ($F_{6,181}$=1.490, P=0.184) on behaviour duration (see Figure 1 below).



Supplementary Material 4, Figure 1. Average duration of calf action under feeding, grooming, resting, and social interaction, play, and exploration behavioural classes by calves <3 months, 3-6 months, and 6-12 months old. Error bars are 95% CI.

CHAPTER 4

Proximity and Behavioural Interactions between Calves and Conspecific Females in the Kabini Asian Elephant Population, Southern India

Title: Proximity and behavioural interactions between calves and conspecific females in the Kabini Asian elephant population, southern India

Authors: T. Revathe and T.N.C. Vidya*

Affliation: Evolutionary and Organismal Biology Unit, Jawaharlal Nehru Centre for Advanced Scientific Research (JNCASR), Bengaluru, India.

* Corresponding author.
Email: tncvidya@jncasr.ac.in; ORCID iD: 0000-0002-7143-9008.

Manuscript to be posted on bioRxiv

Author contributions

T. Revathe and T.N.C. Vidya conceived this study. TR collected field data and carried out the analyses. TR primarily and TNCV wrote the manuscript.

Abstract

Spatial positioning and interactions between young ones and conspecifics are important in understanding the ontogeny of social relationships, including that between an allomother and a young one. We studied the spatial positions and behavioural interactions of 20 calves up to 6 months old with conspecific subadult and adult females in free-ranging Asian elephants (*Elephas maximus*) in the Kabini elephant population (Nagarahole and Bandipur National Parks), southern India, to identify allomothers and to understand the nature of calf-female relationships. Calves initiated more proximity contacts and behavioural interactions than conspecific females did towards calves. We found significant main or interaction effects of calf age-class (newborns: <3 months old; infant calves: 3-<6 months old) on proximity to conspecifics and calf-conspecific behaviours, with newborns being closer to their mothers than were infants, and newborns being part of more interactions with conspecifics than were infants. We did not find an effect of calf sex on calf-conspecific behaviours in these young calves, but the sample sizes were limited in such tests. Calves spent most of their time near their mothers and one other female, whom we call an escort. Calves interacted with mothers and escorts significantly more frequently than with other females in their groups, and initiated similar numbers of interactions towards their mothers and escorts. The number of non-suckling interactions initiated by calves was even higher towards escorts than towards the mothers. Escorts in turn initiated more interactions towards calves than the mothers or other females did. Feeding and social interactions were more frequently initiated by calves than resting-related interactions. Calves not only initiated more interactions, but also terminated more interactions than conspecifics. Mothers and escorts did not significantly differ in the proportions of calf-initiated interactions that they terminated, or in the proportions of positive and negative responses they showed towards calves, but other females showed a higher proportion of negative interactions than mothers and escorts, and a lower proportion of positive than negative responses towards calves. Thus, calves and escorts seem to have an important relationship, even closer than that with mothers at times, and escorts can be considered allomothers. Thus, differentiated social relationships are found at an early age in elephants, which may develop further as they age.

Keywords

Allomaternal care, calf and female interactions, escort, Kabini, Asian elephants.

Introduction

A central component of ontogeny in social species is the development of social relationships. These relationships may be heterogeneous from a young age itself or become gradually differentiated over time (Berman 1982a,b, de Waal 1996, Berman *et al.* 1997). In many social mammals, individuals apart from the mother/parents may take care of the young, and this is called alloparental care (Wilson 1975) or allocare (for example, Rowell *et al.* 1964, McKenna 1979 in primates, Pusey and Packer 1994 in the African lion, Estes and Goddard 1967 in the African wild dog, Paul *et al.* 2014, Pal *et al.* 2021 in dogs, Rood 1978, Clutton-Brock *et al.* 2000, Hodge 2005 in mongooses, Whitehead 1996, Gero *et al.* 2013, Hill and Campbell 2014 in cetaceans, Lee 1987 in the African savannah elephant). The development and survival of young may be affected by the presence of or interactions with such alloparents and social partners (Hrdy 1976, Lee 1987, Hodge 2005). In contrast to these positive or primarily affiliative interactions, interactions between some females and young ones that are not their own may also be primarily aggressive, or fall somewhere along the continuum of the two depending on the age and reproductive status of the females (Rowell *et al.* 1964, Nicolson 1987). Thus, studies of the frequencies and nature of interactions between young ones and various conspecifics contribute to an ontogenic understanding of the patterning of social relationships.

Female social structure and the costs of interacting with group members are thought to influence the frequency and nature of young-conspecific interactions. For example, in matrilineal kin-based societies, allocare, if present, is expected to be shown by adult females and not males, and there may be differences amongst male and female offspring in their interactions with group members, acting as a precursor to their sex-specific adult lifestyles (Lee and Moss 2014). Socioecological theory, which was proposed to explain the evolution of different kinds of societies in relation to ecological conditions such as resource-risk distributions (see Wrangham 1980, van Schaik 1989, Sterck *et al.* 1997, Isbell and Young 2002), has also been extended to explain how food competition regime and the ensuing dominance structure may affect the nature of interactions of females with young ones in a social unit and select for or against allocare (Maestripieri 1994a, Chism 2000). In societies in which female relationships are primarily based on contest competition within groups (such as a resident nepotistic society), females are expected to show relatively more aggressive than affiliative interactions towards unrelated young (Maestripieri 1994a). Aggressive behaviours towards unrelated infants may especially be shown by females who have their own dependent young (Rowell *et al.* 1964, Maestripieri 1994b). When within-group contest is low, with dominant females being more tolerant of the subordinates in the group due to high between-group contest (resident-nepotistic-tolerant society), the relative frequency of aggressive to affiliative interactions by females towards unrelated young is expected to be lower than in the former case (Maestripieri 1994a). The potential social risks to the young ones from unrelated or distantly-related females within social units as a result of female dominance structure may also influence the permissiveness of mothers in the movement of their newborns or their handling by other females (Rowell *et al.* 1964, McKenna 1979, Maestripieri 1994a), especially in altricial species.

Alloparental care in mammals is also often associated with traits such as prolonged period of offspring dependency, well-defined parental care and high levels of parental investment, low life-time reproductive success, and complex social organisation with well-established kinship ties (Wilson 1975, Riedman 1982). Young adult or subadult, nulliparous females often act as allomothers/escorts/babysitters in several species (for example, Hrdy 1976, Lee 1987, O'Brien and Robinson 1991, Förster and Cords 2005, Konrad *et al.* 2019), obtaining direct or indirect benefits, or simply due to natal attraction if the allocare is not costly (Riedman 1982, Chism 2000). The frequency of initiation of interactions by young ones and allomothers towards each other is expected to vary with the degree of neonatal development (Hill and Campbell 2014). Altricial neonates, at one end of the continuum, are poorly developed at birth and are highly dependent on their mothers for nutrition, thermoregulation, locomotion, and sensory processing; whereas precocial neonates, at the other end, have high developmental maturity and show independence since birth in many or all the above-mentioned traits (Derrickson 1992). Thus, in altricial species, the mother and allomother(s) take more initiative in maintaining proximity and initiating interactions with the neonates than vice versa, and this dynamic shifts as neonates grow and achieve locomotory independence (for e.g., see Spencer-Booth 1968, Hinde and Spencer-Booth 1967, Mann and Smuts 1999, Kumar and Solanki 2014).

Elephants have a long period of offspring-dependency, high maternal investment, and complex social organisation, and allomothering has been reported in captive and wild African savannah elephants (*Loxodonta Africana*; Woodford and Trevor 1970, Douglas-Hamilton 1972, Dublin 1983, Lee 1987, Garaï 1997, Lee and Moss 2011), a wild population of African forest elephants (*Loxodonta cyclotis*; Chelluri 2009), and captive (Williams 1950, Eisenberg 1980, Rapaport and Haight 1987), semi-captive (Gadgil and Nair 1984), and wild (McKay 1973, Jayantha *et al.* 2009, Vidya 2014, Webber 2017) Asian elephant populations. Allomothering has been conjectured to be important in the evolution and cohesiveness of female elephant societies (Douglas-Hamilton and Douglas-Hamilton 1975, Wilson 1975, Dublin 1983, Gadgil and Nair 1984). However, the only detailed studies on allomothering in elephants come from the Amboseli African savannah elephant population (Lee 1987, Lee and Moss 2011), and, to a lesser extent, semi-captive Asian elephants in southern India (Gadgil and Nair 1984) and wild African forest elephants in Dzanga-Ndoki National Park (Chelluri 2009). In the Amboseli African savannah elephant population, calves (under 2 years of age) had non-random neighbours and were spatially closer to females than males (Lee 1987, Lee and Moss 2011). High frequencies of interactions were seen between calves and others in the group, but although calves interacted to a greater extent overall with non-mothers (females apart from the calf's mother) than their mother, the single highest rate of interaction was with the mother. Allomothers, who assisted calves, were generally older female siblings, and allosuckling was rare and generally from nulliparous females (Lee 1987). Due to smaller group sizes in the African forest elephant compared to the African savannah elephant, it was expected that interactions with calves in the former would mostly involve the mother, which would be far more frequent than the interactions with non-mothers (Chelluri 2009). However, it was found that calf-mother interactions occurred at similar frequencies and were of similar nature in the two species (Chelluri 2009). In semi-captive Asian elephants, Gadgil and Nair (1984) found that calves showed a preference for interacting with a specific non-mother female in the group. Non-mother adult females were found to be spatially closer to certain calves, and allosuckling was also observed.

Asian elephants live in matrilineal societies (Sukumar 1989). Female Asian elephants in southern India are organized into distinct clans, with the clan being the most inclusive level of social organization (Nandini *et al.* 2018). Males disperse away from their natal clans as they reach puberty and do not permanently associate with female groups thereafter (Sukumar 1989, Desai and Johnsingh 1995, Keerthipriya *et al.* 2021). Fission-fusion dynamics (see Aureli *et al.* 2008) are seen within clans (Sukumar 1989, Nandini *et al.* 2017, 2018), and between-clan interactions are almost always agonistic in the Kabini Asian elephant population (Shetty 2016, Gautam and Vidya 2019), where the current study was carried out (see Methods). As a result of fission-fusion dynamics, all the females of a clan are not always together, and a set of females seen together is called a group (see Methods, Nandini *et al.* 2018). Elephants are uniparous, and calves are precocial at birth but are nutritionally and socially dependent on their mothers for long periods of time (Nair 1989, Revathe *et al.* 2020). Young ones are weaned only around 4-5 years of age or after the birth of a sibling, whichever is earlier (Mar *et al.* 2012). Calves (considered as individuals under one year of age here because of high mortality until that time; Kabini Elephant Project unpublished data) can be predated by tigers (Williams 1950).

As elephant calves are precocial (Nair 1989, Revathe *et al.* 2020) and are quick to explore their surroundings (Nair 1989), we expected calves to initiate more interactions towards conspecifics than conspecifics towards calves. However, if there was natal attraction, one might expect conspecific females to initiate more interactions towards calves. In that case, one would also expect multiple females, and not only the mother and allomother(s) to initiate those interactions. Higher initiation of interactions by calves than adult females was seen in semi-captive elephants in southern India (Gadgil and Nair 1984), but they were not natural groupings of related females.

A restriction on group size and feeding competition have been found in the Kabini Asian elephant population (Nandini *et al.* 2017, 2018, Gautam 2019, Gautam and Vidya 2019). Therefore, it was possible that calves might not have many other individuals to interact with in groups or, even if they did, that those individuals might not spend time interacting with calves due to feeding competition. This would suggest that the number of calf-conspecific interactions in Kabini might be lower than that seen in the African savannah elephant. However, group sizes were larger in the presence of calves (Chapter 2) and, since there was a weakly-expressed dominance hierarchy within clans in Kabini (Shetty 2016, Gautam 2019), compared to that in Amboseli (Archie *et al.* 2006) and calves are not direct competitors of adult females, it was also possible that calf-conspecific female proximity and behavioural interactions would be seen with multiple adult females in Kabini. On the other hand, even if multiple females interacted with calves, it was likely that all of them would not show equal amounts of care.

We, therefore, examined calf-conspecific proximity and behavioural interactions in the Asian elephant (*Elephas maximus*) by addressing the following questions in order to find out if females showed allomaternal care, if so, how comparable was allomaternal care to maternal care, and to obtain baseline data to eventually understand the ontogeny of social relationships through initially comparing behaviours of different categories of females towards calves and *vice versa*.

Calf-conspecific spatial interactions

a) Do calves or conspecifics initiate and terminate more proximity contacts, and is there a difference across conspecific categories (mothers, escorts, other females; see Methods) in this?
b) How do calf age-class and conspecific category affect calf-conspecific proximity?

Calf-conspecific behavioural interactions

c) Do calves or conspecifics initiate more behavioural interactions, and is this affected by calf age-class and conspecific category?
d) Do calves initiate a greater number of interactions of certain behavioural classes towards particular conspecific categories?
e) Do calves or conspecifics terminate interactions more frequently and is there a difference across conspecific categories in the kinds of responses shown towards calf-initiated interactions?
f) Do the results from the questions above remain unchanged when only non-suckling interactions rather than all interactions initiated by calves are considered (as calves are dependent on the mother but not on others for milk)?

Methods

Field data collection

We carried out field data collection from December 2015 to June 2018 in Nagarahole National Park and Tiger Reserve and Bandipur National Park and Tiger Reserve in southern India. These two parks primarily comprise dry and moist deciduous forests, and are separated by the Kabini reservoir, resulting from the construction of the Beechanahalli Dam on the River Kabini. During the dry season (mid-December to mid-June), as the water recedes, abundant fresh grass becomes available in the reservoir area, resulting in a high density of elephants and other herbivores around the backwaters. Tiger density is also high in the area (Jhala *et al.* 2008).

We carried out field sampling, following fixed sampling routes, from ~6:30 AM to ~5:45-6:45 PM, depending on daylight hours and permits during the wet and dry seasons (see Nandini *et al.* 2017 for 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 (see Nandini *et al.* 2018). We aged, sexed, and identified the individuals seen based on natural physical characteristics (see Vidya *et al.* 2014). The Kabini Elephant Project has recorded hundreds of individually identified elephants from 2009 (Vidya *et al.* 2014). Animals born before the beginning of the study were aged based on shoulder height, body size and other characteristics, and in comparison to semi-captive elephants in the area of known ages (Vidya *et al.* 2014). Individuals were age-classified 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 paper, since we examine calves of different ages, we refer to those less than three months old as newborn calves and to those from 3-<6 months of age as infant calves.

Since the area around the Kabini backwaters provides good visibility, the majority of the behavioural data presented here were obtained from this area. We used focal animal sampling (Altmann 1974) to record interactions between calves and conspecifics in a group. 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 so as 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 separately. 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. We refer to females other than the focal calf's mother and escort(s) in a focal session as 'other females'.

The purpose of using the three categories of females was to find out whether females that showed coordinated movement with the calf (i.e., escorts) also showed more affiliative behaviour than other females. If that were the case, coordinated movement could be used as a proxy for allomothering. This was also done to avoid circularity in quantifying allomothering behaviour in females who were assumed to be allomothers based on such behaviour. Thus, we first defined escorts using coordinated movement and then measured various escort-calf behaviours. Mother-escort comparison in their behaviours towards calves and *vice versa* allowed us to understand how comparable allomaternal care is to maternal care if escorts indeed showed allomaternal care. The ‘Other females’ category was used for comparison in the analyses (see data analysis section) to satisfy the purpose of running complete models and quantifying the behaviour of other females, which had not been previously studied in any Asian elephant population. This also set the stage to understand the ontogeny of differential social relationships.

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). 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 for the reasons mentioned above.

Calf-conspecific proximity initiation and leaving

We scored 3 focal videos per calf to look at calf position changes on a second-by-second basis for 20 calves, 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 (1 hour in total per calf; 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 1 calf-body length. A calf could be near multiple individuals simultaneously. 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 leaving by a calf, and L_{cf} by a conspecific) was recorded when the calf-conspecific distance increased from ≤1 to >1 calf-body length. Hinde’s proximity index (Hinde and Spencer-Booth 1967, see Supplementary Material 3) was calculated as follows to see whether calves showed more approaches or leavings towards each conspecific of interest: Hinde's index = the percentage of approaches (% Ap_c) made by the calf towards a conspecific – the percentage of leavings made by that calf away from that conspecific (% L_c). Positive Hinde's index values (>0 to +100) indicate that the calf more frequently approached than left the conspecific. We also calculated Brown's proximity index (Brown 2001; Supplementary Material 3) to measure the relative contributions of the calf and conspecific to changes in proximity contacts between the pair: Brown's proximity index = $\frac{Ap_c+L_c}{Ap_c+L_c+Ap_{cf}+L_{cf}} \times 100$. Brown's index values (which range from 0 to 100) above 50 indicate that the calf contributed more than the conspecific to changes in proximity, and *vice versa*. While Brown's (2001) 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, as both would give a Brown's index greater than 50.

Since a focal calf could have more than one escort within a focal sample, the Hinde's index and Brown's index in such cases 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. Since the number of calves for which the index could be calculated for all three conspecific categories was small, 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 then separately 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 higher. Here, conspecific category (fixed factor with 2 levels: Mother, Escort), calf identity (random factor), and their interaction were examined. Only calves that had Hinde's and Brown's index values in at least two of their focals were used.

Calf-conspecific proximity

During each 20-minute focal, we took a scan every 4 minutes to obtain six independent calf positions in terms of who was 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. 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 number of scans near all the females in that conspecific category / number of females in that conspecific category x 6 (i.e., the number of total scans in the focal). As a result of this and simultaneous proximity of calves to more than one category of conspecifics sometimes, the three proportions did not add up to 1.

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 used for proximity, 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. The behaviours shown were classified into three behavioural 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 the conspecific-initiated interactions, as well as the responses shown by conspecifics to 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. It must be noted that as in the case of proximity, it was possible for more than one conspecific to simultaneously interact with the same calf.

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 checked for interaction effects.

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

We found that the number of calf-initiated interactions was much higher than the number of conspecific-initiated interactions (see Results), and wanted to find out whether the former varied based on behavioural class of interaction and conspecific category. Therefore, 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 of each focal calf, we 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 (there were insufficient data for other females) were compared. 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). As calves initiated interactions towards other females in their groups in only some of their focals, we analysed the proportions of calf-initiated interactions that elicited a positive or a neutral response only from mothers and escorts. 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

Since only (or primarily) the mothers provide milk to their calves in Asian elephants, we modified the original dataset by removing all the suckling-related interactions that the focal calves initiated towards the conspecifics. We used this to find out if calves interacted primarily with their mothers, even if suckling was not considered. The same analyses carried out on calf-conspecific interactions were also carried out on this modified dataset.

Thus, to check if calves behaved in a similar manner towards different kinds of conspecific females, we compared calf-conspecific proximity initiation and leaving, calf-conspecific proximity, and the number of calf-initiated interactions, overall and under different behavioural classes. To check if 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. 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) *Calf proximity contacts*

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. (In certain cases, 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.) There was no significant difference in the calf Hinde's (Friedman ANOVA: χ^2= 2.000, *N*=7, *df*=2, *P*=0.368, Figure 1a) or Brown's (Friedman ANOVA: χ^2= 4.571, *N*=7, *df*=2, *P*=0.102, Figure 1b) proximity indices across 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 calf ID ($F_{16,54}$=0.992, P=0.479), conspecific category ($F_{1,16}$=3.849, P=0.067), or their interaction ($F_{16,54}$=0.724, P=0.757) (Figure 1c). 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 was more likely to approach than to leave escorts (confidence intervals in Figure 1c)

The average Brown's proximity indices of calves were greater than 50 with the mother, escort, and other females (Figure 1b,d), indicating that calves contributed more than the conspecifics to changes in proximity. ANOVAs on the logit Brown's index with mothers and escorts (17 calves, 44 focals) showed no significant effect of calf ID ($F_{16,54}$=1.484, P=0.140), conspecific category ($F_{1,16}$=0.888, P=0.360), or their interaction ($F_{16,54}$=0.365, P=0.985) (Figure 1c). Due to low sample size, the effects of calf age and sex on proximity initiation could not be checked.

b) *Calf-conspecific proximity*

Calves spent a very small proportion of their time without any female conspecific within a reachable distance (Average ± 95% CI: newborn calves: 0.033 ± 0.033; infant calves: 0.044 ± 0.027). There was no significant effect of calf age-class on the proportion of scans that calves spent near conspecific females (ANOVA: $F_{1,18}$=0.205, P=0.656), with newborn calves (average ± 95% CI=0.475 ± 0.076) and infant calves (0.439 ± 0.069) spending similar proportions of scans near conspecific females. 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 and 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, Figure 2) or other females (P<0.001, Figure 2), 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 they 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; Figure 2), but both spent similar proportions of time near their escorts

(P=0.871; Figure 2), and near other females (P=0.529; Figure 2). There was no significant effect of calf identity ($F_{18,120}$=0.984, P=0.482) or its interaction with conspecific category ($F_{36,120}$=1.389, P=0.097) on the proportion of scans that calves spent near a conspecific. The sample sizes were not large enough to include calf sex in the ANOVA above. However, when tested for infant calves separately, there was no effect of calf sex on the proportion of scans spent near conspecifics (Supplementary Material 5).

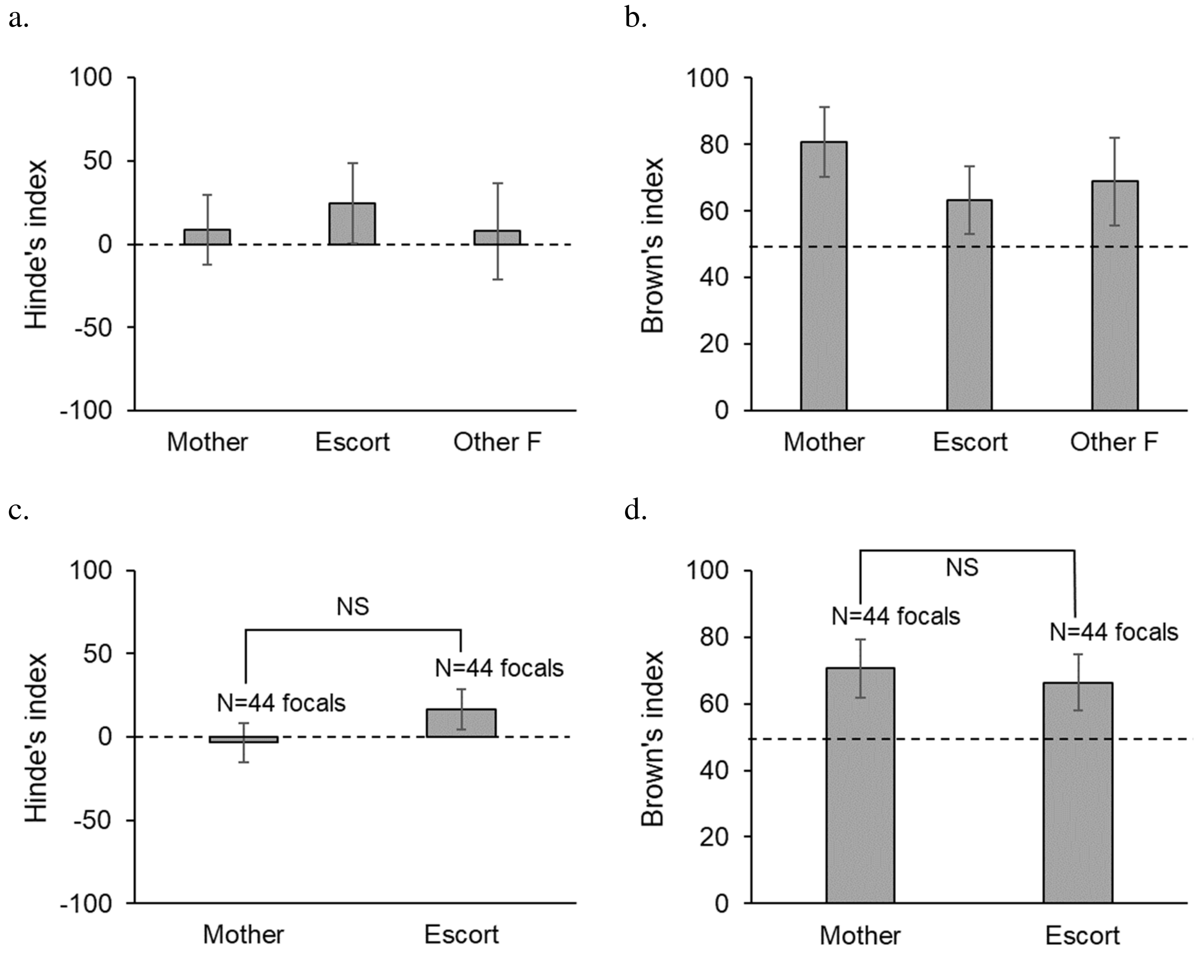
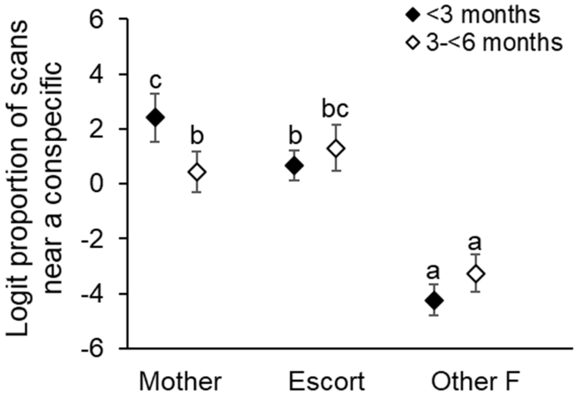


Figure 1. Average a) Hinde’s and b) Brown’s proximity indices of 7 calves for which data were available with all three conspecific categories, and c) Hinde’s and d) Brown’s indices of 17 calves with mothers and escorts. Error bars are 95% CI. Dashed lines indicates the expected Hinde’s index of 0 and expected Brown’s index of 50 in the respective graphs.



0.8 ± 0.09	0.6 ± 0.10	0.6 ± 0.08	0.7 ± 0.10	0 ± 0.02	0.1 ± 0.05

Figure 2. Logit proportions of scans that a calf spent near the three conspecific categories of females. Error bars are 95% CI. Letters above the data points indicate pattern of statistical significance based on Tukey's HSD tests (a<b<c). Shared letters above the bars indicate no significant difference between comparisons. The average values of the proportion of scans near a conspecific (averaged over all the focals of all the calves in the category) ± 95% CI are shown below the graph for each case.

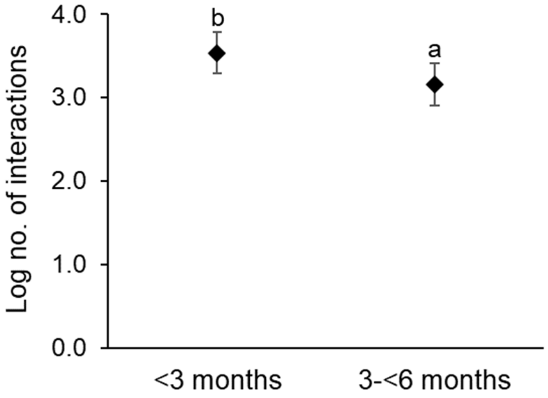
Calf-conspecific interactions

We recorded a total of 1332 interactions between calves and their mothers, escorts, or other females in their groups (calf-initiated: 1184, conspecific-initiated: 148) during the total focal duration of 1200 minutes. Most of these interactions were of very short duration (average ± 95% CI: calf-initiated: 20.4 ± 4.14 seconds; conspecific-initiated: 24.0 ± 14.5 seconds; Supplementary Material 6).

c) Initiation of interactions

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 ± 95% CI per 30-min focal: 29.60 ± 4.931) than conspecific females initiated towards calves (3.70 ± 1.634; Table 1, Figure 4a). Newborn calves were part of a significantly greater number of interactions with conspecifics (initiated by either) than were infant calves with conspecific females (Table 1, Figure 3). 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), whereas 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 4a), and a lower number of interactions towards other females (*P*<0.05 for both the comparisons; Figure 4a). 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; Figure 4a), with the latter two not being significantly different (*P*>0.05; Figure 4a). None of the random effects was significant (Table 1). The sample sizes were not large enough to include calf sex as a factor in the current ANOVA, but there was no effect of calf sex on the numbers of calf-conspecific interactions involving infant calves tested separately (Supplementary Material 8).



