Social Structure, Genetic Relatedness, and Dominance Relationships in Female Asian Elephants in Nagarahole and Bandipur National Parks, Southern India

A thesis submitted for the degree of

Doctor of Philosophy

by

Nandini R Shetty

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

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CERTIFICATE

This is to certify that the work presented in this thesis titled "**Social Structure, Genetic Relatedness, and Dominance Relationships in Female Asian Elephants in Nagarahole and Bandipur National Parks, Southern India**" has been carried out by Ms. Nandini R Shetty 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.

Date: Dr. T.N.C. Vidya

DECLARATION

I declare that the matter presented in my thesis titled "**Social Structure, Genetic Relatedness, and Dominance Relationships in Female Asian Elephants in Nagarahole and Bandipur National Parks, 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, Bangalore, India, under the supervision of Dr. 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.

Place: Bengaluru   Nandini R. Shetty

Date:

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Contents

THESIS ABSTRACT

This thesis describes the first detailed quantitative study of female Asian elephant social organisation in India. Social organisation may be shaped by ecological factors and individual relationships, and understanding the relative roles of these factors in shaping animal societies has long been a central objective of mammalian behavioural research (Crook and Gartlan 1966, Clutton-Brock and Harvey 1977, Wrangham 1980). Individual relationships may further depend on inclusive fitness benefits, direct fitness benefits, and conflict from conspecifics. Using data collected over five years, between March 2009 and July 2014, on identified females from Nagarahole and Bandipur National Parks (the Kabini population; see Vidya *et al*. 2014) in southern India, I studied some aspects of the social organisation of female Asian elephants and how they might be affected by ecological factors or individual relationships. Elephants offer a superb system for investigating the role of ecological factors and individual relationships on behaviour as they are socially advanced, inhabit diverse habitats, and possibly offer an opportunity for kin selection. Female Asian elephants live in matrilineal societies and show fission-fusion dynamics, which, in other species allow community members to split away or associate together in groups of different sizes in response to spatio-temporally varying resources. However, being long-lived species, elephants have to be studied over a long period so that their societies can be properly understood.

The introductory ***Chapter 1*** provides a general introduction to socioecological theory, the Asian elephant, and the study population. As this was the first detailed study of female Asian elephant social organisation in India, I began by characterising the social structure of female elephants in the Kabini population based on associations between individually identified females. This is described in ***Chapter 2***, titled ***Female Asian elephant social structure in southern India and a comparison with other elephant populations***. I identified 330 females above the age of ten years, which were used for analysis. Upon constructing association networks and using network methods, I found that female social structure in the Kabini population was highly modular, with discrete communities that I call clans. Associations amongst females were nonrandom, with individuals associating almost exclusively with their clan-mates. Fission-fusion dynamics were found within clans and

group sizes were small compared to clan sizes. A comparison of social structure of the Kabini population, suitably modified to account for sampling differences, with those of the Uda Walawe Asian elephant population (de Silva *et al*. 2011, de Silva and Wittemyer 2012) and Samburu African savannah elephant population (Wittemyer *et al*. 2005) showed the African savannah elephant population to be more connected and cohesive than the Asian elephant populations based on association strengths and network statistics. The Samburu population seemed to be a hierarchically nested multilevel society while the Asian elephants did not appear to be nested. However, I was able to detect hierarchical clustering levels in all three populations using a network community detection method, and the average community sizes at two levels of clustering were not different across populations, pointing to some basic underlying similarities in social structure. Since average group sizes were significantly larger in Samburu compared to Kabini and Uda Walawe, I examined whether the differences seen in association and network statistics could be explained by group size. Using random datasets, I found that the higher average strength of association, number of associates, and smaller network distance to other associates in Samburu compared to Kabini could possibly be explained by group size differences. Thus, differences in average group size may mask basic underlying similarities in the social structures of related species.

I then examined whether seasonality affects female social structure in the Kabini population, which is detailed in ***Chapter 3***, titled ***Seasonal variation in female Asian elephant social structure in Nagarahole-Bandipur, southern India***. Fission-fusion dynamics in other species allow for group sizes and compositions to change in response to resources. I found in the Kabini population that clan identity was maintained across seasons, within-clan network statistics did not change across seasons, and within-clan associations were moderately correlated across seasons. Group sizes also did not change seasonally within individual clans. However, there were population-level effects of season, with larger group sizes in the dry season and a greater number of strong associations in the wet season. Since population-level results arise as a combination of results from different clans, they may be misleading, and previous studies at the population-level may need to be interpreted cautiously. I also found that group sizes did not increase with clan size, suggesting a constraint on group size. This resulted in lower strengths of association in larger clans. The constraint on group size possibly explains the lack of seasonal effects. However, the constraint in group size did not restrict clan-mates to remaining in fixed small groups.

Groups remained roughly similar in size, but were fluid, with changing associates, suggesting benefits of extended associations with clan-mates.

I examined the role of genetic relatedness in female social structure in ***Chapter 4***, titled ***Genetic relatedness and associations in female Asian elephants in Nagarahole-Bandipur, southern India***. I collected fresh dung samples from identified females, upon observed defecation, and genotyped dung-extracted DNA at 14 nuclear microsatellite loci. Females belonging to first-level communities within clans were closely related, as first- and second-order relatives. Females were also closely related to their top associate, and significantly more related to the top and second associate compared to the average associate. These results indicate that close associations were based on genetic relatedness between females, thus presenting opportunities for indirect fitness benefits. However, although females were also significantly related at the clan-level overall, many clans had females with low relatedness or relatedness of zero. Significant correlations between association strength and genetic relatedness were found in less than half the clans examined. These results suggest that genetic relatedness between females was not the only prerequisite for bonding amongst them and that direct fitness benefits may also be important at the level of the clan.

I went on to examine dominance relationships within and between clans. This is described in ***Chapter 5*** titled ***Dominance relationships amongst female Asian elephants in Nagarahole-Bandipur, southern India***. Socioecological theory suggests that the quality and distribution of resources will affect food competition (which may be of scramble or contest type), which in turn will affect dominance relationships within societies (Wrangham 1980, van Schaik 1989, Isbell 1991, Sterck *et al*. 1997). Since elephants are bulk foragers that range widely and feed primarily on grasses, scramble competition might be expected, leading to egalitarian relationships within, and possibly between, clans. However, age/size based linear dominance hierarchies within clans had been observed in the African savannah elephant (Archie *et al*. 2006, Wittemyer and Getz 2007) and it was possible that the Asian elephant might also show this pattern. I collected data on agonistic interactions using *ad libitum* and focal sampling, and found that there was a low frequency of within-clan agonistic interactions, but a high frequency of between-clan agonistic interactions. Upon analysing within-clan dominance in five focal clans, I found no linear dominance hierarchy, although there was unidirectionality of interactions and interactions almost always had clear winners. Older individuals were often more dominant than younger individuals, but this effect of age was smaller than that in the African savannah elephant populations studied. Moreover, the matriarch (the oldest adult female) was not the single most dominant female in any clan, unlike that seen in the African savannah elephant. Between-clan interactions were more intense than within-clan interactions, involved retaliation, and resulted in decided winners (when one clan displaced the other from its feeding spot) only in half the interactions. Group size had an effect on between-clan interactions, with larger groups tending to win, suggesting that this might be a direct benefit of associating with clan-mates. The Kabini reservoir was artificially created in the 1970s and offers a large point resource for elephants in the dry season, during which most observations of dominance could be made. I speculate that this change in resource distribution for elephants traditionally using the area might have led to high levels of dominance between clans and suppression of dominance within clans. Radiocollaring of females to examine dominance levels across their entire ranges would be required to test this in the future.

Chapter 6 is a short conclusions chapter, summarising the main results. This thesis provides new information on female Asian elephant social organisation by describing the female social structure of the species and making comparisons across populations, examining the effects of seasonality and genetic relatedness on social structure, and presenting the first information on dominance relationships in the species. The results here suggest that ecological factors, in the form of resource availability, may play an important role in social organisation by constraining group sizes and, thereby, affecting social structure. Individual relationships, in the form of relationships with close relatives may be important, but direct fitness benefits are also probably important at the level of the clan, which is the most inclusive social unit in this population.

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CHAPTER 1

General Introduction

Introduction

I describe the first detailed study of female Asian elephant socioecology in India. This study was carried out in Nagarahole and Bandipur National Parks and Tiger Reserves in southern India. Using data from individually identified females, I describe social structure, genetic relatedness, and dominance relationships in the different chapters. In this chapter, I give an introduction to socioecological theory, to Asian elephants, the study area, and the broad objectives of the study.

Socioecological theory

A society is a set of consistently associating conspecific animals. Social organisation describes the size, demography, and spatio-temporal cohesion of the members of a society, and social structure describes the patterning of interactions and resulting social relationships among the members (Kappeler and van Schaik 2002). Social organisation and structure impact various aspects of an animal's life, such as access to resources (for example, Gompper 1996), reproductive opportunities (Clutton-Brock 1989a, Silk 2007, Clutton-Brock and Huchard 2013), predation risk (Ebensperger *et al*. 2006), and exposure to disease (Altizer *et al*. 2003). Social structure can also affect population genetic structure (Storz 1999, Parreira and Chikhi 2015) and population dynamics (Crook 1970, Courchamp *et al*. 1999), making it very important in the study of a species. Social behaviour arises as a response to both ecological factors and individual relationships, and understanding the relative roles of these factors in shaping animal societies has been central to mammalian behavioural research (Crook and Gartlan 1966, Eisenberg *et al*. 1972, Clutton-Brock and Harvey 1977, Wrangham 1980). Individual relationships may depend on inclusive fitness (an individual's personal reproductive success plus the indirect reproductive success contributed by relatives, who share the individual's genes, as a result of the individual's intervention in their reproductive activities, Hamilton 1964) benefits, direct fitness benefits, and conflict from conspecifics (Kummer 1978, Walters and Seyfarth 1987).

Socioecological theory predicts that female dispersion in polygynous mammals relate to spatio-temporally varying resource-risk distributions (Clutton-Brock and Harvey 1977, Wrangham 1980, Terborgh and Janson 1986, Clutton-Brock 1989b, van Schaik 1989, Isbell 1991, Wrangham *et al*. 1993, Chapman *et al*. 1995, Janson and Goldsmith 1995, Sterck *et al*. 1997, Rubenstein and Hack 2004, Snaith and Chapman 2007). When food does not limit female reproductive success, egalitarian societies with female transfer between groups and no dominance hierarchies within groups are expected (Isbell 1991). When food resources limit female reproductive success, female-bonded groups may be formed, with different extents of inter- and intra- group competition (Wrangham 1980, van Schaik 1989, Isbell 1991, Sterck *et al*. 1997, Isbell and Young 2002) because within-group feeding competition is a major cost of group living (Jarman 1974, van Schaik *et al*. 1983, Terborgh and Janson 1986, Dunbar 1988, van Schaik 1989, Wrangham *et al*. 1993, Janson and Goldsmith 1995, see Koenig 2002, Wittiger and Boesch 2013). Food competition may occur through non-interference or scramble competition, which occurs over non-monopolisable resources, or through interference or contest competition, which occurs over usurpable resources such that there is a winner and a loser (Nicholson 1954). If resources limit female reproductive success but cannot be monopolised by single females within groups, resident egalitarian societies may be formed, while if important resources can be monopolised by single females within groups, contest competition leading to despotic societies with strong dominance hierarchies is expected (Wrangham 1980, van Schaik 1989, Isbell 1991, van Hooff and van Schaik 1992, Isbell and van Vuren 1996, Sterck *et al*. 1997, Isbell and Young 2002). If there is both within- and between- group contest, the within-group contest may be lowered by dominants, who become tolerant of the subordinates, and a resident-nepotistic-tolerant society may be formed (Sterck *et al*. 1997). Within-group dominance hierarchies may be nepotistic or individualistic, depending on the role of kinship in social organisation.

A solution to within-group food competition from spatio-temporally changing food resources is exhibited by species that show fission-fusion dynamics (see Aureli *et al*. 2008). Previously called fission-fusion societies, these societies exhibit changing group sizes and compositions over time, by the fission of groups and fusion of subgroups depending on resource availability and distribution (Kummer 1971). Such flexible organisation is thought to have evolved to reduce the cost of group living, and is seen in species such as chimpanzees, spider monkeys, geladas, hamadryas baboons, whales, dolphins, spotted hyenas, humans, bats, zebras, and elephants (Kummer 1968, 1971, Milton 1984, Dunbar 1988, Symington 1988, van Schaik 1989, Whitehead *et al*. 1991, Strier 1992, Chapman 1990, Chapman *et al*. 1995, Kerth and König 1999, Connor *et al*. 2000, Rubenstein and Hack 2004, Hill and Dunbar 2003, Wittemyer *et al*. 2005, Lehmann *et al*. 2007, Smith *et al*. 2008). Species showing high fission-fusion dynamics may be useful for examining predictions from the socioecological theory relating to ecological factors, competition, group size, and relatedness.

The Asian elephant (Elephas maximus)

The Asian elephant is one of three surviving species of the Order Proboscidea. Ranging from the Tigris-Euphrates basin in western Asia, eastwards across the Indian subcontinent, to southeast Asia and Yangtze-Kiang in China about 4,000 years ago (Sukumar and Santiapillai 1996), the Asian elephant's range is now reduced to approximately 3.5% of its historic range (Baskaran *et al*. 2011). The Asian elephant is listed as Endangered and there are an estimated 41,400-52,300 individuals worldwide, distributed across 13 countries, and 26,000-28,000 wild elephants in India (Sukumar 2003, Baskaran *et al*. 2011). Elephants are distributed across four regions in the country, northern India in the foothills of Himalayas, northeastern India, central (East-centra) India, and southern India (see Vidya *et al*. 2005a). Population sizes in these four regions are estimated at ~1,700, 9,000-9,500, ~2,650, and ~14,000 elephants respectively (Baskaran *et al*. 2011). Within southern India are three large elephant populations, the Brahmagiri-Nilgiri-Wyanad-Mysore or the Nilgiris-Eastern Ghats landscape, the Anamalai–Nelliyampathy–High Ranges or the Anamalai-Parambikulam landscape, and the Periyar–Agasthyamalai or Periyar-Kalakkad-Mundanthurai landscape (see AERCC 1998, Vidya *et al*. 2005b, Baskaran *et al*. 2011). The three landscapes harbour approximately 8,800, 3,000, and 2,000, elephants, respectively (Baskaran *et al*. 2011). Habitat loss and fragmentation, human-elephant conflict, and, to a much smaller degree, poaching of males for ivory (only males carry ivory in Asian elephants) are threats to the Asian elephant.

Perhaps understandably, most studies of the Asian elephant have focused on counting elephant numbers, assessing habitats available, and human-elephant conflict (Sukumar 1989, Leimgruber *et al*. 2003, see Sukumar 2003, Fernando *et al*. 2008a). A little less common are studies of ecology. The Asian elephant is wide-ranging (although variable, Baskaran *et al*. 1995, Fernando *et al*. 2008b) and inhabits a variety of habitats, ranging from wet evergreen forests to dry thorn forests (Sukumar 2003). They are ecosystem engineers and seed dispersers, and can modify their habitat considerably (Botkin *et al*. 1981, Campos-Arceiz and Blake 2011). Asian elephants feed on a large number of grasses, herbs, shrubs, and trees, and show differences in feeding patterns across habitats and seasons (Sukumar

1989, Baskaran *et al*. 2010). Being megaherbivores with poor digestion, they are bulk foragers, and spend about 60% of daytime hours feeding (Baskaran *et al*. 2010).

Not much work exists on the social organisation of the Asian elephant, and social structure in the species had been largely assumed to be similar to that of the well-studied African savannah elephant (see Sukumar 2003), although the two lineages diverged about 7.6 million years ago (Rohland *et al*. 2007). Female Asian elephants are philopatric, whereas males disperse away from the group when they are about 10-15 years old (McKay 1973, Sukumar 1989, Desai and Johnsingh 1995). Studies of female social structure in Sri Lanka had identified “herds”, comprising adult females and their offspring, that showed fission-fusion dynamics, with entire herds breaking up into subunits and reassociating (McKay 1973). Subsequently, based on observations of large aggregations of elephants in southern India, a hierarchical social structure was suggested, with family groups, joint-family groups, bond groups, and clans forming nested levels (Sukumar 1989), similar to that seen in the African savannah elephant (Douglas-Hamilton 1972, Moss and Poole 1983). Fernando and Lande (2000), based on a study using radio-telemetry and genetic relatedness between females, suggested that female social structure of Asian elephants was restricted to the family-level. More recently, the first detailed, quantitative study of female associations in Asian elephants, carried out in Uda Walawe, Sri Lanka, reported a multilevel society. Females showed long-term associations with a few associates and all the adult females were connected to one another in a social network at the level of the population (de Silva *et al*. 2011).

Objectives of my study

I worked on female Asian elephant socioecology in a population in southern India. Since the social structure of female Asian elephants was not clear, my first objective was to carry out a quantitative study of female social structure. I aimed to find out whether female social structure in the Asian elephant was indeed limited to family groups or whether there was a nested, multileveled social structure. I also wanted to find out how this social structure changed with seasons. I expected that social organisation of the Asian elephant would be different from that of the African savannah elephant because of the different nature of habitats that the two species inhabited: open savannah versus forest. After I began my work, results from the study in Uda Walawe were published, and provided an additional comparison of female Asian elephant social structure. Another objective of my study was to examine whether sociality in female Asian elephants was based on genetic relatedness. Finally, I also wanted to examine the nature of within- and between-group dominance amongst female Asian elephants.

The Kabini Elephant Project

Elephants offer a superb system for investigating the role of ecological factors and individual relationships on behaviour as they are socially advanced (Wilson 1975), inhabit ecologically diverse habitats (see Sukumar 2003), and offer an opportunity for kin selection by forming social groups of closely related individuals (Vidya and Sukumar 2005, Archie *et al*. 2006). Moreover, our understanding of mammalian social organisation and behaviour was largely based on studies of primates (for e.g. Kummer 1968, Wrangham 1980, van Schaik 1989, Isbell 1991, Dunbar 1992, Sterck *et al*. 1997). Although there were long-term studies of the African savannah and African forest elephants (Douglas-Hamilton and Douglas-Hamilton 1975, Moss 1988, Turkalo and Fay 1995), there were no similar studies of Asian elephants. Long-term studies (e.g., Isle of Rum red deer, St. Kilda soay sheep, Kalahari meerkats, Amboseli baboons, Amboseli and Samburu African elephants) have been indispensable to the study of behaviour in mammals, as changing environments may confound patterns observed over short periods (see Clutton-Brock and Sheldon 2010). Understandably, such long-term datasets are particularly important for the study of long-lived animals like elephants. The Kabini Elephant Project had been set up with the above in mind in March 2009 (Vidya *et al*. 2014), and I carried out my work as part of this long-term programme of monitoring and behavioural research on individually identified Asian elephants.

The Kabini Elephant Project was set up in Nagarahole National Park and Tiger Reserve (Nagarahole; 11.85304°-12.26089° N, 76.00075°-76.27996° E, 644 km^2) and the adjoining Bandipur National Park and Tiger Reserve (Bandipur; 11.59234°-11.94884° N, 76.20850°-76.86904° E, 872 km^2), in the Nilgiris-Eastern Ghats landscape in Karnataka, southern India. The Nilgiris-Eastern Ghats landscape holds the single largest population of Asian elephants in the world, with over 8,500 elephants (Rangarajan *et al*. 2010, Baskaran *et al*. 2011), of which about 2,600 (Baskaran and Sukumar 2011) elephants probably use Nagarahole and Bandipur. The parks together have a range of habitat types including dry and moist deciduous forests, thorn forest, and teak and eucalyptus plantations (Pascal 1982). However, the dominant habitats are dry and moist deciduous forests in both parks.

Nagarahole and Bandipur are separated by the Kabini reservoir on the river Kabini, formed by the construction of the Beechanahalli Dam in 1974. The Kabini reservoir and the area around its receding backwaters are a major source of water and fresh grass to herbivores during the dry season. The Kabini area receives an annual rainfall of about 950 mm from the seasonal southwest and northeast monsoons (I considered mid-June to November to be the wet season, see chapter 3). Elephants congregate around the backwaters during the dry season and are more scattered in the forest during the wet season. The area around the backwaters affords good visibility for behavioural observations. Both Nagarahole and Bandipur also have a good network of roads and elephants are moderately habituated to vehicles because of tourism.

I carried out fieldwork from January 2011 - May 2013, and labwork during 2010 and 2014.

Outline of the thesis

This thesis is written in manuscript format with self-contained chapters in the form of manuscripts. However, not being constrained by length as in an actual manuscript, detailed results are presented. In the second chapter, we examined the social structure of female Asian elephants in the Kabini population to find out whether social structure was limited to the family-level or whether there was a nested or non-nested multilevel society. We also compared this with the social structures of female African savannah elephant populations and the Uda Walawe Asian elephant population. If both Asian elephant populations showed similar social structures, the observed differences with the African savannah elephant would likely have ecological origins. In the third chapter, we analysed the observed social structure of female elephants from Kabini seasonally and annually. As resource distribution and abundance were expected to change with season, we examined whether group sizes and social network cohesiveness changed between the dry season and the wet season. In the fourth chapter, we examined whether female social structure was based on genetic relatedness by genotyping females from collecting dung samples. We analysed the strength of associations and relatedness to find out the possible roles of indirect and direct fitness benefits in organizing female Asian elephant societies. We then describe dominance relationships amongst females within and between groups in the fifth chapter. This is especially of interest since there are different contrasting predictions relating to the expected type of dominance relationships in elephants. The sixth chapter is a short summary of the main findings.

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CHAPTER 2

Female Asian Elephant Social Structure in Southern India and a Comparison with Other Elephant Populations

Title: Female Asian elephant social structure in southern India and a comparison with other elephant populations

Authors: Nandini Shetty, P. Keerthipriya, T.N.C. Vidya

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

Abstract

Societies with fission-fusion dynamics allow for community members to split away or associate together in groups of different sizes in response to spatio-temporally varying resources. We examined the role of group size in affecting the outcome of social structure analysis in female elephants, which show high fission-fusion dynamics. We carried out the first quantitative study of female Asian elephant social organisation in India. Using over five years of data on associations between females from Nagarahole and Bandipur National Parks (the Kabini population) in southern India, and network methods, we found that female social structure in this population is highly modular, with discrete communities that we call clans. Clans almost never associated with one another. There was some variability in within-clan structure, which was related to clan size. In keeping with the highly modular social network, only a small fraction of all possible associations between females was non-zero, while there were a large number of connections within clans. We also created a dataset (the Kabini 500-m dataset) from our original field data to match the sampling methods previously used in a study each of Asian and African savannah elephants, so that network and association statistics could be properly compared across populations. We found that the Samburu African savannah elephant social network was more connected than the Uda Walawe and Kabini 500-m Asian elephant networks. Association index distributions, network structure curves, and cumulative bifurcation curves were more similar amongst the Asian elephant populations compared to those from the Samburu population, and the latter seemed to be a hierarchically nested multilevel society while the former did not show signs of nestedness. However, when we analysed the social networks using the Louvain method of community detection, we uncovered hierarchical clustering levels in all three populations. Moreover, the average community sizes at the first and second levels of clustering were not significantly different across populations, indicating some basic similarities in social structure across the species. The average group size was significantly larger in the Samburu population compared to the Asian elephant populations. An examination of the effect of group size on AI and network statistics using random association data with different average group sizes revealed that the higher average AI and average degree, and lower average path length in Samburu compared to the Kabini 500-m dataset could be explained by differences in group size. Thus, underlying similarities in the social network structures of related species showing fission-fusion dynamics may be obscured because of differences in average group size.