39.4±8.87 27.3±6.24

Figure 3. Log numbers of all interactions (initiated by either calf or conspecific) 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 (averaged over all the focals of all the calves in the category) ± 95% CI per focal are shown below the category.

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 9) for comparison.

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	_	_

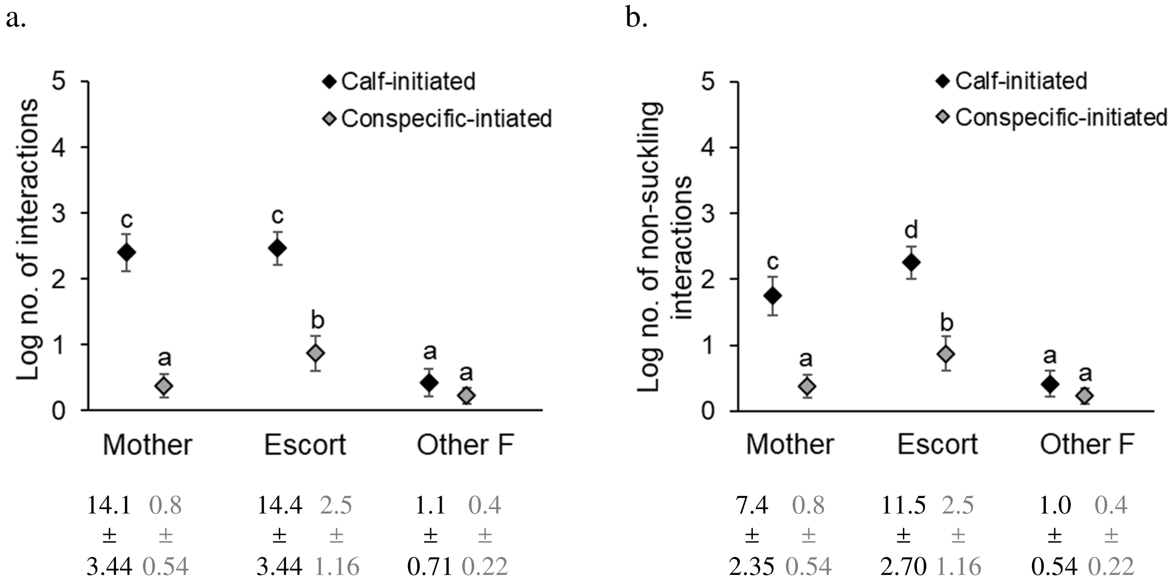


Figure 4. Log numbers of a) all interactions and b) non-suckling interactions initiated by calves towards the three conspecific categories of females, and the log numbers of interactions initiated by these conspecific females towards calves. Error bars are 95% CI. Letters above

the data points indicate the pattern of statistical significance based on Tukey's HSD tests (a<b<c<d; shared letters indicate no statistical significance). The values of the number of interactions (averaged over all the focals of all the calves in the category) ± 95% CI are shown below the X-axis categories.

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 even after removing the suckling-related interactions (794 non-suckling interactions, see Supplementary Material 7, 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 4b). The random effects of calf identity and its interaction with conspecific category were significant (Supplementary Material 9).

d) Calf-initiated interactions: Frequency in different contexts

Of the calf-initiated interactions, there were a total of 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). Newborn and infant calves initiated similar numbers of interactions towards conspecific females (Figure 5; and 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). They initiated more interactions towards mothers and escorts than towards other females as seen above (Initiator category x Conspecific category in Table 1, Figure 4a). 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 6a) and social interactions (Mother versus Other Females: $P<0.05$; Escort versus Other Females $P<0.05$, Figure 6a), but the number of resting-related interactions initiated by calves was higher only towards the 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 6a). There was no effect of sex on the number of calf-initiated interactions for infant calves examined separately (see Supplementary Material 10), but since the sample sizes were small, sex as a factor could not be included in this analysis.

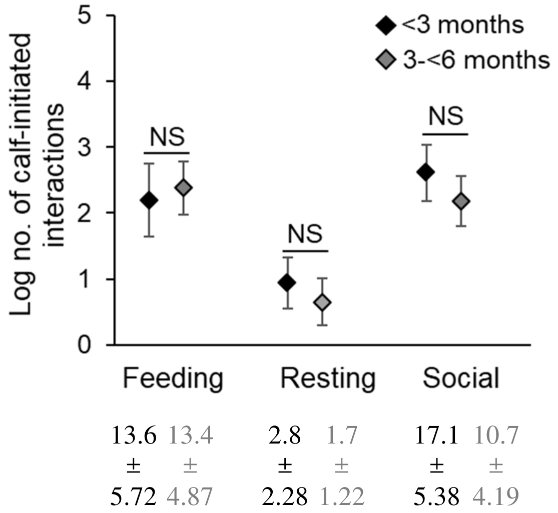


Figure 5. Log numbers of calf-initiated interactions of the three behavioural classes by newborn and infant calves towards conspecific females. Error bars are 95% CI. Letters above the data points indicate the pattern of statistical significance. The values of the number of interactions (averaged over all the focals of all the calves in the category) ± 95% CI are shown below the X-axis categories

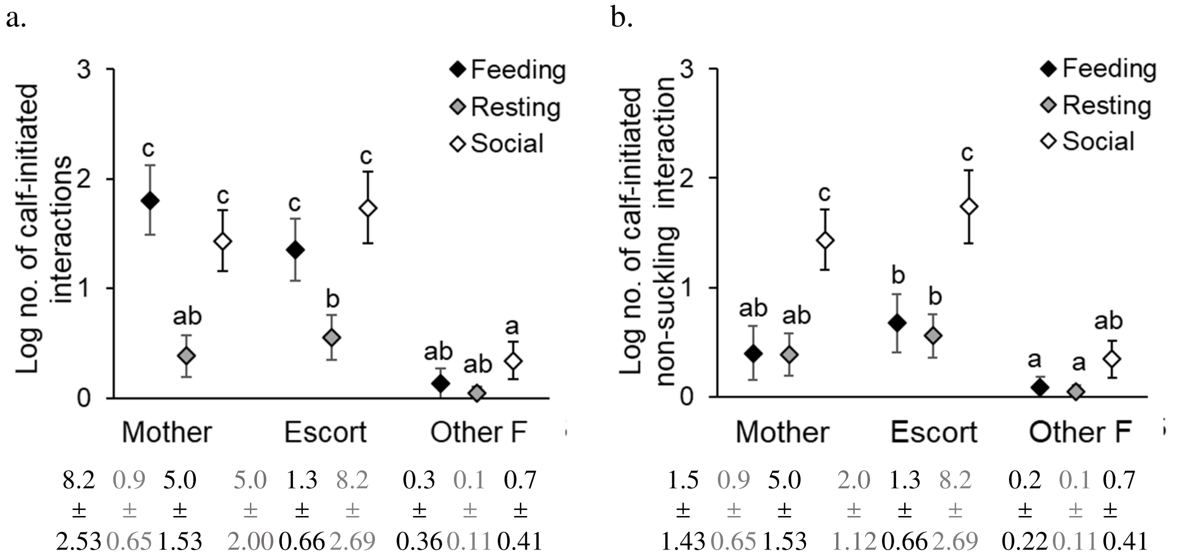


Figure 6. Log numbers of a) all calf-initiated interactions and b) calf-initiated non-suckling

interactions of three behavioural classes towards the three conspecific categories of females. Error bars are 95% CI. Letters above the data points indicate patterns of statistical significance based on Tukey's HSD tests (a<b<c). Shared letters above the bars indicate no statistical significance in pairwise comparisons. The numbers of calf-initiated interactions (average ± 95% CI) are shown below the graphs.

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*
All calf-conspecific interactions						
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	_	_

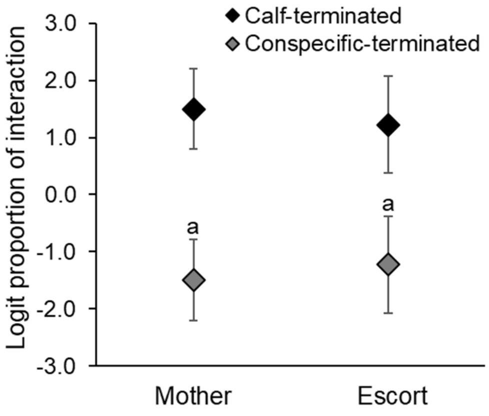
The ANOVA on the log number of calf-initiated non-suckling interactions (149 interactions) also showed similar results (Supplementary Material 11). However, since the number of feeding-related interactions (average ± 95% CI per 30-minute focal: 3.72 ± 2.451) was lowered because of the removal of suckling 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 6b). 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 6b) 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 6a,b).

e) Calf initiated interactions: Terminations

Of the 1184 calf-initiated interactions, calves terminated 868 interactions while conspecifics terminated the remaining. Since calves did not initiate interactions towards other females in their groups in the many of the focals, we could only check the difference in proportions of terminations by mothers and escorts. We found that mothers and escorts terminated similar logit proportions of calf-initiated interactions towards them (Table 3, Figure 7). The same pattern was seen in the termination of non-suckling interactions (Supplementary Material 12). In both the cases, mothers and escorts terminated similar logit proportions of interactions initiated by newborn and infant calves.

Table 3. 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) 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	_	_



0.8	0.2	0.7	0.3
±	±	±	±
0.08	0.08	0.08	0.08

Figure 7. 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 above the data points indicate pattern of statistical significance based on ANOVA. Proportions of calf-initiated interactions terminated by calf and mother and by calf and escort (average ± 95% CI) are shown below the graphs.

e) Calf-initiated interactions: Responses by conspecifics

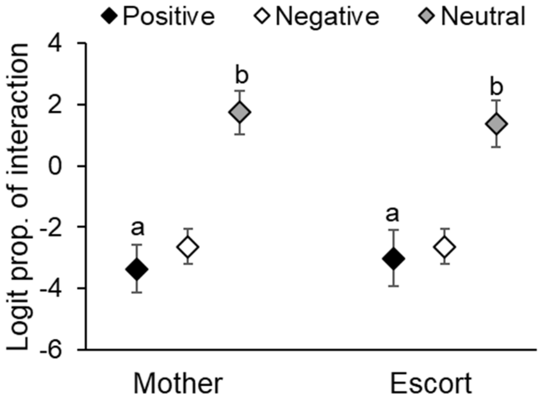
Calves received different types of responses, but the majority of their interactions did not elicit a response from conspecific females (*N*=885 out of 1184 calf-initiated interactions received no response). There were more negative (192) than positive (107) responses overall, but only 17 of the 192 negative responses were aggressive, such as kick, lash, push, pull trunk, and beat with tail. Since not all the negative interactions directed towards calves caused physical and/or social distress, we split them into aggressive and non-aggressive negative interactions. Non-aggressive negative conspecific-initiated interactions included only nudge (to make the calf move from a feeding spot).

Negative aggressive interactions included kick, push, pull trunk, beat with tail, and lash. Escorts never initiated any aggressive interaction towards calves, and 9 out of the 10 of the conspecific-initiated aggressive interactions towards calves was by other females in their groups; the remaining was by a mother. The percentage of positive conspecific-initiated interactions (93 in total) towards calves initiated by mothers was 20.4%; escorts initiated 77.4% of these interactions, and other females initiated 2.2%. Most of the neutral interactions (i.e., sniffing in the direction of calf) were initiated by escorts (8 out of 10; 1 out of 10 by mothers; 1 out of 10 by other females). 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.

We found that the proportions of calf-initiated interactions towards mothers and escorts that elicited a neutral response were significantly higher than the proportion that elicited a positive response from them (Table 4, Figure 8). There was no significant effect of conspecific category or its interaction with response type or of most random factors (Table 4) 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).

Table 4. Results of the ANOVA on the log 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) 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	_	_



0.1	0.1	0.8	0.1	0.1	0.8
±	±	±	±	±	±
0.06	0.04	0.07	0.08	0.04	0.08

Figure 8. 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).

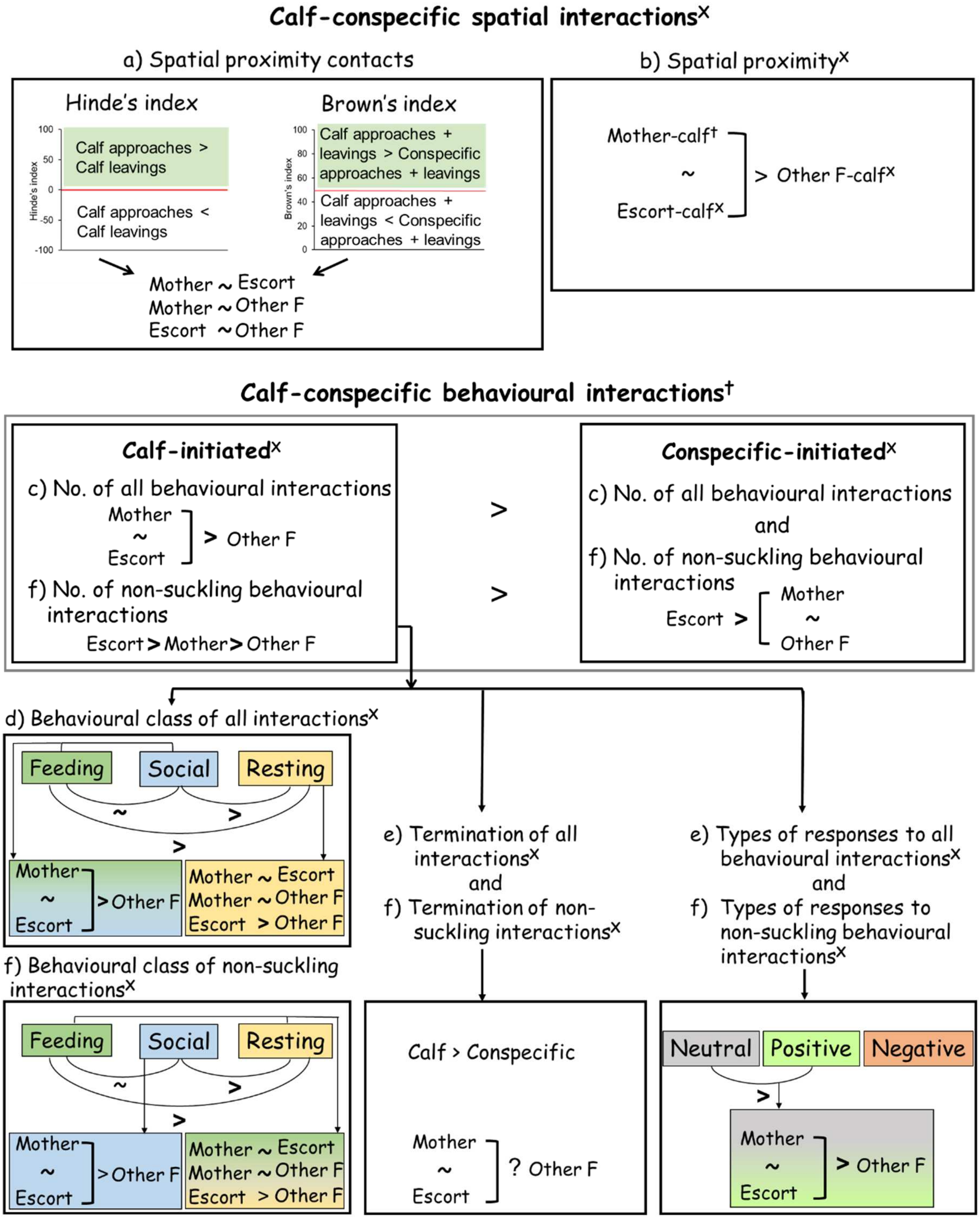


Figure 9. A schematic with results of analyses on calf-conspecific proximity and proximity initiation, calf-conspecific behavioural interactions, and calf-conspecific non-suckling behavioural interaction results. '†' indicates a significant effect of calf age and 'x' indicates no significant effect of calf age on the variable. The alphabets correspond to the ones in the questions and results.

Discussion

To understand possible links between fission-fusion dynamics and cooperative offspring care, understanding the nature, frequency, and functions of allomothering in the study population is essential. Therefore, we carried out one of the first studies to examine the relationship between calves and conspecific females ≥5 years of age in wild Asian elephants, to ascertain that there is allomaternal care in the study population, to identify allomothers, and to eventually understand the ontogeny of social relationships and their benefits. This study provides a baseline for calf-female interactions, specifically maternal and allomaternal interactions for calves less than six months of age.

Calf-conspecific female proximity and proximity initiation

As expected based on the precociality of Asian elephant calves, we found that calves (even from a young age) were responsible for initiating more changes in proximity with females than *vice versa*. This was true of mothers, escorts, and other females, amongst which there was no difference in Brown's index. Hinde's proximity index showed that calves approached their mothers, escorts, and other females more often than they left them (positive Hinde's indices). Contrary to this, the Hinde's index between mother and calf had been found to be negative during the first six months of life and positive only after that 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. Whether the Hinde's index is negative in our study using a 5-m distance remains to be seen. Calves under six months of age are highly dependent on their mother for nutrition, which may make it less likely for them to leave their mothers 5 m away even in our study. Offspring have been found to contribute more to proximity changes than mothers in other precocial species also, such as belugas (Hill and Campbell 2014), Saharan arrui (Cassinello 1997), and sorraia horses (Heitor and Vincete 2008) also. However, although calves initiate proximity (and behavioural) interactions in the study population, we do not yet know whether calves initiate these towards the nearest non-mother female, and therefore the escort, or whether they seek out the specific escort female even when it is away.

Calves up to six months of age spent a majority of their time near at least one female conspecific in their group, and had non-random neighbours as seen in African savannah elephants (Lee 1987). As individuals in the periphery face increasing predation risk (Hamilton

1971), calves might be positioned within a group such that their risk of predation is reduced. In fact, we often found calves to be between their mothers and escorts (as also seen by Gadgil and Nair 1984). The proportion of scans in which calves were near female conspecifics was much higher than those that near males, as also found in semi-captive Asian elephants and wild African savannah elephants (Gadgil and Nair 1984, Lee 1987), as male elephants do not show offspring care. Newborn calves spent a greater proportion of time near their mothers than escorts, as also seen in Gadgil and Nair's (1984) study on semi-captive elephants (in which calves <3 months old were near (≤1 m) their mothers more often (~65% of the time) than near allomothers (around 20%-40% of the time)). However, the groups included in that study were artificially constituted as they were semi-captive elephants, and information on familiarity amongst group members was not available. African savannah elephant calves (<2 years old) were closer (≤1 m) to non-mother individuals than their mothers (Lee 1987), but we do not have this information for newborn calves in that population.

As calves grew, they started to spend more time away from their mothers, and this period (3-<6 months) coincided with an increase in trunk motor skills and adult-like feeding behavioural expression (Chapter 3 of this thesis). An effect of calf age on mother-calf proximity has also been reported in wild Asian elephants in Sri Lanka and captive Asian elephants (Webber 2017), and in wild African savannah elephants across broader immature age-classes (Lee 1986). Unlike mother-calf proximity (which was higher in newborns than infants), the proximity between escorts and calves (and also between other females and calves) did not decrease at least till 6 months of age because of which mother-calf and escort-calf proximity were similar for infant calves. In the African savannah elephant also, 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). Therefore, this seems to be a broader pattern. The calf-non-mother neighbour distance was also found to be shorter than the calf-mother distance (Lee 1987). In line with a previous study on wild and captive Asian elephant populations (Webber 2017), we also did not find sex-based differences in calf-female conspecific proximity. As calves under six months of age are highly dependent on their mothers and are in the initial stages of physical maturation, sex differences in proximity might develop only beyond that. However, we did not have sufficient sample sizes to test the effects of calf sex along with calf age in the same analyses.

As mentioned above, we do not know the extents to which the mother, escort, and calf exert a choice resulting in their proximity patterns. Mother-escort spatial proximity before calf birth, and calf-escort spatial proximity controlling for mother-escort proximity may help to understand if escorts are choosing calves or their mothers, and if calves choose specific escorts or the individuals nearest to themselves.

Calf-conspecific female behavioural interactions

In general, we found a high rate of interaction (around 1.1 interactions/minute) between calves and conspecific females, whereas interactions with males were rare, as also seen in captive Asian (Gadgil and Nair 1984) and African savannah elephants (Lee 1987). Newborn calves had more interactions with conspecific females than infant calves, which was a result of females initiating more interactions towards newborn calves than infant calves (there was no significant difference in the interactions initiated by newborn calves and by infant calves towards conspecific females). In the Amboseli elephants, calves less than a year old were greeted more often than those 13-24 months old (Lee 1987). Similar to spatial proximity contacts, the majority of the behavioural interactions were initiated by calves towards conspecific females. While comparisons are not available in other populations for the same age-classes, similar results were reported by Gadgil and Nair (1984) in semi-captive Asian elephants and by Lee (1986) in the Amboseli elephants. The lack of calf sex difference in initiation of interactions towards conspecific females (which we would like to confirm with larger sample sizes) was also found in Amboseli (Lee 1987), although differences between the sexes developed with age as found in play behaviours in Amboseli (Lee and Moss 2014).

In more than half the focals, calves did not initiate an interaction with females other than the mother and escort; when they did interact with other females, it was almost 14 times less frequent than that with escorts. 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 African forest elephants, calves interacted significantly more with familiar (family) than unfamiliar ("extra-group") individuals (Chelluri 2009), and in African savannah elephants, allomothers were siblings and other family members (Lee 1987). It is also possible that escorts were younger than other females, and were, therefore, preferred by calves. Calves (≤12 months old) had a higher rate of interaction with young juvenile and adolescent females than with adult females in Amboseli (Lee 1987). However, in our analysis, the number of interactions initiated by calves during the entire set focal duration was used rather than the focal duration during which different conspecific categories of females were near calves (which would facilitate interactions).

We found that calves (all <6 months) interacted with their mothers (7.40 ± 2.354 / 30 min) and escorts (11.50 ± 2.708 / 30 min) at similarly high rates, whereas African elephant calves (≤12 months old) interacted with their mothers more than with any other single individual (Lee 1986, 1987). However, African savannah elephant calves (≤12 months) had an interaction rate of 2.3 interactions / h with their mothers (Lee 1987). If the pattern of higher interaction rates in Kabini holds after including calves that are six to 12 months old, it would be interesting to compare the group compositions and the behaviours of mothers in the two species to find out whether the larger number of individuals available in African savannah elephant groups, mothering styles, or the calves themselves are responsible for the difference in interaction rates. It is possible that calves interact to a smaller extent with mothers when there are other age-peers present (calves in Amboseli had the highest rate of interactions with age-peers when interactions across different age-classes were compared; Lee 1987); larger groups and those with multiple calves in Kabini can also be examined to check this. Possible differences in scoring between the two studies (Lee 1987, this study) also have to be ruled out, but Webber (2017) also suggested that wild African elephant calves interacted for a lower proportion of time than Asian elephant calves (although interaction rates were not available).

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 sucked from them, as was seen in African savannah elephants (Lee 1987). This is expected as lactation is energetically costly. However, allomothers who did not have dependent young of their own have been observed to provide milk in semi-captive and captive Asian elephants, (Gadgil and Nair 1984, Rapaport and Haigh 1987, in which case, the grandmother provided milk).

Calves initiated different behavioural classes of interactions with all the conspecific categories of females, but to varying extents, as seen in the Amboseli population (Lee 1986). However, calves preferred their mothers and escorts (to other females), and seemed to interact similarly with them in feeding, resting, and social interactions. Feeding interactions involved passive food sharing and included behaviours such as calves taking scraped off grass from a conspecific (TGC; *N*=89; see Supplementary Material 4) or feeding in the same spot as the conspecific (TGS; *N*=21). These behaviours required close contact between calves and conspecifics, and social tolerance, which is a prerequisite for social transmission of knowledge and skills (van Schaik 2003), and were almost always initiated towards mothers (proportion towards the mother: 0.46; TGS: 0.38) and escorts (proportion towards escorts: TGC: 0.54; TGS: 0.52), and almost never towards other females (TGC: 0; TGS: 0.10). Similarly, calves initiated preparatory feeding behaviours (Chapter 2 of this thesis) such as locating the nipple correctly or investigating what conspecifics were feeding on, probably to learn to identify food species, primarily towards their mother and escorts. Social interactions through which calves probably sought protection (from heat or predation) by standing under a conspecific's belly or between their trunk and forelegs were also with their mothers or 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).

However, calves initiated more non-suckling interactions towards their escorts than even their mothers, which might have led to foraging freedom for the mothers. Almost all the play interactions with conspecific females were also initiated towards escorts (95%; the rest with mothers 5%). We found 1.7% of all the calf-initiated interactions towards conspecific females at least five years old (*N*=1184 interactions) to be play. This might be similar to that in Amboseli, in which we do not have directly comparable data, but 4.4% of all the calf-initiated interactions towards conspecifics of all age-sex-classes except the mother was play (Lee 1986). Whether the proportion of social interactions that is play is affected by group size and the number of other calves or juveniles remains to be seen. The common social interactions included rubbing against a conspecific (~27%) and touching a conspecific (~23%). 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).

Just as calves behaved similarly towards mothers and escorts, with some interactions being higher towards escorts, mothers and escorts also behaved with similarity towards calves, with escorts showing more interactions at times. Mothers and escorts guarded calves during longer periods of calf resting; this behaviour was never exhibited by other females in the groups. They also showed positive responses that required them to stop feeding (see above), terminating comparable numbers of calf-initiated interactions, and rarely directed aggression towards the calf. 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. This pattern of results may change when immatures attain foraging and/or social independence as that found in orangutans during food solicitations (Mikeliban *et al.* 2021). Whether the time spent in showing positive responses translates into feeding costs for mothers and escorts remains to be seen. It would also be worthwhile to separate interactions that necessitated a response (many interactions initiated by a calf did not require a response and did not get one) and then compare the responses of conspecific females.

While females initiated very low numbers of interactions towards calves overall, escorts initiated more interactions than mother and other females. They also initiated the highest proportion of positive interactions (followed by mothers – about one-fourth that of escorts), and more positive than negative interactions. Mothers also initiated more positive than negative interactions but the difference was small, and other females initiated more negative than positive or neutral interactions towards calves. However, pooling together negative responses to calf-initiated interactions and negative conspecific female-initiated interactions to calves, the rate of aggression received by calves less than six months old was the lowest from mothers (0.15/h), followed by escorts (0.4/h). The latter was similar to that found in Amboseli, with the rate of aggression from allomothers being 0.38 interactions/hour spent near the calf (Lee 1987). The rate of aggression received from other females in Kabini was 0.8/h despite calves spending the least proportion of time with other females. Although not directly comparable, the overall rate of aggression received by calves less than six months old from conspecific females (>=5 years old) was 1.35 interactions/hour (27 instances of aggression/20 focal hours) in Kabini, whereas the overall rate of aggression received by calves <2 years old from conspecific adult females was 0.58 interactions/hour spent nearby in Amboseli (Lee 1987).

Our observations that other females showed more negative interactions towards calves than mother or escorts, and escorts showed positive interactions towards calves were not a given. Some primate studies have found that inexperienced females who act as allomothers are not gentle and can even accidentally harm the young ones (for e.g., see discussion in Hrdy 1976). Similarly, escort-calf interactions could have potentially been negative/harmful. It can also be seen from the results that calf-female interaction patterns do not necessarily mirror the proximity patterns. For instance, we found that the proximity of newborn calves towards the mother was greater than that towards escorts, and the proximity of 3-6-month-old calves was similar towards these two conspecific categories. If the rate of interactions mirrored proximity, one would expect more interactions with mothers overall than with escorts. However, calves initiated similar numbers of interactions with mothers and escorts, and a greater number of non-suckling interactions with escorts than mothers. Also, escorts initiated more interactions towards calves than mothers did. Thus, analysing number of interactions apart from proximity provided us with additional information about calf-conspecific relationships.

Overall, there were remarkable similarities between mothers and escorts in their behaviours towards calves and in the behaviours of calves towards them (see Figure 9), with the primary difference being that escorts did not provide milk. Escorts thus provided allomaternal care, which was primarily positive and helpful in nature. Moreover, females who were classified as escorts in a focal always provided allomaternal care in that focal and were physically close to the calf ~70% of the time during that focal. Therefore, potentially, by looking at coordinated movement for a short period of time, it is possible to identify the allomother of a calf in a particular sighting. Mothers did not restrict calf-escort contacts or interactions, unlike the case in some primates with strict dominance hierarchies (for e.g., see Kaufmann 1966, Liu *et al.* 2018), and in fact, nudged their calves towards escorts while they fed (field observations). Moreover, although mother-calf behavioural interactions decreased with calf age, allomaternal care by escorts did not decrease during at least the first 6 months of life, probably ensuring adequate care for calves during their crucial development period. Thus, allomaternal care is likely to be an integral part of developmental care in Asian elephants. O'Brien and Robinson (1991) also found that allomaternal care was more frequent than maternal care during later stages of infant development in capuchin monkeys. Escort motivation, including age and body condition, and mother-escort relationships, including relatedness and previous associations (female relationship are heterogeneous; Shetty 2016), may influence who acts as the escort (allomother). Thus, there is heterogeneity in the nature of interactions between calves and different categories of females. It would be interesting to examine whether these lead to differentiated relationships persisting into the future. The presence of calves and their interactions with other females and immatures in the group might also increase close social interactions amongst mothers, and between mothers and escorts, which may establish new relationships or strengthen existing relationships. It would be interesting to see if the presence of calves influences inter-female spatial and behavioural interactions in the study population.

To summarise, we found that elephant groups with calves comprised females who provided active care (mother and escort) and those who did not provide active care (other females); therefore, there is allomaternal care and differentiated calf-female relationships in the study population, and escorts are the allomothers. We found that allomaternal care is comparable to maternal care without nutritional support through lactation. From the results so far, we cannot rule out the speculation that cooperative offspring care (this chapter) may be a reason for increased female sociality in calf presence (chapter 2 of this thesis).

Acknowledgements

This work was funded by the Council of Scientific and Industrial Research, Government of India, under Grant No. 37(1613)/13/EMR-II and Jawaharlal Nehru Centre for Advanced Scientific Research (JNCASR). TR was supported as a student by JNCASR. This work is part of TR's Ph.D. thesis. We thank the offices of the PCCF, Karnataka Forest Department, and of the Conservators of Forests of Nagarahole and Bandipur National Parks and Tiger Reserves for field permits. We also thank various officials of Karnataka Forest Department and officials and staff of Nagarahole and Bandipur National Parks for their support. Krishna, Shankar, Pramod, and others provided field assistance. We thank Hansraj Gautam for some focal videos.

References

1. Altmann J (1974). Observational study of behaviour: sampling methods. *Behaviour* 49: 227-267.
2. Archie EA, Morrison TA, Foley CAH, Moss CJ and Alberts SC (2006). Dominance rank relationships among wild female African elephants, *Loxodonta africana*. *Animal Behaviour* 71: 117-127.
3. Berman CM, Rasmussen KL and Suomi SJ (1997). Group size, infant development and social networks in free-ranging rhesus monkeys. *Animal Behaviour* 53: 405-421.

4. Berman CM (1982a). The ontogeny of social relationships with group companions among free-ranging infant rhesus monkeys I. Social networks and differentiation. *Animal Behaviour* 30: 149-162.
5. Berman CM (1982b). The ontogeny of social relationships with group companions among free-ranging infant rhesus monkeys II. Differentiation and attractiveness. *Animal Behaviour* 30: 163-170.
6. Brown GR (2001). Using proximity measures to describe mother-infant relationships. *Folia Primatologica* 72: 80-84.
7. Cassinello J (1997). Mother—offspring conflict in the Saharan Arrui, *Ammotragus lervia sahariensis*: Relation to weaning and mother's sexual activity. *Ethology* 103: 127-137.
8. Chelluri G (2009). *Ontogeny of the Mother-Calf Relationship in African Forest Elephants, Loxodonta africana cyclotis.* Honours thesis, Cornell University, Cornell.
9. Chism J (2000). Allocare patterns among cercopithecines. *Folia Primatologica* 71: 55-66.
10. Clutton-Brock TH, Brotherton PN, O'Riain MJ, Griffin AS, Gaynor D, Sharpe L, Kansky R, Manser MB and McIlrath GM (2000). Individual contributions to babysitting in a cooperative mongoose, *Suricata suricatta. Proceedings of the Royal Society of London B: Biological Sciences* 267: 301-305.
11. de Waal F (1990). Do rhesus mothers suggest friends to their offspring? *Primates* 31: 597-600.
12. Derrickson EM (1992). Comparative reproductive strategies of altricial and precocial eutherian mammals. *Functional Ecology* 6: 57-65.
13. Desai AA and Johnsingh AJT (1995). Social organization and reproductive strategy of the male Asian elephant (*Elephas maximus*). In: Daniel JC and Datye H (eds), *A Week with Elephants*. Bombay Natural History Society, Oxford University Press, Bombay, pp. 532.
14. Douglas-Hamilton I and Douglas-Hamilton O (1975). *Among the Elephants*, Penguin, London.
15. Douglas-Hamilton I (1972). *On the Ecology and Behaviour of the African Elephant: The Elephants of Lake Manyara.* Ph.D. thesis, University of Oxford, Oxford.
16. Dublin HT (1983). Cooperation and reproductive competition among female African elephants. *Social Behaviour of Female Vertebrates* 1: 291-313.
17. Eisenberg JF (1980). Ecology and behaviour of the Asian elephant. *Elephant* 1: 36-56.
18. Estes RD and Goddard J (1967). Prey selection and hunting behaviour of African wild dogs. *Journal of Wildlife Management* 31: 52-70.

19. Förster S and Cords M (2005). Socialization of infant blue monkeys (*Cercopithecus mitis stuhlmanni*): Allomaternal interactions and sex differences. *Behaviour* 142: 869-896.
20. Gadgil M, Hegde M, Joshi NV and Gadgil S (1985). On the communication of well-being. *Proceedings of the Indian Academy of Sciences: Animal Sciences* 94: 575-586.
21. Gadgil M and Nair VP (1984). Observations on the social behaviour of free ranging groups of tame Asiatic elephants (*Elephas maximus Linn*). *Proceedings of the Indian Academy of Sciences (Animal Science)* 93: 225-233.
22. Garai ME (1997). *The Development of Social Behaviour in Translocated Juvenile African Elephants Loxodonta africana (Blumenbach).* Ph.D. thesis, University of Pretoria, Pretoria.
23. Gautam H (2019). *Resource Availability, Within-clan and Between-Clan Agonistic Interactions, and Dominance Relationships amongst Female Asian Elephants in Nagarahole National Park, Southern India.* Ph.D. thesis, Jawaharlal Nehru Centre for Advanced Scientific Research, Bengaluru.
24. Gautam H and Vidya TNC (2019). A test of the socioecological model in female Asian elephants: the effects of food abundance, food distribution, and competitor density on within-clan and between-clan contests. *bioRxiv* 754515. https://doi.org/10.1101/754515.
25. Gero S, Gordon J and Whitehead H (2013). Calves as social hubs: dynamics of the social network within sperm whale units. *Proceedings of the Royal Society B: Biological Sciences* 280: 20131113.
26. Hamilton WD (1971). Geometry for the selfish herd. *Journal of Theoretical Biology* 31: 295-311.
27. Heitor F and Vicente L (2008). Maternal care and foal social relationships in a herd of Sorraia horses: Influence of maternal rank and experience. *Applied Animal Behaviour Science* 113: 189-205.
28. Hill HM and Campbell C (2014). The frequency and nature of allocare by a group of belugas (*Delphinapterus leucas*) in human care. *International Journal of Comparative Psychology* 27: 501-514.
29. Hinde RA and Atkinson S (1970). Assessing the roles of social partners in maintaining mutual proximity, as exemplified by mother-infant relations in rhesus monkeys. *Animal Behaviour* 1: 169-176.
30. Hinde RA and Spencer-Booth Y (1967). The behaviour of socially living rhesus monkeys in their first two and a half years. *Animal Behaviour* 15: 169-196.

31. Hodge SJ (2005). Helpers benefit offspring in both the short and long-term in the cooperatively breeding banded mongoose. *Proceedings of the Royal Society B: Biological Sciences* 272: 2479-2484.
32. Hrdy SB (1976). Care and exploitation of nonhuman primate infants by conspecifics other than the mother. *Advances in the Study of Behaviour* 6: 101-158.
33. Isbell LA and Young T (2002). Ecological models of female social relationships in primates: similarities, disparities, and some directions for future clarity. *Behaviour* 139: 177-202.
34. Jayantha D, Dayawansa PN, Padmalal UK and Ratnasooriya WD (2009). Social relationships of wild juvenile Asian elephants *Elephas maximus* in the Udawalawa National Park, Sri Lanka. *Journal of Threatened Taxa* 26: 211-214.
35. Jhala YV, Gopal R, and Qureshi Q (eds.) (2008). *Status of Tigers, Co-predators and Prey in India*. Report. National Tiger Conservation Authority and Wildlife Institute of India. TR08/001.
36. Kaufmann JH (1966). Behaviour of infant rhesus monkeys and their mothers in a free-ranging band. *Zoologica* 51: 17-28.
37. Keerthipriya P, Nandini S and Vidya TN (2021). Effects of male age and female presence on male associations in a large, polygynous mammal in southern India: The Asian elephant. *Frontiers in Ecology and Evolution* 9: 616666.
38. Konrad CM, Frasier TR, Whitehead H and Gero S (2019). Kin selection and allocare in sperm whales. *Behavioural Ecology* 30: 194-201.
39. Kumar A and Solanki GS (2014). Role of mother and allomothers in infant independence in capped langur *Trachypithecus pileatus*. *Journal of the Bombay Natural History Society* 111: 3-9.
40. Lee PC and Moss CJ (2014). African elephant play, competence and social complexity. *Animal Behaviour and Cognition* 1: 144-156.
41. Lee PC (1986). Early social development among African elephant calves. *National Geographic Research* 2: 388-401.
42. Lee PC (1987). Allomothering among African elephants. *Animal Behaviour* 35: 278-291.
43. Lee PC and Moss CJ (1999). The social context for learning and behavioural development among wild African elephants. In Box HO and Gibson KR (eds.), *Mammalian Social Learning: Comparative and Ecological Perspectives*, pp. 102–125. Cambridge University Press, Cambridge.

44. Lee PC and Moss CJ (2011). Calf development and maternal rearing strategies. In: Moss CJ, Croze H and Lee PC (eds.), *The Amboseli Elephants: A Long-Term Perspective on a Long-Lived Mammal,* pp 224-237. University of Chicago Press, Chicago.
45. Liu BJ, Wu CF, Garber PA, Zhang P and Li M (2018). Effects of group size and rank on mother–infant relationships and reproductive success in rhesus macaques (*Macaca mulatta*). *American Journal of Primatology* 80: e22881.
46. Maestripieri D (1994a). Social structure, infant handling, and mothering styles in group-living Old World monkeys. *International Journal of Primatology* 15: 531-553.
47. Maestripieri D (1994b). Influence of infants on female social relationships in monkeys. *Folia Primatologica* 63: 192-202.
48. Mann J and Smuts BB (1999). Natal attraction: allomaternal care and mother–infant separations in wild bottlenose dolphins. *Animal Behaviour* 55: 1097-1113.
49. Mar KU, Lahdenpera M and Lumma V (2012). Causes and correlates of calf mortality in captive Asian elephants (*Elephas maximus*). *PLOS One* 7: e32335.
50. McKay GM (1973). Behaviour and ecology of the Asiatic elephant in southeastern Ceylon. *Smithsonian Contributions to Zoology* 125: 1-113.
51. McKenna JJ (1979). The evolution of allomothering behaviour among colobine monkeys: function and opportunism in evolution. *American Anthropologist* 81: 818–840.
52. Mikeliban M, Kunz B, Rahmaeti T, Uomini N and Schuppli C (2021). Orangutan mothers adjust their behaviour during food solicitations in a way that likely facilitates feeding skill acquisition in their offspring. *Scientific Reports* 11: 1-4.
53. Nair PV (1989). Development of nonsocial behaviour in the Asiatic elephant. *Ethology* 82: 46–60.
54. Nandini S, Keerthipriya P and Vidya TNC (2017). Seasonal variation in female Asian elephant social structure in Nagarahole-Bandipur, southern India. *Animal Behaviour* 134: 135-145.
55. Nandini S, Keerthipriya P and Vidya TNC (2018). Group size differences may mask underlying similarities in social structure: a comparison of female elephant societies. *Behavioural Ecology* 29: 145–159.
56. Neter J, Wasserman W and Kutner MH (1990). *Applied Linear Statistical Models*, 3rd Edition. Irwin, Homewood, Illinois.
57. Nicolson NA (1987). Infants, mothers, and other females. In Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW and Struhsaker TT (eds.), *Primate Societies*, pp. 330-342. University of Chicago Press, Chicago.

58. O'Brien TG and Robinson JG (1991). Allomaternal care by female wedge-capped capuchin monkeys: effects of age, rank and relatedness. *Behaviour* 119: 30-50.
59. Pal SK, Roy S and Ghosh B (2021). Pup rearing: The role of mothers and allomothers in free-ranging domestic dogs. *Applied Animal Behaviour Science* 234: 105181.
60. Paul M, Majumder SS and Bhadra A (2014). Grandmotherly care: a case study in Indian free-ranging dogs. *Journal of Ethology* 32: 75-82.
61. Pusey AE and Packer C (1994). Non-offspring nursing in social carnivores: minimizing the costs. *Behavioural Ecology* 5: 362-374.
62. Rapaport L and Haight J (1987). Some observations regarding allomaternal caretaking among captive Asian elephants (*Elephas maximus*). *Journal of Mammalogy* 68: 438-442.
63. Revathe T, Anvitha S and Vidya TNC (2020). Development of motor control and behaviour in Asian elephants in the Kabini elephant population, southern India. *International Journal of Developmental Biology* 64: 377-392.
64. Riedman ML (1982). The evolution of alloparental care and adoption in mammals and birds. *Quarterly Review of Biology* 57: 405-435.
65. Rood JP (1978). Dwarf Mongoose Helpers at the Den. *Zeitschrift für Tierpsychologie* 48: 277-287.
66. Rowell TE, Hinde RA and Spencer-Booth Y (1964). “Aunt”-Infant interaction in captive rhesus monkeys. *Animal behaviour* 12: 219-226.
67. Shetty NR (2016). *Social Structure, Genetic Relatedness, and Dominance Relationships in Female Asian Elephants in Nagarahole and Bandipur National Parks, Southern India.* Ph.D. thesis, Jawaharlal Nehru Centre for Advanced Scientific Research, Bengaluru.
68. Spencer-Booth Y (1968). The behaviour of group companions towards rhesus monkey infants. *Animal Behaviour 16*: 541–557.
69. StatSoft, Inc. (2004). STATISTICA (data analysis software system), version 7. www.statsoft.com.
70. Sterck EHM, Watts DP and van Schaik CP (1997). The evolution of female social relationships in nonhuman primates. *Behavioural Ecology and Sociobiology* 41: 291-309.
71. Sukumar R (1989). *The Asian Elephant: Ecology and Management*. Cambridge University Press, Cambridge.
72. van Schaik CP (1989). The ecology of social relationships amongst female primates. In: Standen V and Foley RA (eds), *Comparative Socioecology: The Behaviour of Humans and Other Mammals*, pp. 195-218. Blackwell Scientific Publications, Oxford.

73. van Schaik CP (2003). Local traditions in orangutans and chimpanzees: Social learning and social tolerance. In Fragaszy DM and Perry S (eds.), *The Biology of Traditions: Models and Evidence*, pp. 297–328. Cambridge University Press, Cambridge.
74. Vidya TNC (2014). Novel behaviour shown by an Asian elephant in the context of allomothering. *Acta Ethologica* 17: 123-127.
75. Vidya TNC, Prasad D and Ghosh A (2014). Individual identification in Asian elephants. *Gajah* 40: 3-17.
76. Webber CE (2017). *A Comparison of Behavioural Development of Elephant Calves in Captivity and in the Wild: Implications for Welfare*. Ph.D. thesis, University of Stirling, Stirling.
77. Whitehead H (1996). Babysitting, dive synchrony, and indications of alloparental care in sperm whales. *Behavioural Ecology and Sociobiology* 38: 237–244.
78. Williams JH (1950). *Elephant Bill*. Rupert Hart-Davis, London.
79. Wilson EO (1975). *Sociobiology: The New Synthesis*. The Belknap Press, Cambridge, MA.
80. Woodford MH and Trevor S (1970). Fostering a baby elephant. *African Journal of Ecology* 8: 204-205.
81. Wrangham RW (1980). An ecological model of female-bonded primate groups. *Behaviour* 7: 262-300.

Supplementary Material

Supplementary Material 1. Details of calves sampled.

Supplementary Material 1, Table 1. Individual and clan identities and age-class (at the time of sampling), sex-class categorisation of calves sampled to get durations of calf positions, calf proximity, and calf behavioural interactions data.

S.No.	Calf name	Clan	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. Individual and clan identities and age-, sex-class categorisation of calves sampled to get durations of calf positions to calculate the time to independence of calf positions.

Calf name	Clan	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.

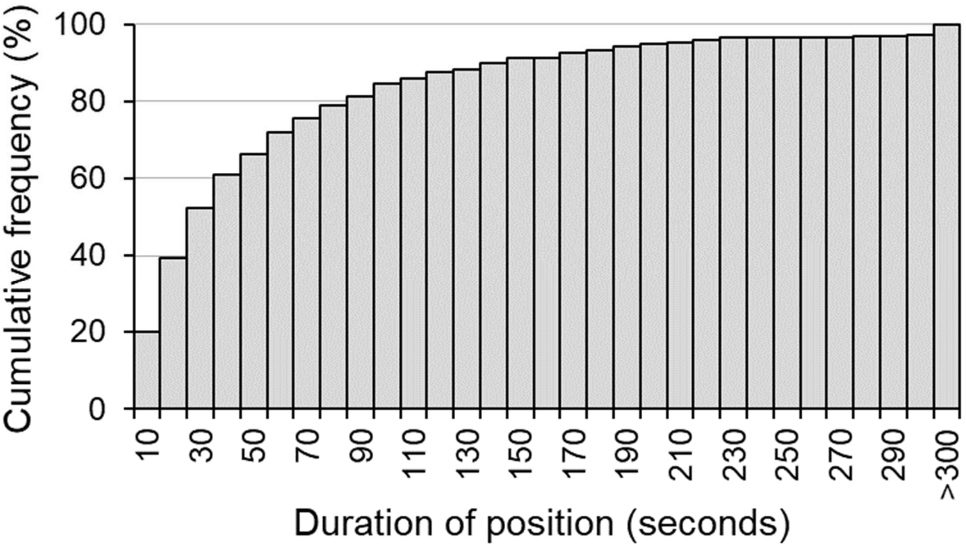
S.No.	Focal calf position code	Code description
1	ALO	Alone
2	SNC	Near another calf
3	SCE	Near another calf and an escort
4	CCJ	Near another calf and a juvenile
5	FCJ	Near another calf, a juvenile, and an other female
6	SCM	Near another calf and the mother
7	CCC	Near another calf and two other females
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.

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. We found that 95% of the calf positions 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.

As mentioned in the main text, 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. It can be calculated for each young one-conspecific pair in a group as follows:

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 and, to do this, the Brown's index (Brown 2001) was used. This calculates the total percentage of changes in proximity contacts that were due to the movement of the calf.

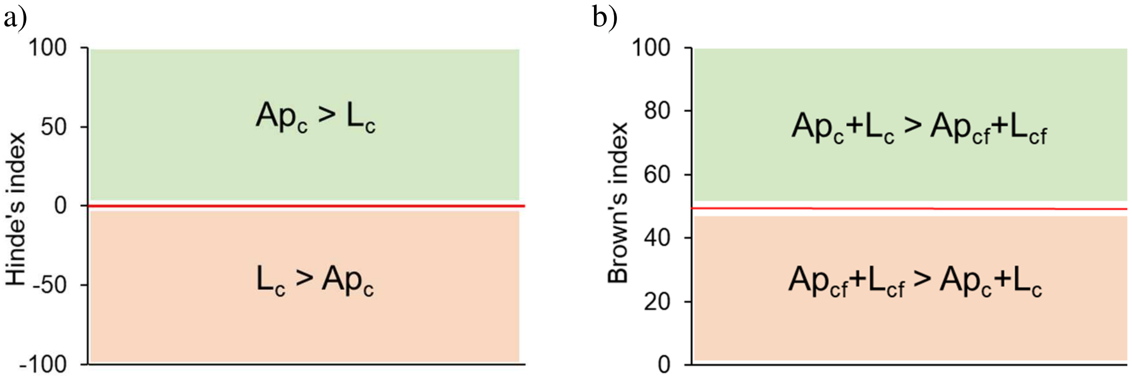
Brown's proximity index = $\frac{Ap_c+L_c}{Ap_c+L_c+Ap_{cf}+L_{cf}} \times 100$

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. 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, Scott *et al.* 2020), 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).

Supplementary Material 4. Details of behavioural interactions recorded.

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 nipple in the wrong direction	9	Feeding	Try to locate nipple between the hind legs (also 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.

Code	Interaction	Frequency	Behavioural class	Description
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).
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).

Code	Interaction	Frequency	Behavioural class	Description
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	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	Kick a conspecific, even if it misses.
LSH	Lash	0	0	1	Social	Negative	Lash out at a conspecific with the trunk.
NGE	Nudge calf towards escort	2	0	0	Social	Negative	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	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			Behavioural class	Type	Description
		Mom	Escort	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.

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.

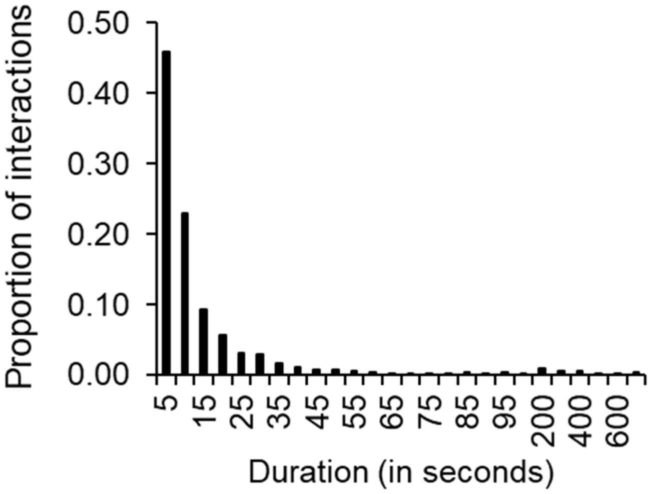
Code	Response	Frequency	Type	Description
RES	Rescue	1	Positive	Walk/run towards the calf when distress is expressed and reach the calf.
SMA	Smell anus	1	Positive	Check the calf by smelling the anus.
STG	Stand guard	16	Positive	Stand guard while the calf sleeps. The calf should be next to at least one 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	_	_

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. Details of focals that had calf-conspecific interactions.

Supplementary Material 7, 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 8. 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 8, 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).

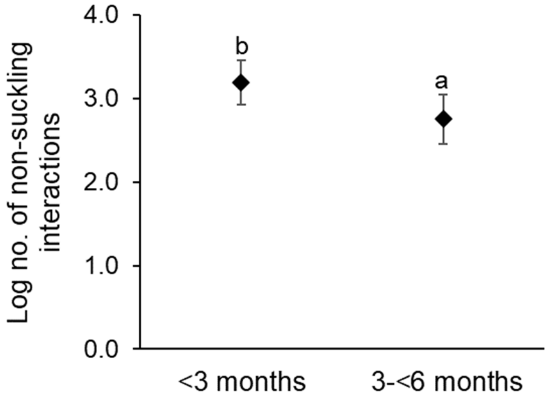
Effect	Effect (F/R)	*SS*	*df*	*MS*	*F*	*P*
Calf ID(calf sex)	Random	7.209	8	0.901	2.195	**0.040**
Calf sex	Fixed	0.074	1	0.074	0.082	0.782
Initiator category	Fixed	58.964	1	58.964	133.247	**<0.001**
Conspecific category	Fixed	27.505	2	13.753	35.559	**<0.001**
Calf ID(calf sex)*Initiator category	Random	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	_	_

Supplementary Material 9. 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 9, 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	_	_



27.9±6.46 19.2±6.39

Supplementary Material 9, 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 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	_	_

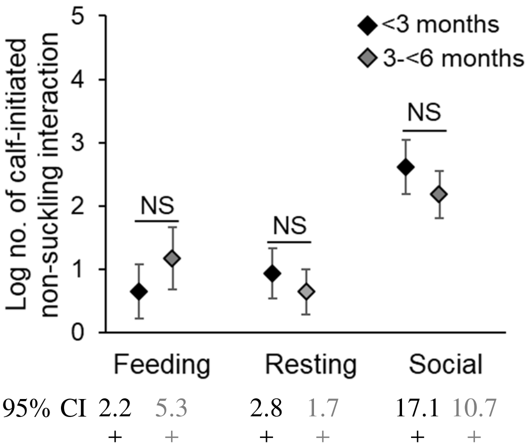
Supplementary Material 11. Behavioural classes of calf-initiated non-suckling interactions.

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	_	_



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

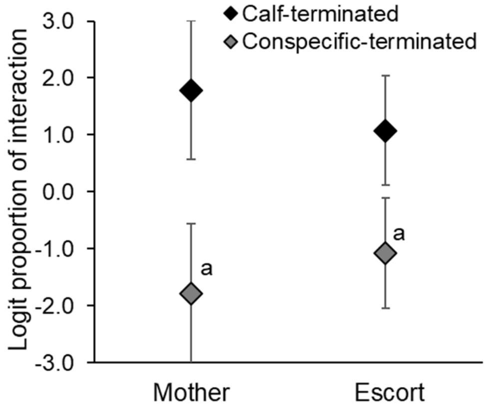
Supplementary Material 11, Figure 1. Log numbers of calf-initiated non-suckling interactions of the three behavioural classes by newborn and infant calves towards conspecific females. Error bars are 95% CI. NS indicates lack of statistical significance.

Supplementary Material 12. Termination of calf-initiated non-suckling interactions.

As mentioned in the main text, we looked at terminations of calf-initiated 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 1. 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	_	_



Mother		Escort	
0.7 ± 0.12	0.3 ± 0.12	0.7 ± 0.10	0.3 ± 0.10

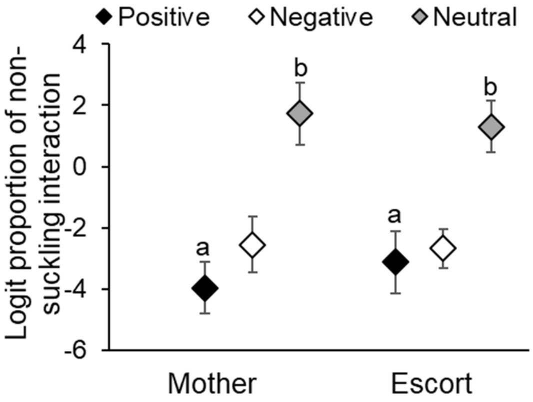
Supplementary Material 12, Figure 1. Logit proportions of calf-initiated non-suckling interactions towards their mothers and escorts that were terminated by the calves and by the conspecific females. Error bars are 95% CI. Letters above the data points indicate pattern of statistical significance. Proportions 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 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 1 below, Figure 1 below). None of the other effects was significant.

Supplementary Material 13, Table 1. Results of the ANOVA on the log 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	_	_



0.1	0.2	0.7	0.2	0.1	0.7
±	±	±	±	±	±
0.07	0.09	0.10	0.09	0.04	0.09

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).

Supplementary Material 14. Conspecific-initiated interactions towards calves.

Of the 148 conspecific-initiated interactions, there were a total of 31 feeding interactions (Mother: 9, Escort: 19, Other Females: 3; duration of these interactions: Mother: 0.37 minutes, Escort: 1.03 minutes; Other Females: 0.07 minutes), 0 resting interactions, and 117 social interactions (Mother: 23, Escort: 82, Other Females: 12; duration of these interactions: Mother: 23.55 minutes, Escort: 33.43 minutes, Other Females: 0.52 minutes). These interactions were either positive, negative, or neutral (Table 1 below), with positive interactions being higher than negative or neutral interactions.

Supplementary Material 14, Table 1. Types of interactions initiated by conspecific female towards calves and their numbers and proportions.