Keywords

Asian elephant, female social structure, fission-fusion, multilevel societies, group size, association network, Louvain community detection, Nagarahole-Bandipur, southern India, Kabini elephant population.

Introduction

Social structure and organisation, which include the patterning of relationships and the system of interactions between individuals, are important in foraging (for example, Gompper 1996, Vásquez and Kacelnik 2000), reproductive opportunities (see Clutton-Brock 1989a, Silk 2007, Clutton-Brock and Huchard 2013), disease (for example, see Altizer *et al*. 2003, Cross *et al*. 2004, Hock and Fefferman 2012), population genetic structure (for example, Storz 1999, Rossiter *et al*. 2012, Parreira and Chikhi 2015), and population dynamics (for example, Crook 1970, Courchamp *et al*. 1999, Langwig *et al*. 2012), through factors such as dominance (for example, see Sterck *et al*. 1997, see Sapolsky 2005, Smith *et al*. 2007, Wittemyer *et al*. 2007), anti-predatory benefits (for example, Dehn 1990, Hass and Valenzuela 2002, Ebensperger *et al*. 2006), information flow (for example, Zachary 1977, Lusseau 2007, Voelkl and Noe 2010), social learning (for example, White 2004, Van der Post and Hogeweg 2008, Aplin *et al*. 2013), and pathogen transmission (for example, Vander Waal *et al*. 2014). Social organisation is thought to evolve in response to spatio-temporally varying resource-risk distributions (Clutton-Brock and Harvey 1977, Wrangham 1980, Clutton-Brock 1989b, van Schaik 1989, Isbell 1991, Wrangham *et al*. 1993, Chapman *et al*. 1995, Janson and Goldsmith 1995, Sterck *et al*. 1997, Rubenstein and Hack 2004, Snaith and Chapman 2007), making ecological factors an important consideration when comparing societies. One of the modal types of social organisation observed in mammals was called the fission-fusion society, in which groups fuse together or split away in response to spatio-temporally varying resources, thus balancing the costs and benefits of group-living (Kummer 1971, Milton 1984, Dunbar 1988, Symington 1988, van Schaik 1989, Whitehead *et al*. 1991, Strier 1992, Chapman 1990, Chapman *et al*. 1995, Connor *et al*. 2000, Rubenstein and Hack 2004, Wittemyer *et al*. 2005a, Smith *et al*. 2008). Distinct types of fission-fusion societies were identified (see van Schaik 1999, Grüter and Zinner 2004), such as multilevel societies that were either strictly hierarchically nested (as seen in hamadryas, Kummer 1968, Abegglen 1984, Stammbach 1987), or flexibly nested (as seen in gelada baboons, Dunbar and Dunbar 1975, Kawai *et al*. 1983, Dunbar 1988), and the classical or individual-based fission-fusion society (as seen in chimpanzees and spider monkeys, Nishida and Hiraiwa-Hasegawa 1987, Symington 1990). It has since been recognized that fission-fusion societies actually form a continuum of different extents of fission-fusion dynamics (see Aureli *et al*. 2008). Here, we examine whether group size could be a factor that bridges the modal types within species showing high fission-fusion dynamics. Group size is the number of individuals in a sighting of animals and is often smaller than the size of socially-meaningful communities in species showing fission-fusion dynamics.

Female elephants show high fission-fusion dynamics (see Aureli *et al*. 2008), but previous studies have suggested hierarchically nested, multileveled (multitiered) social structure in African savannah elephants (Moss and Poole 1983, Wittemyer *et al*. 2005a) and non-nested, multileveled social structure in an Asian elephant population (de Silva and Wittemyer 2012). The differences between these social structures may arise from group size limitation in the Asian elephant, preventing hierarchical structure from being apparent, but this has not been examined previously, as only one detailed study of Asian elephant social structure (de Silva *et al*. 2011) was available. Since observed social structure may reflect evolved patterns, as well as plastic responses to the current environment (DiFiore and Rendall 1994, Kappeler and van Schaik 2002, see Chapman and Rothman 2009), studies of multiple populations are required to understand the social structure of a species. Here, we examine the role of group size in affecting social structure by collecting the first large-scale quantitative data on Asian elephant social structure from India, from the Nagarahole-Bandipur (Kabini) population, and by comparing this with data from the Uda Walawe Asian elephant population in Sri Lanka, and the Amboseli and Samburu African savannah elephant populations, for which published data on female social structure are available (Moss and Poole 1983, Wittemyer *et al*. 2005a, Archie *et al*. 2006, de Silva *et al*. 2011, Archie and Chiyo 2012, de Silva and Wittemyer 2012).

The Asian elephant (*Elephas maximus*) is an endangered species, whose social organisation may have been impacted to varying extents across its range by long, historic manipulation by humans. Therefore, there have justifiably been calls for detailed studies of social organisation in multiple elephant populations in order to understand the drivers of social organisation (Fernando and Lande 2000, Vidya and Sukumar 2005a,b, de Silva *et al*. 2011, de Silva and Wittemyer 2012). Asian and African savannah elephants form matriarchal societies, with females and their dependent offspring living together in groups, and adolescent males dispersing from the groups and leading largely solitary lives thereafter (Douglas-Hamilton 1972, McKay 1973, Moss and Poole 1983, Sukumar 1989, Vidya and Sukumar 2005a,b). Female groups show high fission-fusion dynamics (see Aureli *et al*. 2008). However, based on previous studies, there seemed to be differences in social structure within and between elephant species, possibly from different sampling methods and ecology (see below).

The African savannah elephant exhibits a multitiered female society (Douglas-Hamilton 1972, Moss and Poole 1983, Wittemyer *et al*. 2005a). The basic unit of this society is the mother-offspring unit, and the term "family group" was used to refer to one to a few closely related females and their offspring (Buss and Smith 1966). Social organisation in Amboseli was described to consist of family groups or core groups, comprising several female-dependent offspring units, that were identified at the beginning of the study (from 1972) based on spatial associations and behavioural criteria, and associations of family or core groups that were termed bond groups (Moss and Poole 1983, Archie *et al*. 2006). Family groups that shared dry-season home ranges were called clans (Moss and Poole 1983), which were, therefore, spatially identified. Social tiers in Samburu were identified statistically through cluster analysis and included, hierarchically, second-tier units (family groups), third-tier units (kinship groups of Douglas-Hamilton (1972) or bond groups of Moss and Poole (1983)), and fourth-tier units (Wittemyer *et al*. 2005a). Groups themselves were differently identified in the field, with individuals of core groups having to be within 100 m of one another in order to qualify as being associated in Amboseli (Archie *et al*. 2006), and individuals within a 500-m radius of an aggregation centre being classified as a group in Samburu (Wittemyer *et al*. 2005a). Amboseli and Samburu have also experienced different extents of poaching (Poole *et al*. 1992, Moss 2001), but the association network in Samburu was found to be resilient to the elevated levels of poaching because of daughters replacing their mothers in network roles (Goldenberg *et al*. 2016). Therefore, differences in the female social networks of the two populations, with the Samburu network being much more interconnected than the Amboseli network (Figure 1), are likely to stem from differences in sampling methods. Samburu and Amboseli are similar in elephant density and ecology (Wittemyer *et al*. 2009) and social tiers are similar in the two populations (Table 1).

Studies on female Asian elephant social organisation had long suggested a matriarchal society with fission-fusion dynamics, inferred from female social groups of varying sizes (McKay 1973, Sukumar 1989). However, the precise nature of female social organisation was ambiguous, with studies from Sri Lanka largely not describing multitiered societies but those from southern India implying them (see below). McKay (1973), in southeastern Sri Lanka, described the most inclusive female social group (containing females, their dependent offspring, and juveniles and subadults) as a “herd”, which could contain subunits that showed fusion and fission, but which did not associate with other “herds” that shared their home range. “Herds” were found to contain 15-40 individuals. Fernando and Lande (2000) found smaller group sizes subsequently based on radio-telemetry and limited observational data (see Table 1), but these groups too did not associate with other groups that shared their home range, and were referred to as family groups. A study in southern India, albeit not specifically on social organisation, suggested the existence of a multitiered female elephant society with “family groups” (with a single adult female and her dependent offspring), “joint-family groups” (with two or more adult females), “bond groups”, and “clans” (comprising 50-200 individuals; Sukumar 1989, 2003). Daniel *et al*. (1987) and Baskaran *et al*. (1995), in studies of habitat use and ranging in southern India, referred to social associations of females that showed coordinated movement and were presumably related as a “clan” (of up to 65 individuals), but did not demarcate social tiers within clans. The first large, quantitative study of Asian elephant social organisation, carried out in Uda Walawe, Sri Lanka, found female social organisation with long-term associates, and larger social units than typically seen associating at any time in the field (de Silva *et al*. 2011), which was also the case with the previous, less quantitative studies (and indeed expected in fission-fusion societies in general). What was different from the previous studies (insofar as the data that previous studies contained that could be compared) was that the larger social units (“herds” or “family groups” or “clans” as the term might be) were connected to one another in a social network at the level of the entire population (de Silva *et al*. 2011, de Silva and Wittemyer 2012). In a comparative analysis, it was found that female groups were smaller, showed weaker associations, and were less connected at the population level than that seen in the Samburu African savannah elephant population (de Silva *et al*. 2011, de Silva and Wittemyer 2012). The Uda Walawe population thus showed a non-nested, multilevel society, with individuals associating differently with two types of social affiliates, in contrast to a multitiered society in Samburu with nested social tiers (de Silva and Wittemyer 2012). Although some of the initial confusion relating to female Asian elephant social organisation seems to have stemmed from an attempt to equate social levels in the Asian elephant with those described in the better-studied African savannah elephant, there was also the possibility of female Asian elephant social organisation being different between Sri Lanka and the mainland. A plausible reason for this could be the extensive historical disturbance to elephants in Sri Lanka compared to southern India (see Sanderson 1879, pp. 68-69, Lorimer and Whatmore 2009).

We used data from the Nagarahole-Bandipur (Kabini) population in southern India to find out whether female social structure in this population was similar to that in Sri Lanka, and, if so, whether the difference in social structure from that of the African savannah elephant could be explained by a constraint on group size. We also wanted to find out whether the wider social network in Uda Walawe compared to associations found in previous studies in Sri Lanka could have resulted from differences in methods. A 100-m distance cutoff had been traditionally used to delineate Asian elephant groups (Fernando and Lande 2000), while a 500-m cutoff, similar to the one in Samburu, had been used in Uda Walawe (de Silva *et al*. 2011). We expected that there might be lower levels of connectedness in the Uda Walawe population compared to the Kabini population because of extensive historical disturbance in the former. However, on the whole, we expected greater similarity between Kabini and Uda Walawe, with smaller group sizes and lower network connectivity in the Asian elephant populations than in the African savannah elephant because of ecological differences.

Methods

Field data collection

The field study was carried out in Nagarahole National Park and Tiger Reserve (henceforth, Nagarahole; 11.85304°-12.26089° N, 76.00075°-76.27996° E, 644 km^2) and the adjacent Bandipur National Park and Tiger Reserve (henceforth, Bandipur; 11.59234°-11.94884° N, 76.20850°-76.86904° E, 872 km^2), in the Nilgiris-Eastern Ghats landscape in Karnataka, southern India (Supplementary Material 1). The greater landscape holds the single largest population of Asian elephants in the world, with over 8,500 elephants (Rangarajan *et al*. 2010), of which about 2,600 (Baskaran and Sukumar 2011) elephants probably use Nagarahole and Bandipur. The dominant habitats in the study area are dry and moist deciduous forests. The Kabini reservoir, resulting from the construction of the Beechanahalli Dam on the River Kabini, lies between Nagarahole and Bandipur, and is a major source of water and fresh grass to herbivores during the dry season (see Vidya *et al*. 2014). The area sampled was centred around the Kabini reservoir and extended into the forests of Bandipur and Nagarahole, and we refer to the population as the Kabini population. The area receives an annual rainfall of about 950 mm from the seasonal southwest and northeast monsoons, dividing the year, roughly equally, into wet and dry seasons.

Field data collection was carried out from the beginning of March 2009 to July 2014, on a total of 878 field days. Sampling could not be carried out during several months in 2010 because of field permit issues. Sampling was carried out by driving along pre-selected routes from about 6:30 AM to 6:00-6:45 PM (depending on daylight hours and field permits). Elephants in the study area have been exposed to tourist vehicles for many years, which facilitated observation. Female elephant "groups" were identified as an aggregation of female elephants, usually along with their young, that showed coordinated movement (especially towards or away from a water source or salt lick), coordinated behaviours (such as bunching and facing the same direction when perceiving a threat from other elephants or heterospecifics), or affiliative behaviour, and were usually within 50-100 m of one another. Members of a group were said to be associating with one another. During our original data collection, we did not use a 500-m distance cutoff as had been used in Uda Walawe or Samburu because it was clear from the uncoordinated, and sometimes aggressive, interactions between different aggregations of elephants within 500 m of one another that they did not belong to a single social group. Sighting details of elephant groups, including group size, time of sighting, and GPS location were recorded. Individuals were photographed and sketched, and identified based on multiple natural physical characteristics, and aged based on body size, skull size, and body characteristics, using the Forest Department's semi-captive elephants of known ages in the area as a reference (see Vidya *et al*. 2014). Although individuals older than 15 years have previously been referred to as adults (Sukumar 1989, Vidya *et al*. 2014), since we subsequently found that females were often sexually mature at 10 years of age (as in other elephant populations, see Moss *et al*. 2011, de Silva *et al*. 2013), we analysed associations for females that were 10 years old or older (referred to simply as females in the rest of this paper).

Association data

Animals were sighted only briefly sometimes, in which case all the individuals in a group could not be identified. We excluded such sightings and retained only sightings in which all the females could be identified. We considered sightings of the same group to be independent if they were observed again after 2.5 hours because this interval yielded roughly similar probabilities of groups either changing in composition or not (see

Supplementary Material 2). Changes in group composition within this time period were not recorded as separate sightings. Since we wanted to compare our data with the Uda Walawe and Samburu populations in which a 500-m distance cutoff had been used to identify associations, in addition to using our original sighting dataset for analyses, we created a sighting dataset (referred to henceforth as the Kabini 500-m dataset) in which we grouped together females that were within 500 m of one another based on GPS data. In this new dataset, sightings sharing a common female during the day were merged together into a single sighting, after the manner of de Silva *et al*. (2011). Only sightings with all the females identified were used for the Kabini 500-m dataset also. Further, only females sighted at least 20 times were retained in the dataset as had been done in the Uda Walawe and Samburu datasets. Data on female group sightings were used to calculate the Association Index (AI) between pairs of females, as the ratio of the number of times two females A and B were seen together (N_{AB}) to the number of times either A or B was observed (N-D, where N is the total number of sightings and D the number of times neither A nor B was seen) (Ginsberg and Young 1992). The percentage of non-zero AI values, average AI, and kurtosis of AI were also calculated. Unless otherwise mentioned, data manipulation and analyses were carried out using MATLAB 7 R2004a (The MathWorks, Inc, 1984-2011, www.mathworks.com).

Social structure using networks

We examined social structure using network and cluster analyses. Social networks were constructed based on AI between individuals and visualized using Gephi 0.8.2 (Bastian *et al*. 2009). The network statistics that were calculated included *degree* (the number of connections or *edges* arising from an individual or *node*), *clustering coefficient* (the proportion of all possible edges between the immediate neighbours of a focal node that actually exist, and, therefore, the probability that two randomly chosen neighbours of a focal individual are connected), *path length* (the number of edges on the shortest path between two nodes), and *distance-weighted reach* (the sum of the reciprocal of path lengths from a focal node to other nodes), calculated for individual nodes, and *density* (the proportion of all possible connections in the network that actually exist) and *modularity* (see below) calculated for the entire network (Wasserman and Faust 1994, Borgatti 2006, Latapy 2008). Most network statistics were calculated using MATLAB but distance-weighted reach (reach centrality) was calculated using UCINET ver. 6.528 (Borgatti *et al*. 2002). In order to find out whether the network was different from a random network, we compared the degree distribution of the observed network against Poisson expectation that would arise from an Erdös-Rényi random network (Erdös and Rényi 1960). We also tested for preferred associations by randomly permuting the association data following Whitehead (2008; see Supplementary Material 3). Network statistics of the Kabini 500-m dataset were compared with available statistics from previously studied populations. Since the mean and SD of these statistics were generally available from other populations, but the distributions were likely to be skewed and/or have different variances, we compared statistics across populations using Welch's two-sample tests (Welch 1937). It has been shown through simulations that the Welch's test performs well under several scenarios involving the comparison of skewed distributions with unequal variances and sample sizes (Fagerland and Sandvik 2009). As a further precaution, we used this test to compare statistics between the Uda Walawe and Samburu populations that had earlier been analysed using randomisation tests (de Silva and Wittemyer 2012), and found the same results in all eight tests performed. While comparing the statistics from the Kabini population with the Uda Walawe and Samburu populations (as shown in de Silva and Wittemyer 2012), we used the Kabini 500-m dataset with only females that were sighted at least 20 times (n=109 females) so that the datasets were comparable.

Community structure within networks, and hence *modularity* (a measure of the extent to which a community is partitioned; this can be measured by comparing the fraction of edges within communities to that between communities), was identified using the Louvain method (Blondel *et al*. 2008). The Louvain method clusters communities hierarchically and is known to be accurate. It uses a weighted network (in which edge weights, which are AI values between females, are incorporated rather than mere presence or absence of associations between females) in which each node is initially considered a separate community. Changes in modularity upon rearrangements of nodes are evaluated and rearrangements are stopped when a local maxima of modularity is obtained. The communities detected at this point are used as nodes for the next step. Since the algorithm begins with rearrangements of single nodes across communities, this method does not suffer from the problem of identifying communities at a small scale. The algorithm is repeated iteratively until the maximum modularity is obtained, resulting in hierarchical partitions of communities within communities (Blondel *et al*. 2008). This method allows for structure to be meaningfully examined at different hierarchical levels because the intermediate partitions correspond to local modularity maxima (Blondel *et al*. 2008). This method, therefore, naturally lends itself to the investigation of social organisation, when one is interested in finding out whether there are hierarchies or not. The Louvain method was implemented by calling the C++ codes made available by the authors (https://sites.google.com/site/findcommunities/) from MATLAB. We carried out the Louvain hierarchical community detection for the Uda Walawe and Samburu data also (from de Silva and Wittemyer 2012, data kindly provided by the authors) for comparison with the Kabini (Kabini 500-m dataset) population. We also constructed network structure curves following de Silva *et al*. (2011) for comparison across populations. The number of clusters with more than one female, determined using the Louvain method, after removing edges below different AI thresholds, was plotted against AI threshold. The network structure curve provides information on the cohesiveness of the social network at different association strengths. Significant changes in the slope of the network structure curve were detected by comparing the values of number of clusters to the left and right of each point within a moving window of 0.3 using the Wilcoxon rank sum test (see de Silva *et al*. 2011).

Effect of group size on AI and network statistics

Since differences in group sizes are likely to affect AI and network statistics, we examined the effect of group size on these statistics in random datasets, to find out whether differences across populations in network statistics could simply be a result of differences in group size. We created random datasets, each with 100 individuals in 1500 sightings, distributed in group sizes following beta distributions with parameters that resulted in group size distributions that mimicked known elephant group size distributions (α=1, β=7, maximum group size=19 for Uda Walawe, α=2, β=9, maximum group size=26 for Samburu, and α=1, β=9.5, for the Kabini population, maximum group size=18 for the original data, maximum group size=27 for the 500-m data; Kabini group size distributions from this study, Uda Walawe and Samburu group size distributions from de Silva and Wittemyer 2012). The maximum group size was altered to change average group size. We calculated the average, SD, and kurtosis of AI, and network statistics including average degree, average clustering coefficient, and average path length for the random datasets. One hundred random datasets were created for each beta distribution type with each maximum group size. Therefore, average group size and the AI or network statistics were averaged across these 100 replicates. We then plotted the statistic under consideration against average group size based on the random dataset, for each of the three beta distributions of group sizes, to visualize how the statistic changed with increasing average group size. For each observed statistic (calculated from field populations with an observed average group size), we calculated an expected random value of the statistic by interpolating the appropriate random curve (with matching beta distribution). Interpolation was done using cubic spline in CurveExpert version 1.37 (Hyams 2001). Using the 95% CI of the observed estimates, we calculated an interval with (expected - lower 95% CI of observed)/expected and (expected - higher 95% CI of observed)/expected values for each population. If these intervals overlapped across populations, it indicated that the populations differed from the random lines to the same extent and, therefore, differences in the statistic between the populations could be explained by differences in observed average group size. If the intervals of (E-O)/E did not overlap, it indicated that differences in the statistic between populations were significant beyond the effect of average group size. This was a conservative test because it was possible that the intervals of (E-O)/E could actually be larger than what we calculated based on 95% CIs.

Table 1. Details of social tiers in previously studied elephant populations and from the present study in Kabini. Clan sizes in Kabini are based on 16 clans seen at least 40 times each. The other data come from Fernando and Lande (2000) for Ruhuna National Park (Sri Lanka), de Silva *et al*. (2011) for Uda Walawe (Sri Lanka; the values were calculated using Louvain clustering from data kindly provided by Shermin de Silva), Moss and Poole (1983), Lee (1991), and Moss and Lee (2011) for Amboseli (Kenya), and Wittemyer *et al*. (2005a) and Goldenberg *et al*. (2016) for Samburu (Kenya) (except for the cell marked ‡, whose values were calculated using Louvain clustering from data in de Silva and Wittemyer 2012, kindly provided by the authors).