Type of interaction	Total no. of interaction	Proportion of interactions		
		Mother	Escort	Other F
Positive	93	0.20	0.77	0.02
Negative	45	0.27	0.47	0.27
Negative non-aggressive	35	0.31	0.60	0.09
Negative aggressive	10	0.01	0.00	0.90
Neutral	10	0.10	0.80	0.10

CHAPTER 5

Possible Functions of Allomaternal Care in the Kabini Asian Elephant Population, Southern India

Title: Possible functions of allomaternal care in the Kabini Asian elephant population, southern India

Authors: T. Revathe and T.N.C. Vidya

Affiliation: Evolutionary and Organismal Biology Unit, Jawaharlal Nehru Centre for Advanced Scientific Research (JNCASR), Bengaluru, India.

[*] Corresponding author.
Email: tncvidya@jncasr.ac.in; ORCID iD: 0000-0002-7143-9008.

Manuscript to be posted on bioRxiv

Author contributions

T. Revathe and T.N.C. Vidya conceived this study. TR collected field data and carried out the analyses. TR primarily and TNCV wrote the manuscript.

Abstract

We examined hypotheses to explain allomothering in Asian elephants by collecting field behavioural data from 2016-2018 on 30 unique calves, and group size data on seven female clans in the Kabini Asian elephant population (Nagarahole and Bandipur National Parks), southern India. Young, nulliparous females were primarily, although not exclusively, the allomothers, and showed a higher frequency of allomothering than expected in keeping with the learning-to-mother hypothesis. In accordance with the mother-benefit hypothesis, calves with an allomother spent a higher proportion of their time away from and had fewer social interactions with their mothers than calves without an allomother. Calves with an allomother also had the advantage of being close to, interacting with, and receiving support from their allomothers apart from their mothers, which calves without an allomother lacked (supporting the infant-benefit hypothesis). Moreover, female group sizes were not only larger in calf presence than in their absence, but were even larger in calf presence when an allomother was present, affording allomothered calves the possible benefits of group size against predation. Thus, we found preliminary support for all three hypotheses that we examined. Whether these advantages translate into increased future reproductive success of allomothers, enhanced foraging freedom for mothers, or improved social skills and survival of calves need to be further studied.

Keywords

Allomothering, Asian elephant calf, learning to mother, mother-benefit, infant-benefit, group size.

Introduction

Allomothers are females other than the biological mother who care for conspecific young (Hrdy 1980), and allomothering (allomaternal care) has been observed in diverse species (see Hrdy 1976, Quiatt 1979, Riedman 1982, Nicolson 1987, König 1997, Chism 2000, Ross and MacLarnon 2000, Dunayer and Berman 2018). The occurrence and patterns of allomaternal care are hypothesised to be influenced by many interlinked factors, such as ecological factors, life history traits, and female social structure (McKenna 1979, Riedman 1982, Maestripieri 1994, Paul 1999, Chism 2000, Ross and MacLarnon 2000), giving rise to various, often non-mutually exclusive, adaptive explanations to explain such care. These hypotheses include *learning to mother*, *alliance formation*, and *reciprocity*, which involve direct fitness benefits, and *mother-benefit* and *infant-benefit* hypotheses, which invoke indirect benefits. We carried out preliminary examination of three of these hypotheses in a population of Asian elephant.

Learning to mother hypothesis

Allomothering is found in species with well-developed maternal and/or paternal care, often with relatively low female lifetime reproductive success, with mothers investing heavily in slow-maturing offspring that have a long period of dependency (Riedman 1982). Therefore, the learning or development of parenting skills is likely to be very important, and allomothering could facilitate the acquisition of maternal experience and skills before the birth of one's offspring (Lancaster 1971, Hrdy 1976, Quiatt 1979, Ross and MacLarnon 2000). Previous experience in parenting has been found or predicted to increase offspring growth and survival in several mammalian species (Rodents: Wright and Bell 1978, Wang and Novak 1994; Reindeer: Weladji *et al.* 2008; Primates: Jay 1962, Lancaster 1971, Fairbanks 1990). If allomothering were based solely on learning to mother, one would expect a) differences in the patterns of caretaking behaviour amongst females based on their parity, with a positive relationship between parity and maternal competence (i.e., adequate care in the form of appropriate comforting and responsive behaviours; see Seay 1966), and b) maternal competence translating into reproductive success (Hrdy 1976). A majority of the allomothers would then be expected to be young, nulliparous females without previous maternal experience, caring for related or unrelated young (for example, Lancaster 1971, Nishida 1983, Jin *et al.* 2015, Boose *et al.* 2018, Zhang *et al.* 2018), and allomothering would influence parental behaviour and increase the survival of firstborns (for example, Tardif *et al.* 1984, Fairbanks 1990, Stone *et al.* 2010).

Mother-benefit and infant-benefit hypotheses

Since individuals can obtain indirect fitness by helping relatives (Hamilton 1964), the mother-benefit hypothesis proposes that allocarers selectively care for the young of closely related females leading to a) a decrease in the energetic costs associated with maternal care, b) reduction in inter-birth interval, and/or c) increased survival of related females (Ross and MacLarnon 2000). Similarly, allocarers can also obtain indirect fitness by enhancing the survival and reproduction of related young (infant-benefit hypothesis; Ross and MacLarnon 2000). Species in which individuals exhibit kin-based associations might have the opportunity to increase their indirect fitness through cooperative offspring care (König 1997). In many species, allomothers have been found to be closely related to infants, and siblings are taken care of preferentially compared to unrelated or distantly-related individuals (chimpanzees, Lawick-Goodall 1971; baboons, Rowell *et al.* 1964; vervet monkeys, Fairbanks 1990; African wild dogs, Estes and Goddard 1967; Humans, Crittenden and Marlowe 2008; Bonobos, Boose *et al.* 2018; Sperm whales, Konrad *et al.* 2019; Dogs, Paul *et al.* 2014). In the case of the mother-benefit and infant-benefit hypotheses, females of all ages may show allocare if they do not have offspring themselves.

We did not specifically examine the *alliance formation hypothesis*, according to which lower-ranking females preferentially care for the offspring of higher-ranking females in order to develop social bonds and secure their own, as well as their offsprings', future alliances (Deag 1974, de Waal 1990, Maestripieri 1994), or to reduce agonism directed towards them (Deag and Crook 1971). We also did not examine *reciprocity* (Trivers 1971) in providing care for each other's offspring.

Asian elephants

Asian elephants (*Elephas maximus*) show female-based societies, with the clan being the most inclusive level of social organisation (Shetty 2016, Nandini *et al.* 2017, 2018). Males disperse from their natal clans as they reach puberty and only temporarily associate with female groups thereafter (Sukumar 1989, Desai and Johnsingh 1995, Keerthipriya *et al.* 2021). Fission-fusion dynamics within clans allow females to be part of different groupings (de Silva *et al.* 2011, Nandini *et al.* 2017). Females generally associate with relatives (Vidya and Sukumar 2005, Shetty 2016). There is a weakly expressed age-based dominance hierarchy within clans (Shetty 2016, de Silva *et al.* 2017, Gautam 2019); however, there was no rank-related benefit in obtaining food within clans in the study population (Gautam 2019).

Female elephants give birth to single young – very rarely, twins – who are slow maturing and highly dependent on the mother, being weaned fully only around 4-5 years of age. Thus, females invest heavily in the development of their offspring and have relatively few offspring during their lifetime. Calves (less than a year old) have the highest age-specific mortality (Mar *et al.* 2012, unpublished data, Kabini Elephant Project), which makes allomothering potentially beneficial for the mother, calf, and the allomother. Males are not involved in parental care.

Allomothering in elephants

Allomothering is known in African savannah, African forest, and Asian elephants (Gadgil and Nair 1984, Lee 1987, Rapaport and Haight 1987, Chelluri 2009, Vidya 2014, Chapter 4 of this thesis). In African savannah elephants (*Loxodonta africana*), older female siblings were generally the allomothers, and calves without an older female sibling had one of their close relatives as an allomother – i.e., related young, nulliparous females were usually the allomothers (Lee 1987). Communal defense of the calves by forming a defensive circle around the calves during external disturbances was also seen. In the forest elephant (*Loxodonta cyclotis*), only older male and female siblings were seen to allomother calves through accompanying calves during wandering (Chelluri 2009). There was also occasional nursing of calves by related adult females (see Payne 2013). In semi-captive Asian elephants in southern India, calves preferred specific non-mother females, and these non-mother females were in turn near specific calves (Gadgil and Nair 1984). Non-parturient females allomothered related calves in captive Asian elephants in a zoo population (Rapaport and Haight 1987). We also found allomaternal care to be frequent and an integral part of the calf's developmental period in the Kabini Asian elephant population (Chapter 4 of this thesis). However, the reasons for allomaternal care and the direct consequences of such care have not been examined in detail. While reports on Asian elephants are based on small sample sizes, since young females were usually the allomothers in the African savannah elephant population studied, there was indirect support for the learning to mother hypothesis (Lee 1987). There was also some evidence for the infant-benefit hypothesis in that species: the presence of allomothers significantly lowered calf mortality, although they did not appear to enhance the growth rate of calves (Lee 1987).

In this study, we examined the non-mutually exclusive learning to mother, mother-benefit, and infant-benefit hypotheses in the Asian elephant. We expected young, nulliparous females to disproportionately show allomothering compared to non-lactating, older, parous females if the learning to mother hypothesis were true, whereas this would not be expected in the case of the mother-benefit or infant-benefit hypotheses. We expected calf-mother proximity and interactions to decrease in the presence of an allomother in the case of the mother-benefit hypothesis; this would not be expected if the other two hypotheses alone were correct because the presence of allomothers near the calf would not result in the mother moving away to feed. We expected calf sociality and female group size to increase in the presence of an allomother if the infant-benefit hypothesis were true. We also expected younger calves to be allomothered more than older calves in the case of the infant-benefit hypothesis, and calves of the youngest mothers to be allomothered more than mothers of other age-classes in the case of the mother-benefit hypothesis.

Methods

Field sampling

The study was carried out from January 2016 to June 2018 in Nagarahole and Bandipur National Parks and Tiger Reserves, southern India, primarily in and around the Kabini reservoir area (see Vidya 2014 and Chapter 2 of this thesis for details about the study area). The Asian elephants in this area have been studied since 2009 (Kabini Elephant Project), and hundreds of individuals have been identified based on multiple natural physical characteristics, including ear shape, markings on the ear that include nicks, tears, holes, etc., back shape, tail length and tail hair, and tusk length and shape in the case of males (see Vidya *et al.* 2014). We drove along pre-decided weekly routes from morning to evening and aged, sexed, and identified the elephants seen. Individuals were aged based on height and other characteristics (see Vidya *et al.* 2014) and classified as calves (<1 year old; further classified as newborn calves: <3 months old, infant calves: 3-<6 months, and old calves: 6-<12 months), juveniles (1–<5 years old), subadults (5–<10 years old in the case of females and 5–<15 years old in the case of males), and adults (≥10 years old in the case of females and ≥15 years old in the case of males). Adult females were further classified into five- or ten-year age-classes. A female group was defined as a set of females and, often, dependent young that showed coordinated movement and were usually within 50-100 m of one another (see Nandini *et al.* 2018). In the study population, the clan is the most inclusive level of female social organisation and fission-fusion dynamics occur within each clan; therefore, female groups sighted were usually subsets of clans. We almost never saw females of different clans to associate together as a single group.

To study the functions of allomaternal care, we collected data on calf-conspecific proximity, behavioural interactions (for newborn and infant calves) and female group size (for calves of all three age-classes). We conducted focal sampling (Altmann 1974) in the open habitat around the Kabini reservoir and video-recorded (using SONY HDR-XR 100E or HDR-PJ 540E video cameras) all the calf-conspecific interactions. Observers were at least about 50 m away from the elephant groups so that the groups were not disturbed.

Focal video scoring and analysis

We scored the focal videos (played back on Windows Media Player 12.0) recorded from elephant groups in which all the individuals were identified to obtain data on calf-conspecific proximity and calf-conspecific interactions (see below). We defined three categories of conspecific females: mother, allomother, and other females for each focal calf during each focal session. ‘Other females’ were non-mother, non-allomother females in the group that were at least 5 years old; these were females who did not show coordinated movement with the focal calf beyond that required of a group. Escorts, i.e., individuals that showed coordinated movement with a calf (beyond that required of a group) throughout most of the focal duration, were considered allomothers, as frequent affiliative interactions were found to occur between them and the calves (see Discussion of Chapter 4 of this thesis). Identification of the allomother was carried out separately for each focal session. This female did not necessarily always allomother a particular calf (or any calf) in all of that calf’s focals in which she was present. Therefore, if the female did not allomother the calf in a subsequent focal, she was considered an other female in that focal. Thus, only being an escort in a focal resulted in a female’s categorization as an allomother, and only in that focal. There could also be more than one allomother for a calf during a focal. Though coordinated movement was necessary through most of the focal, we did not set an *a priori* arbitrary cut-off on the number of allomaternal behaviours shown by a female during a focal to decide if she would be considered an allomother in that focal, as it would artificially reduce the variance observed in the extent of allomaternal care shown within a focal and impede one from exploring why certain allomothers showed more care than others.

We noted down the parity of all the females (nulliparous: never seen with her own calf or with enlarged mammary glands / lactation; parous: females know to have given birth, having either surviving or no surviving offspring). We obtained data on 30 calves, of which 20 had an allomother in each of their focals analysed (allomothered calves; data on these also used in Chapter 4) and 10 did not have an allomother in any of their focals analysed (non-allomothered calves) (Supplementary Material 1). Each focal was from a different day of observation for each calf. Each calf appeared in only one age-class (<3 months or 3-<6 months). All three conspecific categories of females were present in all the focals of the allomothered calves, and mothers and other females were present in all the focals of the non-allomothered calves.

Calf-conspecific proximity

We scored three 20-minute focals for each of the 30 calves in order to obtain data on calf-conspecific proximity (the focal videos of the 20 allomothered calves were the same as those used in Chapter 4 of this thesis). As explained in Chapter 4, we scanned individuals every four minutes (based on the time to independence of calf positions, see Chapter 4, Supplementary Material), obtaining 18 scans of calf positions per calf (3 focals x 6 scans/focal). At each scan of calf position, we noted down the conspecific categories of females that were within one calf body length of the focal calf. For each focal, we calculated the proportions of the six scans in which the focal calf was near its a) mother, b) allomother (where applicable), and c) other females. Since a calf could simultaneously be near more than one individual, these three proportions did not necessarily add up to 1. As there were often more than one ‘other female’ in the group or, sometimes, more than one allomother for a calf, we calculated the average proportion of scans that a calf spent near a single escort or other female (i.e., proportion of scans near a conspecific category / number of females in that conspecific category in that focal for the focal calf).

Calf-conspecific interactions

We scored two half-hour focal videos per calf for 30 calves (focal videos of the 20 allomothered calves were the same as those used in Chapter 4) and noted down all the interactions that occurred between the focal calf and females of the three conspecific categories. During each interaction, we noted down the identity and conspecific category of the initiator and terminator, the duration of the interaction, and the behavioural class of the interaction (feeding-related, resting-related, or social; see Chapter 4, Supplementary Material 4). For the focal calf-initiated interactions, we also recorded the types of response (positive, neutral, or negative; see Chapter 4, Supplementary Material 4) received by the calf from the mother, allomother, and other females.

For each focal, we calculated the proportion of calf-initiated interactions towards females of each conspecific category terminated by conspecific females of that category. Calves that had not initiated any interaction towards females of a particular conspecific category in the focal were excluded from the analyses that examined behavioural class of interaction (if conspecifics had also not initiated any interaction towards calves), and termination of and responses to calf-initiated interactions. The proportions of calf-initiated interactions towards mothers, allomothers, and other females that elicited positive, neutral, and negative responses (proportions for the three kinds of responses would together add up to 1 for each conspecific category) were calculated.

Data analysis

Age-classes of allomothers and frequency of allomothering

To examine whether young females were disproportionately allomothers (learning to mother hypothesis), we compared the numbers of females of different age-classes who ever allomothered a calf in each clan with the numbers of females of those age-classes available for allomothering in each of those clans, using a Pearson's X^2 test. Females who were at least 5 years old and did not have dependent young (up to 3 years old) of their own during each sighting were considered available for allomothering in that sighting. We also compared, within each clan, the numbers of independent sightings (based on 2.5-hour cut-off; see Nandini *et al.* 2017) during which females of different age-classes were allomothers (i.e., observed frequency of allomothering) with the numbers of sightings of females of those age-classes available for allomothering, using the Pearson's X^2 test. Parity was not tested independent of age due to the small sample sizes. Certain clans did not have females of all the age-classes. So, while doing the Pearson's X^2 test for each clan, only those age-classes in which there was at least one available female were used (see Supplementary Material 2). Tests were done on the clans that had available females in at least five age-classes (see Supplementary Material 2).

Calf-conspecific proximity and behavioural interactions

For each focal calf, we calculated the average value of each of the different proximity and behavioural measures across its focals (averaged across 3 focals for proximity related variables and across 2 focals for behavioural interaction related variables). To examine whether calf-mother proximity and interactions varied between the presence and absence of the allomother (mother-benefit hypothesis), we carried out ANOVAs with the average value as the dependent variable, and allomother presence/absence, calf age-class (2 levels: <3 months and 3-<6 months), and their two-way interactions as fixed-factors for each of the dependent variables; the dependent variables were the average proportion of scans near the mother, average mother-calf distance, average number of interactions with mothers, average number of interactions with mothers under different behavioural classes, average proportion of calf-initiated interactions terminated by the mothers, and average proportions of positive and negative responses from mother to the calf-initiated interactions.

Similarly, to assess the infant-benefit hypothesis in terms of calf sociality, all the above variables calculated for other females (by taking into account the number of other females), except proximity in terms of distance (because other females were often not near calves), were analysed in allomother presence and absence using the same ANOVA design as stated above.

We used a total of 540 scans of calf positions for the proximity analysis (allomother-present: calf <3 months old: 18 scans x 10 calves; calf 3-<6 months old: 18 scans x 10 calves; allomother-absent: calf <3 months old: 18 scans x 5 calves; calf 3-<6 months old: 18 scans x 5 calves), of which the scans in allomother presence (360 scans) had also been used in Chapter 4. There were a total of 1765 mother-calf, allomother-calf, and other female-calf behavioural interactions.

We also compared the proximity and behavioural measures between young allomother (<20 years in age)-calf pairs and older allomother (>=20 years in age)-calf pairs using Mann-Whitney *U* tests, in order to find out whether young allomothers showed a greater extent of allomothering than older allomothers (learning to mother hypothesis) during calf focal sessions. For certain calves, the identity of the allomother did not remain the same across focals. Therefore, we chose only those calves that had the same allomother in its focals (that led to 2 or 3 focals per calf) when examining the proportion of scans near the allomother (*N*=13 young allomother-calf dyads, 6 older allomother-calf dyads), and the average was used. Similarly, we only used those calves that had the same allomother in both its focals for analyses of behavioural interaction related variables (*N*=10 young allomother-calf dyads, 6 older allomother-calf dyads).

The sample sizes for proximity and behavioural variables were not the same because, for certain calves, the same focal videos could not be used for both; behavioural interaction scoring required calf visibility throughout the focal, but proximity had to be scored only once every four minutes. However, for most of the calves, the videos used for proximity and behavioural interaction scoring were the same. Mann-Whitney *U* tests and ANOVAs were carried out in Statistica (StatSoft, Inc. 2004).

Calf and mother age and the probability of allomothering

To examine whether calf age (infant-benefit hypothesis) and mother's age (mother-benefit hypothesis) affected the probability of a calf having an allomother, we analysed all the independent female group sightings with at least one calf during which a focal had been taken (so that we could confirm the presence/absence and identity of the allomother/s; N=881 such sightings when a focal was taken from January 2016-June 2018; Supplementary Material 3) using a generalised linear mixed-effects model. The presence or absence of an allomother for each calf in a sighting was considered a binomial dependent variable (allomother absence: 0, allomother presence: 1), calf age-class (<3 months, 3-<6 months, and 6-<12 months), and mother age-class (10-<20, 20-<30, 30-<40, 40-<50, and ≥50 years; Supplementary Material 3) were categorial fixed factors, the number of available females at least 5 years old without a dependent calf was a continuous factor, and calf ID was a categorical random factor. Each calf could appear multiple times within an age-class (sample sizes were not the same across calves), and each calf could also appear across age-classes. All the mothers had only one surviving calf during the study period on whom sighting data were collected and used here. Therefore, the mother's ID was not included as a random factor. We ran the models using the *fitglme* function in MATLAB R2011a, with a binomial distribution for the dependent variable (logit link).

Female group size

We had previously found that female group sizes increased in the presence of calves (Chapter 2 of this thesis). Following this, we wanted to check here whether this group size increase was due to the presence of an allomother. Therefore, we compared the number of females, who were at least 5 years old, in each sighting when there were no calves, when there was at least one calf in the sighting but no allomother (i.e., no female ≥5 years showed allomaternal care), and when there was at least one calf in the sighting and at least one allomother (i.e., at least one female ≥5 years showed allomaternal care). We used sighting data from 7 clans (which had at least five sightings in each of these three categories; Supplementary Material 5). Female group sizes were not normally distributed, and female group size could not be zero. There was also overdispersion. Therefore, we used a zero-truncated negative binomial model with log link for female group size. We used calf/allomother presence/absence as a fixed factor with three levels (1. calf absent, 2. calf present and allomother absent, and 3. calf present and allomother present; calf absent and allomother present would not be logically possible), and clan and its interaction with calf/allomother presence/absence as random factors. We assessed the significance of random effects using the same method as followed in Chapter 2 of this thesis (see Chapter 2, Methods). Group size analyses were run in R (version 4.1.1) using the package 'glmmTMB' (Magnusson *et al.* 2017). R^2 was calculated (see Chapter 2, Methods) using the R package 'RVAideMemoire' (Hervé 2022)).

Results

A majority of the female groups sighted had only one calf (N=618 sightings; Figure 1). An allomother was present in 72% of the calf sightings, and 62% of the calves had at least one allomother (Figure 1; there could be a single allomother in a sighting with multiple calves, leading to a lower percentage of calves with an allomother than the percentage of calf sightings with allomothers). We obtained data on 60 calf-allomother pairs, comprising 48 different allomothers (569 allomother sightings) and 36 different calves from 11 clans (see Supplementary Material 4). The proportion of sightings of calves in which specific females that had ever allomothered them was present varied from 0.2-1, but was mostly 1 (see Figure 2a). Therefore, while there were some allomothers that were seen only occasionally with the calf that they allomothered, most allomothers were seen in most of the sightings of the calf. Each allomother cared for only one calf at a time, and the number of allomothers for a calf ranged from one to four, but about half (53%) of the calves had only one allomother (31% had two allomothers, 14% had three allomothers, and 3% had four allomothers during the study period when they were calves). Periods of allomothering amongst females who allomothering a particular calf overlapped to different extents, however, that was not examined in this study. The proportion of sightings in which a particular female who had ever allomothered a particular calf was present with that calf and was seen to show allomothering varied from 0.1-1.0 (Figure 2b). Again, while some females who ever allomothered a calf showed a low proportion of allomothering, the majority showed allomothering whenever they were present in the group with the calf. This would be a minimum estimate because we were only examining allomothering within 20-minute focals, and it was possible that the allomother showed allomothering outside of that.

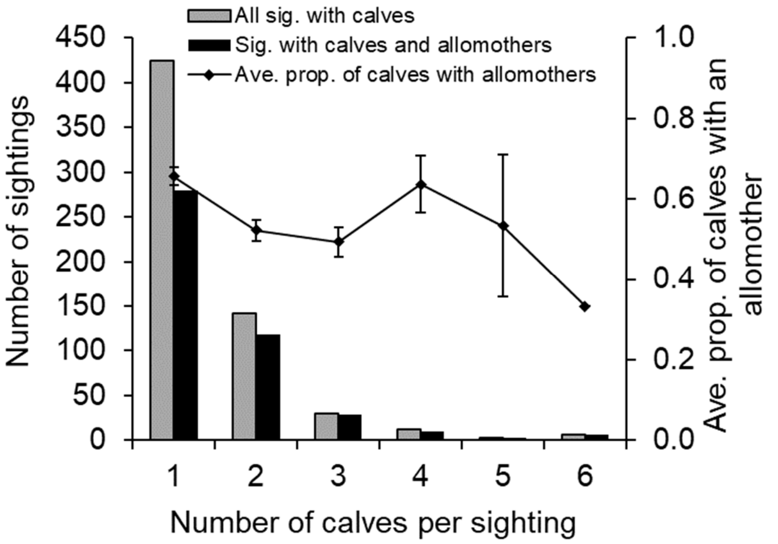


Figure 1. Numbers of female group sightings with varying number of calves (grey bars; *N*=618 sightings), numbers of such female group sightings (with varying number of calves) that had at least one allomother in the sighting (black bars), and the average proportion of allomothered calves in the sighting (number of calves with an allomother in the sighting divided by the total number of calves in the sighting, and averaged across sightings) for sightings with different numbers of calves (points). The line connecting the points is only for visualisation and does not signify anything. Error bars are 95% CI around the means.

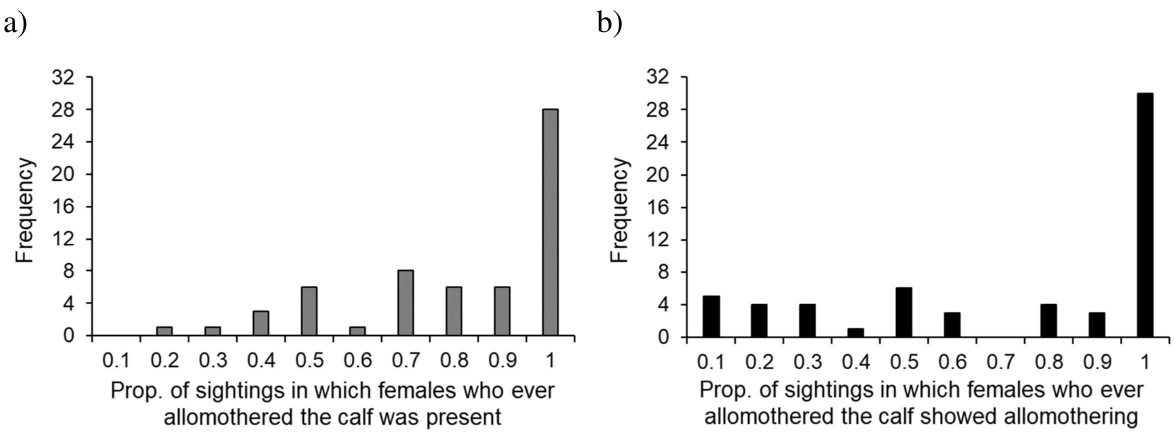


Figure 2. Frequency distribution of the a) proportions of sightings of calves in which females

who had allomothered particular calves, at least in one of their sightings, was present (i.e., number of focal sightings of a calf in which a particular female that ever allomothered a calf was present / number of focal sightings of the calf) and b) proportions of sightings of calves in which specific females showed allomothering (i.e., number of focal sightings of a calf in which a specific female who had allomothered the calf at any point showed allomothering / number of focal sightings of that calf in which that female was present). Plots are based on data from 60 unique calf-allomother dyads (but not unique allomother, as during the course of the study period, a particular female could have allomothered more than one calf) from 11 clans.

Age class of allomothers and allomothering behaviour

The median age of all the females who ever allomothered a calf was 17.7 years; here, each female who ever allomothered a calf was included only once, and their ages were calculated using the mid-point of the study period. Nulliparous females comprised 67% of all the females who ever allomothered a calf; here, each female was included as many times as the number of unique calves they allomothered because the parity of females could change over time (for e.g., Koyna was nulliparous when she allomothered Kokila_2015_F and Ketki_2016_F, but she was parous when she allomothered Kasturi_2018_M; Koyna had given birth to a still-born calf before she allomothered Kasturi's calf). Females who had dependent young less than 5 years of age never showed allomaternal care. Grandmothers were allomothers for two calves (Genette_2017_F, Floppy_ears_2018_F). Of the 60 mother-allomother pairs, mothers were older than allomothers in 67% of the dyads (Figure 3). Excluding the three pairs that were very close in age (i.e., the same age-class; Gemini, Dominique: 18.2 and 18.3 years; Suhrita, Suvrata: 12.7 and 14.2 years; Floppy_ears, Sushma: 15.3 and 15.8 years), mothers were older than allomothers in 71% of the dyads.

We found some variation across age-classes in the proportion of females that were available to allomother calves (i.e., the number of females without dependent young <3 years divided by the number of females within a female age-class), as well as in the proportion of females who actually allomothered calves (i.e., the number of female who ever showed allomothering divided by the number of females within a female age-class) (Figure 4; clans that did not have even a single female in a particular age-class were omitted in the calculations of the above two proportions only for that age-class, see Supplementary Material 2). The proportions of females that ever allomothered calves were much smaller than those available. Therefore, allomothering was probably not limited by the lack of available females.

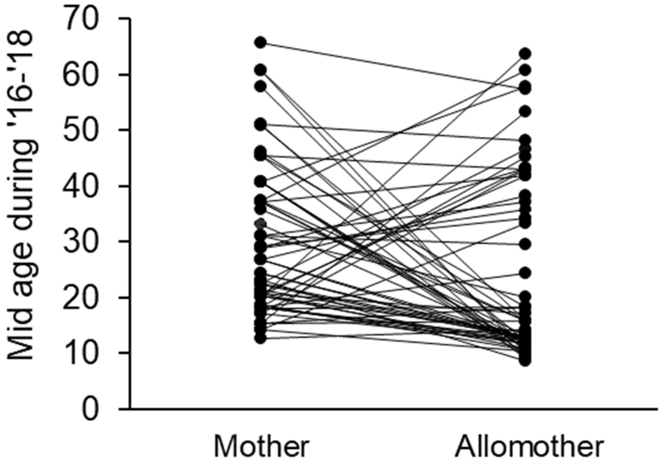


Figure 3. Ages of the 60 unique mother-allomother dyads (but not all unique allomothers, as during the course of the study period, a particular female could have allomothered more than one calf) with lines connecting the mothers and allomothers. Ages were calculated using the mid-point of the sampling period.

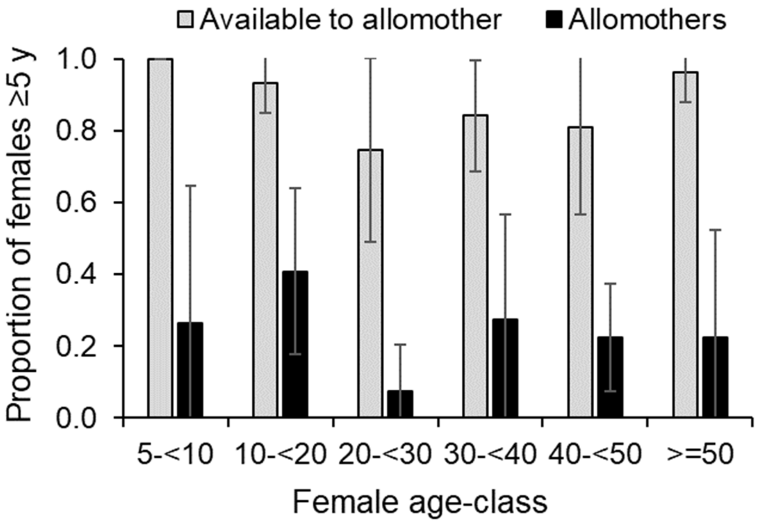


Figure 4. Proportions of females of different age-classes that were available to allomother and were ever allomothers across clans (see Supplementary Material 2 for sample sizes). Error bars are 95% CI around the means.

Table 1. Results of the X^2 tests on seven clans to compare the observed and expected age-classes of females who ever allomothered a calf and observed and expected frequencies of allomothering by females of different age-classes. The age-classes used were the same as that shown in Figure 2. Sufficient sample sizes were not available in the other four clans.

	Age-class of females who ever allomothered			Frequency of allomothering by females of different age-classes		
Clan ID	X^2	*df*	*P*	X^2	*df*	*P*
Katrina	54.328	4	**<0.001**	64.867	4	**<0.001**
Lisa	64.000	5	**<0.001**	127.444	5	**<0.001**
Menaka	5.333	4	0.255	25.253	4	**<0.001**
Nakshatra	9.600	5	0.087	26.667	5	**<0.001**
Osanna	37.615	5	**<0.001**	29.438	5	**<0.001**
Patricia	4.950	5	0.422	37.388	5	**<0.001**
Victoria	14.866	5	**0.011**	137.129	5	**<0.001**

The observed age-classes of females who ever allomothered a calf were significantly different from those expected in four of the seven clans that could be tested (see Supplementary Material 2; Table 1). There was a greater number of 10–20-year-old females who ever allomothered a calf than the expected values in four clans (Katrina, Lisa, Osanna, and Victoria), a greater number of 30–40-year-old females who ever allomothered a calf also than expected in one clan (Lisa), and a greater number of 40–50-year-old females who ever allomothered a calf also than expected in one clan (Osanna). Their (30–40-year-olds and 40–50-year-olds) numbers were the same as the numbers of 10–20-year-old females who ever allomothered a calf in their respective clans. In all but one of the clans (Patricia), 20–30-year-old females were never the allomothers (Figure 5a). Similarly, in all but one of the clans (Victoria), >=50-year-old females were never the allomothers. There was no significant correlation between the age of the allomother and that of the calf – i.e., females of all ages allomothered calves of all ages (Supplementary Material 5).

The observed frequencies of allomothering by females of various age-classes were different from those expected in all the seven clans tested (Table 1), with the frequencies of allomothering being higher than expected in 10–20-year-old females in six of the seven clans (Figure 5b). In one of the clans (Menaka), subadult females were allomothers in more sightings than expected. In four of the clans, older females (40–50 years old in three clans and >50 years old in one clan) were also allomothers in more sightings than expected, apart from

10–20-year-old females. In only one clan, 30–40-year-old females were allomothers in a greater number of sightings than expected. In all the 7 clans, the frequency of allomothering by 10–20-year-old females was greater than the frequencies of allomothering by females of other individual age-classes (Figure 5b).

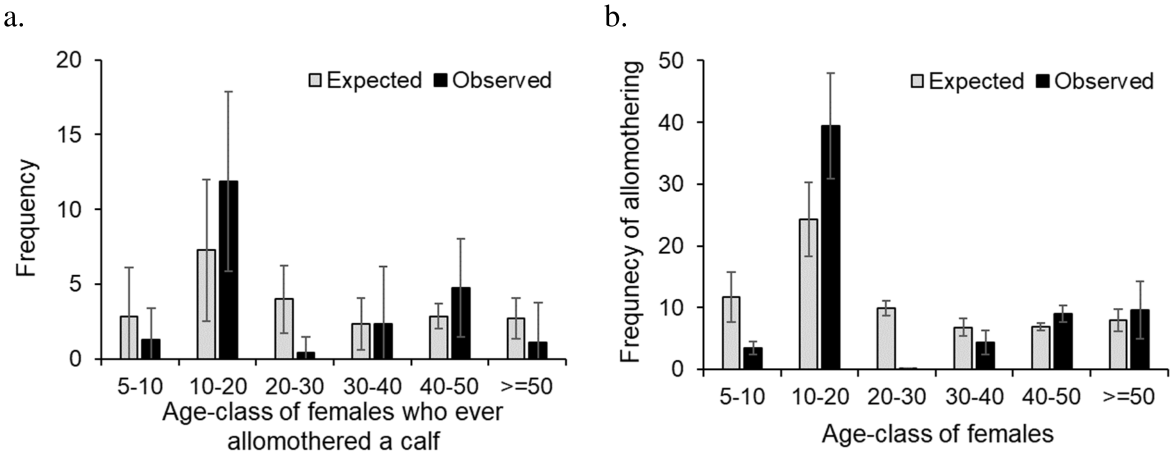


Figure 5. Observed versus expected frequency of a) age-classes of females who ever allomothered a calf and b) allomothering (i.e., number of sightings as allomothers) by females of different age-classes. The values were averaged across six or seven clans, depending on the presence of females available to allomother in each age-class (seven clans used for X^2 tests, but not all the clans had females available for allomothering in all the six age-classes; Supplementary Material 1). Error bars are 95% CI around the means.

While young females were more frequently the allomothers compared to older females, both young and older females showed similar proximity (during focal sessions) to calves when they were allomothers: there was no significant difference between young and older allomothers in the average proportion of scans calves spent near them (Mann-Whitney *U* test: U=30.5, Z_{adj}=-0.769, P=0.467, Figure 6a). There was also no significant difference in the average number of interactions between calves and allomothers of the two broad age-classes (U=24.5, Z_{adj}=-0.597, P=0.562, Figure 6b) or the average proportion of calf-initiated interactions terminated by allomothers of the two broad age-classes (U=22.0, Z_{adj}=0.868, P=0.428, Figure 6d). However, the average number of positive (helpful) interactions initiated by allomothers towards calves was higher among young than older allomothers (U=10.0, Z_{adj}=2.169, P=0.031, Figure 6c). While not statistically significant, there was also a trend of a slightly higher average proportion of interactions that received a positive response (U=18.5, Z_{adj}=-1.247, P=0.220, Figure 6e) and slightly lower average proportion of interactions that received a negative response from (U=19.0, Z_{adj}=1.197, P=0.231, Figure 6f) the young than older allomothers.

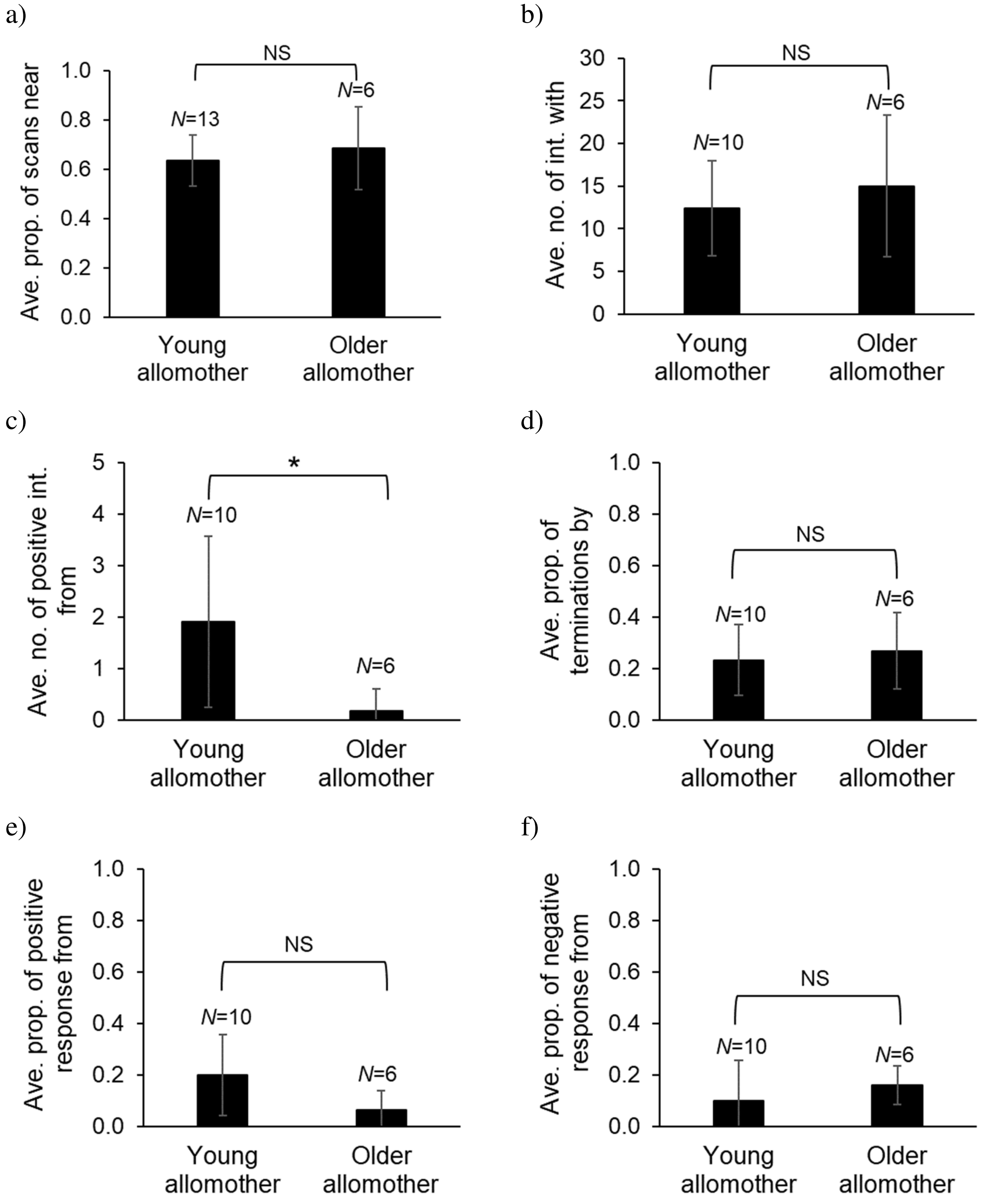


Figure 6. a) average proportion of scans spent by calves near, b) average number of interactions with, c) average proportion of positive interactions from, d) average proportion

of calf-initiated interactions terminated by, e) average proportion of calf-initiation interactions that elicited a positive response from, and f) average proportion of calf-initiation interactions that elicited a negative response, from young and older allomothers. Error bars are 95% CI around the mean. The numbers of allomothers are written above the bars. Asterisks indicates significance based on Mann-Whitney *U* test.

Allomothering and mother-calf interactions

Calves with allomothers spent a significantly smaller proportion of their time near (within one calf body length) their mothers than did calves without allomothers (Table 2, Figure 7a) during focal sessions. The average mother-calf distances in the presence of allomothers seemed higher than those in the absence of allomothers, but this was not statistically significant (Table 2, Figure 7b). Newborn calves (<3 months old) spent a significantly smaller proportion of their time near their mothers and were significantly closer to their mother than were infant calves (3-<6 months old) (Table 2, Figure 7c,d).

Calves with and without an allomother (during the focal session) did not significantly differ in the average total number of interactions (Table 3, although was there a lower trend in allomother presence, Figure 8a), feeding-related interactions (Table 3, Figure 8b), or resting-related interactions (Table 3, Figure 8c), that they (calves) initiated towards their mothers. However, calves with an allomother initiated fewer social interactions with their mothers than those without an allomother (Table 3, Figure 8d). Newborn and infant calves did not significantly differ in the numbers of interactions, either total or in different behavioural classes, initiated towards their mothers, although there was a trend towards lower values by infant calves in the numbers of social and resting interactions (Table 3, Figure 9 a-d).

Table 2. Results of the ANOVA on the average proportion of scans near the mother and on the average distance (in calf body lengths) between mother-calf pairs. Significant *P* values are marked in bold. P/A refers to presence/absence.

Effect	SS	*df*	*MS*	*F*	*P*
Average proportion of scans near the mother					
Intercept	15.111	1	15.111	1038.318	**<0.001**
Calf age-class	0.185	1	0.185	12.724	**0.001**
Allomother P/A	0.198	1	0.198	13.587	**0.001**
Calf age-class*Allomother P/A	0.030	1	0.030	2.036	0.166
Error	0.378	26	0.015		
Average mother-calf distance					
Intercept	5.653	1	5.653	29.407	**<0.001**
Calf age-class	0.936	1	0.936	4.870	**0.036**
Allomother P/A	0.684	1	0.684	3.558	0.070
Calf age-class*Allomother P/A	0.338	1	0.338	1.760	0.196
Error	4.998	26	0.192		

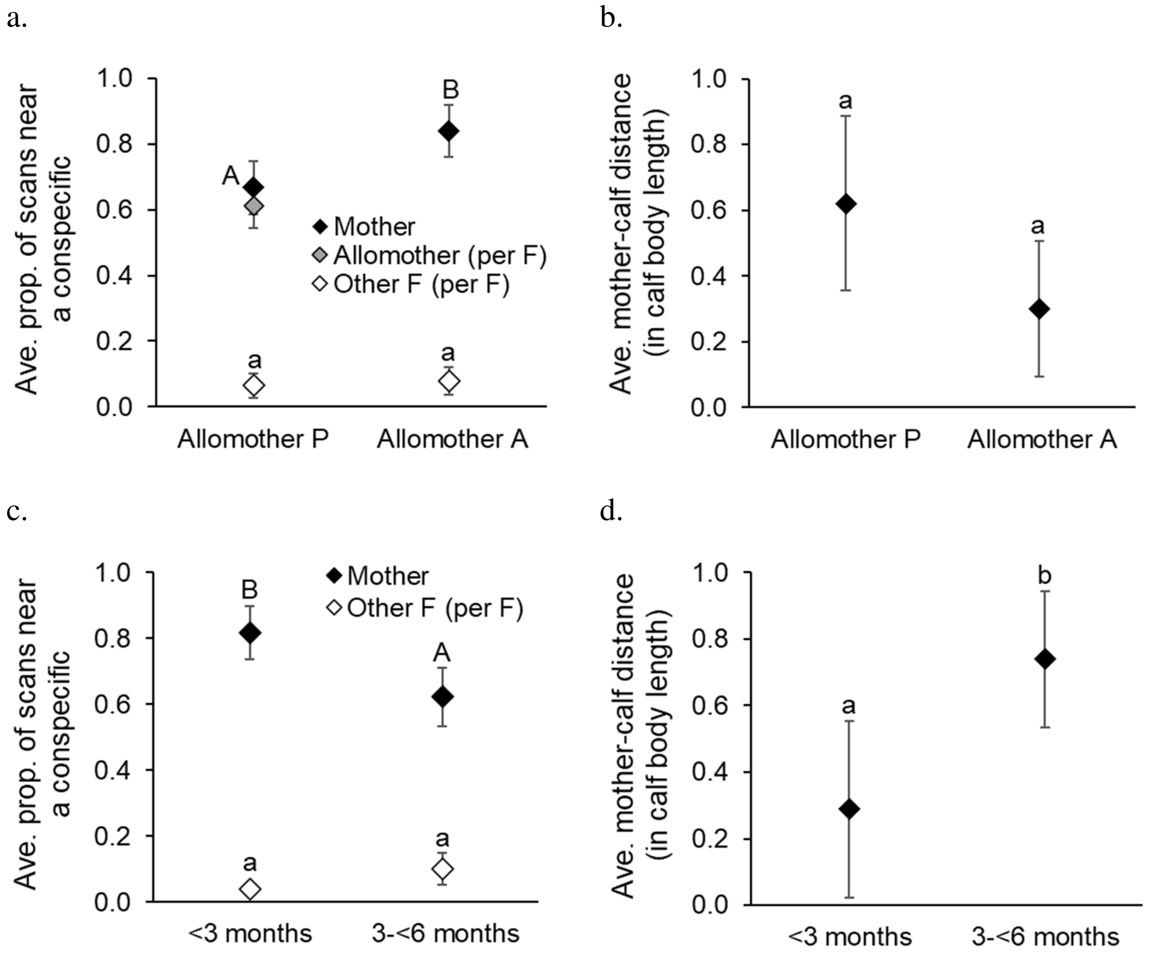


Figure 7. a) average proportion of scans spent by calves near their mothers, allomothers (per allomother), or other females (per other female) in allomother presence (*N*=20 calves) and

absence (*N*=10 calves), b) average mother-calf distance in allomother presence and absence, c) average proportion of scans spent by newborn calves (<3 months old; *N*=15 calves) and infant calves (3-<6 months old; *N*=15 calves) near their mothers, and d) average mother-calf distance for newborn and infant calves. Error bars are 95% CI around the means. Letters above the data points indicate patterns of statistical significance (a<b; A<B; shared letters indicate no statistical significance).

Table 3. Results of the ANOVA on the average numbers of all interactions, feeding interactions, resting interactions, and social interactions, initiated by calves towards their mothers. Significant *P* values are marked in bold. P/A refers to presence/absence.

Effect	SS	*df*	*MS*	*F*	*P*
Average number of all calf-initiated interactions with mother					
Intercept	6923.004	1	6923.004	132.408	**<0.001**
Calf age-class	28.704	1	28.704	0.549	0.465
Allomother P/A	110.704	1	110.704	2.117	0.158
Calf age-class*Allomother P/A	0.938	1	0.938	0.018	0.895
Error	1359.425	26	52.286		
Average number of calf-initiated feeding interactions with mother					
Intercept	1960.817	1	1960.817	60.855	**<0.001**
Calf age-class	0.600	1	0.600	0.019	0.893
Allomother P/A	3.750	1	3.750	0.116	0.736
Calf age-class*Allomother P/A	4.267	1	4.267	0.132	0.719
Error	837.750	26	32.221		
Average number of calf-initiated resting interactions with mother					
Intercept	18.150	1	18.150	10.886	**0.003**
Calf age-class	1.067	1	1.067	0.640	0.431
Allomother P/A	0.150	1	0.150	0.090	0.767
Calf age-class*Allomother P/A	1.667	1	1.667	1.000	0.327
Error	43.350	26	1.667		
Average number of calf-initiated social interactions with mother					
Intercept	1201.538	1	1201.538	88.467	**<0.001**
Calf age-class	26.004	1	26.004	1.915	0.178
Allomother P/A	80.504	1	80.504	5.927	**0.022**
Calf age-class*Allomother P/A	3.038	1	3.038	0.224	0.640
Error	353.125	26	13.582		

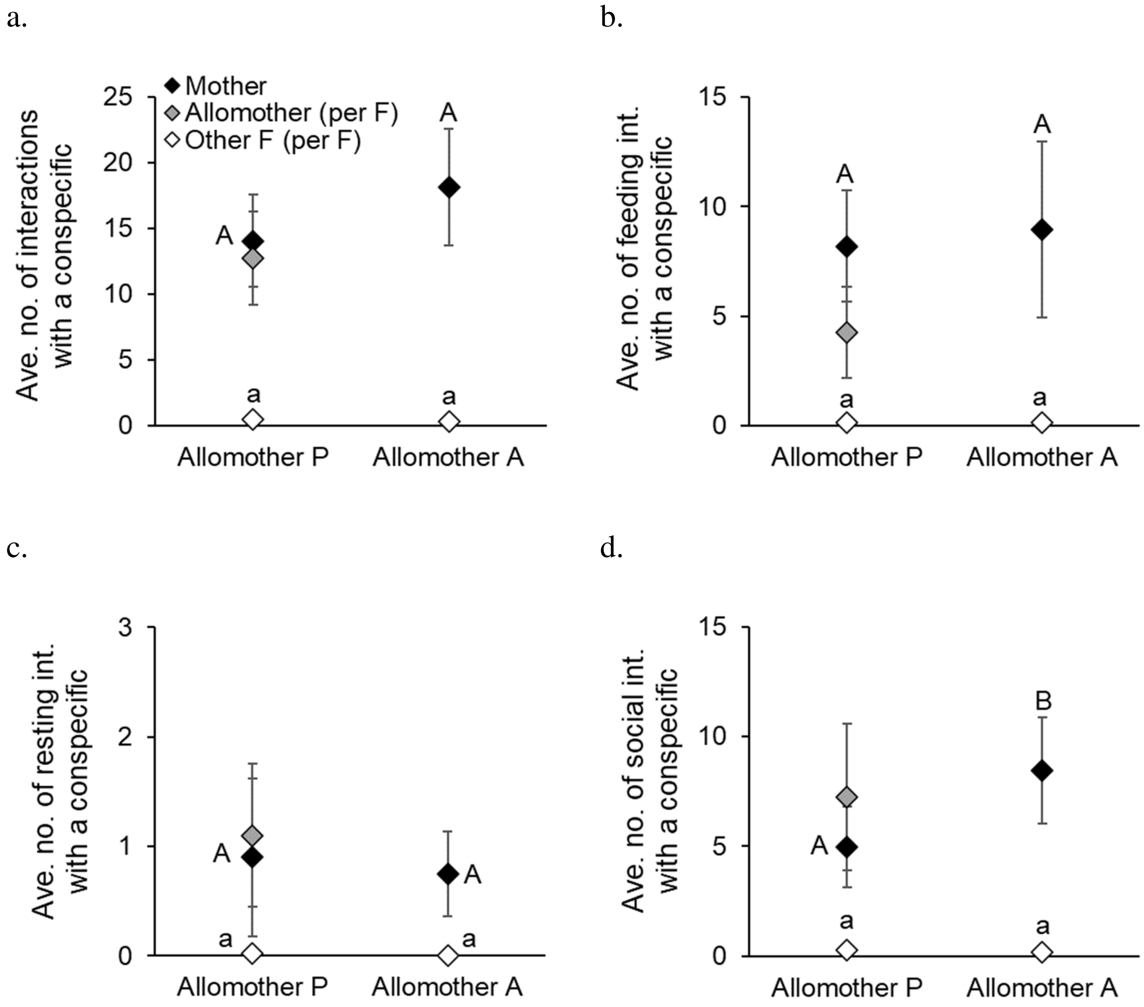


Figure 8. a) average total numbers of calf-initiated interactions, and average numbers of b) feeding, c) resting, and d) social calf-initiated interactions (towards their mothers, allomothers (per allomother), or other females (per other female)) in allomother presence (*N*=20 calves) and absence (*N*=10 calves). Error bars are 95% CI around the mean. Letters above the data points indicate patterns of significance (a<b; A<B; shared letters indicate lack of significance between categories).

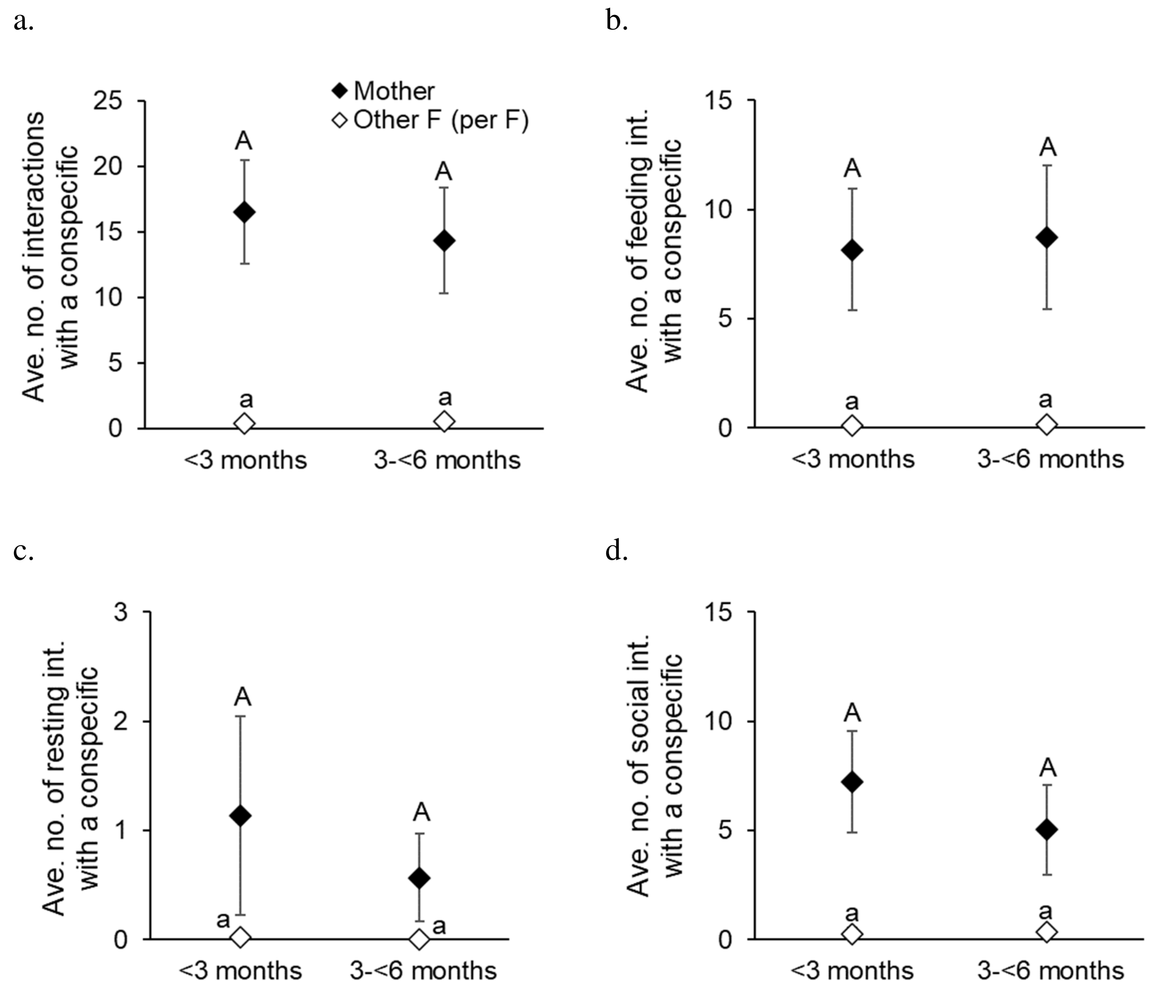


Figure 9. a) average total numbers of calf-initiated interactions, and average numbers of b) feeding, c) resting, and d) social interactions initiated by newborn (<3 months old; *N*=15 calves) and infant calves (3-<6 months old; *N*=15 calves) towards their mothers and other females (per other female). Error bars are 95% CI around the means. Letters above the data points indicate patterns of significance (a<b; A<B; shared letters indicate lack of significance between categories).