Population	Ave. no. of females in a family group (range)	Ave. no. of individuals in a family group (range)	Ave no. of females / family groups in a bond group	Ave. no. of individuals in a bond group (range)	No. of females in a clan / fourth-tier unit / most inclusive unit	No. of individuals in a clan / fourth-tier unit / most inclusive unit
Kabini	–	–	–	–	Mean: 13.31, SD: 7.78, Median: 11.5, IQR: 7.5-18.5, Max: 32	Mean: 29.19, SD: 19.76, Median: 21, IQR: 17-39.5, Max: 83
Kabini 500m, ≥20 sightings	–	–	–	–	Mean: 15.57, SD: 9.74, Median: 18, IQR: 9-19.5, Max: 31	–
Uda Walawe	–	–	–	–	Mean: 11.67, SD: 7.47, Median: 12, IQR: 5-17, Max: 23	–
Ruhuna	–	–	–	–	7.75 (4-11)[†]	14.75 (7-24)[†]
Amboseli	2.35 (1-9)*	7.22 (2-23)*	2-5 family groups	–	5-9 family groups	Range: 50-250
Samburu	2.2[•] (1-5)	7.64 (1-15)	2.0 family groups (4.4 females on ave., based on •)	16 (6-40)	[‡]Mean: 13.75, SD: 7.46, Median: 11, IQR: 8.8-16, Max: 28	Median: 33.5, IQR: 28.8-80.3; Median: 32, IQR: 23.5-38 during a subsequent period.

*Family groups in Amboseli comprised, on average, 2.35 females and 7.22 total individuals in 1976, while core groups (erstwhile family groups that had expanded) in 2002 comprised an average of 7.08 females (Moss and Lee 2011). The former are shown so that appropriate comparisons can be made across populations. †These were described as family groups originally (because families contained up to 10-20 females and their offspring according to Wilson 1975), but Asian elephant populations are placed in the last two columns here as the most inclusive social units. IQR: Inter-Quartile Range.

Cluster analysis and cumulative bifurcation curve using AI

In addition to using the Louvain method to detect hierarchical structure in the Kabini population, we carried out hierarchical cluster analysis for comparison across populations. Although hierarchical cluster analysis may not be useful for detecting hierarchical structure if social units at each tier of social structure show variability in AIs (also see de Silva and Wittemyer 2012), we used this method so that the shapes of the cumulative bifurcation curves could be compared across populations. We constructed dendrograms based on associations between individuals and used the plot of the cumulative number of bifurcations in the dendrogram at different linkage distances to identify knots, which indicate significant slope changes, corresponding to different social tiers (see Wittemyer *et al*. 2005a). The UPGMA method was chosen for clustering because it yielded the maximum cophenetic correlation coefficient value (CCC=0.976). Knots were identified by comparing the number of bifurcations in 0.2 and 0.3 windows above and below each point in the cumulative bifurcations plot, using a Wilcoxon rank sum test. If multiple adjacent points yielded significant *P* values, the point with the most significant *P* value was considered the knot and, if adjacent points gave identical *P* values, the average of the linkage distances at these points was considered the knot value.

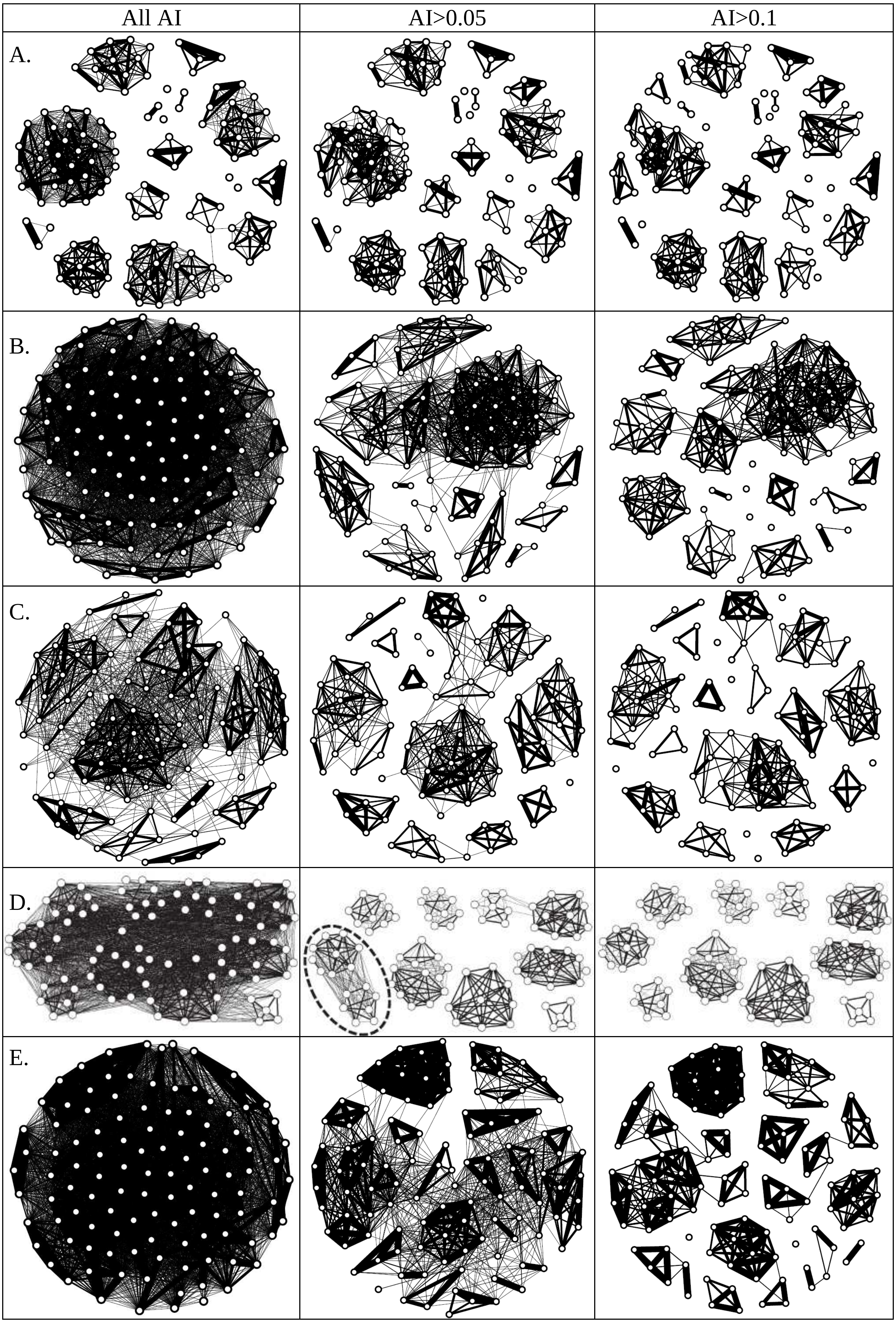


Figure 1. Social networks in A) Kabini, original dataset, B) Kabini 500-m dataset, C) Uda

Walawe (Sri Lanka), D) Amboseli (Kenya), and E) Samburu (Kenya), based on all associations (first column), associations with an AI cutoff of 5% (second column), and an AI cutoff of 10% (third column). The networks in C and E are based on de Silva and Wittemyer (2012; data kindly provided by the authors) and those in D, from Archie and Chiyo (2012; reproduced with the permission of the publisher, John Wiley and Sons, license number 3960250419556). The dashed oval in D indicates a bond group. Only individuals sighted at least 20 times are included in the Kabini networks, as was the case in the Uda Walawe and Samburu networks. Networks for the Kabini data based on individuals sighted at least 10 times are shown in Supplementary Material 4.

Results

The dataset used to examine female associations comprised 3893 female group sightings in which all the females could be identified (9551 individual females, including repeat sightings of the same individual; the 3893 sightings, in which all the females could be identified, comprised 87% of all the female group sightings we had during the study period). The number of uniquely identified females from this dataset was 330.

Association network and AI in the Kabini population based on the original dataset

The association network based on the entire dataset showed clearly demarcated communities (Figure 2). Therefore, associations between females were highly non-random based on comparison with Poisson expectation (G-test for goodness of fit, G=1514.46, df=23, P<0.001) and through the permutation test (both short- and long-term preferences, see Supplementary Material 3). The overall network modularity was high (0.936). We refer to communities obtained through the Louvain method as clans, in keeping with previous terminology used to refer to the most inclusive female social grouping of elephants in southern India. The largest clan in our study consisted of 32 females (83 individuals, including their offspring). We did not find female associations across clans during over five years except on seven occasions (Figure 1). Execution of the Louvain algorithm based on the 330 females yielded 90 communities after the first round of clustering, 70 after the second, and 69 after the third. Excluding 30 communities of single females, there were 60 communities after the first round of clustering, 40 communities after the second round, and 39 communities after the third round (which corresponded to the eventual 39 clans).

Fourteen of the 39 clans went through more than one round of clustering, suggesting more than one level of social organisation in these clans. One clan showed three levels of clustering, while the remaining 13 did not form larger clusters after the second round of clustering. The clans formed after more than one round of clustering were significantly larger (average=14.4, SD=7.57, N=14) than those whose compositions remained intact from the first round of clustering (average, SD, N of clan size: 3.9, 2.74, 25, excluding singletons; Mann-Whitney U test: U=20.0, Z_{adj}=-4.598, P<0.001, see Supplementary Material 5). Based on clans that were sighted over 150 times, we found that 95% of the clan members were sighted on average within the first 40 sightings of the clan (and 92% within the first 30 sightings). Since under-sampling could lead to incomplete clans, we examined the clans sighted more than 40 times and found that they were also significantly larger when they had more than one clustering level (average=17.0, SD=7.29, N=10) than when they had a single clustering level (average=7.2, SD=3.66, N=6; Mann-Whitney U test: U=6.0, Z_{adj}=-2.609, P=0.009, Supplementary Material 5).

In keeping with the clearly defined clusters with few associations between them, the overall AI distribution was highly skewed (Figure 3), with only 2.5% of the AI values being non-zero (average AI=0.004, SD=0.040, median=0). This increased to 10.8% when only individuals that were seen at least 20 times were included in the dataset (Table 2). The average degree and average distance-weighted reach were low (average degree=8.32, average distance-weighted reach=12.45, Table 2) because of female associations being restricted to the clan. The average clustering coefficient was high (0.87; 0.95 based on females seen at least 20 times, Table 2) due to the large number of connections within clusters, and density, which measures connectedness across the entire network, was low (0.025, Table 2).

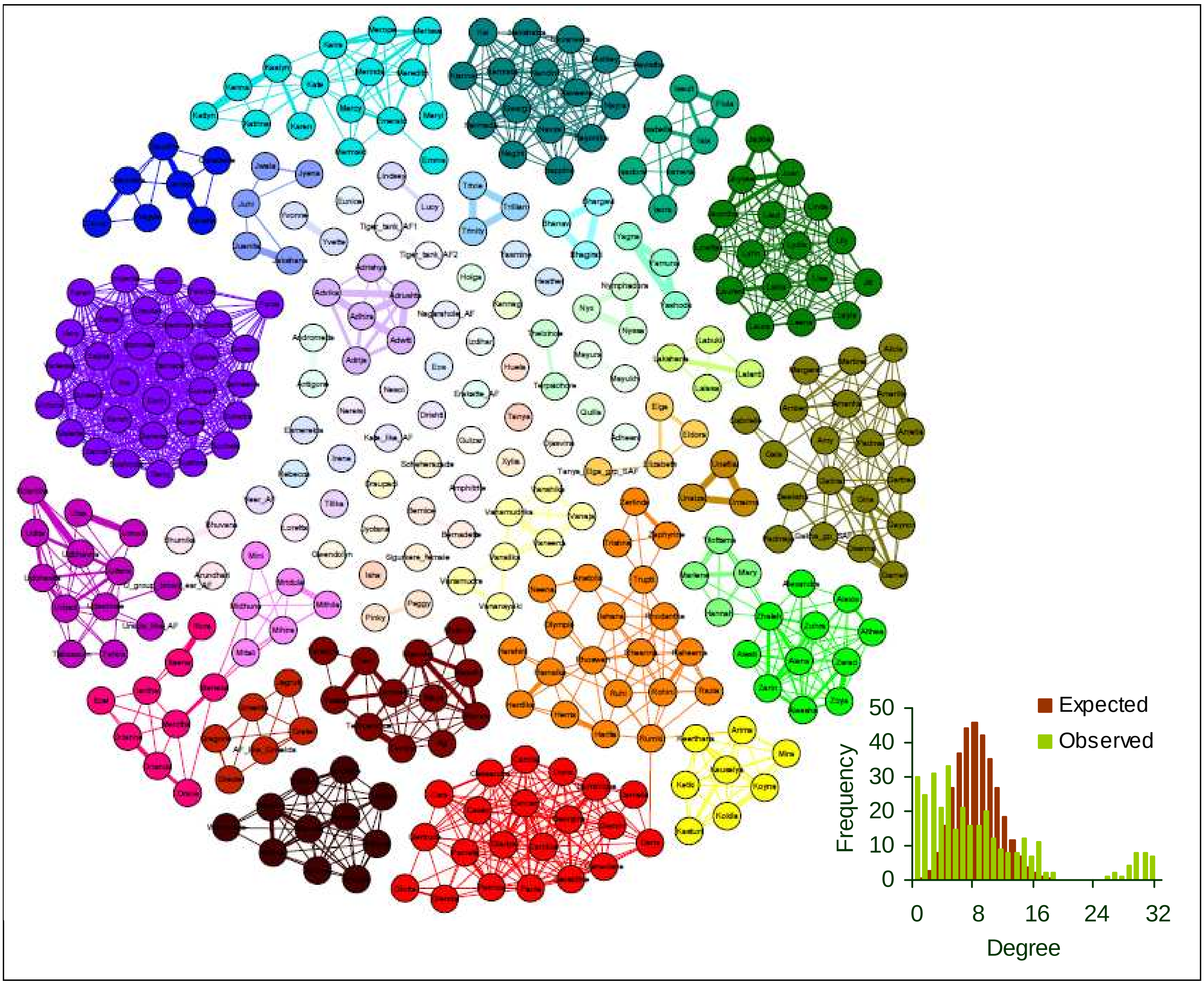


Figure 2. Social network based on the entire dataset of 330 females drawn using the Fruchterman Reingold layout (Fruchterman and Reingold 1991) in Gephi. Each node here is a female and the edges between the nodes indicate nonzero AI between females (edge thickness is proportional to AI). Nodes are coloured based on modularity classes and we refer to nodes of the same colour as a clan. The expected (Poisson) and observed degree distributions based on this social network are shown at the bottom right. The average degree was 8.32 based on this network, which includes individuals seen only once; when such individuals were removed, the average degree was 9.55 (274 individuals). Most of the solitary nodes towards the centre are females that were seen only once or a few times. The small number of connections across clans arose from seven sightings during the five year study period. Four of these were due to associations of Rumki (orange) with Arima (yellow), and later, with Dana (red) when the former had a very small calf that could not keep pace with the group, and the latter also had calves. Olympia's clan (that Rumki belonged to) was seen a total of 164 times, Kasturi's clan (yellow) was seen 436 times, and

Patricia’s clan (red) was seen 688 times. The other connections between clans were between Tilottama’s clan (light green; seen 76 times) and Alexandra’s clan (bright green; seen 48 times), and between Menaka’s clan (dark rose; seen 73 times) and Mridula’s clan (light pink; seen 70 times).

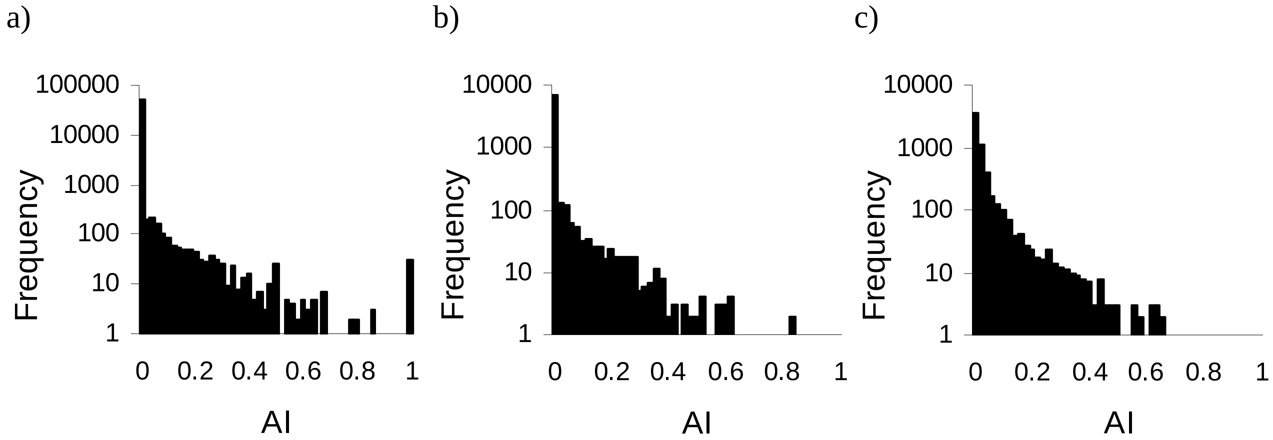


Figure 3. AI distributions based on a) the entire data, b) only females sighted at least 20 times, and c) only females sighted at least 20 times but based on the Kabini 500-m dataset. The relatively high frequency of AI=1 in a) is because of small number of sightings of some individuals, and this disappears in the other graphs.

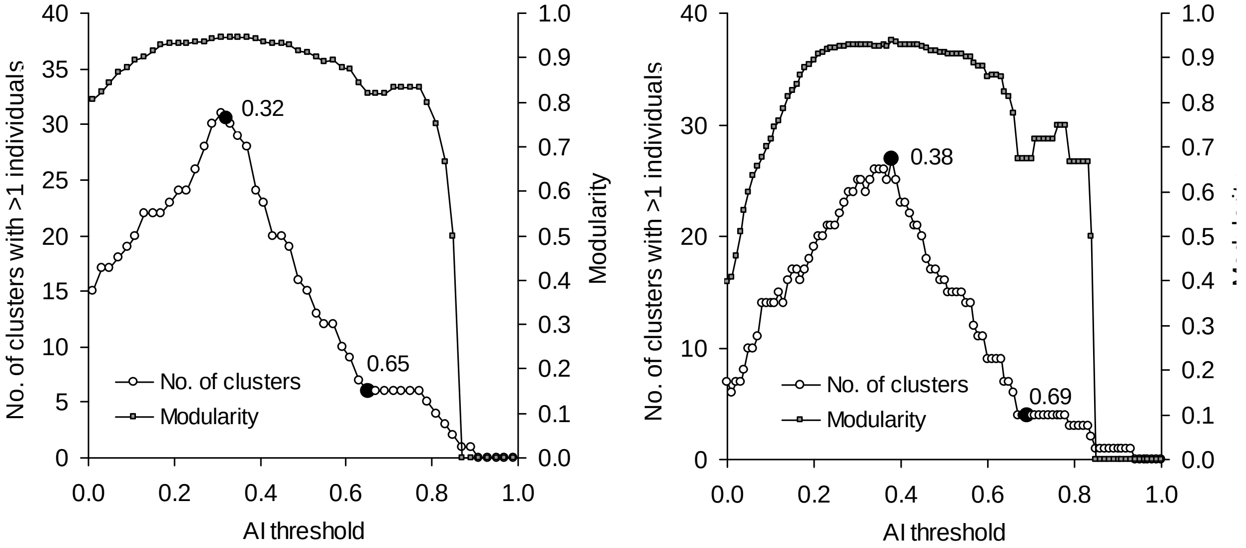
Table 2. Average group size (number of females), AI statistics, and network statistics for different elephant populations. Statistics for the Uda Walawe and Samburu populations are reproduced from de Silva and Wittemyer (2012) and the ones with asterisks were calculated from network files (of de Silva and Wittemyer 2012) kindly provided by Shermin de Silva and George Wittemyer. Statistics for the Lopé forest elephant population are reproduced from Schuttler *et al.* (2014). Statistics such as the degree and density might be underestimates in Lopé because the number of times individuals were sighted was very small (network statistics based on individuals sighted at least twice) and there was a significant correlation between the number of sightings and the number of associates (Schuttler *et al.* 2014). The small average group size is, however, in keeping with that found in forest elephants in Dzanga Bai (average female group size including dependants: 2.7, SD=1.3) in a long-term study (Turkalo *et al.* 2013). The average group size for Kabini ≥20 sightings is the average of group sizes of only those sightings in which all the females were seen at least 20 times (this is shown for the sake of completeness). Significant differences in metrics based on the Welch's two-sample test are shown using superscripted alphabets (a<b<c), with α set to 0.0017 based on a flat Bonferroni correction for 29 tests.

Population	Average group size (SD)	Percentage of non-zero AI values	Kurtosis of AI	Average degree (SD)	Average clustering coefficient (SD)	Average distance weighted reach (SD)	Average path length (SD)	Modularity	Density
Kabini	2.38 (1.83)^b	2.5	315.42	8.32 (8.15)	0.87 (0.165)	12.45 (9.14)	2.17 (1.433)	0.936	0.025
Kabini ≥20 sightings	2.35 (1.84)^b	10.8	67.97	13.34 (9.95)	0.95 (0.082)	15.87 (9.85)	1.60 (1.160)	0.803	0.108
Kabini 500-m, ≥20 sightings	3.16 (3.14)^c	69.4	37.71	74.95 (19.50)^b	0.81 (0.056)^b	92.46 (9.75)^b	1.31 (0.463)^b	0.398	0.694
Uda Walawe	3.07 (2.34)^c	20.8	10.35	22.53 (11.85)^a	0.63 (0.13)^a	59.46 (9.04)^a	* 2.07 (0.740)^c	* 0.701	* 0.217
Samburu	5.03 (4.61)^d	82.8	27.59	88.87 (16.00)^c	0.88 (0.04)^c	99.94 (7.96)^c	* 1.18 (0.388)^a	* 0.474	* 0.815
Lopé	1.48 (0.80)^a	1.4	-	2.06	0.86	-	2.157	-	0.033

Comparison of association networks across populations

The association network based on the original Kabini data was highly disconnected, unlike female social networks in the previously studied African savannah elephant and Uda Walawe Asian elephant populations (de Silva and Wittemyer 2012, Figure 1, first column), but more connected than the network in the Lopé African forest elephant population (Schuttler *et al*. 2014). However, since different criteria had been used for grouping these networks, we compared the Kabini 500-m network with the Uda Walawe and Samburu networks that had also been based on a 500-m distance cutoff, and the original Kabini network with the Amboseli network (in which associations had been recorded somewhat similarly, see Archie *et al*. 2006). Visual comparison showed the Kabini 500-m networks to be intermediate in connectedness between the Samburu and Uda Walawe networks (Figure 1). This was supported statistically, with the average degree (74.95), average distance-weighted reach (92.46), and clustering coefficient (0.81) in the Kabini 500-m network being significantly smaller than those in Samburu (Welch's two-sample test: average degree: U=5.772, df=208.3, P<0.001, average distance-weighted reach: U=6.216, df=207.9, P<0.001, clustering coefficient: U=10.636, df=195.3, P<0.001), but significantly larger than those in Uda Walawe (Welch's two-sample test: average degree: U=23.862, df=179.3, P<0.001, average distance-weighted reach: U=25.687, df=211.7, P<0.001, clustering coefficient: U=13.068, df=140.2, P<0.001; Table 2). The average path length in the Kabini 500-m network was also intermediate, being larger than that in Samburu (Welch's two-sample test: U=16.573, df=11452.6, P<0.001) and smaller than that in Uda Walawe (U=64.999, df=9038.0, P<0.001). Visual comparison of networks based on our original data with the Amboseli networks showed a more connected network in the Amboseli population with no AI cutoff, but similar networks in Kabini and Amboseli at AI cutoffs of 5% and 10% (Figure 1).