The proportion of calf-initiated interactions that their mothers terminated, the proportion of calf-initiated interactions to which mothers showed a positive response, and the proportion to which mothers showed a negative response neither increased nor decreased if their calf had an allomother (Table 4, Figure 10a,c,e). There was no significant effect of calf age-class on the proportion of interactions that elicited a positive or negative response from mothers either (Table 4, Figure 10b,d,f).

Table 4. Results of the ANOVA on the average proportion of calf-initiated interactions that elicited a positive and a negative response from mothers. P/A refers to presence/absence.

Effect	SS	*df*	*MS*	*F*	*p*
Proportion of interactions terminated by mothers					
Intercept	1.812	1	1.812	95.990	**<0.001**
Calf age-class	0.015	1	0.015	0.798	0.380
Allomother P/A	0.006	1	0.006	0.324	0.574
Calf age-class*Allomother P/A	0.055	1	0.055	2.923	0.099
Error	0.491	26	0.019		
Proportion of interactions that elicited a positive response from mothers					
Intercept	0.033	1	0.033	18.738	**<0.001**
Calf age-class	0.001	1	0.001	0.647	0.428
Allomother P/A	0.000	1	0.000	0.178	0.677
Calf age-class*Allomother P/A	0.002	1	0.002	0.917	0.347
Error	0.046	26	0.002		
Proportion of interactions that elicited a negative response from mothers					
Intercept	2.521	1	2.521	115.784	**0.000**
Calf age-class	0.003	1	0.003	0.138	0.713
Allomother P/A	0.043	1	0.043	1.959	0.173
Calf age-class*Allomother P/A	0.004	1	0.004	0.173	0.681
Error	0.566	26	0.022		

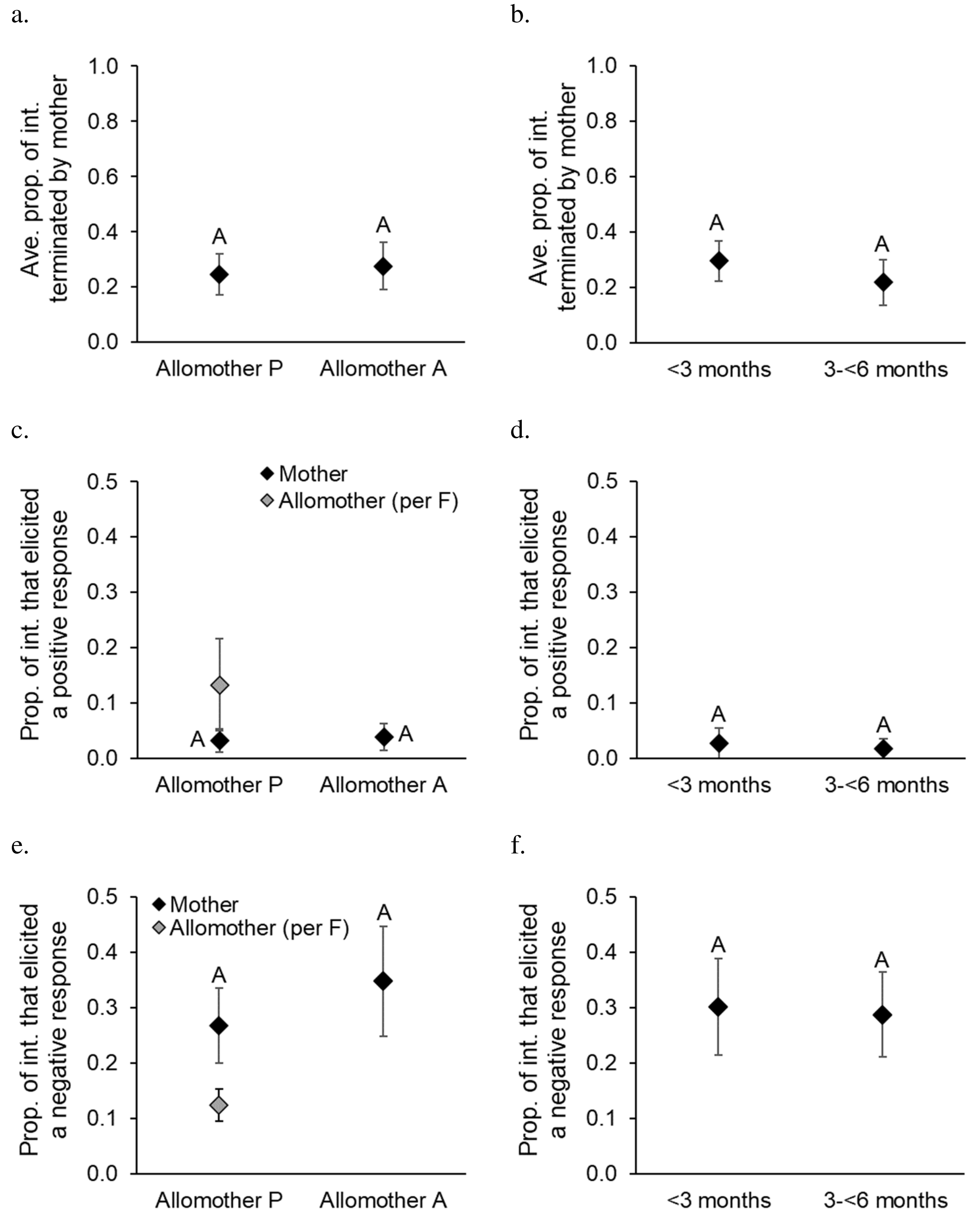


Figure 10. Proportion of calf-initiated interactions that a) mothers terminated, and that elicited a c) positive and d) negative response from their mothers and allomothers (per allomother) where applicable in allomother presence (*N*=20 claves) and absence (*N*=10 claves), and proportion of newborn and infant calf-initiated interactions that b) mothers terminated, and that elicited a d) positive and f) negative response from their mothers. Error bars are 95% CI around the means. Letters above the data points indicate patterns of significance; shared letters indicate a lack of significance between categories.

Allomothering and calf-other female behaviours

Calf proximity with females other than its mother or allomother did not increase in the presence of an allomother for a focal calf (Other F; Table 5, Figure 7a) nor did the the total number of interactions (Table 5, Figure 8a) or the number of feeding (Table 5, Figure 8b), resting (Table 5, Figure 8c), or social interactions (Table 5, Figure 8d) initiated by calves towards other females increase in the presence of an allomother during focal sessions; however, calves with an allomother had the advantage of being close to and interacting with their allomothers, as much as they did with their mothers (Chapter 4 of this thesis, Figure 7a, 8a-d), and receiving positive responses from both (Chapter 4 of this thesis and Figure 10a), which the calves without an allomother did not enjoy.

Newborn and infant calves did not significantly differ in the average proportion of scans near other females (Table 5, Figure 7c), in the total number of interactions (Table 5, Figure 9a) or in each of the different behavioural classes of interactions towards other females (Table 5, Figure 9b-d). As calves <6 months rarely interacted with females other than their mothers or allomothers, we could not include other females while analysing the proportion of positive responses received by calves; nevertheless, such responses from other females towards calves with and without an allomother were almost non-existent.

Calf and mother age and the probability of a calf being allomothered

When we examined the factors that influenced the probability of a calf being allomothered, we found that the best model consisted of calf age-class, mother age-class, and calf ID, and there was one other good model with ΔAIC <2 (Supplementary Material 2). In both models, newborn (<3 months) calves were allomothered significantly more frequently than calves of the other two age-classes (Table 6, Figure 11a). Calves of the oldest age-class of mothers were allomothered significantly less frequently than calves of mothers of other age-classes (Table 6, Figure 11b). Although the number of available females appeared in one of the best models, the parameter estimate was not statistically significant (Table 6).

Table 5. Results of the ANOVA on the average proportion of scans near other females (per other female), average numbers of all calf-initiated interactions, and feeding, resting, and social interactions towards other females (per other female). Significant *P* values are marked in bold. P/A refers to presence/absence.

Effect	SS	*df*	*MS*	*F*	*p*
Average proportion of scans near (per) other female					
Intercept	0.109	1	0.109	45.124	**<0.001**
Calf age-class	0.008	1	0.008	3.254	0.083
Allomother P/A	0.007	1	0.007	2.729	0.111
Calf age-class*Allomother P/A	0.007	1	0.007	2.933	0.099
Error	0.063	26	0.002		
Average number of all calf-initiated interactions with other females					
Intercept	3.649	1	3.649	10.121	**0.004**
Calf age-class	0.284	1	0.284	0.626	0.436
Allomother P/A	0.286	1	0.286	0.631	0.434
Calf age-class*Allomother P/A	0.383	1	0.383	0.845	0.366
Error	11.784	26	0.453		
Average number of calf-initiated feeding interactions with other females					
Intercept	0.501	1	0.501	4.901	**0.036**
Calf age-class	0.052	1	0.052	0.510	0.481
Allomother P/A	0.001	1	0.001	0.009	0.927
Calf age-class*Allomother P/A	0.202	1	0.202	1.978	0.171
Error	2.660	26	0.102		
Average number of calf-initiated resting interactions with other females					
Intercept	0.002	1	0.002	0.582	0.452
Calf age-class	0.001	1	0.001	0.381	0.542
Allomother P/A	0.002	1	0.002	0.582	0.452
Calf age-class*Allomother P/A	0.001	1	0.001	0.381	0.542
Error	0.101	26	0.004		
Average number of calf-initiated social interactions with other females					
Intercept	1.973	1	1.973	10.468	**0.003**
Calf age-class	0.090	1	0.090	0.477	0.496
Allomother P/A	0.251	1	0.251	1.330	0.259
Calf age-class*Allomother P/A	0.030	1	0.030	0.160	0.693
Error	4.899	26	0.188		

Table 6. Results of the generalised linear mixed-effects models of the probability of calves being allomothered.

Effect	Estimate	SE	*t*	*df*	*P* value	95% CI of estimate	
Model: Allomother A/P ~ 1 + Calf age-class + Mother age-class + (1 |Calf ID)							
Fixed effects							
Intercept	1.226	1.150	1.066	874	0.287	-1.031	3.482
Calf age-class - <3	**0.622**	**0.269**	**2.315**	**874**	**0.021**	**0.095**	**1.149**
Calf age-class - 3-<6	-0.453	0.268	-1.692	874	0.091	-0.979	0.073
Mother age-class - 10-<20	1.862	1.490	1.249	874	0.212	-1.063	4.786
Mother age-class - 30-<40	0.866	2.047	0.423	874	0.672	-3.151	4.883
Mother age-class - 40-<50	-1.816	2.347	-0.774	874	0.439	-6.423	2.791
Mother age-class - >=50	**-6.126**	**2.585**	**-2.370**	**874**	**0.018**	**-11.199**	**-1.053**
Random effects		SD					
Calf ID intercept		6.918		51 levels			
Model: Allomother A/P ~ 1 + Calf age-class + Mother age-class + No. of available females + (1| Calf ID)							
Fixed effects							
Intercept	1.310	1.177	1.113	873	0.266	-1.000	3.620
Calf age-class - <3	**0.622**	**0.269**	**2.313**	**873**	**0.021**	**0.094**	**1.150**
Calf age-class - 3-<6	-0.448	0.268	-1.670	873	0.095	-0.975	0.079
Mother age-class - 10-<20	1.876	1.495	1.255	873	0.210	-1.059	4.810
Mother age-class - 30-<40	0.852	2.055	0.415	873	0.678	-3.181	4.885
Mother age-class - 40-<50	-1.809	2.355	-0.768	873	0.443	-6.432	2.814
Mother age-class - >=50	**-6.161**	**2.594**	**-2.375**	**873**	**0.018**	**-11.253**	**-1.069**
No. of available females	-0.019	0.059	-0.330	873	0.742	-0.135	0.096
Random effects		SD					
Calf ID intercept		6.942		51 levels			

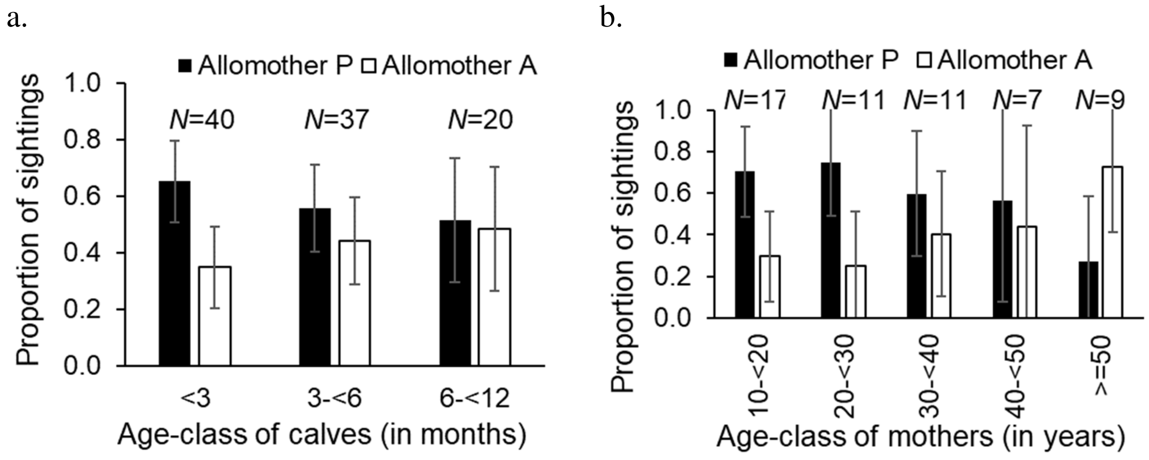


Figure 11. a) proportion of sightings of calves of the three age-classes in which they were and were not allomothered and b) proportion of sightings of mothers of the five age-classes in

which their calves were and were not allomothered. Numbers above the bars indicate sample sizes (i.e., number of sightings of calves and number of sightings of mothers, respectively) for each age-class. Error bars are 95% CI around the means.

Allomothering and female group size

There was a significant effect of calf/allomother presence/absence on female group size, with group size being significantly higher in calf presence-allomother presence (i.e., when at least one of the females ≥5 years showed allomaternal care), followed by calf presence-allomother absence (when none of the females ≥5 years showed allomaternal care) (Table 7, Figure 12). Group size was the lowest in calf absence (Figure 12). There was also a significant effect of clan identity as well as its interaction with calf/allomother presence/absence (Supplementary Material 5).

Table 7. Results of the full GLMM using log link for female group size. Intercept and category (i.e., calf absence-allomother absence, calf presence-allomother absence, and calf presence-allomother presence) are fixed effects (for which SE of the estimate is calculated), whereas Clan and Clan x Calf/Allomother presence/absence (P/A in table) are random effects (for which SD is given). Significant *P* values are marked in bold. Asterisks mark significant random effects based on comparison with reduced models (see Supplementary Material 5).

Dependent variable	Estimate	*SE* of estimate	95% CI of estimate		*z*	*P*
			Lower	Upper		
Intercept	0.313	0.170	-0.020	0.646	1.837	0.066
Category: calf presence-allomother absence	0.938	0.161	0.622	1.254	5.810	**<0.001**
Category: calf presence-allomother presence	1.207	0.154	0.905	1.509	7.825	**<0.001**
Clan		0.318				*
Clan x Calf/Allomother P/A		0.220				*

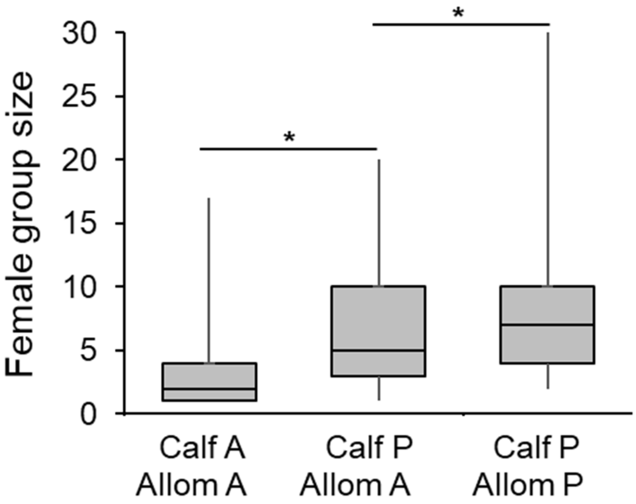


Figure 12. Female group size (number of females at least five years old) in calf absence-allomother absence, calf presence-allomother absence, and calf presence-allomother presence. Boxes show the 25th percentile, median, and 75th percentile, and bars indicate the minimum and maximum. Significant pairwise differences are marked with asterisks.

Discussion

We examined three functional hypotheses, namely the learning to mother hypothesis (direct benefits; Lancaster 1971, Hrdy 1976, Quiatt 1979, Chism 2000, Ross and MacLarnon 2000), mother-benefit hypothesis, and infant-benefit hypothesis (indirect benefits; Chism 2000, Ross and MacLarnon 2000), to explain allomothering in Asian elephants for the first time. We found preliminary support for all of three of these hypotheses, i.e., allomothering may potentially benefit all three participants – the allomother, mother, and calf. As expected by the learning to mother hypothesis, young, nulliparous females were primarily the allomothers. In accordance with the mother-benefit hypothesis, calves with an allomother spent a higher proportion of their time away from and had fewer social interactions with their mothers than calves without an allomother. Apart from one's mother, calves with an allomother had the advantage of being close to, interacting with, and receiving support from their allomothers, but calves without an allomother were close only to their mothers. Female group sizes were larger in calf presence than in their absence; additionally, allomother-present groups were larger than allomother-absent groups, suggesting that calves might experience increased group size benefits in the presence of an allomother, probably against predation. These results lend support to the infant-benefit hypothesis through increased sociality and protection. The various results of the three hypotheses are discussed in detail below.

Learning to mother hypothesis

As offspring survival is an important component of female reproductive fitness, learning mothering skills prior to the birth of one's calf could be vital (Quiatt 1979), especially in a species with high first-birth mortality regardless of maternal age (see Mar *et al.* 2012). We found that the majority of the females who ever allomothered a calf were young adult females (10-20 years) as expected if this hypothesis were true. Moreover, a majority of the females who ever allomothered a calf were also nulliparous females. However, on an average, young females who ever allomothered a calf did not show allomaternal care in around 30% (± 11%) of their sightings with calves (the value was very similar for older females who ever allomothered a calf also). Young females have been reported as allomothers previously also, in studies of small numbers of semi-captive and captive Asian elephants (Gadgil and Nair 1984, Rapaport and Haight 1987, Garai 1992). Young, nulliparous females were often the allomothers in African savannah elephants also (Dublin 1983, Lee 1987, Lee and Moss 2011). When we looked at allomothering behaviour, we found no significant pattern in how spatially close and responsive allomothers were with respect to their age; however, young age allomothers extended slightly more help than older allomothers. Since the calves of young African savannah elephant females experienced more frequent distress situations than the calves of older and more experienced females, Lee (1987) suggested that allomothering might not enhance maternal skills. However, whether females that have been allomothers are more responsive or have a higher reproductive success than those who have never allomothered a calf is yet to be examined in this and the Amboseli population.

Since the majority of the females who ever allomothered a calf were young females, this resulted in mothers being older than allomothers (i.e, females who ever allomothered their calves) in about two-thirds of all mother-allomother dyads, as in the case of African savannah elephant (Dublin 1983). Allomothers being (of any age but) younger than the mothers would be expected in the case of the alliance formation hypothesis also. A positive effect of age on within-clan dominance relationships is known in the Kabini population, but the within-clan dominance hierarchy is weakly expressed (Shetty 2016, Gautam 2019). There was also no rank-related effect on food abundance in feeding sites (Gautam 2019). Thus, caring for the calves of older, dominant females, is unlikely to yield more food resources for the allomother, as has also been suggested in the African savannah elephant (Lee 1987). However, Dublin (1983) had found that subordinate females had better access to resources when they were caring for the calf of dominant females than when they were not in the African savannah elephant, in which there is a linear age or size-based dominance structure (see Archie *et al.* 2006).

Allomothers may also accrue social benefits rather than food resources through allomothering the calves of older or more dominant females (see de Waal 1990), and longer-term data would be required to test the alliance formation hypothesis through comparing the agonism experienced by females to check if reduced agonism is a potential reason for allomothering the calves of older females. The oldest females were not found to be the most central in Kabini (Shetty 2016); therefore, social connectedness may not be a reason for allomothers being younger than mothers. However, allomothering might itself bring advantages in terms of social connectedness as found in sperm whales (Gero *et al.* 2013), in which connectedness of a female was higher when caring for a calf than otherwise. We also saw between-clan allomaternal interactions involving five distinct allomother-calf dyads and one adoption of what seemed to be an orphan calf. One between-clan allomaternal relationship (Pinky_2006_F from Peggy's clan became the allomother of Jacintha_2015_M from Lisa's clan after the death of the other females of Peggy's clan) led to a female having regular associations with another clan (Lisa's clan; see Figure 6 of Chapter 2) in the absence of her own clan. Thus, apart from the above two discussed hypotheses, being an allomother may also facilitate the integration of unrelated females into non-natal social units.

We found that some older females (30–40-year-old females and 40–50-year-old females) also showed allomothering. Thus, learning to mother or alliance formation cannot be the sole reason for allomothering, and it is possible that young and older allomothers extend allomaternal care for different reasons.

Indirect fitness benefits

As an individual's behaviour towards its relatives may influence its overall fitness according to the theory of inclusive fitness (Hamilton 1964), the role of kinship in the evolution of allomaternal care has been discussed by many, primarily in primates (for e.g., see Hrdy 1976, Riedman 1982, Nicolson 1987, Chism 2000, Ross and MacLarnon 2000). In elephants also, apart from direct fitness benefits, allomothers may gain indirect fitness benefits through offering protection against predation (see Dublin 1983, McComb *et al.* 2011) and allomaternal care for the calves of related females (Lee 1987). In line with the expectation based on kin selection theory, allomothers were found to help related individuals in the African savannah elephants (Lee 1987), and a grandmother was found to show allomothering in one small set of captive Asian elephants (Rapaport and Haight 1987). However, allomaternal care may not be restricted to close relatives as expected from theory and, even when females discriminate based on relatedness, not all participants may reap fitness benefits: it is possible for allomothers to gain direct fitness benefits through practicing maternal behaviours and for mothers and calves to obtain no benefit or experience negative effects due to the allomother's inexperience (for discussion, please see Quiatt 1979). Thus, to understand the role of kin selection in allomaternal care in the study population, we first assessed if there was some support to mothers and calves receiving any benefit at all in the presence of allomaternal care. The various results of the mother-benefit and infant-benefit hypotheses are discussed below.

Mother-benefit hypothesis

It has been hypothesised that mothers would gain fitness benefits if allomothering could facilitate mothers to spend more time foraging (foraging freedom; Ross and MacLarnon 2000). We found that the time calves spent near their mothers and the number of social interactions with their mothers were lower when the calves had allomothers than when they did not, in keeping with the hypothesis. However, whether the time calves spend with allomothers facilitates feeding by mothers needs to be examined. In the African savannah elephant, mothers were not found to engage in increased feeding at greater distances from their calves in the presence of potential allomothers (Lee 1987).

The average mother-calf distances in the presence and absence of the allomother were not significantly different, but there was a trend towards higher distances in allomother presence. The number of total, feeding, and resting interactions were not different in the presence and absence of allomothers. Since mother's milk is the primary mode of nutrition for young calves, the lack of significant difference in feeding interactions with their mothers between calves with and without an allomother was not very surprising. We did not find allomothers to nurse calves, although calves did suck from their allomothers (Chapter 3 of this thesis), perhaps as a source of comfort (Lee 1987, Vidya 2014).

Infant-benefit hypothesis

Elephant calves are slow maturing and have a prolonged period of dependency and social learning (Nair 1989, Chapter 3 of this thesis). Hence, additional support and assistance from females apart from the mother can be potentially beneficial for the calf. We found that many of the calves had at least one allomother, and they were close to and had frequent interactions with their allomothers. Young calves were more frequently allomothered than older calves, in keeping with the infant-benefit hypothesis.

We then checked if calf sociality was higher in the presence than in the absence of an allomother. For instance, if the calf initiated movements and the allomother followed the calf at a distance (or vice versa, with the allomother leading and the calf following), calves could have potentially interacted with other females in the group more frequently than if there was no allomother. It could have also potentially been the case that when there was an allomother near a calf, other females came near the allomother to interact with her and then also interacted with the calf. In either case, the presence of an allomother could have increased calf proximity with other females. In African forest elephants, it had been found that calves or juveniles with an older offspring wandered (moved away from their mothers) more than those without an older offspring (Chelluri 2009). However, we found that calves (≤6 months) with an allomother were usually only near their mothers and allomothers and mostly interacted with them only. It is possible that differences between allomothered and non-allomothered calves appear in sociality later in life.

Though the presence of an allomother did not alter calf-other female sociality in terms of proximity and interactions, calves had frequent feeding interactions with their allomothers that involved obtaining grass, which constitutes a major portion of elephant diet (Baskaran *et al.* 2010). Calves often sniff, touch, grab, and place in mouth the grass being collected by conspecifics, especially their mothers and allomothers, and place their trunk tip in the mouths of others while those individuals chew on grass. Such frequent feeding interactions are thought to facilitate ‘food learning’ in young calves (Lee and Moss 1999) who are yet to develop adequate motor skills to engage in adult like foraging activities (Chapter 2 of this thesis).

Both mothers and allomothers watch over calves as they lie on the ground to rest. With the presence of an allomother, such resting interactions between mothers and calves did not decrease. However, longer datasets may be required to examine this. During longer resting periods, calves may be more vulnerable to predation attempts; therefore, mothers could have invested similar amounts of time in guarding calves regardless of the presence of an allomother, thus enhancing protection. There were scenarios when mothers woke up their calves when they changed feeding sites (field observation). If the presence of an allomother allows mothers to find new feeding sites without leaving their calves alone, such calves may get to rest for a longer duration than those without an allomother, which may ultimately enhance the foraging time of mothers.

We found frequent social interactions between calves and their allomothers, referred to as ‘allomothering play’ in the African savannah elephants (Lee and Moss 2014). Such frequent social interactions may increase social information that a calf has, which could improve social competence later in life resulting in increased sociality (see Burton 1972, Deag 1974, Taborsky and Oliveira 2012). Thus, the presence of an allomother might be helpful for calves to practice and learn crucial social skills and reach independence sooner than calves without an allomother. Whether the current differences in sociality between calves with and without an allomother translate into future differences in sociality has to be studied. Close social interactions with females other than the mother could also help in social integration into one’s social unit (Poirier and Smith 1974, Cheney 1978). Lee (1987) found a significant positive association between the number of potential allomothers in a family and calf survival. Whether the presence of an actual allomother increases calf survival through support and/or protection in elephants is yet to be studied.

We found that female group sizes were higher in calf presence than calf absence even when there was no allomother present (i.e., when females in a group did not show allomaternal care). Therefore, the increase in group size in calf presence was not due to the presence of the allomother alone. In fact, there were many sightings of mother, calf, and an other female, with no allomother (see Supplementary Material 3). The larger group size in allomother presence than in allomother absence could either be due to an allomother joining or one (or a few) of the existing females becoming the allomother(s) and an other female joining the group. We cannot differentiate between these yet in the absence of continuous data on the same calf’s group from the time the calf is born. Whether larger group sizes benefit the calf, say, in terms of protection, needs to be examined.

We found 30–40-year-old and 40–50-year-old females, but never 20–30-year-old females, to allomother calves. It is possible that the older females have the opportunity to extend grandmaternal care and hence were seen to be allomothers. We found grandmaternal care in two cases, so there is support for females helping related individuals, but we do not yet know the genetic relatedness between other mother-allomother pairs to conclude if allomothering is restricted to close relatives.

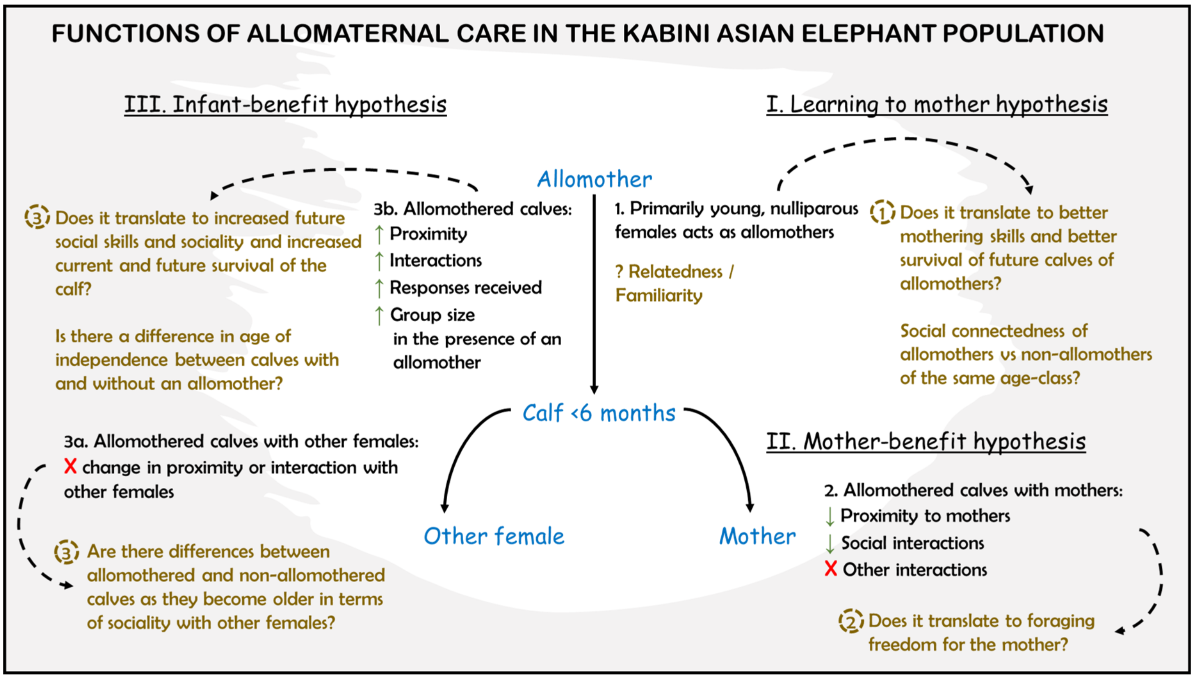


Figure 13. Schematic of the results of the three functional hypotheses of allomothering in the study population and future directions. Arrows indicate an increase or decrease and a cross indicates no significant difference. Future directions are shown with dashed lines.

As mentioned in the introduction, we did not test the *natal attraction* and *phylogenetic inertia* hypotheses, which do not invoke any benefits. In the first case, one would expect all females except those with dependent young to show non-expensive allomaternal care (Scollay and DeBold 1980, Paul and Keuster 1996, Silk 1999). High inter-female variation in the kinds and frequency of allomaternal behaviour are also expected (Scollay and DeBold 1980). Contrary to this hypothesis, we found young females and not all non-lactating females to allomother calves. Although there was variation across females in the amount of allocare shown and allocare decreased with calf age, we found that each allomother allomothered only one calf at a time. Thus, the natal attraction hypothesis is not sufficient to explain allomothering in this elephant population. Phylogenetic inertia (Edwards and Naeem 1993), with alloparenting having arisen in the lineage and simply persisting because of no selection against it, is also unlikely as allomothering does not seem to be trivial. However, the costs that allomothers incur are yet to be quantified.

Overall, we found some evidence for the learning to mother (direct benefits), mother-benefit, and infant-benefit (indirect benefits) hypotheses (Figure 13). As several predictions of these hypotheses are not mutually exclusive, investigating the consequences of these results (Figure 13) in the future is important to understand which functions are responsible for the maintenance of allomaternal care in Asian elephants. Further exploring the avenues that our results have opened up will allow us to understand if allomothering functions in similar ways in Asian and African savannah elephants.

Acknowledgements

This work was funded by the Council of Scientific and Industrial Research, Government of India, under Grant No. 37(1613)/13/EMR-II and Jawaharlal Nehru Centre for Advanced Scientific Research (JNCASR). TR was given a Ph.D. fellowship by JNCASR. This work is part of TR’s Ph.D. thesis. We thank the offices of the PCCF(WL), Karnataka Forest Department, and Conservators of Forests and DCFs of Nagarahole and Bandipur National Parks and Tiger Reserves, for field permits. We are grateful to various officials and staff of Nagarahole and Bandipur National Parks for permissions and support. We thank Krishna, Shankar, and Pramod for help in the field, and Hansraj Gautam for some focal videos.

References

1. Archie EA, Moss CJ and Alberts SC (2006). The ties that bind: genetic relatedness predicts the fission and fusion of social groups in wild African elephants. *Proceedings of the Royal Society of London B: Biological Sciences* 273: 513-522.
2. Baskaran N, Balasubramanian M, Swaminathan S and Desai AA (2010). Feeding ecology of the Asian elephant *Elephas maximus Linnaeus* in the Nilgiri Biosphere Reserve, southern India. *Journal of the Bombay Natural History Society* 107: 3-13.

3. Boose K, White F, Brand C, Meinelt A and Snodgrass J (2018). Infant handling in bonobos (*Pan paniscus*): exploring functional hypotheses and the relationship to oxytocin. *Physiology and Behaviour* 193: 154-166.
4. Burton FD (1972). The integration of biology and behaviour in the socialization of *Macaca sylvana* of Gibraltar. In: Poirier FE (ed.), *Primate Socialization*, pp. 29-62. Random House, New York.
5. Chelluri G (2009). *Ontogeny of the Mother-Calf Relationship in African Forest Elephants, Loxodonta africana cyclotis.* Honours thesis, Cornell University, Cornell.
6. Cheney DL (1978). Interactions of immature male and female baboons with adult females. *Animal Behaviour* 26: 389-408.
7. Chism J (2000). Allocare patterns among cercopithecines. *Folia Primatologica* 71: 55-66.
8. Crittenden AN and Marlowe FW (2008). Allomaternal care among the Hadza of Tanzania. *Human Nature* 19: 249-262.
9. de Silva S, Ranjeewa AD and Kryazhimskiy S (2011). The dynamics of social networks among female Asian elephants. *BMC Ecology* 11: 1-6.
10. de Silva S, Schmid V and Wittemyer G (2017). Fission–fusion processes weaken dominance networks of female Asian elephants in a productive habitat. *Behavioural Ecology* 28: 243-252.
11. de Waal F (1990). Do rhesus mothers suggest friends to their offspring? *Primates* 31: 597-600.
12. Deag JM (1974). *A Study of the Social Behaviour and Ecology of the Wild Barbary Macaque Macaca sylvanus L.* Ph.D. thesis, University of Bristol, England.
13. Deag JM and Crook JH (1971). Social behaviour and 'agonistic buffering' in the wild Barbary macaque *Macaca sylvana L. Folia Primatologica* 15: 183-200.
14. Desai AA and Johnsingh AJT (1995). Social organization and reproductive strategy of the male Asian elephant (*Elephas maximus*). In: Daniel JC and Datye H (eds.), *A Week with Elephants*, pp. 532-532. Bombay Natural History Society, Bombay.
15. Dublin HT (1983). Cooperation and reproductive competition among female African elephants. In: Wasser S (ed), *Social Behaviour of Female Vertebrates*, pp. 291-313. Academic Press, Inc., New York.
16. Dunayer ES and Berman CM (2018). Infant handling among primates. *International Journal of Comparative Psychology* 31.
17. Edwards SV and Naeem S (1993). The phylogenetic component of cooperative breeding

in perching birds. *The American Naturalist* 141: 754-789.

18. Estes RD and Goddard J (1967). Prey selection and hunting behaviour of the African wild dog. *The Journal of Wildlife Management* 1: 52-70.
19. Fairbanks LA (1990). Reciprocal benefits of allomothering for female vervet monkeys. *Animal Behaviour* 40: 553-562.
20. Gadgil M and Nair VP (1984). Observations on the social behaviour of free ranging groups of tame Asiatic elephants (*Elephas maximus Linn*). *Proceedings of the Indian Academy of Sciences (Animal Science)* 93: 225-233.
21. Garaï ME (1992). Special relationships between female Asian elephants (*Elephas maximus*) in zoological gardens. *Ethology* 90: 187-205.
22. Gautam H (2019). *Resource Availability, Within-clan and Between-Clan Agonistic Interactions, and Dominance Relationships amongst Female Asian Elephants in Nagarahole National Park, Southern India*. Ph.D. thesis, Jawaharlal Nehru Centre for Advanced Scientific Research, Bengaluru.
23. Gero S, Gordon J and Whitehead H (2013). Calves as social hubs: dynamics of the social network within sperm whale units. *Proceedings of the Royal Society B: Biological Sciences* 280: 20131113.
24. Hamilton WD (1964). The Genetical Evolution of Social Behaviour I. *Journal of Theoretical Biology* 7: 1-16.
25. Hervé M (2022). Package 'RVAideMemoire'. https://cran.r-project.org/web/packages /RVAideMemoire/RVAideMemoire.pdf
26. Hrdy SB (1976). Care and exploitation of nonhuman primate infants by conspecifics other than the mother. *Advances in the Study of Behaviour* 6: 101-158.
27. Jay PC (1963). Maternal Behaviour among Langurs. *Annals of the New York Academy of Sciences* 102: 468-476.
28. Jin T, Wang D, Pan W and Yao M (2015). Nonmaternal infant handling in wild white-headed langurs (*Trachypithecus leucocephalus*). *International Journal of Primatology* 36: 269-287.
29. Keerthipriya P, Nandini S and Vidya TN (2021). Effects of male age and female presence on male associations in a large, polygynous mammal in southern India: the Asian elephant. *Frontiers in Ecology and Evolution* 9: 616666.
30. König B (1997). Cooperative care of young in mammals. *Naturwissenschaften* 84: 95-104.
31. Konrad CM, Frasier TR, Whitehead H and Gero S (2019). Kin selection and allocare in

sperm whales. *Behavioural Ecology* 30: 194-201.

32. Lancaster JB (1971). Play mothering: the relations between juvenile females and young infants among free-ranging vervet monkeys (*Cercopithecus aethiops*). *Folia Primatologica* 15: 161-182.
33. Lawick-Goodall J (1971). *In the Shadow of Man.* Houghton Mifflin Harcourt, United States.
34. Lee PC and Moss CJ (2011). Calf development and maternal rearing strategies. In: Moss CJ, Croze H and Lee PC (eds.), *The Amboseli Elephants: A Long-Term Perspective on a Long-Lived Mammal,* pp 224-237. University of Chicago Press, Chicago.
35. Lee PC and Moss CJ (2014). African elephant play, competence and social complexity. *Animal Behaviour and Cognition* 1: 144-156.
36. Lee PC and Moss CJ (1999). The social context for learning and behavioural development among wild African elephants. In: Box HO and Gibson KR (eds.), *Mammalian Social Learning: Comparative and Ecological Perspective*, pp 102-125. Cambridge University Press, Cambridge.
37. Lee PC (1987). Allomothering among African elephants. *Animal Behaviour* 35: 278-291.
38. Maestripieri D (1994). Social structure, infant handling, and mothering styles in group-living Old World monkeys. *International Journal of Primatology* 15: 531-553.
39. Magnusson A, Skaug H, Nielsen A, Berg C, Kristensen K, Maechler M, van Bentham K, Bolker B, Brooks M and Brooks MM (2017). Package ‘glmmTMB’. R Package Version 0.2.0.
40. Mar KU, Lahdenperä M, and Lummaa V (2012). Causes and correlates of calf mortality in captive Asian elephants (*Elephas maximus*). *PLoS One* 7: e32335.
41. McComb K, Shannon G, Durant SM, Sayialel K, Slotow R, Poole J and Moss C (2011). Leadership in elephants: the adaptive value of age. *Proceedings of the Royal Society B: Biological Sciences* 278: 3270-3276.
42. McKenna JJ (1979). The evolution of allomothering behaviour among Colobine monkeys: function and opportunism in evolution. *American Anthropologist* 81: 818-840.
43. Nair PV (1989). Development of nonsocial behaviour in the Asiatic elephant. *Ethology* 82: 46-60.
44. Nandini S, Keerthipriya P and Vidya TNC (2017). Seasonal variation in female Asian elephant social structure in Nagarahole-Bandipur, southern India. *Animal Behaviour* 134: 135-145.
45. Nandini S, Keerthipriya P and Vidya TNC (2018). Group size differences may mask

underlying similarities in social structure: a comparison of female elephant societies. *Behavioural Ecology* 29: 145-159.

46. Nicolson NA (1987). Infants, mothers, and other females. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW and Strusaker TT (eds.), *Primate Societies*, pp. 330-342. University of Chicago Press, Chicago.
47. Nishida T (1983). Alloparental behaviour in wild chimpanzees of the Mahale mountains, Tanzania. *Folia Primatologica* 41: 1-33.
48. Paul A (1999). The socioecology of infant handling in primates: is the current model convincing? *Primates* 40: 33-46.
49. Paul A and Kuester J (1996). Infant handling by female Barbary macaques (*Macaca sylvanus*) at Affenberg Salem: testing functional and evolutionary hypotheses. *Behavioural Ecology and Sociobiology* 39: 133-145.
50. Paul M, Majumder SS and Bhadra A (2014). Grandmotherly care: a case study in Indian free-ranging dogs. *Journal of Ethology* 32: 75-82.
51. Payne K (2013). Sources of social complexity in the three elephant species. In: de Waal FBM and Tyack PL (eds.), *Animal Social Complexity: Intelligence, Culture, and Individualized Societies*, pp. 57-86. Harvard University Press, Cambridge, MA, USA.
52. Poirier FE and Smith EO (1974). Socializing functions of primate play. *American Zoologist* 14: 275-287.
53. Quiatt D (1979). Aunts and mothers: adaptive implications of allomaternal behaviour of nonhuman primates. *American Anthropologist* 81: 310-319.
54. Rapaport L and Haight J (1987). Some observations regarding allomaternal caretaking among captive Asian elephants (*Elephas maximus*). *Journal of Mammology* 68: 438-442.
55. Revathe T, Anvitha S and Vidya TNC (2020). Development of motor control and behaviour in Asian elephants in the Kabini elephant population, southern India. *International Journal of Developmental Biology* 64: 377-392.
56. Riedman ML (1982). The evolution of alloparental care and adoption in mammals and birds. *The Quarterly Review of Biology* 57: 405-435.
57. Ross C and MacLarnon A (2000). The evolution of non-maternal care in anthropoid primates: a test of the hypotheses. *Folia Primatologica* 71: 93-113.
58. Rowell TE, Hinde RA and Spencer-Booth Y (1964). "Aunt"-Infant interaction in captive rhesus monkeys. *Animal Behaviour* 12: 219-226.
59. Scollay PA and DeBold P (1980). Allomothering in a captive colony of Hanuman langurs (*Presbytis entellus*). *Ethology and Sociobiology* 1: 291-299.

60. Seay B (1966). Maternal behaviour in primiparous and multiparous rhesus monkeys. *Folia Primatologica* 4: 146-168.
61. Shetty NR (2016). *Social Structure, Genetic Relatedness, and Dominance Relationships in Female Asian Elephants in Nagarahole and Bandipur National Parks, Southern India*. Ph.D. thesis, Jawaharlal Nehru Centre for Advanced Scientific Research, Bengaluru.
62. Silk JB (1999). Why are infants so attractive to others? The form and function of infant handling in bonnet macaques. *Animal Behaviour* 57: 1021-1032.
63. StatSoft, Inc. (2004). STATISTICA (data analysis software system), version 7. www.statsoft.com.
64. Stone AI, Mathieu D, Griffin L and Bales KL (2010). Alloparenting experience affects future parental behaviour and reproductive success in prairie voles (*Microtus ochrogaster*). *Behavioural Processes* 83: 8-15.
65. Sukumar R (1989). *The Asian Elephant: Ecology and Management*. Cambridge University Press, Cambridge.
66. Taborsky B and Oliveira RF (2012). Social competence: an evolutionary approach. *Trends in Ecology and Evolution* 27: 679-688.
67. Tardif SD, Richter CB and Carson RL (1984). Effects of sibling-rearing experience on future reproductive success in two species of Callitrichidae. *American Journal of Primatology* 6: 377-380.
68. Trivers RL (1971). The evolution of reciprocal altruism. *The Quarterly Review of Biology* 46: 35-57.
69. Vidya TN and Sukumar R (2005). Social organization of the Asian elephant (*Elephas maximus*) in southern India inferred from microsatellite DNA. *Journal of Ethology* 23: 205-210.
70. Vidya TNC (2014). Novel behaviour shown by an Asian elephant in the context of allomothering. *Acta Ethologica* 17: 123-127.
71. Vidya TNC, Prasad D and Ghosh A (2014). Individual identification in Asian elephants. *Gajah* 40 3-17.
72. Wang Z and Novak MA (1994). Parental care and litter development in primiparous and multiparous prairie voles (*Microtus ochrogaster*). *Journal of Mammalogy* 75: 18-23.
73. Weladji RB, Loison A, Gaillard JM, Holand Ø, Mysterud A, Yoccoz NG, Nieminen M and Stenseth NC (2008). Heterogeneity in individual quality overrides costs of reproduction in female reindeer. *Oecologia* 156: 237-247.
74. Wright L and Bell RW (1978). Interactive effects of parity and early pup stress on the

open field behaviour of laboratory rats. *Developmental Psychobiology* 11: 413-418.

75. Zhang D, Xia DP, Wang X, Zhang QX, Sun BH and Li JH (2018). Bridging may help young female Tibetan macaques *Macaca thibetana* learn to be a mother. *Scientific Reports* 8: 1-8.

Supplementary Material

Supplementary Material 1. Details of focal calves.

Supplementary Material 1, Table 1. Calf ID, calf sex, clan ID, calf age-class, and allomother presence/absence in all their focals of the 30 calves used for behavioural analyses.

Calf ID	Calf sex	Clan ID	Age class	Allomother Presence (P) / Absence (A)	Other female Presence (P) / Absence(A)
Alena_2017_M	M	Alexandra	<3 months	P	P
Amarilla_2016_M	M	Osanna	<3 months	P	P
Gemini_2017_M	M	Patricia	<3 months	P	P
Genette_2017_F	F	Patricia	<3 months	P	P
Georgina_2017_F	F	Patricia	<3 months	P	P
Ilaena_2016_F	F	Menaka	<3 months	P	P
Iliora_2015_M	M	Menaka	<3 months	P	P
Ipomoea_2018_M	M	Victoria	<3 months	P	P
Kai_2016_M	M	Nakshatra	<3 months	P	P
Kasturi_2018_M	M	Kasturi	<3 months	P	P
Camila_2017_M	M	Patricia	3-<6 months	P	P
Floppy_ears_2018_F	F	Victoria	3-<6 months	P	P
Kausalya_2015_M	M	Kasturi	3-<6 months	P	P
Marlene_2015_F	F	Tilottama	3-<6 months	P	P
Namrata_2017_F	F	Nakshatra	3-<6 months	P	P
Orlanda_2015_M	M	Menaka	3-<6 months	P	P
Suhrita_2016_F	F	Victoria	3-<6 months	P	P
Valerie_2016_M	M	Victoria	3-<6 months	P	P
Vanessa_2015_M	M	Victoria	3-<6 months	P	P
Zarin_2015_F	F	Alexandra	3-<6 months	P	P
Ilsa_2016_F	F	Menaka	<3 months	A	P
Linda_2016_F	F	Lisa	<3 months	A	P
Patricia_2016_M	M	Patricia	<3 months	A	P
Sarayu_2016_M	M	Victoria	<3 months	A	P
Serena_2016_M	M	Victoria	<3 months	A	P
Cancan_2017_M	M	Patricia	3-<6 months	A	P
Hannah_2016_F	F	Tilottama	3-<6 months	A	P
Ketki_2016_F	F	Kasturi	3-<6 months	A	P
Kokila_2015_F	F	Kasturi	3-<6 months	A	P
Suveera_2016_M	M	Victoria	3-<6 months	A	P

Supplementary Material 2. Details of clans used to compare the expected and observed age-classes of allomothers and frequency of allomothering by females of different age-classes.

Supplementary Material 2, Table 1. The presence (P) or absence (A) of females of different age-classes without dependent young (<3 years) (i.e., females available for allomothering) are shown for the clans in which allomothering was observed at least once (*N*=11 clans). For each clan, the number of female age-classes available to perform X^2 tests are also shown. We performed X^2 tests on only those clans (marked by asterisks) that had available females in at least 5 age-classes (*N*=7 clans).

	Female age-class (in years)						
Clan ID	5-<10	10-<20	20-<30	30-<40	40-<50	>=50	No. of age-classes available for X^2 test
Alexandra	A	P	P	P	A	P	4
Kasturi	P	P	A	P	A	P	4
Katrina*	A	P	P	P	P	P	5
Lisa*	P	P	P	P	P	P	6
Menaka*	P	P	P	A	P	P	5
Mystique	P	P	A	P	P	A	4
Nakshatra*	P	P	P	P	P	P	6
Osanna*	P	P	P	P	P	P	6
Patricia*	P	P	P	P	P	P	6
Tilottama	A	P	A	P	P	P	4
Victoria*	P	P	P	P	P	P	6
No. of clans used to look at the proportion of available females for allomothering and the proportion of allomothers	8	11	8	10	9	10	-

Supplementary Material 3. GLMM to examine the probability of having an allomother.

Supplementary Material 3, Table 1. Numbers of sightings of calves of different age-classes and numbers of unique calves within each age-class. As there can be more than one calf in a group sighting, the number of sightings of calves will be more than the number of group sightings. There was a total of 51 unique calves across all calf age-classes.

Calf age-class	No. of sightings of calves	No. of unique calves within an age-class
<3 months	338	40
3-<6 months	373	37
6-<12 months	170	20
Total	881	97

Supplementary Material 3, Table 2. Number of sightings of each calf with only its mother, with mother and allomother/s but no other female/s, with mother and other female/s but no allomother/s, with mother, allomother/s, and other female/s based on a total of 881 sightings of 51 calves. Calves that were ever allomothered are marked with Y (Yes; *N*=36), and those that were never allomothered are marked with N (No; *N*=15). For the calves that were ever allomothered, the proportions of sightings without an allomother are also shown. "-" implies that for calves that were never allomothered the number of sightings with an allomother (either without or without other female/s) is not applicable.

Calf ID	Allomothered (Y/N)	Total no. of sightings	No. of sightings with				Prop. of sightings without an allomother
			Only mother	Mother + Allomother	Mother + Other F	Mother + Allomother + Other F	
Alena_2017_M	Y	11	0	4	0	7	0.00
Amarilla_2016_M	Y	9	0	0	0	9	0.00
Ashley_2016_M	Y	7	0	4	0	3	0.00
Camila_2017_M	Y	9	0	2	0	7	0.00
Emerald_2016_F	Y	13	0	0	1	12	0.08

Calf ID	Allomothered (Y/N)	Total no. of sightings	No. of sightings with				Prop. of sightings without an allomother
			Only mother	Mother + Allomother	Mother + Other F	Mother + Allomother + Other F	
Fawzia_2015_M	Y	1	0	0	0	1	0.00
Floppy_ears_2018_F	Y	24	0	0	0	24	0.00
Gemini_2017_M	Y	12	1	1	1	9	0.17
Genette_2017_F	Y	24	0	11	0	13	0.00
Georgina_2017_F	Y	22	0	0	0	22	0.00
Ilaena_2016_F	Y	11	0	0	3	8	0.27
Iliora_2015_M	Y	6	0	0	0	6	0.00
Ipomoea_2018_M	Y	10	0	0	0	10	0.00
Kai_2016_M	Y	2	0	0	0	2	0.00
Kasturi_2018_M	Y	16	0	3	0	13	0.00
Kausalya_2015_M	Y	28	0	3	0	25	0.00
Keerthana_2017_M	Y	35	0	0	34	1	0.97
Ketki_2016_F	Y	25	0	4	19	2	0.76
Kokila_2015_F	Y	18	2	6	5	5	0.39
Leena_2017_F	Y	21	0	3	3	15	0.14
Lynn_2015_F	Y	31	0	0	1	30	0.03
Marlene_2015_F	Y	14	0	1	0	13	0.00
Merinda_2017_F	Y	5	1	1	3	0	0.80
Merope_2016_F	Y	4	0	2	0	2	0.00
Myrla_2016_M	Y	7	0	0	5	2	0.71
Namrata_2017_F	Y	7	2	1	0	4	0.29
Narmada_2015_M	Y	10	0	1	0	9	0.00
Navaneeta_2017_F	Y	8	0	3	0	5	0.00
Orlanda_2015_M	Y	11	0	5	0	6	0.00
Paula_2017_M	Y	4	0	0	2	2	0.50
Salvia_2016_F	Y	18	0	0	0	18	0.00
Suhrita_2016_F	Y	42	0	1	0	41	0.00
Suneeti_2016_F	Y	12	0	0	3	9	0.25
Valerie_2016_M	Y	68	0	1	21	46	0.31
Vanessa_2015_M	Y	65	0	1	4	60	0.06
Zarin_2015_F	Y	16	0	2	0	14	0.00
Andrea_2017_F	N	1	0	-	1	-	-
Cancan_2017_M	N	5	0	-	5	-	-
Faiza_2016_M	N	3	3	-	0	-	-
Gretel_2015_M	N	2	0	-	2	-	-
Hannah_2016_F	N	37	17	-	20	-	-
Ilsa_2016_F	N	15	0	-	15	-	-
Lily_2017_M	N	3	3	-	0	-	-
Linda_2016_F	N	32	2	-	30	-	-

Calf ID	Allomothered (Y/N)	Total no. of sightings	No. of sightings with Only mother	Mother + Allo-mother	Mother + Other F	Mother + Allo-mother + Other F	Prop. of sightings without an allo-mother
Merissa_2017_F	N	2	0	-	2	-	-
Nayonika_2015_M	N	12	1	-	11	-	-
Patricia_2016_M	N	6	0	-	6	-	-
Sarayu_2016_M	N	28	1	-	27	-	-
Serena_2016_M	N	31	2	-	29	-	-
Suveera_2016_M	N	72	0	-	72	-	-
Zerad_2015_M	N	6	1	-	5	-	-
Total	-	881	36	60	330	455	-

Supplementary Material 3, Table 3. Numbers of sightings of mothers of different age-classes and the number of unique mothers within each age-class, in the dataset used for group size analysis. There was a total of 51 mothers across all age-classes. As the sightings are over a 2.5-year study period, certain mothers could occur in two consecutive age-classes for the same calf.

Age-class of mothers	No. of sightings of mothers	No. of unique mothers within an age-class
10-<20	242	17
20-<30	125	11
30-<40	147	11
40-<50	209	7
>=50	158	9
Total	881	57

Supplementary Material 3, Table 4. Results of the generalized linear mixed-effect models run using *N*=881 sightings of calves to examine the effects of calf age-class, mother age-class, number of available females (all fixed factors), and calf ID (random factor) on the probability of calves being allomothered.

	Model parameters				
S. No.	Fixed effects	Random effects	AIC	ΔAIC	Deviance
1	Calf age-class, Mother age-class	Calf ID	418.84	0.00	402.84
2	Calf age-class, Mother age-class, No. of available females	Calf ID	420.73	1.89	402.73
3	Calf age-class	Calf ID	423.15	4.31	415.15
4	Mother age-class	Calf ID	423.56	4.72	411.56
5	Calf age-class, No. of available females	Calf ID	425.05	6.21	415.05
6	Mother age-class, No. of available females	Calf ID	425.33	6.49	411.33
7	_	Calf ID	428.12	9.28	424.12
8	No. of available females	Calf ID	429.89	11.05	423.89
9	Calf age-class, Mother age-class	_	1084.9	666.06	1070.9
10	Calf age-class, Mother age-class, No. of available females	_	1086.7	667.86	1070.7
11	Mother age-class	_	1091.7	672.86	1081.7
12	Mother age-class, No. of available females	_	1093.7	674.86	1081.7
13	Calf age-class	_	1196.6	777.76	1190.6
14	Calf age-class, No. of available females	_	1198.3	779.46	1190.3
15	No. of available females	_	1199.7	780.86	1195.7

Supplementary Material 4. Details of data used for the analysis of group sizes and clans with allomothers.