The original Kabini network did not change substantially when an AI cutoff of 0.05 was used, unlike networks from all the other datasets (Figure 1). The Kabini 500-m network changed dramatically at an AI cutoff of 0.05 like the Samburu network. However, the network structure curve of the Kabini 500-m dataset was roughly similar in shape to that obtained from the Uda Walawe population previously rather than the Samburu population (de Silva and Wittemyer 2012). It differed from the Uda Walawe network structure curve though in showing two points of significant slope change (at AI threshold values of 0.38 and 0.69, Figure 4) rather than a single point of significant slope change. The AI distribution based on the Kabini 500-m dataset (Figure 3c) bore a greater visual similarity to that of Uda Walawe than to that of Samburu, as high AI values were absent (see de Silva and Wittemyer 2012) and this similarity in AI distribution could have given rise to the similarity in network structure curves. The average AI was, however, significantly smaller in Uda Walawe (0.019) compared to that in Kabini 500-m dataset (0.034; Welch's two-sample test: *U*=11.195, *df*=11295.3, *P*<0.001), which was in turn significantly smaller than that in Samburu (0.049; Welch's two-sample test: *U*=8.209, *df*=9544.9, *P*<0.001). However, the percentage of non-zero AI values was much higher in the Kabini 500-m dataset than in Uda Walawe (Table 2). The kurtosis of the Kabini 500-m dataset was higher than those of both Samburu and Uda Walawe (Table 2).


a) Original data

b) 500-m cutoff

Figure 4. Network structure curve (of females seen at least 20 times) for a) the original data and b) data based on a 500-m distance cutoff, showing two points of slope change based on window of 0.3 (*P*<0.001 for AI threshold of 0.32 and *P*=0.006 for AI threshold of 0.65, points of slope change were 0.33 and 0.665 based on a window of 0.2; *P*=0.001 for AI threshold of 0.38 and *P*=0.012 for AI threshold of 0.69, *P*=0.082 for the AI threshold of 0.69 based on the 0.2 window).

The Louvain clustering carried out on the Kabini 500-m, Uda Walawe, and Samburu datasets showed two levels of clustering in the first two datasets and three levels of clustering in the third dataset (although Uda Walawe sometimes also showed three levels of clustering and Samburu, two, see Supplementary Material 6). The numbers of communities after the first round of clustering were 20, 16, and 24 in the Kabini 500-m, Uda Walawe, and Samburu, datasets, respectively, and the numbers of communities after the second round of clustering were 7, 9, and 9, respectively. Eight communities were detected after the third round of clustering in Samburu. In the Kabini 500-m dataset, five of the seven eventual communities changed from the first to the second rounds of clustering, while the other two remained compositionally the same from the first level to the second level. The numbers of second-level communities that changed in composition from the first to the second rounds of clustering were four out of nine in Uda Walawe, and seven out of nine in Samburu. Although the community sizes at different levels of clustering had remained the same in the original Kabini dataset, there were small differences in the number of communities and community sizes/composition in the Kabini 500-m, Uda Walawe, and Samburu datasets, upon repeating the same analysis multiple times (see Supplementary Material 6). As in the original Kabini dataset, the communities formed after the second clustering level were larger than those formed after the first clustering level, although this was not statistically significant in the Uda Walawe dataset (Mann-Whitney U tests: Kabini 500-m: U=25.5, Z_{adj}=-2.480, P=0.013; Uda Walawe: U=39.5, Z_{adj}=-1.856, P=0.063; Samburu: U=15.0, Z_{adj}=-3.808, P<0.001). Interestingly, community sizes at a particular clustering level were not different across populations (average ± SD after the first clustering level: Kabini 500-m: 5.45 ± 3.05, Uda Walawe: 6.56 ± 4.87, Samburu: 4.58 ± 2.34, Kruskal-Wallis test: $H_{2,69}$=0.380, P=0.827; average ± SD after the second clustering level: Kabini 500-m: 15.57 ± 9.74, Uda Walawe: 11.67 ± 7.47, Samburu: 12.22 ± 7.60, Kruskal-Wallis test: $H_{2,25}$=0.594, P=0.743; Figure 5; Mann-Whitney U tests, Kruskal-Wallis test, and test for homogeneity of slopes below carried out using Statistica 8, Weiß 2007). There was a correlation between second-level community sizes and the number of first-level communities within second-level communities (Figure 6), and a test for homogeneity of slopes showed no difference in slopes across the three populations (Multiple R^2=0.765, P<0.001, Effect of population: F[2,19]=0.502, P=0.613; Effect of the number of first level communities: F[1,19]=52.608, P<0.001).

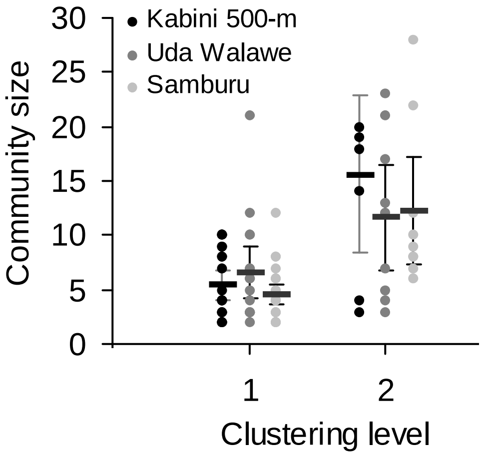


Figure 5. Community sizes after the first and second levels of clustering using the Louvain algorithm, based on the Kabini 500-m, Uda Walawe, and Samburu datasets. Communities after the second level of clustering that did not change in composition after the first level are also included in the second level. Means and 95% CI (1.96 SE) are also shown.

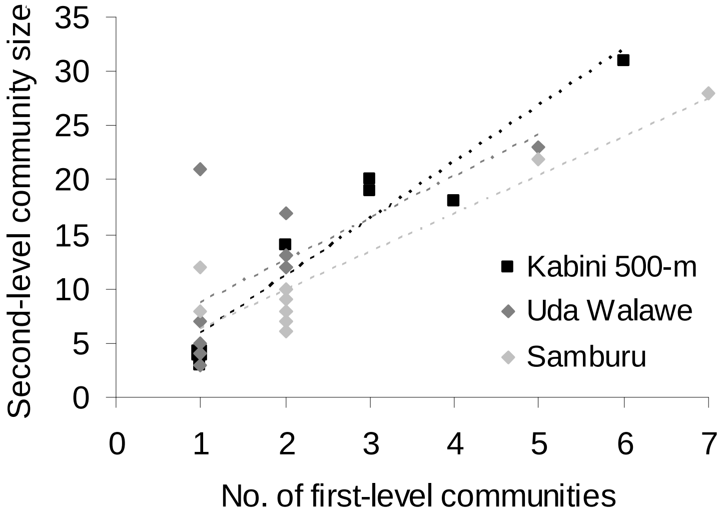


Figure 6. Sizes of second-level communities composed of varying numbers of first-level communities in the Kabini 500-m, Uda Walawe, and Samburu datasets. Equations of the trendlines (in the same colours as the data points of the respective populations) for the three populations are: Kabini 500-m: y=5.227x+0.636, R^2=0.904, Uda Walawe: y=3.861x+4.803, R^2=0.453, Samburu: y=3.521x+2.833, R^2=0.859.

Cluster analysis and cumulative bifurcation curve in the Kabini population

The cumulative bifurcation curve based on average linkage clustering (dendrogram in Supplementary Material 7) showed one point of significant slope change at linkage distance 0.32 (Wilcoxon rank sum test: rank sum=121.5, Z=-3.805, P<0.001, 0.3 window) for both the 0.2 and 0.3 windows. A second knot was seen at linkage distance of 0.62 only based on the 0.2 window (Wilcoxon rank sum test: rank sum=57.5, P=0.010, 0.2 window) (Figure 7a). The curve was concave-up, indicating a smaller number of linkages at small linkage distances (tight associations) than at large linkage distances (loose associations). A similar bifurcation curve was obtained from the Kabini 500-m dataset also (Figure 7b).

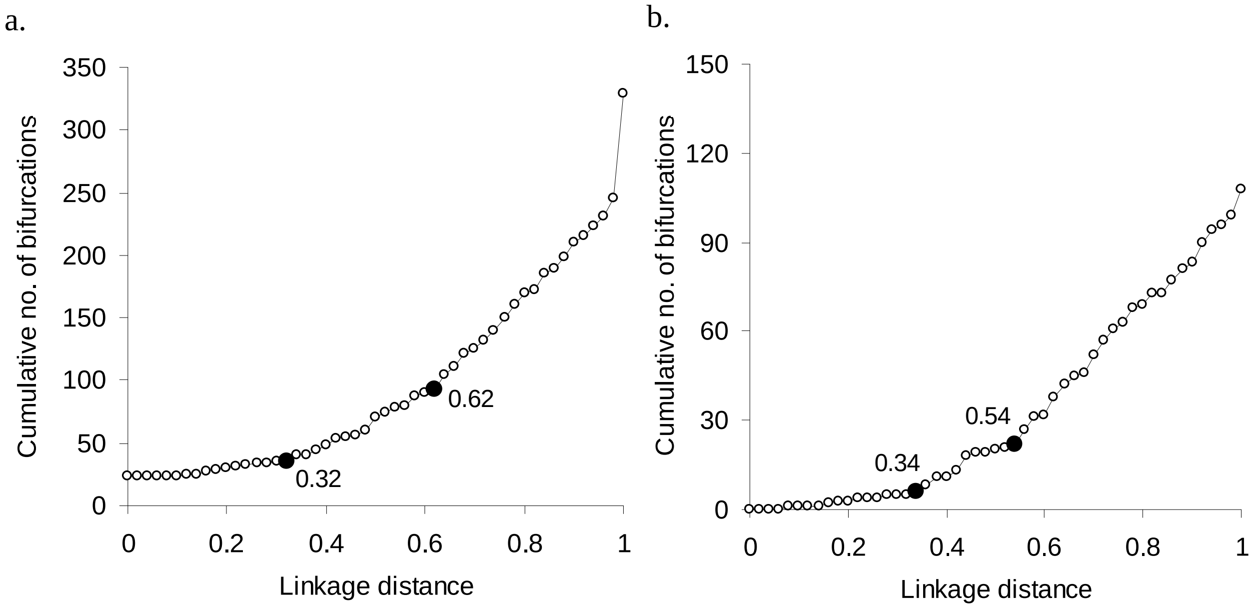


Figure 7. a. Cumulative bifurcation curve based on the original Kabini data showing knots (knot at linkage distance of 0.32 based on 0.3 and 0.2 windows and knot at linkage distance of 0.62 based on only the 0.2 window). A similar graph based on only females seen at least 20 times showed knots at 0.36 and 0.62, and 0.36 and 0.56 based on 0.2 and 0.3 windows, respectively. b. Cumulative bifurcation curve based on the Kabini 500-m dataset showing knots based on a 0.3 window (the 0.34 knot based on a 0.2 window had a P value of 0.067 and a knot at 0.56 was seen).

Observed group sizes and the effect of group size on AI and network statistics in random networks

The average group size in the Kabini population was small, with 2.38 females per group (Table 2, median=2) and the group size distribution was skewed to the right (Figure 8). A comparison of group sizes across populations showed Lopé to have a significantly smaller average group size than that in Kabini, the Kabini 500-m dataset and Uda Walawe to have similar group sizes, and Samburu to have a significantly larger group size than the Kabini 500-m and Uda Walawe datasets (Welch’s two-sample tests, Table 2).

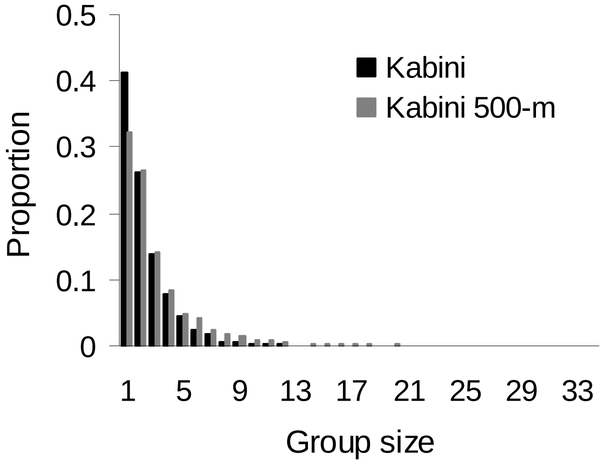


Figure 8. Group size distributions in the original Kabini population and in the Kabini 500-m dataset. The absolute frequencies are shown in Supplementary Material 8.

As mentioned above (Methods), we created random datasets to examine the effect of group size on AI and network statistics. With the exception of some values at very small group sizes, the three different beta distributions (α=1, β=9.5; α=1, β=7; α=2, β=9) of group sizes did not significantly change the expected value of AI or network statistic considered under random association (Figure 9). Under all three beta distributions of group sizes, the average expected AI increased linearly with increasing average group size, the average degree and average clustering coefficient increased and plateaued with increasing average group size, and kurtosis of AI, and average path length decreased with increasing average group size (Figure 9). The higher average AI in Samburu compared to the Kabini 500-m dataset (see *Comparison of association networks across populations* above) was an effect of group size, with the average AIs being similar when average group sizes were taken into account. The observed average AI in both Samburu and Kabini 500-m datasets were larger than the expected average AI for the corresponding average group sizes to the same extent ([*E*-*O*]/*E*=-0.667, interval: -0.578 to -0.756 for Kabini 500-m, [*E*-*O*]/*E*=-0.626, interval: -0.522 to -0.730 for Samburu). The higher average AI in the Kabini 500-m data compared to that in Uda Walawe remained after accounting for the effect of average group size ([*E*-*O*]/*E*=-0.014, interval: 0.085 to -0.113 for Uda Walawe). Although kurtosis does not have an error associated with it for a particular dataset, the higher kurtosis of AI in the Kabini 500-m dataset compared to Samburu and Uda Walawe did not seem to be an effect of smaller average group size visually. The smaller average degree in the Kabini 500-m dataset (75) compared to Samburu (89) could be explained as an effect of group size differences in the two populations as the observed average degrees in both these datasets were smaller than the expected average degrees for the corresponding average group sizes to the same extent ([*E*-*O*]/*E*=0.111, interval: 0.154-0.067 for Kabini 500-m cutoff, [*E*-*O*]/*E*=0.092, interval: 0.122-0.061 for Samburu). On the other hand, the smaller average degree in Uda Walawe compared to the Kabini 500-m cutoff dataset was again not simply a result of average group sizes as the group sizes in these two populations were not significantly different from each other (see above; [*E*-*O*]/*E*=0.722, interval: 0.750-0.694 for Uda Walawe). The higher average path length in the Kabini 500-m cutoff network than in Samburu (Table 2) could also be explained by differences in average group size (Supplementary Material 9). We had previously found the clustering coefficient in the Kabini 500-m cutoff network to be significantly smaller than that in Samburu (see above), but the former was 5.5% smaller than expected for a random network of the same average group size while the latter was 11% smaller than expected for its average group size. Therefore, corrected for group size, the Kabini 500-m dataset would have a significantly higher clustering coefficient than the Samburu population, although this difference was small (Supplementary Material 9).

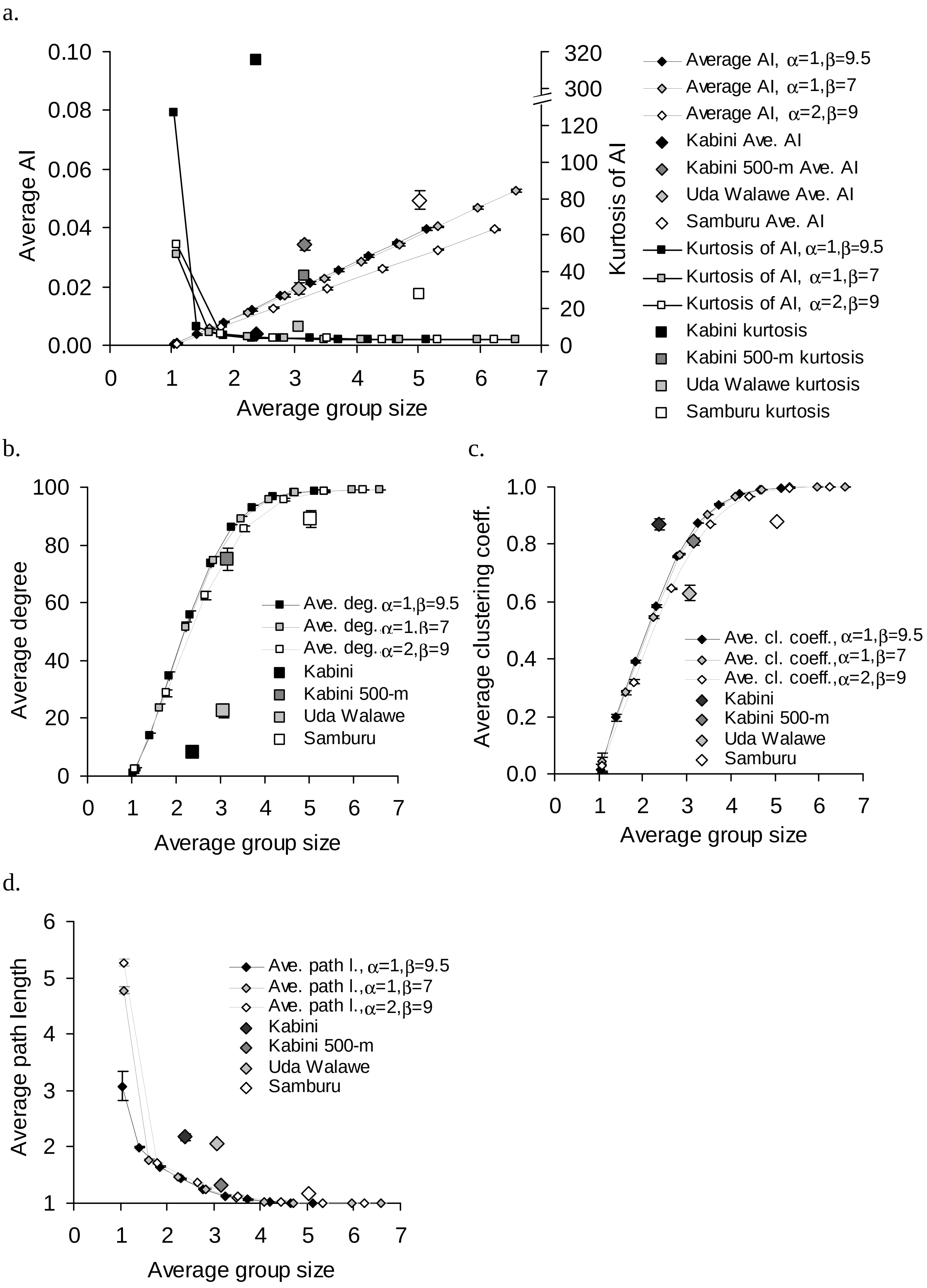


Figure 9. AI and network statistics based on 100 random datasets of 100 individuals each, under three different beta distributions (*α*=1, *β*=9.5; *α*=1, *β*=7; *α*=2, *β*=9) of group sizes,

and the corresponding observed values in different populations. a. Average AI and kurtosis of AI, b. average degree of individuals, c. average clustering coefficient, and d. average path length, for different average group sizes. All the error bars are 1.96 SE.

Discussion

Social structure in the Kabini population

Based on the first quantitative data on social structure of female Asian elephants from India, we found highly non-random associations between females, with the association network being clearly demarcated into communities that we call clans. That there were only seven associations between clans during over five years suggests that the clan is the most inclusive level of meaningful social structure in the Kabini population. Using the Louvain method of clustering, we found up to three hierarchical levels of clustering. However, there was variability in clan structure, with 38% of the clans seen over 40 times showing a single level of clustering, 56% showing two levels of clustering, and a single clan showing three levels. Clans with a single level of clustering were smaller than those with more than one level. It is not clear whether the clans with a single level of clustering represent those that have undergone recent permanent fission, whether the single level arose from demographic factors (see *Implications for Asian elephant social structure* section below), or whether it arose from clans not being fully identified. While the last is possible, it is not very likely as we used a 40-sighting cutoff for clans (as we had found, based on clans sighted over 150 times, that 95% of the clan members were sighted on average within the first 40 sightings of the clan and 92% within the first 30 sightings). However, given small group sizes, a large number of sightings may be required to uncover all the associations. It would be interesting to examine the attributes, other than clan size, of clans showing different levels of hierarchical clustering in order to understand the differences in clan structure. In keeping with the highly modular social network, only a small fraction of AI values were non-zero because of the lack of between-clan associations, and the AI distribution was highly skewed. The clustering coefficient was high because of connections within clans.

Comparison of social structure across populations and the role of group size

Asian and African savannah elephants were initially thought to share largely similar social organisations (Eltringham 1982, Sukumar 1989, 2003). Subsequently, they were found to differ in their social structure (de Silva and Wittemyer 2012), with larger groups and stronger associations within and across groups in the African savannah elephant. Indeed, we also found from our study that the Samburu social network was more connected than the Asian elephant networks (Uda Walawe and Kabini 500-m). The Kabini 500-m network was intermediate in network statistics, such as average degree, average distance-weighted reach, clustering coefficient, and path length, compared to those of Samburu (which had significantly higher values of these statistics, except for path length which was lower) and Uda Walawe. The network structure curve and cumulative bifurcation curve from the Kabini 500-m network were more similar to those based on the Uda Walawe network compared to those based on the Samburu network (see de Silva and Wittemyer 2012). The cumulative bifurcation curve was concave-up, indicating a smaller number of linkages at small linkage distances (tight associations) than at large linkage distances (loose associations). Although the average AI from the Kabini 500-m dataset was significantly larger than that from the Uda Walawe dataset, the AI distributions were also more similar to each other than to the AI distribution from the Samburu dataset. However, contrary to previous finding that kurtosis was higher in African savannah than in Asian elephants (de Silva and Wittemyer 2012), we found that the kurtosis of the Kabini 500-m dataset was higher than those of both Samburu and Uda Walawe populations (Table 2). This difference was seen despite the higher absolute values of AIs in Samburu compared to Kabini. Since kurtosis measures the heaviness of the tail compared to the normal distribution, this result reflects the difference between the average AI and AIs in the tail of the distribution, and not the latter alone. Visual comparison of the original Kabini dataset's network with the Amboseli (in which associations had been recorded somewhat similarly, see Archie *et al*. 2006) network showed a more connected network in the Amboseli population with no AI cutoff, but similar networks in Kabini and Amboseli at AI cutoffs of 5% and 10% (Figure 1). However, in the absence of access to the Amboseli network data (of Archie and Chiyo 2012), we were not able to make any further comparisons.