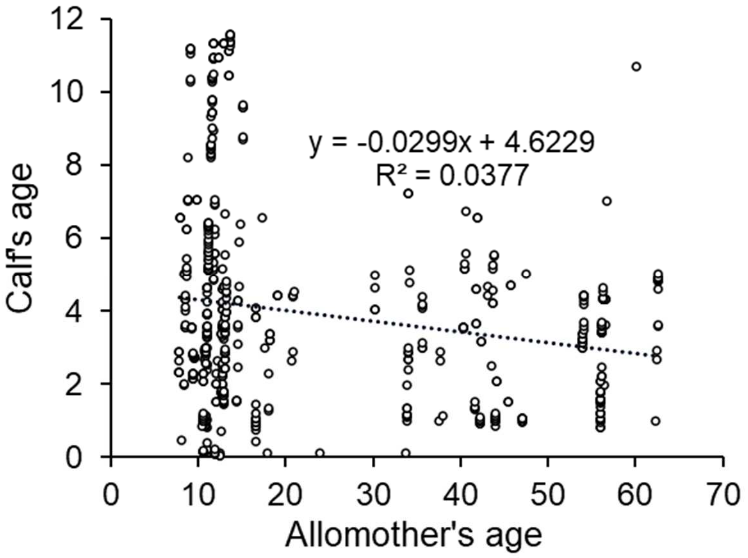
Supplementary Material 4, Table 1. Numbers of female group sightings of 13 clans in the presence and absence of calves and allomothers during 2016-2018. The clans that had at least 5 sightings under all three categories were used for group size analysis (*N*=7 clans, marked with '*'). Clans that had an allomother in at least one of their sightings (*N*=11 clans) were used to make Figure 1 (main text). 'A' denoted absence; 'P' denotes presence.

Clan ID	No. of sightings in calf A	No. of sightings in allomother A	No. of sightings in allomother P
Alexandra	27	2	27
Anabelle	70	1	0
Gregoria	9	2	0
Kasturi*	101	34	58
Katrina*	17	7	17
Lisa*	218	29	48
Menaka	95	3	25
Mystique	2	5	2
Nakshatra*	135	13	31
Osanna	40	0	9
Patricia*	351	11	60
Tilottama*	49	25	14
Victoria*	317	40	155
Total	1431	172	446

Supplementary Material 4, Table 2. Results of the full and the two reduced GLMMs (Zero-truncated Negative Binomial Model) using log link for female group size. The fixed factor calf/allomother presence/absence (P/A in table) had three levels: 1. calf absent, 2. calf present and allomother absent, and 3. calf present and allomother present. Significant *P* values of model comparisons are marked in bold, which indicates that a particular reduced model is significantly different from the model that is above it in the table. 95% CI of *R* calculated using 1000 replicates.

Model parameters		AIC	*R* 95%*CI*	R^2	*P*
Fixed effect	Random effect				
Calf/Allomother P/A	Clan, Clan x Calf/Allomother P/A	6813.9	0.51 (0.47 - 0.55)	0.26	_
Calf/Allomother P/A	Clan	6825.7	0.49 (0.45 - 0.52)	0.24	**<0.001**
Calf/Allomother P/A	_	6970.1	0.46 (0.42 - 0.50)	0.21	**<0.001**

Supplementary Material 5. Allomother age and calf age.



Supplementary Material 5, Figure 1. Plot of the ages of calves allomothered against the ages of the allomothers (ages on the date they were seen) using 446 sightings of calves in allomother presence. The Spearman's r was -0.065 (not significant).

CHAPTER 6

Conclusions

Conclusions

This is the first study to quantify the role of calves (<1 year) and juveniles (1-<2 years) on the female social structure of an elephant species, using long-term data from the Kabini elephant population. This is also one of the first quantitative studies to examine calf development, explore the nature of calf-conspecific female interactions, and assess the functions of allomaternal care in any wild Asian elephant population using a substantial number of individually identified elephants. In this chapter, I briefly discuss my findings and suggest several lines of work following the current results.

Increased group size and associations in the presence of young ones due to fission-fusion dynamics

From the present study, we found that the presence of dependent young was a predictor of group size in the Kabini Asian elephant population. Female group sizes, including the numbers of adult, young adult, and subadult females in the group, increased in the presence of calves and juveniles. While we did not check for this (because of many of the measures of group size that we initially considered being correlated with one another), it is likely that the numbers of females of other age-classes also increase in the presence of calves and juveniles. Large group sizes in immature presence were previously noted by McKay (1973) based on a small sample size of Asian elephants in Sri Lanka. If the increase in group size is to provide protection against predation and/or show allomaternal care towards calves, a reduction in female group sizes would be expected as the juveniles grow. This has to be examined in the future with respect to offspring mortality (with respect to predation) and level of dependence on mothers and allomothers. Since carcasses of calves are seldom found in dense forest, it is difficult, however, to assign mortality to predation versus other causes such as disease. Increased group size in the presence developing offspring may also enhance the socialisation of young ones, as seen in orangutans (see van Schaik 1999). While we did not find increased socialisation of calves with adult females apart from the allomother, it is possible that there could be increased socialisation with other calves or juveniles. This needs to be examined by finding out whether the probability of mothers being together is higher than that expected by chance, and whether, if so, it benefits the mothers and/or the calves.

Apart from increased group sizes, we also found the strength of associations amongst adult females to increase in the presence of calves. Network measures such as degree, which is the number of direct associates (adult females here), and clustering coefficient, which is the proportion of neighbours of a female who are associates of one another, were also higher in calf presence than in their absence. Path length, which the shortest number of edges connecting two nodes, was smaller in calf presence than in their absence in each clan. Thus, females were more connected and neighbours had stronger and closer associations in the presence than in the absence of calves. Fission-fusion dynamics are thought to allow individuals to maximize their fitness by flexibly adjusting group sizes and compositions in response to fluctuating environmental conditions and to maximize social benefits (Aureli *et al.* 2008, Sueur *et al.* 2011). We found that fission-fusion dynamics facilitated changes in group size and associations, resulting in what are likely to be social advantages, since there had been no such change in group size or associations across ecologically different seasons previously (Nandini *et al.* 2017). Indeed, apart from ecological factors, a growing body of studies indicates that social factors, such as the presence of young ones, influence individual sociality (Gadgil and Nair 1984, Wells *et al.* 1987, Baird and Dill 1996, van Schaik 1999, Smith *et al.* 2008, Gero *et al.* 2013, Wey *et al.* 2013, Holmes *et al.* 2016, Saito and Idani 2016, Marealle *et al.* 2020), and our study adds to this.

Since a constraint on female group size had been found in this population (Nandini *et al.* 2017), and feeding competition also seemed to increase with increasing group size (Gautam and Vidya 2019), there might be increased feeding competition in the presence of calves. Whether this is indeed the case or whether females use different behavioural tactics to offset this would be interesting to examine in the future. Feeding costs may potentially be tempered by frequent changes in association so that individuals do not remain in groups of large sizes for long periods of time (higher rate of fission-fusion in the presence than in the absence of calves, although this would not help the mothers of dependent young), greater spread while feeding, or temporal spacing of feeding over short time periods (which might be limited as elephants have to feed during most of their waking hours). Individual variation in how females respond to the presence and absence of calves also remains to be explored. Moreover, while we looked at differences in the presence and absence of calves, whether females behaved differently in the presence and absence of their own calves was not investigated. Additionally, although we found that female association networks differed between calf presence and absence, we do not know if the closest associates remain the same or change between calf presence and absence.

Development of calves

In order to examine any social benefits of female group size, composition, or associations, we had to analyse calf-conspecific behavioural data. However, before that, we studied calf physical and social and non-social behavioural development to understand when, how, and how long calves take to develop crucial skills and to understand their behavioural repertoire, on which there were no previous data from any wild Asian elephant population in India. The previous studies on Asian elephant calf development included a detailed one by Nair (1989) on nine semi-captive elephant calves, and one by Webber (2017) comparing captive and wild populations.

Elephant calves are precocial and can follow their mothers within hours of being born (Nair 1989, Sukumar 2003). However, if precociality were to be measured in terms of adeptness in trunk usage and trunk-limb coordination necessary for feeding behaviours, nutritional and social independence, elephants are not much more precocial than primate or carnivore young. Thus, although calves are precocial in nature, they take a prolonged duration to learn various non-social and social behaviours. We found that physical development was important for the development of certain behaviours as that found in captive calves (Nair 1989). However, trunk lateralization happened early on in life, even before the development of proper trunk motor control. As even young calves were lateralized for trunk movements, it is likely that lateralization is innate in Asian elephants. Thus, trunk lateralisation may not be a reliable developmental marker in Asian elephants. In Asian elephants, calves are weaned only around the age of 4-5 years, and calves (<1 year) are entirely reliant on their mothers for nutrition (Nair 1989, Sukumar 2003). Whether the early lateralisation results from phylogenetic inertia is not known.

Young calves spent the most amount of time in preparatory adult behaviours (i.e., insipient stages of adult-like behaviours), especially in preparatory feeding behaviours, and this reduced with age with a simultaneous increase in duration spent in showing adult-like feeding behaviours. However, the average action duration remained similar across calf age-classes, suggesting that adult-like feeding efficiency may still take time to develop. Feeding behaviours involves holding, pulling and extracting, placing in mouth, and chewing grass, which require trunk and foot coordination and strength in trunk usage. An increase in body weight/height is probably needed to perform behaviours that require that strength (see Nair 1989) and practice alone may not explain the observed period of feeding behavioural development. Similarly, first pair of teeth emerges (around 2 months of age; see Nair 1989) well before calves start feeding on grass regularly (i.e., after about 6 months of age), pointing to the importance of development of trunk strength and motor control for feeding. In general, as calves grew, the time spent feeding increased with age and that of resting decreased with age, as found in one other study on wild Asian elephants in Sri Lanka (Webber 2017). Mother-calf behavioural synchrony also simultaneously increased. Calves started expressing most of the adult-like behaviours after about 6 months of age, marking the <6-month period with complete nutritional dependency (see also Nair 1989).

Calf-conspecific interactions

Thus, using calves <6 months of age, we then studied calf-conspecific female interactions and the nature of allomaternal care in the study population. As elephant calves are precocial in nature and have locomotory independence since birth (Nair 1989), we found that calves primarily initiated proximity contacts and behavioural interactions with different classes of conspecific females, unlike altricial young ones, in which conspecifics primarily initiate proximity contacts and interactions till young ones grow (for e.g., see Spencer-Booth 1968, Mann and Smuts 1999, Kumar and Solanki 2014). As elephants of the study population do not show a strong dominance hierarchy (Shetty 2016, Gautam 2019), mothers did not restrict movement of their calves or with whom calves chose to interact probably because of it. However, we found differential nature of calf interactions with mothers, escorts (who showed coordinated movement with a calf beyond what non-calf group members show amongst one another), and other females. Mothers and escorts were similar in all their behaviours towards calves. Calves spent a disproportionate amount of their time near their mothers and escorts and interacted with them more than they did with other females. However, if we control for the amount of time spent near a conspecific category and then recalculate the number of calf-conspecific interactions, the pattern of results may differ with other females. Nevertheless, calves equally preferred their mothers and escorts – similar to that found in semi-captive Asian elephants (Gadgil and Nair 1984), but contrary to calves preferring their mothers the most in the African savannah elephant (Lee 1987).

It is unclear why such a difference exists between Asian and African savannah elephants, and the mechanisms that lead to the development of dissimilar relationships from a young age is still poorly understood. It would be important to examine mothers' relatedness and associations with clan members to understand if these are contributing factors to the differences we see between escort-calf and other female-calf interactions, as social preferences or associations of daughters mirror that of their mothers in some species (for e.g., Berman *et al.* 1997, Gibson and Mann 2008, Goldenberg *et al.* 2016, Maestripieri 2018), and, ultimately, if relationships established at a young age are preserved well into adulthood or if nature of associations change with time. Even though there is a weak dominance relationship amongst clan members, most of the aggressive interactions towards calves were initiated by other females, which again may be a result of differential relationships amongst clan members (see Shetty 2016).

Though we found remarkable similarities between mothers and escorts in their behaviours towards calves, only mothers provided milk in the study population, even though calves frequently sucked from their escorts. However, because of the major mother-escort similarities and as escort interactions with calves were almost never aggressive, and since escorts extended comforting, responsive, and helpful interactions, we conclude that escorts are allomothers. Moreover, although mother-calf proximity duration and number of interactions decreased with calf age, those with escorts did not. Thus, allomaternal care was additional and complementary care that was common during the calf developmental period. Asian elephants have a long gestation period, single offspring at a time (rarely, twins), and prolonged offspring dependency – thus, longer inter-birth intervals and low life-time reproductive success, well-developed maternal care, regular kin associations, and weak within-clan dominance hierarchy, which might make allomaternal care beneficial (see Wilson 1975, McKenna 1979, Riedman 1982).

Functions of allomaternal care

No study on the functions of allomothering had been previously carried out in any wild Asian elephant population. Therefore, using calves up to 1 year of age, we tested three direct and indirect fitness benefits hypotheses of allomothering in the study population. In keeping with the previous studies on wild African savannah elephants (Lee 1987) and semi-captive and captive Asian elephants (Gadgil and Nair 1984, Rapaport and Haight 1987), we found that young, nulliparous females constituted a majority of the allomothers. Additionally, they were more frequently the allomothers than females of other age-classes. However, we also found that when females show allomothering, there was no relationship between allomother's and calf's age. Also, the quantity and quality of care extended by females did not differ with their age except for young allomothers showing more positive interactions towards calves than older allomothers. These results support the learning to mother hypothesis. In a study on semi-captive Asian elephants, it was found that the probability of still birth was high for first born calves as well for older age-class mothers (≥35 years; Mar *et al.* 2012); it was the lowest for females between 20-30 years of age. Probability of calf mortality also increased with maternal age (Mar *et al.* 2012). As female clans are composed of related females (Shetty 2016), which could yield inclusive fitness benefits, whether females belonging to the age-classes with high probability of calf mortality are choosing to invest in related young ones when they themselves do not have dependent offspring remains to be seen.

We found indirect evidence for foraging freedom for the mother in the presence of an allomother for their calves (mother-benefit hypothesis; see Ross and MacLarnon 2000) through reduced calf-mother proximity duration and social interactions. However, behaviours of mothers towards their calves (i.e., kinds of responses showed towards calves and tolerance in terms of proportion of calf-initiated behaviours terminated by mothers) did not change between allomother presence and absence. In keeping with the high mortality and vulnerability during the first six months of life and complete nutritional dependency during the first three months of life, young calves were allomothered more frequently than older calves (≥6 months of age). Contrary to our expectation, we did not find calf proximity duration and interactions with other females to increase in the presence of an allomother; however, an important difference existed between calves with and without an allomother: the former was close to, interacted with, and received positive interactions and support from their allomothers – as much as from their mothers, while the latter had only their mothers as preferred social partners within their groups. Such stark differences during crucial calf development period may have consequences for later life. Apart from these, we also found that calves with allomothers were found in larger groups than calves without allomothers; in addition, average group size was also higher in (calf presence) allomother absence as compared to calf absence (hence, allomother absence), suggesting that there may be multiple benefits to social grouping in calf presence: i.e., protection against predation (communal defense) and allomaternal care.

This is preliminary work pointing to the advantages for the allomother, mother, and the calf, and several questions remain to be answered. Comparison of maternal competence and future reproductive success of allomothers *versus* females of the same age-class who have never been an allomother will help us understand if young, nulliparous females being allomothers translate into increased maternal skills and increased calf survival (learning to mother hypothesis). Apart from learning mothering skills, it is also possible for females to gain social benefits through increased social connectedness when they are allomothers, which was found in sperm whales (Gero *et al.* 2013). We also found that a majority of the allomothers almost always associated with the calves (thus, the mothers of these calves) they allomothered. It remains to be seen how this association pattern changes as the calves grow up.

Comparison of feeding duration and rates of mothers with and without an allomother for their calves will be important to find out if reduced mother-calf closeness translates into enhanced foraging efficiency for the mother (mother-benefit hypothesis). Current and future survival, and future sociality and social skills have to be compared between calves with and without an allomother to understand if allomothering truly benefits the calves (infant-benefit hypothesis). The proportion of older allomothers who are grandmothers needs to be quantified to find out whether kin benefits could be a reason for older allomothers extending allomaternal care (indirect fitness benefits). Mother-allomother (young and older) relatedness also has to be quantified to evaluate the possible role of kin selection on allomothering in Asian elephants. Allomaternal care is unlikely to simply be a byproduct of social structure or due to natal attraction since not all the females who are available show such care. However, it is possible that allomothers do not incur high costs, beyond that of being in larger groups, as a result of showing such caring behaviours (see Augusto *et al.* 2017). The feeding rates of females when they are and are not allomothers have to be compared to estimate the cost.

Fission-fusion dynamics, cooperative offspring care, and female social structure

Asian elephants exhibit a high degree of fission-fusion dynamics (de Silva *et al.* 2011, Nandini *et al.* 2018), and Asian elephants live in stable social units called the clan, which is the most inclusive level of social organization. The long-term stability of clan membership may in part be maintained through the benefits that females potentially gain through strong social bonds as suggested for other species (Kerth *et al.* 2011). In elephants, offspring care is thought to be an important part of female social structure, leading to cooperation and the formation of long-term stable social associations amongst females (Gadgil and Nair 1984, Lee 1987, Schulte 2000, Thitaram *et al.* 2005, Williams *et al.* 2019). One of the benefits of stable social bonds may be allomaternal care or calf protection (Gadgil and Nair 1984, Rapaport and Haight 1987, Jayantha *et al.* 2009, Vidya 2014). Fission-fusion dynamics may thus act as a mechanism by which females can potentially enhance their social benefits in the presence of young ones. It would be then interesting to examine the roles that the additional associating females play in the presence of calves. The increased group size by itself could be beneficial – for e.g., protection of calf against predation through communal defense or increased vigilance or dilution effect (if mothers are found together), apart from increased sociality. We find that in our study population of Asian elephants that there is increased sociality and pronounced allomaternal care. However, to establish cooperative offspring care as a reason for the observed changes in female social structure, one further has to study the roles played by different females in the presence and absence of calves. As Asian and African savannah elephants occupy habitats with diverse ecological habitats, it would be worthwhile to compare the relative effects that dependent young ones have on female group sizes in various populations of these species.

In a highly social species like the Asian elephant, a lack of associates can significantly reduce reproductive fitness and survival. A study on the African savannah elephant found that females who lost their clan mates dispersed into non-natal clans and received higher aggression than clan mates (Goldenberg and Wittemyer 2018). We found a similar pattern in the study population where an orphaned female (Pinky_2006_F alias Pinkisafa), who was the last female survivor of her clan (Peggy's clan), was seen to associate with two non-natal clans (Keerthipriya and Vidya 2021). During the study period 2016-2018, this female was allomothering a juvenile (Jacintha_2015_M) of a female (Jacintha) of one of the non-natal clans (Lisa), and the aggression Pinkisafa received seemed to reduce with time (however, it might have reduced even if she had not allomothered the juvenile, simply due to increasing familiarity with time), with Pinkisafa regularly associating with Lisa's clan (see Chapter 2 of this thesis, Figure 6, last panel). Allomaternal care may thus serve as a mechanism for females without associates from their natal clans – because of demographic reasons such as death of female members of the clan or birth of only male offspring – to integrate into a non-natal clan. A study on captive Asian elephants found that calves were central to the formation of groups that mostly contained unrelated reintroduced females (Thitaram *et al.* 2005). Allomaternal care thus seems to provide an opportunity for female to find new associates, which can be explored in the future using a larger dataset.

References

1. Augusto JF, Frasier TR and Whitehead H (2017). Characterizing alloparental care in the

pilot whale (*Globicephala melas*) population that summers off Cape Breton, Nova Scotia, Canada. *Marine Mammal Science* 33: 440-56.

2. Aureli F, Schaffner CM, Boesch C, Bearder SK, Call J, Chapman CA, Connor R, Di Fiore A, Dunbar RIM, Henzi SP, Holekamp K, Korstjens AH, Layton R, Lee P, Lehmann J, Manson JH, Ramos-Fernández G, Strier KB and van Schaik CP (2008). Fission-fusion dynamics. *Current Anthropology* 49: 627-654.
3. Baird RW and Dill LM (1996). Ecological and social determinants of group size in transient killer whales. *Behavioural Ecology* 7: 408-416.
4. Berman CM, Rasmussen KL and Suomi SJ (1997). Group size, infant development and social networks in free-ranging rhesus monkeys. *Animal Behaviour* 53: 405-421.
5. de Silva S, Ranjeewa AD and Kryazhimskiy S (2011). The dynamics of social networks among female Asian elephants. *BMC Ecology* 11: 1-6.
6. Gadgil M and Nair VP (1984). Observations on the social behaviour of free ranging groups of tame Asiatic elephants (*Elephas maximus* Linn). *Proceedings of the Indian Academy of Sciences (Animal science)* 93: 225-233.
7. Gautam H (2019). *Resource Availability, Within-clan and Between-Clan Agonistic Interactions, and Dominance Relationships amongst Female Asian Elephants in Nagarahole National Park, Southern India*. Ph.D. thesis, Jawaharlal Nehru Centre for Advanced Scientific Research, Bengaluru.
8. Gautam H and Vidya TNC (2019). A test of the socioecological model in female Asian elephants: the effects of food abundance, food distribution, and competitor density on within-clan and between-clan contests. *bioRxiv* 754515. https://doi.org/10.1101/754515.
9. Gero S, Gordon J and Whitehead H (2013). Calves as social hubs: dynamics of the social network within sperm whale units. *Proceedings of the Royal Society B: Biological Sciences* 280: 20131113.
10. Gibson QA and Mann J (2008). The size, composition and function of wild bottlenose dolphin (*Tursiops* sp.) mother–calf groups in Shark Bay, Australia. *Animal Behaviour* 76: 389-405.
11. Goldenberg SZ, Douglas-Hamilton I and Wittemyer G (2016) Vertical transmission of social roles drives resilience to poaching in elephant networks. *Current Biology* 26: 75-79.
12. Goldenberg SZ and Wittemyer G (2018). Orphaning and natal group dispersal are associated with social costs in female elephants. *Animal Behaviour* 143: 1-8.
13. Holmes SM, Gordon AD, Louis EE and Johnson SE (2016). Fission-fusion dynamics in

black-and-white ruffed lemurs may facilitate both feeding strategies and communal care of infants in a spatially and temporally variable environment. *Behavioural Ecology and Sociobiology* 70: 1949-1960.

14. Jayantha D, Dayawansa PN, Padmalal UK and Ratnasooriya WD (2009). Social relationships of wild juvenile Asian elephants *Elephas maximus* in the Udawalawa National Park, Sri Lanka. *Journal of Threatened Taxa*. 1: 211-214.
15. Keerthipriya P and Vidya TNC. (2021). Kabini Elephant Project: A long-term programme for understanding Asian elephant behaviour and ecology. *Trumpet* 2: 14-21.
16. Kerth G, Perony N and Schweitzer F (2011). Bats are able to maintain long-term social relationships despite the high fission–fusion dynamics of their groups. *Proceedings of the Royal Society B: Biological Sciences* 278: 2761-2767.
17. Kumar A and Solanki GS (2014). Role of mother and allomothers in infant independence in capped langur *Trachypithecus pileatus*. *Journal of the Bombay Natural History Society* 111: 3-9.
18. Lee PC (1987). Allomothering among African elephants. *Animal Behaviour* 35: 278-291.
19. Maestripieri D (2018). Maternal influences on primate social development. *Behavioural Ecology and Sociobiology* 72: 130.
20. Mann J and Smuts BB (1999) Behavioural development in wild bottlenose dolphin newborns (*Tursiops* sp.). *Behaviour* 136: 529-566.
21. Mar KU, Lahdenperä M and Lummaa V (2012). Causes and correlates of calf mortality in captive Asian elephants (*Elephas maximus*). *PLoS One* 7: e32335.
22. Marealle WN, Holmern T and Røskaft E (2020). Factors affecting group size and vigilance behaviour of Maasai giraffe (*Giraffa camelopardalis tippelskirchi*) on the Serengeti-Ngorongoro Ecosystem, Tanzania. *East African Journal of Environment and Natural Resources* 2: 14-23.
23. McKay GM (1973). Behaviour and ecology of the Asiatic elephant in southeastern Ceylon. *Smithsonian Contributions to Zoology* 125: 1-113.
24. McKenna JJ (1979). The evolution of allomothering behaviour among colobine monkeys: function and opportunism in evolution. *American Anthropologist* 81: 818–840.
25. Nair PV (1989). Development of nonsocial behaviour in the Asiatic elephant. *Ethology* 82: 46–60.
26. Nandini S, Keerthipriya P and Vidya TNC (2017). Seasonal variation in female Asian elephant social structure in Nagarahole-Bandipur, southern India. *Animal Behaviour* 134: 135-145.

27. Nandini S, Keerthipriya P and Vidya TNC (2018). Group size differences may mask underlying similarities in social structure: a comparison of female elephant societies. *Behavioural Ecology* 29: 145-159.
28. Rapaport L and Haight J (1987). Some observations regarding allomaternal caretaking among captive Asian elephants (*Elephas maximus*). *Journal of Mammalogy* 68: 438-442.
29. Ross C and MacLarnon A (2000). The evolution of non-maternal care in anthropoid primates: a test of the hypotheses. *Folia Primatologica* 71: 93-113.
30. Saito M and Idani GI (2016). How social relationships of female giraffe (*Giraffa camelopardalis tippelskirchi*) change after calving. *African Journal of Ecology* 54: 242-244.
31. Schulte BA (2000). Social structure and helping behaviour in captive elephants. *Zoo Biology* 19: 447-459.
32. Shetty NR (2016). *Social Structure, Genetic Relatedness, and Dominance Relationships in Female Asian Elephants in Nagarahole and Bandipur National Parks, Southern India.* Ph.D. thesis, Jawaharlal Nehru Centre for Advanced Scientific Research, Bengaluru.
33. Smith JE, Kolowski JM, Graham KE, Dawes SE and Holekamp KE (2008). Social and ecological determinants of fission–fusion dynamics in the spotted hyaena. *Animal Behaviour* 76: 619-36.
34. Spencer-Booth Y (1968). The behaviour of group companions towards rhesus monkey infants. *Animal Behaviour* 16: 541–557.
35. Sueur C, King AJ, Conradt L, Kerth G, Lusseau D, Mettke-Hofmann C, Schaffner CM, Williams L, Zinner D, and Aureli F (2011). Collective decision-making and fission–fusion dynamics: a conceptual framework. *Oikos* 120: 1608-1617.
36. Sukumar R (2003). *The Living Elephants: Evolutionary Ecology, Behaviour, and Conservation.* Oxford University Press, Oxford.
37. Thitaram C, Dejchaisri S, Somgird C, Angkawanish T, Brown J, Phumphuay R, Chomdech S, and Kangwanpong D (2015). Social group formation and genetic relatedness in reintroduced Asian elephants (*Elephas maximus*) in Thailand. *Applied Animal Behaviour Science* 172: 52-57.
38. van Schaik CP (1999). The socioecology of fission-fusion sociality in orangutans. *Primates* 40: 69-86.
39. Vidya TNC (2014). Novel behaviour shown by an Asian elephant in the context of allomothering. *Acta Ethologica* 17: 123-127.
40. Webber CE (2017). *A Comparison of Behavioural Development of Elephant Calves in*

Captivity and in the Wild: Implications for Welfare. Ph.D. thesis, University of Stirling.

41. Wells RS, Scott MD and Irvine AB (1987). The social structure of free-ranging bottlenose dolphins. In *Current Mammalogy* pp. 247-305. Springer, Boston, MA.
42. Wey TW, Burger JR, Ebensperger LA and Hayes LD (2013). Reproductive correlates of social network variation in plurally breeding degus (*Octodon degus*). *Animal Behaviour* 85: 1407-1414.
43. Williams E, Carter A, Hall C, and Bremner-Harrison S (2019). Social interactions in zoo-housed elephants: Factors affecting social relationships. *Animals* 9: 747.
44. Wilson EO (1975). *Sociobiology: The New Synthesis*. The Belknap Press, Cambridge, MA.