Despite the above differences between the Samburu African savannah elephant and Asian elephant populations, we found through Louvain clustering that there was hierarchical structuring within social networks in the Kabini (Kabini 500-m dataset), Uda Walawe, and Samburu populations. Since the cumulative bifurcation curve combines data from across the clustering dendrogram, variation across social units in AIs and unequal tiers across social units do not allow for hierarchical structure to be detected (also see de Silva and Wittemyer

2012), which the Louvain clustering algorithm can recover. The number of communities after hierarchical rounds of clustering were similar across populations. Although Samburu often showed a third round of clustering (Uda Walawe sometimes showed a third round and Kabini did not), this only resulted in a small change, with nine communities changing to eight after the third round. Community sizes were not significantly different across populations, both at the first and second level of hierarchical clustering. There was also no difference across populations in the relationship between second-level community sizes and the number of first-level communities within second-level communities (Figure 6). Results from these analyses suggest some basic similarities in social structure across elephant populations.

We show that some of the differences in social structure arose from differences in group sizes across populations. When we tried to account for the effect of group size on AI and network statistics by obtaining expected values using beta distributions of group sizes and random associations of individuals, and matching the expected and observed values for given group sizes, we found that the higher average AI and higher average degree in Samburu compared to Kabini (Kabini 500-m dataset) arose from different average group sizes in the two populations. Average path length was also similar when corrected for group size. The clustering coefficient in Samburu was smaller than expected (11%) at the corresponding group size compared to that in Kabini (Kabini 500-m dataset; 5.5% smaller than expected), but the extents to which they differed was not much. We used 1.96 SE as the 95% confidence intervals for comparisons of the observed and expected values. It is likely that the errors and, therefore, the overlaps in statistics between populations would actually be larger. Therefore, the tests are conservative, and it is possible that group size differences account for more of the social structure differences than we suggest.

Group size has previously been well-recognized as one of the most important factors affecting social behaviour, through competition for resources and increased travel costs (van Schaik *et al*. 1983, Milton 1984, Terborgh and Janson 1986, Dunbar 1988, van Schaik 1989, Wrangham *et al*. 1993, Chapman *et al*. 1995, Chapman and Chapman 2000, see Koenig 2002), and lowered predation risk (van Schaik 1983, 1989, van Schaik and van Noordwijk 1985, Terborgh and Janson 1986, Sterck *et al*. 1997). Ecological constraints may lead to smaller groups (for example, Jarman 1974, Wrangham 1980, Wrangham *et al*. 1993, Chapman *et al*. 1995, Janson and Goldsmith 1995), resulting in differences in group sizes and associations within species across populations (see Chapman and Rothman 2009). The difference in group sizes between the Samburu population and the two Asian elephant populations probably relate to differences in ecology, and more specifically to food resource distribution. Female associations in elephants are useful in cooperative offspring care (Gadgil and Nair 1984, Lee 1987, Lee and Moss 2011, Vidya 2014) and the acquisition and exchange of information (Mc Comb *et al*. 2001, 2011, Mutinda *et al*. 2011, Chiyo *et al*. 2012, Fishlock and Lee 2013), but could result in feeding competition depending on the habitat (also see Fernando and Lande 2000). Asian elephants typically inhabit moister, more forested habitat than African savannah elephants, and possibly face more challenges obtaining food. African forest elephants, which inhabit wetter and denser habitats, with ephemeral and patchily distributed resources (Blake 2002), than the Asian elephant on average, show even smaller group sizes (Turkalo *et al*. 2013, Schuttler *et al*. 2014, see Table 2). Social organisation in the African forest elephant is thought to be limited to nuclear family groups, although they may associate with a larger number of associates in forest clearings (Turkalo and Fay 1995, Fishlock and Lee 2013, Turkalo *et al*. 2013). The social network in the Lopé African forest elephant population (Schuttler *et al*. 2014) was highly disconnected compared to the association network based on the original Kabini data. Adult elephants rarely face predation except from humans, but lions occasionally prey on calves in Samburu (Wittemyer *et al*. 2005b) and tigers occasionally target calves in southern India (personal observation). Turkalo and Fay (1995) suggested that, apart from the patchy distribution of food, low predation by humans might explain the small group sizes of African forest elephants compared to African savannah elephants that have faced high poaching pressure. Elephants in Sri Lanka have historically suffered drastic declines in population size from human depredation, but currently, the leopard is the top predator in Sri Lanka and does not pose a threat even to calves (Fernando and Lande 2000), unlike the tiger in southern India. Despite differences in predation, there was no difference in average group size between Kabini (Kabini 500-m dataset) and Uda Walawe.

As pointed out by several authors (Strier 1994, Kinzey and Cunningham 1994, Struhsaker and Leland 1979, Aureli *et al*. 2008), flexible social grouping is probably more common amongst vertebrates than previously believed, and there is a continuum of different extents of fission-fusion dynamics (Aureli *et al*. 2008), which allow for a balancing of the costs and benefits of group-living in various species (Kummer 1971, Milton 1984, Goodall 1986, Nishida and Hiraiwa-Hasegawa 1987, Stammbach 1987, Dunbar 1988, Symington 1988, 1990, van Schaik 1989, Whitehead *et al*. 1991, Chapman *et al*. 1995, Boesch and Boesch-Achermann 2000, Connor *et al*. 2000, Rubenstein and Hack 2004, Wittemyer *et al*. 2005a, Smith *et al*. 2008, Asensio *et al*. 2009, Kerth *et al*. 2011, Parra *et al*. 2011, Baden *et al*. 2016). Both Asian and African savannah elephant females show high fission-fusion dynamics but there are differences in AI and network statistics and cumulative bifurcation curves between populations. If they had to be compared to the modal types of multilevel organisations (see van Schaik 1999, Grüter and Zinner 2004) based on these analyses, the social structure of the African savannah elephant would correspond to the flexible nested society (according to Grüter and Zinner 2004) or lie between the strict nested and flexible nested multilevel societies, while that of the Asian elephant would correspond to the classical fission-fusion society (with the lower level flexible and the higher level stable) or lie between the flexible nested (with the lower level stable and the higher level flexible) and the classical fission-fusion society. Nestedness does not seem to be complete in the African savannah elephant since partial or whole core groups may associate together to form a larger unit, and single females have a choice of associating or not with their family group members (Moss and Lee 2011, Archie and Chiyo 2012). However, single females are very rarely seen in African savannah elephants (Moss and Lee 2011). African forest elephant social organisation has been previously compared to the individual-based fission-fusion society of chimpanzees (Schuttler *et al*. 2014). Although these would be the classifications based on AI, network statistics, and cumulative bifurcation curves, we find that there are underlying similarities in network structure between the African savannah and Asian elephant populations based on Louvain community detection. The differences observed seem to emanate from group size differences. The average size of first-level communities obtained from Louvain clustering is similar to the average group size in Samburu, while it is about twice the group size in Uda Walawe and Kabini (Kabini 500-m dataset). This allows for individuals of a first-level community to potentially be part of the same group, resulting in high AI values, and nestedness to be easily realised in Samburu. This also results in lower-level social units such as the family/bond group being stable units (see Wittemyer *et al*. 2005). On the other hand, when group sizes are restricted, only subsets of the first-level community can associate together, resulting in lower AIs, unstable lower-level social units, and a less-nested appearance, as in the Asian elephant populations. This would suggest that the multilevel social structure observed in the Asian elephant is a derived condition due to restricted group size (see 'Route A' of Aureli *et al*. 2008), compared to that observed in the African savannah elephant. It is also pertinent to point out that the smaller the group size, the longer the study period required to observe sufficient associations between individuals in order to interpret social structure in a species showing fission-fusion dynamics. Thus, it is very important to carry out long-term studies in such species. It is possible that the African forest elephant too may show some underlying community structure, although the number of observations required in that case would be even larger, given the small group size. It is interesting that the average first-level and second-level community sizes were not different across elephant populations, indicating that there might be something fundamental about these sizes. It is possible that demographic processes play a role in these community sizes (for example, Blumstein 2013, Schradin 2013, Maldonado-Chaparro *et al*. 2015). It has also been suggested that cognitive abilities may constrain the sizes of social groupings because knowledge of complex social relationships might be crucial for group-living (the 'social brain' hypothesis, Byrne and Whiten 1988, Dunbar 1992, 1998).

That group size and social structure are interlinked has been obvious (see Terborgh and Janson 1986). Grouping patterns allow for interaction opportunities, thus resulting in the social structure seen (van Schaik and van Hooff 1983, Terborgh and Janson 1986, Janson 1992, Bourke 1999, Aureli *et al*. 2008, Chapman and Rothman 2009). We show how social structures uncovered by traditional AI and network statistics in fission-fusion societies may differ primarily because of group size differences. Thus group size differences may mask underlying similarities in the social structures of related species showing fission-fusion dynamics, which can be uncovered by hierarchical community detection. Grüter and van Schaik (2010) have also pointed out that modular (nested multilevel) societies require ecological conditions that allow large groups to form, and found that both social factors such as bachelor threat and ecological factors (higher scramble competition in non-modular species) may have led to modular sociality in Asian colobines. Group sizes were shown to have an effect on network statistics in whales, which formed smaller groups when food resources were scarcer. However, they also found that the change in network statistics in times of food scarcity remained significant even after group sizes were accounted for (Foster *et al*. 2012).

Implications for Asian elephant social structure

Despite broad similarities, it appears that there are also some differences in Asian elephant social structure based on the limited detailed comparison between one Sri Lankan (Uda Walawe) and one southern Indian (Kabini 500-m dataset) populations. Network statistics corresponding to the number of associates of females (degree) and reach to other females were higher in the Kabini population (Kabini 500-m dataset) than in Uda Walawe. Thus the social network was more connected in Kabini (Kabini 500-m dataset; higher percentage of non-zero AI) compared to Uda Walawe and the average AI was higher in the former. Group sizes were not different between the two populations (Kabini 500-m dataset and Uda Walawe), therefore, these differences did not arise from group size differences. It is possible that the lower levels of cohesiveness in the Uda Walawe population arose from extensive historical disturbance in Sri Lanka, with thousands of elephants having been hunted and captured during the 1800s and early 1900s (see McKay 1973, Lorimer and Whatmore 2009), and the elephant population being decimated to only about 1500 individuals by the mid-1900s (see McKay 1973). By one estimate, at least 17,000 elephants were hunted, exported, or died in captivity during the 19th century, changing the behaviour and demographics of elephants on the island (see Lorimer and Whatmore 2009). The British hunted and captured elephants in southern India also, but it appears that the numbers caught were very small and there was no decline in population size, unlike the decline in Sri Lanka (Sanderson 1879, pp. 68-69). Moreover, the *kheddah* method used for capturing female elephants in southern India (including in part of our study area, Nagarahole National Park) resulted in the entire group being captured rather than isolated individuals (Sanderson 1879, pp. 70-73; the pit method, in which single elephants fell into concealed pits, was also used for a short period, especially by the Mysore Maharaja, but given up after his death according to Sanderson). Therefore, female social organisation in southern India was probably not as impacted as that in Sri Lanka. Although unrelated females from decimated surviving groups are known to associate together to form social groups in elephant populations subject to anthropogenic mortality (Eltringham 1977, Eltringham and Malpas 1980, Nyakaana *et al*. 2001, Charif *et al*. 2005, Vidya *et al*. 2007, Wittemyer *et al*. 2009), breakdown of social structure itself may or may not change group size. Smaller family groups than normal had been found in the highly poached African savannah elephant populations in Tsavo East, Queen Elizabeth, and Mikumi National Parks (see Nyakaana *et al*. 2001, Gobush *et al*. 2009), and heavy poaching was also thought to have reduced associations and affected social network structure in Lopé, Central Africa (Schuttler *et al*. 2014). Decimation of the population may increase group size where the habitat allows it, but if there is a resource-based constraint on group size, network cohesiveness is likely to decrease (because of associates being killed) while the group size may not change. We think that this might be the likely scenario in Uda Walawe, in which the average group size is not different from that of the Kabini population (Kabini 500-m dataset), but the average degree, average clustering coefficient, and density are lower (Table 2). Recent anthropogenic disturbance appears to be similar in Kabini and Uda Walawe. In both places, dams were built in the late 1960s-early 1970s, submerging forest land and creating reservoirs that elephants now use.

As mentioned previously, associations in the Uda Walawe population had been defined using a 500-m cutoff (de Silva *et al*. 2011, de Silva and Wittemyer 2012), which is why we used the Kabini 500-m dataset for an appropriate comparison. Apart from the distance cutoff, groups that shared common females during a day were combined into a single sighting, which would increase group size and association network connectivity. If a 50-100 m cutoff were used and groups with shared sightings were not combined, the Uda Walawe network would presumably be even less cohesive than it currently is, and consist of small communities of females. Fernando and Lande (2000), in their study in Ruhuna National Park, close to Uda Walawe in southeastern Sri Lanka, had used a 100-m cutoff to identify groups during visual observations (as opposed to using radio-telemetry) and suggested that female social organisation was limited to the family level based on family sizes of 10-20 individuals in African savannah elephants mentioned by Wilson (1975). We suggest that the most inclusive level of female social structure in Asian elephants should be called the clan. The numbers of females in the most inclusive level in the Kabini population were similar to those in Samburu (Table 1), reinforcing the ‘clan’ rather than the ‘family’ nomenclature. We also found structuring within clans, although this is not easy to discern because of groups being small.

A common property of clans in the Asian elephant seems to be the lack of association with other clans, despite proximity. Fernando and Lande (2000) had also found that their study groups, which were smaller in size than the Kabini clans on average (mean number of females: 7.75 in Ruhuna, 13.31 in Kabini based on clans sighted at least 40 times), did not associate with other groups that shared their home range. It is not clear whether the smaller ‘clan’-size in Ruhuna stemmed from the small number of observations, thereby missing other associates, or from demographic factors. There were some small clans in Kabini too, arising from deaths of females and/or a series of male offspring, which do not contribute to clan size. Although most of the single females in Figure 2 are from clans whose ranges are probably at the periphery of our study area, such that we have not yet sighted other females from those clans, there were a few clans that were sighted many times but continued to show a small number of females. The most notable of them included only two females and their dependant offspring (there were older male offspring that occasionally kept in contact), despite being sighted over 300 times. Although a clan of two might as well be called a family group, we prefer to retain the term clan for the most inclusive grouping because the clan seems to be the most stable unit and not the family group. Despite structure within larger clans, the extent of apparent nestedness is low because of limited group size, resulting in individual females associating with different females at different times in small groups. These small groups may be called family groups but, the compositions of these groups keep changing, while (and perhaps because) the sizes remain relatively constant. Therefore, these family groups not stable units, unlike those seen in the African savannah elephant. AI values between females were, therefore, low, as also observed by Fernando and Lande (2000). Since family groups are not the basic unit of association the importance of the matriarch in Asian elephant society is also questionable (de Silva *et al*. 2011). We do not find the nested multitiered organisation suggested by Sukumar (1989, 2003), with ‘joint-family groups’ (which correspond to the family groups of most other authors; a single female and her offspring were called a family group under Sukumar’s classification) and bond groups within clans. The clans of Sukumar (1989) seem to have been based on sharing a common area, as suggested initially by Moss and Poole (1983). We find that different clans use the same general area but do not interact positively. Daniel *et al*. (1987) and Baskaran *et al*. (1995) had referred to females that showed coordinated movement as clans, but had not provided any further details or examined clan structure. Our clans seem to correspond to the ‘herds’ of McKay (1973), who studied elephants in southeastern Sri Lanka. McKay (1973) described fission-fusion between subunits of the herd, with a turnover of herd subunit composition. The herd was the most inclusive unit of female social grouping, and herds remained distinct from one another even when feeding in the same area, which is what we also find. Thus, female Asian elephant social structure in southeastern Sri Lanka and Kabini seem similar, although clan sizes may be smaller in the former. Herd sizes found by McKay (1973; 15-40 individuals) were larger than those found by Fernando and Lande (2000; 7-24 individuals) but smaller than those we found (inter-quartile range: 17-40, maximum: 83 individuals). McKay also seems to have used distance cutoffs of about 100 m because he describes part of a herd that is 150 m away as a different subunit. Although it is possible to find extended networks using a 500-m distance cutoff, we do not think that this is meaningful because of the behaviours observed in the field. Moreover, most of the association strengths of associations obtained by using the larger distance cutoff were low.

Based on our original data, only 1.1% of the AI values lay above a 10% AI cutoff. This was 4% in the original dataset with females seen at least 20 times. Although the percentage of non-zero AI values rose to 69% in the Kabini 500-m dataset (Table 2), the percentage of AI values above a 10% AI cutoff was low (7.8%) in this dataset also, resulting in similar network structure curves (Figure 4a versus 4b). Aggregating sightings over the day also inflates group size and does not reflect the actual competition faced by individuals while feeding within a group. It is interesting that our findings most closely match those from one of the first studies describing social structure in free-ranging Asian elephants (McKay 1973). We suspect that this is because McKay's (1973) study pre-dated detailed observational studies of social structure in the African savannah elephant, preventing any desire to compare social levels found in the Asian elephant to those of the African savannah elephant.

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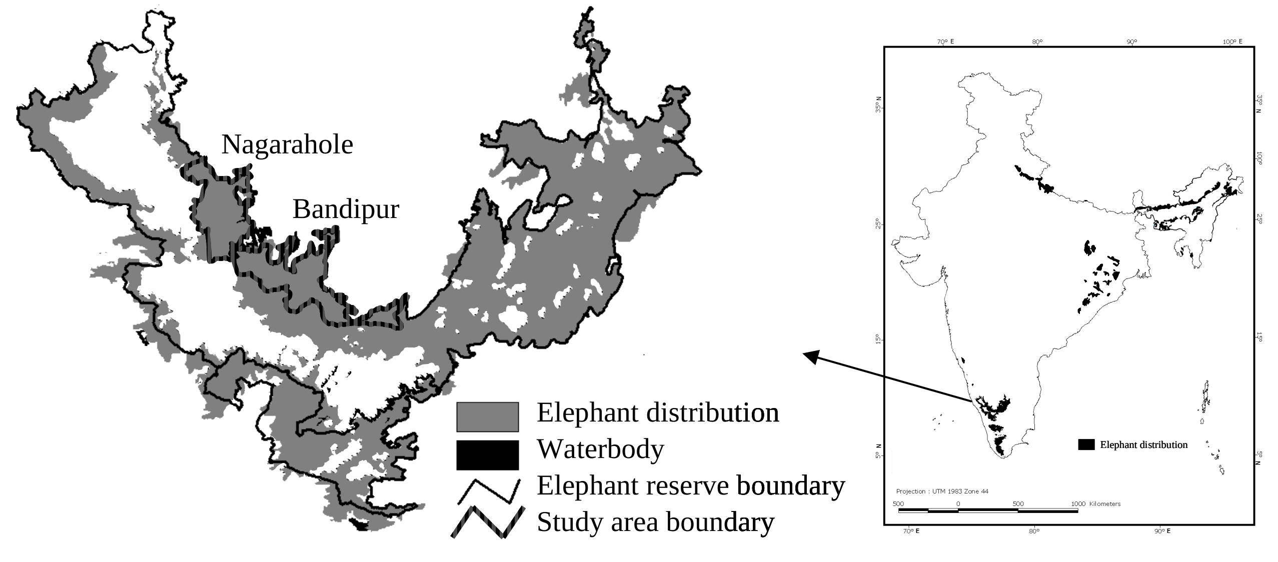
Supplementary Material

Supplementary Material 1. Map of the study area (Nagarahole and Bandipur protected area boundaries shown) and the larger Nilgiris-Eastern Ghats landscape, showing areas of elephant distribution, and elephant reserve boundaries. The northern elephant reserve is the Nilgiris-Eastern Ghats Reserve and the smaller, southern one is the Nilambur-Silent Valley Coimbatore Reserve. The landscape map is based on Vidya *et al*. (2005) and AERCC (1998). Inset: map of India with approximate elephant distribution shown in black (based on Vidya 2004).



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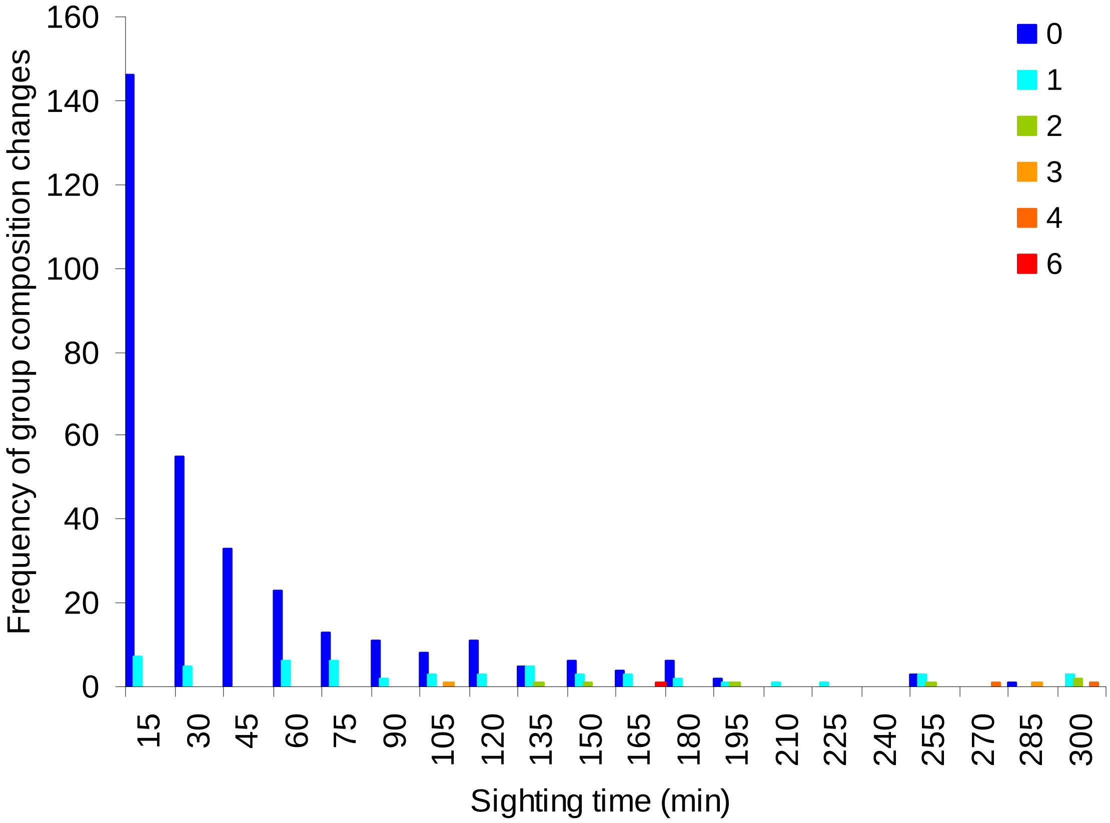
Supplementary Material 2. Change in group composition across time.

Based on elephant sightings from the year 2009, of female associations, in which all adult females were identified and data on the time of individuals joining or leaving a group were available, we plotted a frequency distribution of the number of changes in group composition seen at varying lengths of time (see Figure 1 below). We found that from 135-165 minutes, there were roughly as many groups that changed in composition as groups that did not change in composition and, therefore, used 150 minutes (2.5 hours) as the time cut off when a sighting would be considered an independent sighting.



Supplementary Material 2, Figure 1. Frequency of different numbers of group composition change events for female elephant groups seen for different lengths of time. Zero corresponds to groups that did not change in composition during the time they were observed.

Supplementary Material 3.

We tested for preferred associations by randomly permuting the association data following Bejder *et al*. (1998) and Whitehead (2008, pg. 127-128). Permutations were carried out in SOCPROG 2.4 (Whitehead 2009), retaining the total number of sightings of each individual and the original group sizes of sightings. A 15-day sampling period was chosen and groups were permuted within samples. As suggested by Whitehead (2008), we used the mean AI and proportion of non-zero AIs to detect short-term preferred associations, and the SD and CV of AIs and the SD of non-zero AIs to detect long-term preferred associations. The CV is thought to be a better statistic than SD for long-term preferences though (in the presence of short-term preferences, which may lower SD and the mean). Significantly lower (P<0.05) mean of real AIs than that of permuted AIs indicates short-term (within sampling-period) preferences in association and significantly higher (P>0.95) SD and CV of real AIs than those of permuted AIs indicate long-term (between sampling-period) preferences in association. It is, therefore, possible to find long-term preferences (indicated by significantly higher SD and CV of real AIs than permuted AIs) but no short-term preference (mean AIs of real and permuted data not different) and *vice versa* using the permutation test. A significantly lower proportion of non-zero AIs in the real data than in the permuted data indicates avoidance of some individuals by others in the short term. Permutations were carried out using 20,000 permutations, with 1,000 flips per permutation since the P values seemed to stabilize with these numbers of permutations (see Table 1 below).

We observed significantly lower mean AI in the real data compared to the permuted data, indicating short-term preferences in associations. There was also short-term avoidance as indicated by the significantly lower proportion of non-zero AIs in the real data compared to the permuted data. In addition, SD and CV of real AIs were significantly higher than those of permuted AIs, indicating long-term preferences (Supplementary Material 3, Table 1).

Supplementary Material 3, Table 1. *P* values from the permutation test, carried out on the entire original Kabini dataset, based on different numbers of permutations, using 1000 flips per permutation. Statistically significant values are marked in bold. The observed values are naturally the same, but are listed repeatedly for different numbers of permutations for ease of comparison.

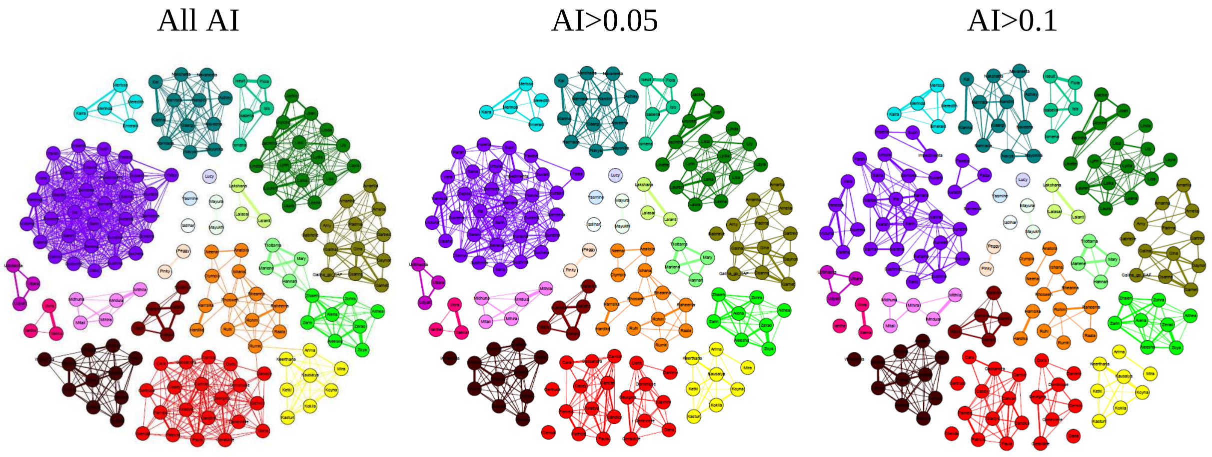
Number of permutations	Statistic	Observed value	Averaged random value	*P* value
5000	Mean AI	0.0057	0.0061	0.058
	SD of AI	0.0486	0.0349	**1.000**
	CV of AI	8.5751	5.7883	**1.000**
	Prop. of non-zero AI	0.0253	0.0862	**<0.001**
	Mean non-zero AI	0.2242	0.0743	1.000
	SD of non-zero AI	0.2110	0.1009	**1.000**
	CV of non-zero AI	0.9410	1.3534	<0.001
10000	Mean AI	0.0057	0.0063	**0.039**
	SD of AI	0.0486	0.0295	**1.000**
	CV of AI	8.5751	4.7217	**1.000**
	Prop. of non-zero AI	0.0253	0.1059	**<0.001**
	Mean non-zero AI	0.2242	0.0626	1.000
	SD of non-zero AI	0.2110	0.0735	**1.000**
	CV of non-zero AI	0.9410	1.1504	0.046
15000	Mean AI	0.0057	0.0063	**0.024**
	SD of AI	0.0486	0.0267	**1.000**
	CV of AI	8.5751	4.2442	**1.000**
	Prop. of non-zero AI	0.0253	0.1146	**<0.001**
	Mean non-zero AI	0.2242	0.0570	1.000
	SD of non-zero AI	0.2110	0.0607	**1.000**
	CV of non-zero AI	0.9410	1.0394	0.396

Number of permutations	Statistic	Observed value	Averaged random value	**P value**
20000	Mean AI	0.0057	0.0063	**0.031**
	SD of AI	0.0486	0.0279	**1.000**
	CV of AI	8.5751	4.4430	**1.000**
	Prop. of non-zero AI	0.0253	0.1103	**<0.001**
	Mean non-zero AI	0.2242	0.0592	1.000
	SD of non-zero AI	0.2110	0.0659	**1.000**
	CV of non-zero AI	0.9410	1.0862	0.224
30000	Mean AI	0.0057	0.0063	**0.008**
	SD of AI	0.0486	0.0264	**1.000**
	CV of AI	8.5751	4.2005	**1.000**
	Prop. of non-zero AI	0.0253	0.1153	**<0.001**
	Mean non-zero AI	0.2242	0.0562	1.000
	SD of non-zero AI	0.2110	0.0593	**1.000**
	CV of non-zero AI	0.9410	1.0292	0.469

References:

1. Bejder L, Fletcher D, Bräger S (1998) A method for testing association patterns of social animals. *Animal Behavior* 56: 719-725.
2. Whitehead H (2008) *Analyzing Animal Societies: Quantitative Methods for Vertebrate Social Analysis*. University of Chicago Press. 320pp.
3. Whitehead H (2009) SOCPROG programs: analyzing animal social structures. *Behavioral Ecology and Sociobiology* 63: 765-778.

Supplementary Material 4. Networks for the original Kabini data based on individuals sighted at least 10 times.

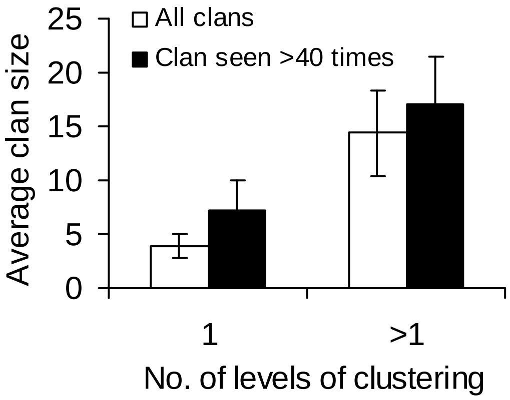


All AI

AI>0.05

AI>0.1

Supplementary Material 5. Average (±1.96 SE) clan size of clans that showed a single social level and more than one social levels, for all clans and clans seen more than 40 times. The median clan sizes (of all clans) of clans with a single social level and more than one social levels were 3 and 14.5, respectively. The median clan sizes of clans seen over 40 times, when clans had a single social level and more than one social levels were 7.5 and 16.5, respectively.



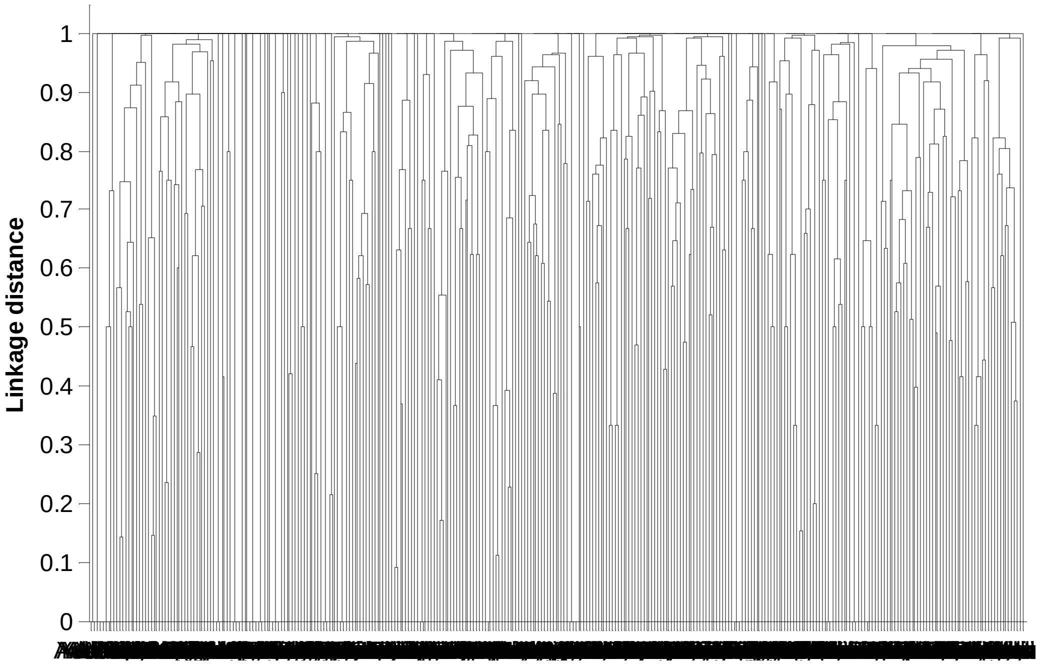
Supplementary Material 6. Louvain clustering results upon replication.

Community detection in the Kabini 500-m, Uda Walawe, and Samburu datasets did not always yield the same communities, unlike the case of the original Kabini dataset. In the Kabini 500-m dataset, the first-level communities remained the same (20 communities) when the analysis was carried out 11 times, and the second-level communities were the same ten out of 11 times. During one replicate, six instead of seven second-level communities were obtained (with one community of size 34 instead of two of sizes 3 and 31, respectively). Therefore, all the results shown in the main text are based on seven second-level communities.

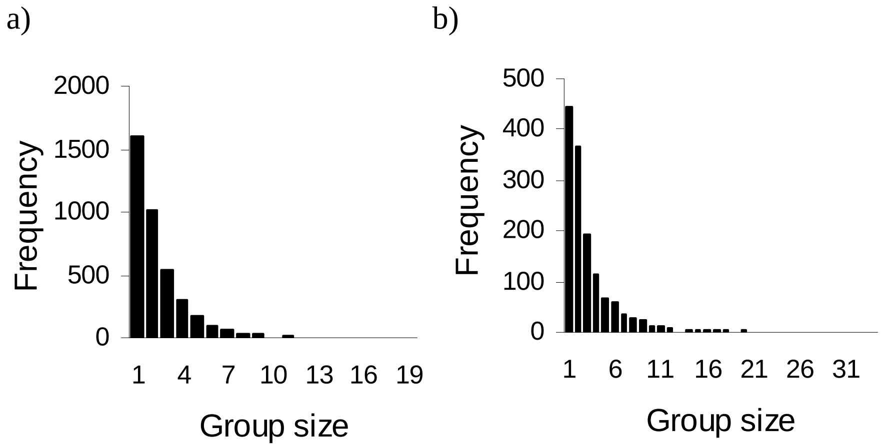
In the case of Uda Walawe, six replicates showed two levels of clustering and five showed three levels of clustering. At the first level of clustering, eight replicates showed 16 communities with the same community sizes across replicates, one showed 15 communities (with community size of 15 instead of 3 and 12), and two showed 17 communities (one replicate with community sizes of 4 and 17 instead of 21, and the other replicate with community sizes of 10 and 11 instead of 21). These first level community sizes did not seem to be dependent on the number of eventual clustering levels. At the second level of clustering, the five replicates that eventually had three clustering levels showed 10 communities each and the six replicates that had two clustering levels showed 8-9 communities each (four replicates with 9 and two with 8; community sizes of 17 and 6 were observed when there were 10 communities instead of a size of 23 when there were nine communities, and a community of size 20 was observed when there were eight communities rather than communities of 7 and 13 when there were nine communities). A third level of clustering in the five replicates with 10 communities in the second level reduced the number of communities to nine in the third level, with identical community sizes as the replicates that showed nine communities in the second level. Based on the majority from the replicates, the Louvain clustering results shown in the main text are based on two levels of clustering with 16 communities in the first round and 9 in the second round. Results shown in Table 1 are also based on this.

In the case of Samburu, seven replicates showed three levels of clustering and four replicates showed two levels of clustering. At the first level of clustering, nine replicates uncovered 24 communities and two uncovered 25 communities. The replicates with 24 communities showed two kinds of group compositions, with a community of size 8 instead of communities of 4 and 4, and communities of 3 and 6 instead of one of 9 (seven replicates with the former sizes and two with the latter sizes). The replicates with 25 communities had community sizes of 4 and 4 instead of 8, and 3 and 6 instead of 9. After the second round of clustering, 9 and 8 communities were found in five replicates each, while 7 communities were found in one replicate. There were three different community compositions in the replicates with 9 communities (one composition occurring three times and the other two, once each) and four different community compositions in the replicates with 8 communities, with slightly different community sizes. Of the seven replicates that showed three levels of clustering, five uncovered 8 communities and one each uncovered 6 and 7 communities, respectively. There were three different community compositions in the five replicates of 8 communities, one composition occurring in three replicates and the others in one each. Based on the majority from the replicates, the Louvain clustering results shown in the main text and Table 1 are based on three levels of clustering, with 24 communities in the first round, 9 communities in the second round (with the most frequent community composition), and 8 communities in the third round.

Supplementary Material 7. Average linkage dendrogram based on the original Kabini dataset. Names of the females at the bottom are not readable because of the large number of females (*N*=330).



Supplementary Material 8. Frequency distributions of group size based on a) the original Kabini dataset and b) the Kabini 500-m dataset.



Supplementary Material 9. Observed (± 95% CI) AI and network statistics, expected averages based on 100 random datasets of 100 individuals each, with three different beta distributions (α=1, β=9.5 for Kabini, α=1, β=7 for Uda Walawe, and α=2, β=9 for Samburu) of group sizes, sample sizes for the statistic under consideration, and proportional differences of the expected (E) and observed (O) statistics. The last column has an interval with (E - lower 95% CI of O)/E and (E - higher 95% CI of O)/E. Sample size was the number of pair-wise associations for AI, the number of females for degree, the number of females with degree>2 for clustering coefficient, and the number of paths, both direct and indirect, between females for path length.

Population	Ave. group size	Obs. ave. AI	Exp. ave. AI	*N*	(E-O)/E interval	
Kabini 500-m	3.16	0.034±0.0018	0.020	5886	-0.578	-0.756
Uda Walawe	3.07	0.019±0.0019	0.019	5460	0.085	-0.113
Samburu	5.03	0.049±0.0032	0.030	5995	-0.522	-0.730
Population	Ave. group size	Obs. Ave. degree	Exp. ave. degree	*N*	(E-O)/E interval	
Kabini 500-m	3.16	74.95±3.661	84.29	109	0.154	0.067
Uda Walawe	3.07	22.53±2.266	81.05	105	0.750	0.694
Samburu	5.03	88.87±2.989	97.86	110	0.122	0.061
Population	Ave. group size	Obs. ave. clust. coeff.	Exp. ave. clust. coeff.	*N*	(E-O)/E interval	
Kabini 500-m	3.16	0.81±0.011	0.86	109	0.067	0.043
Uda Walawe	3.07	0.63±0.025	0.83	105	0.268	0.208
Samburu	5.03	0.88±0.007	0.99	110	0.117	0.102
Population	Ave. group size	Obs. ave. path length	Exp. ave. path length	*N*	(E-O)/E interval	
Kabini 500-m	3.16	1.31±0.012	1.15	5886	-0.130	-0.151
Uda Walawe	3.07	2.07±0.020	1.16	5460	-0.766	-0.800
Samburu	5.03	1.18±0.010	1.02	5995	-0.151	-0.171

CHAPTER 3

Seasonal Variation in Female Asian Elephant Social Structure in Nagarahole-Bandipur, Southern India

Title: Seasonal variation in female Asian elephant social structure in Nagarahole-Bandipur, southern India

Authors: Nandini Shetty, P. Keerthipriya, T.N.C. Vidya

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

Abstract

Fission-fusion dynamics allow for individuals to deal with spatio-temporally changing food resources, with groups of a larger community fusing together when resources are abundant and splitting away when competition for resources is high. Therefore, seasonal changes in resources may affect group sizes and associations in societies showing such dynamics. We examined the seasonal variation in group size and social structure of female Asian elephants, which show high fission-fusion dynamics, in a population in southern India. Associations were non-random, forming social networks with clear communities (clans) in both dry and wet seasons. At the level of the population, we found an effect of season on group size and female associations. Females were sighted in larger group sizes and associated with more uncommon females in the dry season. When associations amongst common females were considered, however, a greater number of stronger associations were observed in the wet season. There were no consistent seasonal differences when associations of clans were separately compared across seasons. Population level results, obtained by a combination of results from different clans, may thus be misleading in this regard, as clans are the relevant social units. This has important implications for the interpretation of previous population-level results seen in this species. Female associations showed some temporal stability, with association indices being moderately correlated across consecutive seasons and years. Group sizes were similar across clans, even though clan sizes were quite different, indicating a restriction on group size, possibly due to resource distribution. In spite of this restriction, most clan-mates showed low, non-zero associations amongst themselves rather than very strong associations with a small set of individuals. So they formed small groups which were fluid, with changing rather than fixed associates. These extended associations hint at a benefit to socialising with other clan-mates, and fission-fusion dynamics in this population appears to be a means of associating with different individuals while holding group size relatively constant, rather than solely a means of increasing or decreasing group size itself in response to ecological factors.

Keywords

Asian elephant, social organisation, group size, association network, seasonality, multilevel society, fission-fusion.

Introduction

Ecological factors and individual relationships may variously affect social structure and group size, and understanding the roles of these factors in shaping animal societies has long been a central objective of mammalian behavioural research (Crook and Gartlan 1966, Eisenberg *et al*. 1972, Clutton-Brock and Harvey 1977, Wrangham 1980, van Schaik 1989). Ecological conditions can lead to societal differences depending on the relative advantages of group living, such as reduced predation risk (van Schaik 1983, 1989, van Schaik and van Noordwijk 1985, Terborgh and Janson 1986) or increased reproductive success (Emlen 1973, Packer and Pusey 1995, Cant 2000, Packer *et al*. 2001, Silk *et al*. 2003, but also see Silk 2007), vis-à-vis the costs of feeding together, especially during periods of low food availability (Jarman 1974, Wrangham 1980, Mitchell *et al*. 1991, Wrangham *et al*. 1993, Janson and Goldsmith 1995, Barton *et al*. 1996, Koenig *et al*. 1998, see Chapman and Rothman 2009, Foster *et al*. 2012, Wittiger and Boesch 2013). According to socioecological theory, within-group feeding competition is a major cost of group living (van Schaik *et al*. 1983, Terborgh and Janson 1986, Dunbar 1988, van Schaik 1989, Wrangham *et al*. 1993, see Koenig 2002), and the ecological-constraints model posits that the additional travel large groups must undertake to meet their energetic requirements would limit group size (Milton 1984, Wrangham *et al*. 1993, Chapman *et al*. 1995, Chapman and Chapman 2000). Fission-fusion dynamics are thought to be a solution to dealing with food competition during varying resource availability, with groups fusing together when resources are abundant and splitting away when competition within groups for resources is high, thus altering the costs and benefits of group living by changing spatio-temporal cohesiveness (Kummer 1971, Dunbar 1988, Symington 1988, Strier 1992, Chapman 1990, Chapman *et al*. 1995, Connor *et al*. 2000, Wittemyer *et al*. 2005, Aureli *et al*. 2008, Smith *et al*. 2008, Asensio *et al*. 2009). However, the effect of ecology on group size or social structure is not entirely straightforward since substantial flexibility has been observed within and between populations of species showing high fission-fusion dynamics (see Strier 2003, Aureli *et al*. 2008). In this context, we examined female social structure and group size in an Asian elephant population to find out how stable or variable they were across seasons and years. Group size is the number of individuals (or subset of individuals, females as in this paper) in a group of animals sighted. Social structure is the patterning of associations or interactions of individuals (or subset of individuals) in the society. Societies with high fission-fusion dynamics may be structured into socially meaningful entities such as communities or clans, but since members of such entities do not remain together all the time, group sizes will often be smaller than community sizes. We find an effect of season on social structure and group size at the level of the entire social network/population, but stability at the level of communities within the social network. We suggest that fission-fusion dynamics may be a means of maintaining multiple associates under conditions of constant but constrained group sizes, rather than solely a means of increasing or decreasing the group size itself in response to ecological factors.

Elephants inhabit ecologically diverse habitats and female elephants live in societies characterized by high fission-fusion dynamics (*sensu* Aureli *et al*. 2008). African savannah elephants (*Loxodonta africana*) show larger group sizes than Asian elephants (*Elephas maximus*) in secondary or deciduous forests, and the latter show larger group sizes than African forest elephants (*Loxodonta cyclotis*) and, possibly, Asian elephants in rain forests (de Silva and Wittemyer 2012, Turkalo *et al*. 2013, Schuttler *et al*. 2014, chapter 2), suggesting that ecological factors affect group sizes across populations/species. Resource availability has been shown to affect within-population female group size and social structure in the African savannah elephant, with groups being larger in the wet season than in the dry season and social cohesion decreasing during the dry season (Wittemyer *et al*. 2005, de Silva and Wittemyer 2012). The African forest elephant faces a different resource distribution regime, with fruits being ephemeral and patchily distributed spatio-temporally (Blake 2002) and, while its effect on group sizes has not been reported, visitations by elephants to the Dzanga Bai forest clearing did not show any seasonality (Turkalo *et al*. 2013). In another study, in Lopé, Schuttler *et al*. (2014) showed that there were no clear seasonal differences in African forest elephant social networks. The effect of ecological factors on social structure within Asian elephant populations has not been clear. McKay (1973) found little seasonal effect on group sizes in Sri Lanka. More recently, de Silva *et al*. (2011), in a large, quantitative study of social structure, found that female social structure in Uda Walawe, Sri Lanka, was not influenced significantly by seasonal differences. Female group sizes were not significantly different between the dry and wet seasons (de Silva *et al*. 2011, de Silva and Wittemyer 2012) and neither was a measure of social associations different between the two seasons (de Silva and Wittemyer 2012). However, Sukumar (2003) reported larger group sizes during the second wet season and dry season than in the first wet season in a southern Indian population. He suggested that larger group sizes during the dry season probably ensued from elephants congregating near water sources and, therefore, encountering one another more frequently (Sukumar 2003). Although plausible when considering only members of socially meaningful entities (communities or clans), congregations themselves may not represent such entities, as different communities might utilize the same resource even if they are otherwise non-interacting or negatively interacting. Therefore, long-term data on identified individuals are required to detect the effects of seasonality on group size and social structure. We examined whether groups, defined as sets of identified females and their young that showed coordinated movement or affiliative behaviour (see chapter 2, Methods), were of significantly different sizes across seasons in Nagarahole and Bandipur National Parks and Tiger Reserves, southern India, and whether there were differences in social structure during this time.

We did not have an *a priori* expectation about the effect of seasonality on group size (only female group size is discussed in this paper). On the one hand, although there was marked seasonality in our study area, it was possible that there would be no effect of seasonality on group size as found in elephants in Sri Lanka. On the other hand, although the difference in rainfall between the dry and wet months was higher in Uda Walawe (about 45 and 230 mm per month on average, respectively, see de Silva and Wittemyer 2012) than in Nagarahole-Bandipur (about 5 and 10 mm per month on average from our study area), the absolute rainfall was much lower in Nagarahole-Bandipur (about 900 mm average annual rainfall at the Kabini reservoir, ~1300-1700 mm in Uda Walawe), which could possibly create differences in group sizes across seasons. However, if there was an effect of season on group size, we expected to find higher group sizes during the dry season. We also expected accompanying differences in social structure between seasons, with greater interconnectedness, although not necessarily connection strengths, between individuals within communities (or clans, defined as the most inclusive social grouping based on network analysis, see community identification in Methods) during the dry season. This was because abundant resources seemed to be concentrated at the Kabini backwaters during the dry season, compared to the wet season, when resources were likely to be more dispersed. We examined differences in social networks and group sizes at the level of the population and the clan.

Methods

Field data collection

Field data were collected as part of the Kabini Elephant Project in Nagarahole National Park and Tiger Reserve (Nagarahole; 11.85304°-12.26089° N, 76.00075°-76.27996° E, 644 km^2) and the adjoining Bandipur National Park and Tiger Reserve (Bandipur; 11.59234°-11.94884° N, 76.20850°-76.86904° E, 872 km^2) in southern India (Figure 1) from March 2009 to July 2014 over 878 field days. Nagarahole and Bandipur comprise primarily dry and moist deciduous forests and are separated by the Kabini reservoir on the river Kabini (see Vidya *et al*. 2014). Elephant density in Nagarahole and Bandipur is high (AERCC 1998, unpublished field data from the Kabini Elephant Project) and large numbers of elephants use the area around the reservoir. Therefore, the area sampled was centred around the Kabini reservoir and extended into the forests of Bandipur and Nagarahole.

The study area receives rainfall from the seasonal southwest and northeast monsoons. The southwest monsoon usually arrives in the beginning of June and withdraws in October, while rains from the northeast monsoon begin in October and last until November or December. Since the forest remains wet between the southwest and northeast monsoons, we considered only two seasons in a year, a dry season and a wet season. The wet season was considered to begin one week after the southwest monsoon’s onset as determined by the India Meteorological Department (Supplementary Material 1). As the study area receives pre-monsoon showers during April and May, a week’s monsoon rain was sufficient to transform the forest. Periods with pre-monsoon showers were not included in the wet season as these showers occurred in otherwise dry and hot months, resulting in little surface water becoming available. The dry season was considered to begin two weeks after the end of the northeast monsoon, in order to ensure that the forest was no longer wet (see Supplementary Material 1). The annual rainfall in Nagarahole ranges from 900-1200 mm and that in Bandipur from 625-1250 mm (Karanth and Sunquist 1992, AERCC 1998), with about 900 mm being the average rainfall at the Kabini reservoir (based on the Beechanahalli Dam weather station records during the study period). Elephants tended to intensively use the area around the Kabini reservoir’s backwaters during the dry season and were more scattered in the forest during the wet season. Heavy rains and low visibility in the forest made sampling during the wet season challenging, and elephant sightings were, therefore, much fewer during the wet season.

We drove along pre-selected routes from about 6:30 AM to 6:00-6:45 PM (depending on daylight hours and field permits) to record elephant sightings. Female elephant “groups” were identified as collections of female elephants and their young that showed coordinated movement or affiliative behaviour, and were within 50-100 m of one another (see chapter 2). Elephants within a group were said to be associating with one another. Elephants were aged and identified (see Vidya *et al*. 2014) and sighting details including GPS location data recorded. Sampling could not be carried out during a large part of 2010 because of field permit issues, restricting some of the analyses to data from 2011-2014.

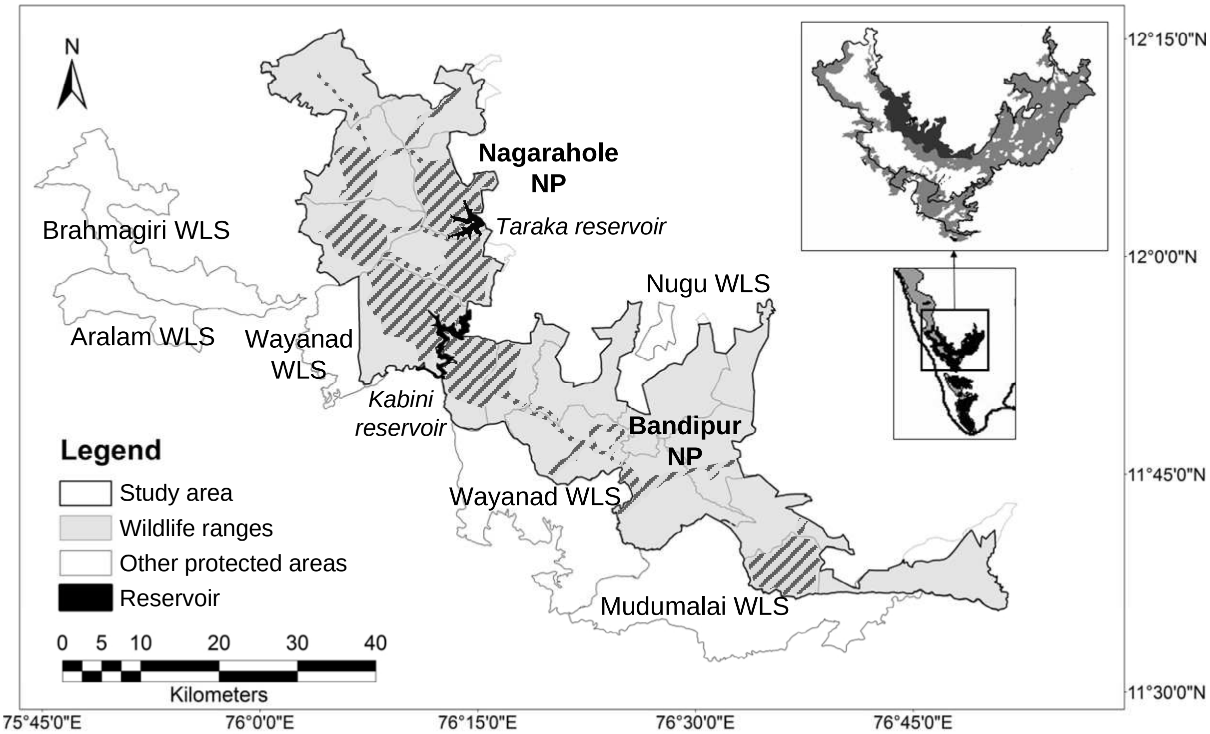


Figure 1. Map of the study area (Nagarahole and Bandipur National Parks, with wildlife ranges within them), with hatching depicting the approximate areas with roads that were sampled. Protected areas other than the study area are also shown. Upper inset: the larger landscape with areas of elephant distribution (based on Vidya *et al*. 2005) in grey, the study area in dark grey, and elephant reserve boundaries (Nilgiris-Eastern Ghats Reserve to the north and the Nilambur-Silent Valley Coimbatore Reserve to the south) in black. Lower inset: map of southern India with elephant distribution shown in black and the Western Ghats in grey.

Data Analysis

Associations between females 10 years or older (referred to simply as females in the rest of the paper; see chapter 2) were analysed from only those sightings in which all the females could be identified. If the same group was sighted after 2.5 hours, it was considered a new sighting (see chapter 2). We calculated the Association Index (AI) between pairs of females, as the ratio of the number of times two females A and B were seen together (N_{AB}) to the number of times either A or B was observed (N-D, where N is the total number of sightings and D the number of times neither A nor B was seen) (Ginsberg and Young 1992). Analyses were carried out on data from the dry and wet seasons separately, and on data from individual dry seasons (2009 and 2011-2014) to address the different questions. Data manipulation and analyses were carried out using MATLAB 7 R2004a (The MathWorks, Inc, 1984-2011, www.mathworks.com) unless otherwise mentioned.

Population-level analysis of group size and social structure comparison across seasons

In order to compare social organisation at the population-level during the dry and wet seasons, we carried out analyses based on a subset of data, in addition to the entire data, so that potential effects arising from differences in the numbers of unique individuals sighted during the two seasons could be eliminated. The entire dataset comprised 3233 sightings during the dry seasons and 653 sightings in the wet seasons, in which all the females could be identified. The total number of uniquely identified females were 298 and 223 during the dry and wet seasons, respectively (330 in all). The subset of data comprised 103 females, which had been seen at least 15 times overall and at least 3 times each during the dry and wet seasons (average number of sightings of these selected females=56.9 during the dry seasons, 11.7 during the wet seasons). We compared average group sizes between seasons using the Welch's two-sample test (Welch 1937, also see Fagerland and Sandvik 2009) and the sampled randomisation test (see below).

We constructed association networks of females seen during the dry and wet seasons and visualized the networks in Gephi 0.8.2 (Bastian *et al*. 2009). These association networks consisted of nodes, indicating females, connected by edges, indicating associations between females. The edges had weights, which were the strengths of associations, represented by AI, between pairs of females. We compared the dry and wet season association networks using the average degree, average clustering coefficient, average path length, modularity, density, and number of shortest paths for each network (see Wasserman and Faust 1994, Latapy 2008). Degree is the number of edges or connections from a node, which, in our association network, was the total number of associates of a female (average degree was averaged across all females being considered). Clustering coefficient of a node is the fraction of all possible edges between its neighbours (nodes that are connected to the focal node directly) that are actually observed (Latapy 2008). This represented the probability that a female's direct associates were themselves directly associated with one another. Average clustering coefficient was averaged across all females with a degree of two or higher, as individuals must have at least two direct associates in order for the associates' connectedness to be measured. Path length is the number of edges between a focal node and another node while traversing the shortest path between those nodes. It was, therefore, a measure of the directness in connections between females in our association networks. Path length can be calculated only between nodes that can be reached (not isolated nodes) and average path length was averaged over the total number of paths. The number of shortest paths is a measure of how connected the network is, with a higher number of shortest paths (for a given number of nodes) indicating a more connected network. Density and modularity are network-level properties and are the proportion of all possible edges that exist in the network, and a measure of the extent to which the network can be meaningfully divided into communities, respectively. Modularity was calculated using the Louvain method (Blondel *et al*. 2008), in which communities are created hierarchically and iteratively, maximizing the density of edges within communities compared to those between communities at each stage of the hierarchy. AI values in the form of edge weights were considered in the calculation of modularity (Blondel *et al*. 2008). The Louvain method was implemented using a MATLAB code written by Antoine Scherrer and made available at the authors' website (https://perso.uclouvain.be/vincent.blondel/research/louvain.html). Apart from these network statistics, we calculated average AI, skew in AI, and kurtosis of AI. We compared these network and AI statistics between the dry and wet seasons using a sampled randomisation test (Sokal and Rohlf 1981, pp. 791-794), in which 10,000 permutations of the data (by randomly assigning rows of data to the dry or wet seasons) were used to assess the significance of the observed dry season-wet season difference in network statistics compared to the differences based on permuted 'dry' season-'wet' season data.

We also utilised two analyses previously used to describe elephant social structure, the network structure curve and hierarchical cluster analysis, for comparison of social networks across seasons. Network structure curves (see de Silva *et al*. 2011) were constructed using the Louvain algorithm to find the number of non-singleton communities at different AI cutoffs (after removing edges below the cutoff), and plotting these against AI cutoff.

Significant changes in slope in this curve were assessed using the Wilcoxon rank sum test to compare the numbers of clusters on either side of each point within a moving window (see de Silva *et al*. 2011). We used a moving windows of 0.3. Since the shape of the curve indicates cohesiveness of the social network at different AI cutoffs, we used this method to look for differences across seasons and compared the curves using Wilcoxon's matched-pairs tests in Statistica 7 (StatSoft, Inc. 2004). For a similar reason, we also carried out hierarchical cluster analysis (see Wittemyer *et al*. 2005), in which AIs between individuals were used to construct a UPGMA-based dendrogram. A plot of the cumulative number of bifurcations in this dendrogram at different linkage distances was used to identify points of slope change (knots), by comparing the cumulative number of bifurcations on either side of each point in a moving window (see Wittemyer *et al*. 2005). The Wilcoxon rank sum test was used again to assess statistical significance. While this analysis is not useful in detecting hierarchical structuring in non-nested multilevel societies (de Silva and Wittemyer 2012, chapter 2 of this thesis), we used it here to look for similarity in social structure across seasons, comparing the curves using the Wilcoxon's matched-pairs test.

Stability/variability of clans across seasons and years

The most inclusive communities found through the Louvain algorithm were called clans (also see chapter 2). These clans were distinct from one another in the social network and represented different modularity classes. Since patterns observed at the population level need not necessarily reflect patterns observed at a finer scale in the social network, we examined whether there were changes in within-clan social structure across seasons. Upon examining the membership of clans that were sighted over 150 times, we found that 95% of the clan members were sighted within the first 40 sightings of the clan on average. Therefore, only clans that were seen at least 40 times were considered for clan-level analyses. There were 16 such clans with over 40 sightings but one of them had only two adult females (despite over 300 sightings), precluding most analyses. Subsets or all of the remaining 15 focal clans were used for analysis depending on the number of sightings of these clans in different comparisons. We constructed association networks for the 15 focal clans and calculated the network statistics mentioned above. Clans with at least 40 sightings overall and at least 10 sightings each in the dry and wet seasons were used for comparison across seasons (nine clans, 76-815 sightings). Differences between the seasons in network statistics for the nine clans were assessed using the sampled randomisation test, as described above. We used a General Linear Model (GLM) to examine the effect of season on average group size, with season as a repeated measure, clan identity as a random factor, and clan size (total membership of the clan) as a covariate. This was also used to examine the effect of season on maximum group size. Group size distributions of the nine clans were compared using Kolmogorov-Smirnov two sample tests. Kolmogorov-Smirnov two sample tests and the GLM were carried out in Statistica 7 (StatSoft, Inc. 2004).

Since we found no effect of clan size on group size from the previous analysis (see Results), we also examined the relationship between clan size and average within-clan AI using a regression to confirm if limited average group sizes affected associations in larger clans to a greater extent. As group sizes were smaller than clan sizes, we also carried out permutation tests following Bejder *et al*. (1998) and Whitehead (2008, pg. 127-128) to detect any preferred associations within the 15 focal clans, against the null hypothesis of random associations. Even if the previous analysis showed a decreasing relationship between average AI and clan size, it would not automatically imply preferred associations, in the absence of the current analysis. These permutations were carried out in SOCPROG 2.4 (Whitehead 2009) using a sampling period of 14 days so that there would be sufficient sightings to carry out the randomisations. The permutation test ensured that the total number of sightings of individuals and sighting group sizes remained the same as those in the original data. The mean AI was used to detect short-term (within sampling-period) non-random associations (significantly lower observed value compared to random values indicate preferences), and the SD and CV of AI to detect long-term non-random associations (significantly higher obseved values compared to random values indicate preferences).

We additionally examined the waiting time (minimum number of sightings) for females in clans of different sizes to meet their clan-mates, as a measure of turnover in associations. If there was an effect of clan size on the extent of non-randomness in associations, it would be seen as a greater departure in the observed waiting time from the expected waiting time. The waiting time is expected to follow a geometric distribution if females are seen randomly and is a type of ‘coupon-collector problem’ in mathematics. However, since females might not be sighted entirely randomly by us, we did not use the theoretical waiting time expectation, instead obtaining the expected waiting time to meet clan-mates by permuting the observed data. We created 5000 permuted datasets for each focal clan by flipping individuals between sightings following the method of Bejder *et al*. (1998). Pairs of sightings and a female from each of those sightings were chosen randomly such that each of the two females chosen was present only in one of the two sightings, and each of the two sightings had only one of the two females (see Whitehead 2008, pg. 124). These females were swapped between the sightings so that the number of sightings, number of females, and group sizes could be preserved. This operation constituted one ‘flip’ and 1000 such flips were carried out for each of the 5000 permutations. Each permuted dataset obtained at the end of 1000 flips was used to calculate how many sightings of each female it took before she encountered each of the other females in her clan. The average of this across females and the 2.5 and 97.5 percentiles were used as the expected values and compared with the observed average minimum number of sightings of females required for them to encounter clan-mates.

We examined the constancy of within-clan associations across time by carrying out Mantel tests (Mantel 1967) on pairs of AI matrices from consecutive seasons or successive dry seasons. These AI matrices were from focal clans that were seen at least 15 times during the particular wet season dataset being compared or 20 times during the other datasets being compared. The observed correlation coefficient, r (r_{XY} of matrices X and Y = $SP(\mathrm{X},\mathrm{Y})/\mathrm{sqrt}[SS(\mathrm{X}).SS(\mathrm{Y})]$, where SP is the cross product of the matrices and SS is the sum of squares), and R^2 between the two matrices were calculated. Rows and columns of one of the matrices were permuted to test for statistical significance in the Mantel test. Since the permutation does not change the denominator for calculating r and actually only changes the Hadamard product (Z_{XY}, which is the sum of the products of corresponding elements in X and Y) of the matrices, the latter ($Z_{observed}$) was compared against a distribution of Z obtained from 1000 permutations to test for statistical significance (see Smouse *et al*. 1986). Clan average group sizes and average AIs were compared across dry seasons of the years 2011-2014 using repeated measures ANOVAs in Statistica 7 (StatSoft, Inc. 2004). Since there were insufficient data from 2010, data from 2009 and 2010 were not used for this comparison, and only clans that had at least ten sightings in each of the four dry seasons were used (seven clans).

Results

Population-level analysis of group size and social structure across seasons

Dry season group sizes (average±SD=2.41±1.837, maximum=14 females) were slightly but significantly larger than wet season group sizes (average±SD=2.21±1.786, maximum=18 females; Welch's two-sample test: *U*=2.523, *df*=951.1, *P*=0.012; sampled randomisation test, *P*=0.004). The group size distributions for the two seasons were also statistically significantly different (Kolmogorov-Smirnov two sample test, *P*<0.05, Figure 2).

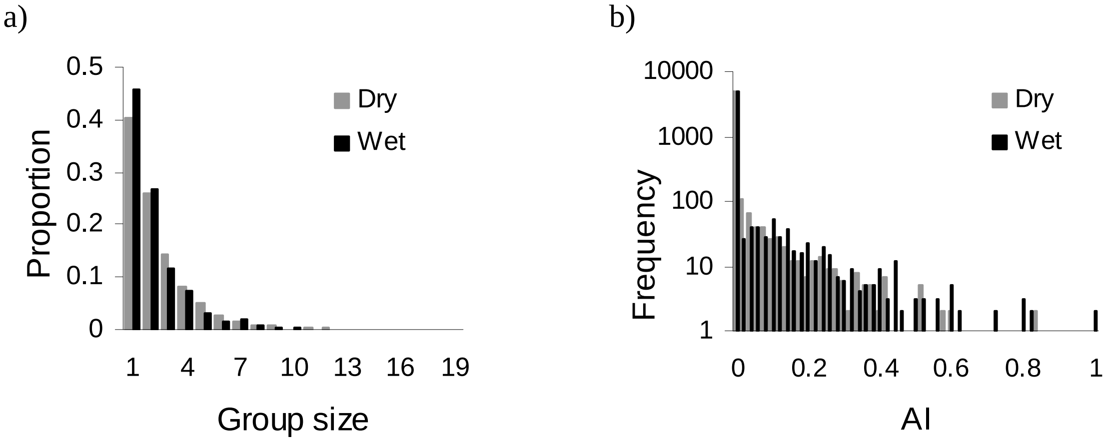


Figure 2. a) Group size distributions based on all groups and b) AI distributions based on 103 common females, during the dry and wet seasons.

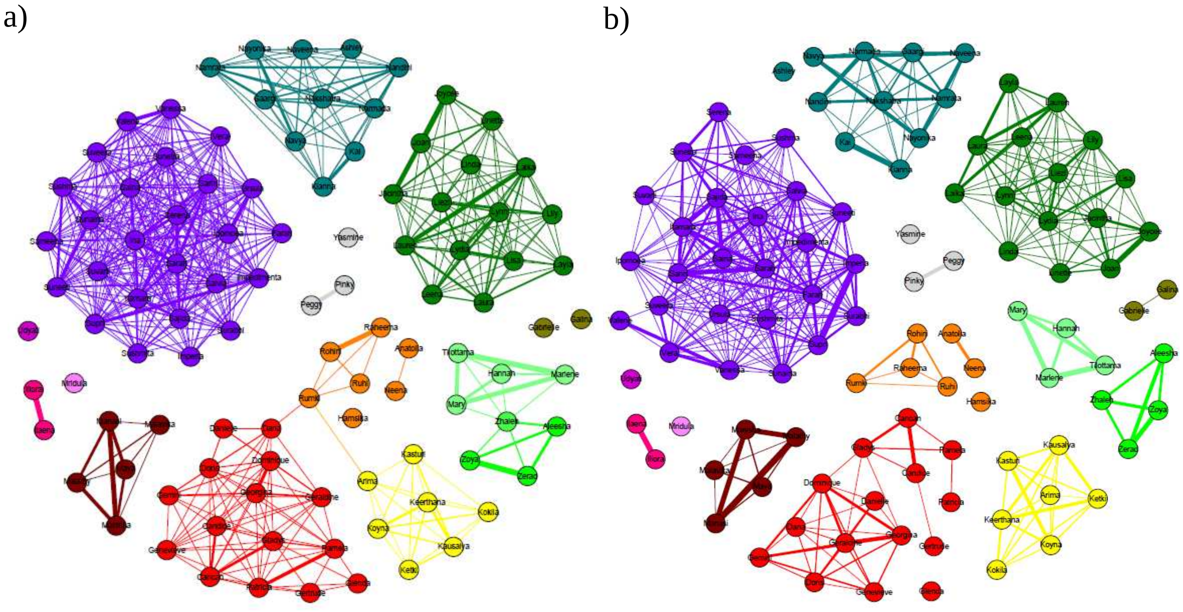


Figure 3. Social networks based on only the 103 common females (seen at least 15 times) during the a) dry and b) wet seasons. Networks based on the entire dry and entire wet season datasets are shown in Supplementary Material 2. Colours of nodes indicate different clans.

Because not all females in each clan were seen 15 times, some of the clans are represented by disconnected individuals in the networks above.

Social networks from the dry and wet seasons looked similar (Figure 3, Supplementary Material 2) and comprised clearly demarcated modularity-based communities that we call clans (see chapter 2). Associations between females were highly non-random in both seasons, being limited almost exclusively to the same clan. Therefore, the proportion of individuals that did not interact was very high. The proportion of non-zero AIs was 2.9% during the dry season and 2.5% during the wet season based on the entire dataset (see Supplementary Material 3), and remained small when the subset of 103 females was examined (10.9% during the dry season, 8.5% during the wet season). Comparison of network statistics based on association networks of only the 103 adult females seen in both the dry and wet seasons showed significantly higher skew and kurtosis of AI distribution in the dry season compared to the wet season, but no significant difference in average AI, average degree, modularity, or other network statistics, between the two seasons (Table 2). If the degrees of all individuals instead of the 103 females were compared across seasons, or if the degrees of the 103 females, but including associations of these females with all the other individuals they were seen with (instead of restricting associations to only amongst the 103 females), were compared across seasons, the average degree was higher in the dry season than in the wet season (average±SD of degree for the 103 females but including anyone they associated with, not restricted to the other 102: dry season: 14.6±9.04, wet season: 9.4±6.90, Wilcoxon's matched-pairs test, T=124, Z=8.206, P<0.001), because of the larger number of rarer individuals sighted during the dry season.

Table 2. AI and network statistics based on sightings of the same 103 females during the dry (no. of sightings=2656) and wet (no. of sightings=545) seasons, and averages of these statistics based on the sampled randomisation test with 10,000 randomisations. *P* values from the sampled randomisation test to test for differences between seasons are shown. Significant values are marked in bold.

Season	Average AI (SD)	Skew in AI	Kurtosis of AI	Average degree (SD)	Average clustering coefficient (SD)	Average path length (SD)	Modu-larity	Density	No. of shortest paths
Dry observed	0.013 (0.0614)	7.378	70.62	11.1 (8.02)	0.92 (0.114)	1.73 (1.244)	0.791	0.109	1702
Dry permuted	0.014 (0.0619)	7.088	65.61	11.4 (8.34)	0.93 (0.115)	1.61 (1.097)	0.784	0.112	1645.1
Wet observed	0.017 (0.0744)	6.405	53.96	8.7 (7.06)	0.89 (0.143)	1.36 (0.654)	0.749	0.085	1238
Wet permuted	0.014 (0.0662)	7.327	70.43	8.4 (6.74)	0.86 (0.146)	1.42 (0.647)	0.785	0.083	1285.4
P value	1.000	**0.003**	**0.008**	0.803	0.937	0.265	0.061	0.785	0.300

The cumulative bifurcation curves based on the dry and wet seasons looked similar in shape with a single knot, but the cumulative number of bifurcations was significantly smaller in the dry season compared to the wet season (Wilcoxon's matched-pairs test: T=0.0, Z=6.093, N=51, P<0.001). The knots were shifted, at linkage distance of 0.56 in the dry season and 0.38 in the wet season (Figure 4a). This arose from a slightly higher number of stronger connections (at lower linkage distance/higher AI) in the wet season compared to the dry season (Figure 4a, see Figure 2b also). The shapes of the network structure curves also looked similar between the dry and wet seasons, with little difference between the knots recovered in the two seasons (Figure 4b). However, the wet season network structure curve was right shifted: in the wet season, a lower number of clusters were found at the same AI values below the knot compared to the dry season (Wilcoxon's matched-pairs test: T=4.0, Z=3.309, N=18, P<0.001), while a higher number of clusters were found in the wet season compared to the dry season at AI values above the knot (Wilcoxon's matched-pairs test:

T=0.0, *Z*=4.860, *N*=32, *P*<0.001). Therefore, there was greater integrity of clusters in the wet season than in the dry season (after the knot, the number if clusters decreases because clusters with single individuals are not plotted; therefore, a larger number of clusters reflects more cohesiveness at those values of AI cutoff).

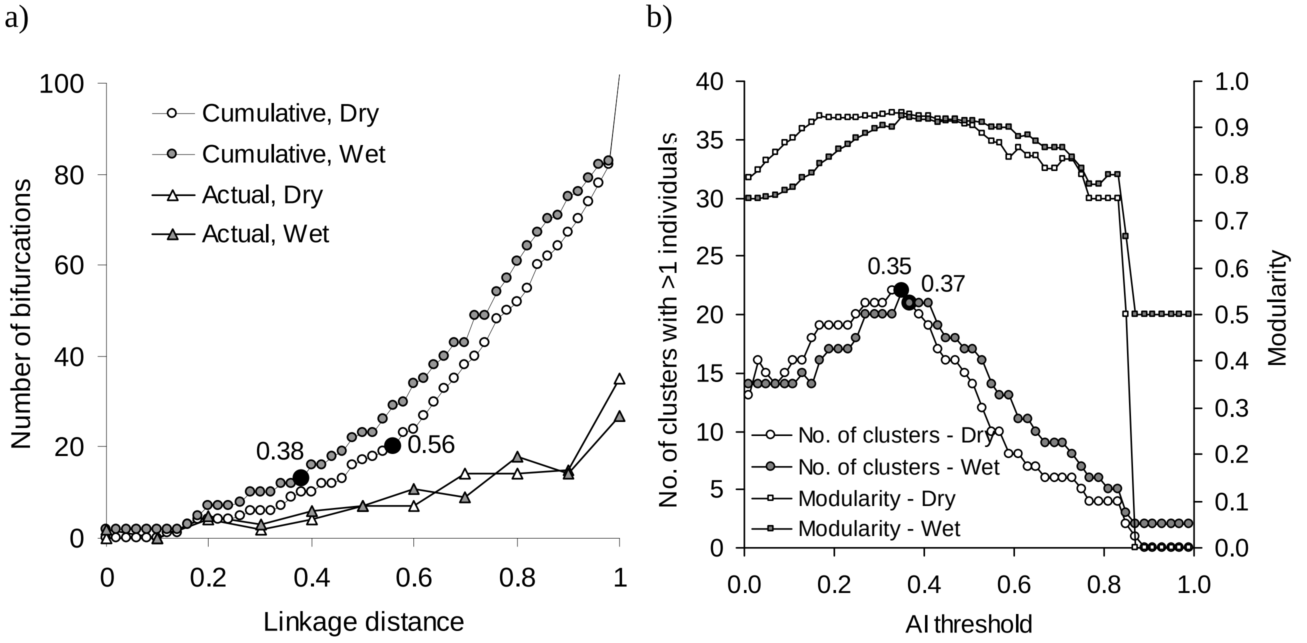


Figure 4. a) Bifurcation curves from the dendrograms in Supplementary Material 4 and b) network structure curves for the dry (open symbols) and wet (grey symbols) seasons, based on 103 females sampled in both the seasons. In the cumulative bifurcation curves in a), knots (black circles) were found at AI=0.56 for the dry season data and 0.38 for the wet season data based on a window of 0.3. The actual numbers of bifurcations binned in units of 0.1 linkage distance are also shown, along with the cumulative numbers of bifurcations. In b), there was a single knot at AI threshold value of 0.37 based on the dry season data and a knot at AI threshold value of 0.35 based on the wet season data.

Comparison of group sizes and social structure within clans across seasons

Visually, the social networks of the 15 focal clans, while showing similarities, showed more connections during the dry season than the wet season (Figure 5). The average within-clan AI in the 15 focal clans ranged from 0.04 to 0.53 overall, with the ranges being similar across seasons (Table 3). There was no significant difference in average within-clan AI across seasons based on the sampled randomisation test, and there were no consistently significant differences across clans between the dry and wet seasons in within-clan skew or kurtosis of AI or within-clan network statistics (Supplementary Material 5). AI distributions compared based on the sampled randomisation test also showed largely no differences between the dry and wet seasons, with the exception of a few differences at the lower end of the AI distributions (Supplementary Material 6, 7).

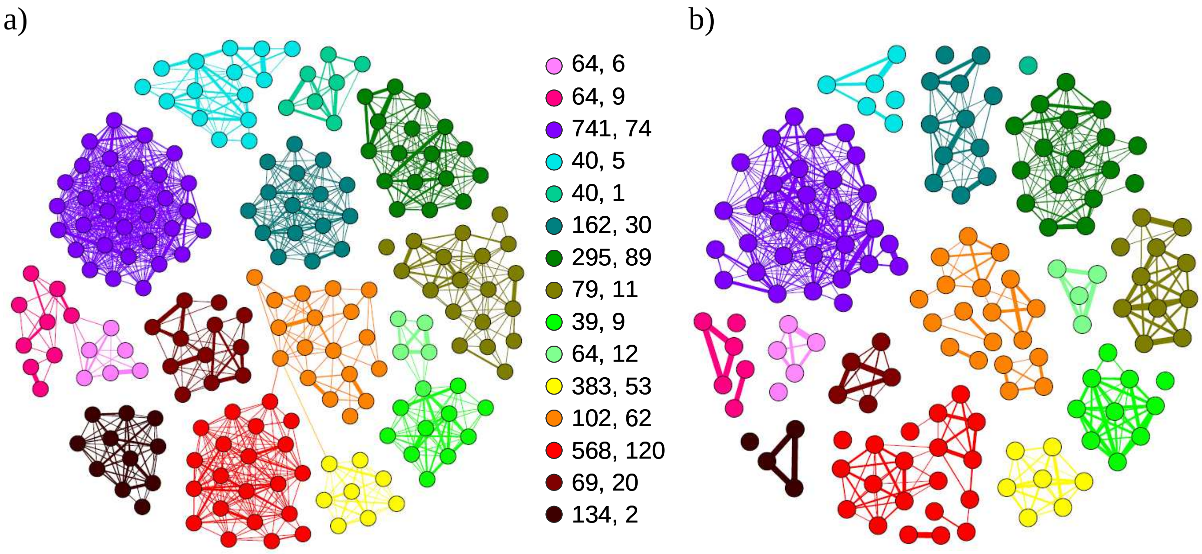


Figure 5. Social network of 15 focal clans during the dry (a) and wet (b) seasons. Circles with numbers written next to them correspond to the number of sightings of focal clans in the dry and wet seasons, respectively. Nodes are coloured based on clan membership based on the entire data. The nine clans with at least 10 sightings during the wet season were used for comparison across seasons.

Average group sizes in the focal clans were small, with 1.7-3.2 females, and similar ranges seen across seasons (Table 3). The GLM to examine the effect of season on average group size showed no significant effect of season ($F_{1,7}$=0.0137, P=0.910) or clan size ($F_{1,7}$=0.9696, P=0.358) on average group size (see Supplementary Material 8, 9). There was an effect of clan size ($F_{1,7}$=10.0534, P=0.016, partial eta-square=0.590) on the maximum group size, but no effect of season ($F_{1,7}$=1.5053, P=0.260). Group size distributions were not significantly different between seasons in any of the nine focal clans tested (Kolmogorov-Smirnov two sample tests, P>0.1), nor were group sizes different between seasons for any individual clan based on sampled randomisation tests (P>0.05 for all clans).

Table 3. Clan size, number of sightings, and average (SD) of AI and group sizes for focal clans for the overall data, dry season and wet season. Apart from the 15 focal clans used for analyses, the clan with only two females is also shown in this table for completeness. Clan size refers to the number of females in the clan and is sometimes different between seasons because all clan members were not sighted. AIs and group sizes are not shown for clans that were seen fewer than 10 times in a particular category.

Clan	Clan size (All, Dry, Wet)	No. of sightings (All, Dry, Wet)	Ave. (SD) AI All data	Ave. (SD) AI Dry	Ave. (SD) AI Wet	Ave. (SD) group size All data	Ave. (SD) group size Dry	Ave. (SD) group size Wet
Alexandra	11, 11, 10	48, 39, 9	0.19 (0.175)	0.19 (0.185)	–	3.02 (1.973)	3.08 (1.897)	–
Anabelle	11, 11, 4	136, 134, 2	0.19 (0.132)	0.19 (0.133)	–	2.92 (2.066)	2.93 (2.075)	–
Fiola	7, 7, 1	41, 40, 1	0.26 (0.232)	0.26 (0.234)	–	2.80 (1.364)	2.85 (1.350)	–
Kasturi	8, 8, 7	436, 383, 53	0.15 (0.123)	0.15 (0.132)	0.29 (0.117)	2.08 (1.356)	2.01 (1.291)	2.64 (1.665)
Katrina	16, 16, 6	45, 40, 5	0.10 (0.166)	0.10 (0.171)	–	2.71 (1.660)	2.83 (1.708)	–
Lisa	17, 17, 17	384, 295, 89	0.10 (0.148)	0.11 (0.161)	0.10 (0.131)	2.51 (1.782)	2.48 (1.749)	2.61 (1.893)
Manasi	12, 12, 5	89, 69, 20	0.13 (0.231)	0.14 (0.227)	0.38 (0.343)	2.42 (1.364)	2.36 (1.403)	2.60 (1.231)
Menaka	9, 9, 6	73, 64, 9	0.11 (0.202)	0.10 (0.183)	–	1.70 (0.720)	1.67 (0.736)	–
Mridula	6, 6, 5	70, 64, 6	0.17 (0.207)	0.18 (0.222)	–	2.01 (0.955)	2.05 (0.933)	–
Nakshatra	16, 16, 12	192, 162, 30	0.09 (0.107)	0.10 (0.103)	0.13 (0.191)	2.61 (1.793)	2.63 (1.875)	2.50 (1.280)
Olympia	21, 21, 19	164, 102, 62	0.04 (0.100)	0.04 (0.119)	0.05 (0.125)	1.71 (1.032)	1.68 (1.064)	1.77 (0.982)
Osanna	20, 19, 11	90, 79, 11	0.07 (0.127)	0.07 (0.133)	0.24 (0.267)	2.46 (1.630)	2.46 (1.584)	2.45 (2.018)
Patricia	21, 21, 20	688, 568, 120	0.07 (0.106)	0.06 (0.103)	0.06 (0.142)	2.06 (1.597)	2.09 (1.613)	1.91 (1.517)
Peggy	2, 2, 2	305, 245, 60	0.58 (NA)	0.58 (NA)	0.57 (NA)	1.58 (0.494)	1.58 (0.494)	1.57 (0.500)
Tilottama	4, 4, 4	76, 64, 12	0.53 (0.222)	0.53 (0.229)	0.56 (0.190)	2.55 (1.148)	2.63 (1.076)	2.17 (1.467)
Victoria	32, 32, 31	815, 741, 74	0.08 (0.098)	0.07 (0.099)	0.09 (0.138)	3.22 (2.570)	3.20 (2.496)	3.47 (3.223)

Clan size and AI relationship, preferred associations within clans, and time to meet clan-mates

The average within-clan AI declined with increasing clan size (Regression using 15 focal clans: β=-0.669, R^2=0.447, $F_{1,13}$=10.511, P<0.006; Figure 6). Since average group size did not change with increasing clan size (Figure 6), there appeared to be a limit on group size, resulting in larger clans showing lower levels of association. This pattern was also seen when the nine focal clans being used for seasonal comparisons were analysed separately based on the dry and wet season data (Supplementary Material 10).

Permutation tests to examine preferred associations within clans showed preferred associations by at least one test (average AI lower than random, SD or CV of AI higher than random; see Supplementary Material 11, 12) in all but two clans. Preferred associations, if present during the dry season, were also present during the wet season (Supplementary Material 12). The average minimum number of sightings of females to meet all clan-mates increased with clan size as expected (GLM using average observed and expected values, matched for clan, with clan size as a covariate: effect of clan size: $F_{1,13}$=8.921, P=0.011, Figure 7). However, the observed minimum number of sightings required to meet all their clan-mates was larger than the expected values in only six of the 15 focal clans (Figure 7, confidence intervals of the observed values lie above the intervals for the expected values) and, therefore, there was no significant difference overall between the average observed and expected minimum number of sightings (GLM: $F_{1,13}$=0.590, P=0.456). There was also no significant interaction between clan size and the observed and expected minimum number of sightings (GLM: $F_{1,13}$=1.287, P=0.277). It must be noted, however, that some of the females did not meet all their clan-mates during the entire period of observation, especially in the larger clans. Therefore, the average observed minimum number of sightings is an underestimate in such clans (see Supplementary Material 13).

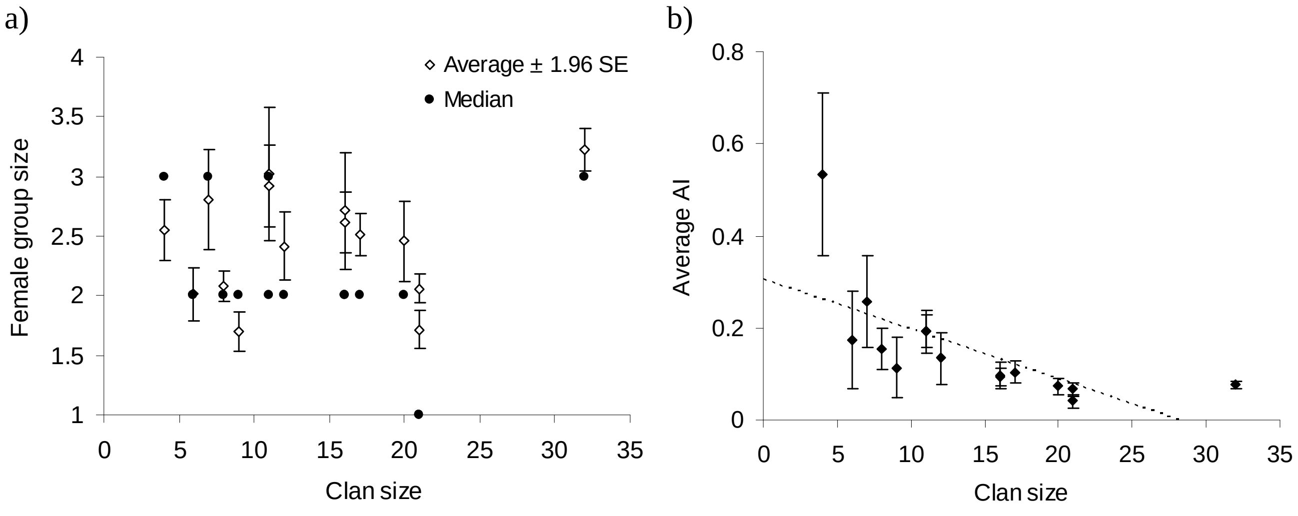


Figure 6. a) Average (±1.96 SE) and median group sizes and b) average (±1.96 SE) AI plotted against clan size for 15 focal clans based on the entire data (also see Supplementary Material 10). The regression is shown as a dotted line in b).

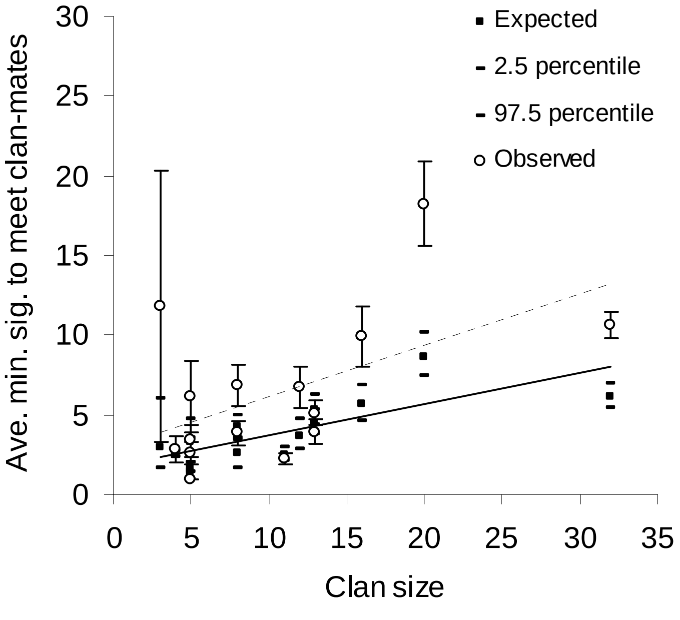


Figure 7. Average observed and expected minimum number of sightings of females required to meet all their clan-mates, in clans of different sizes. The 2.5 and 97.5 percentiles of the expected values are also shown. Error bars for the observed data are 1.96 SE of the mean. Trendlines for the average observed (dotted lines) and average expected (solid lines) values are shown.

Temporal changes in within-clan associations

Although preferred associations might exist in both seasons without being the same preferred associations, based on Mantel tests, we found AI matrices to be significantly positively correlated between successive seasons (18 of 19 tests significant at *P*=0.05, 13 tests significant using a flat Bonferroni correction of 0.0026 for multiple tests), and successive dry seasons (15 of 19 tests significant at *P*<0.05, 10 tests significant after Bonferroni correction) in the majority of the tests performed (Supplementary Material 14). The values of the correlations were medium (*r* from about 0.4 to about 0.8, Supplementary Material 13) and were not different between consecutive seasons or successive dry seasons.

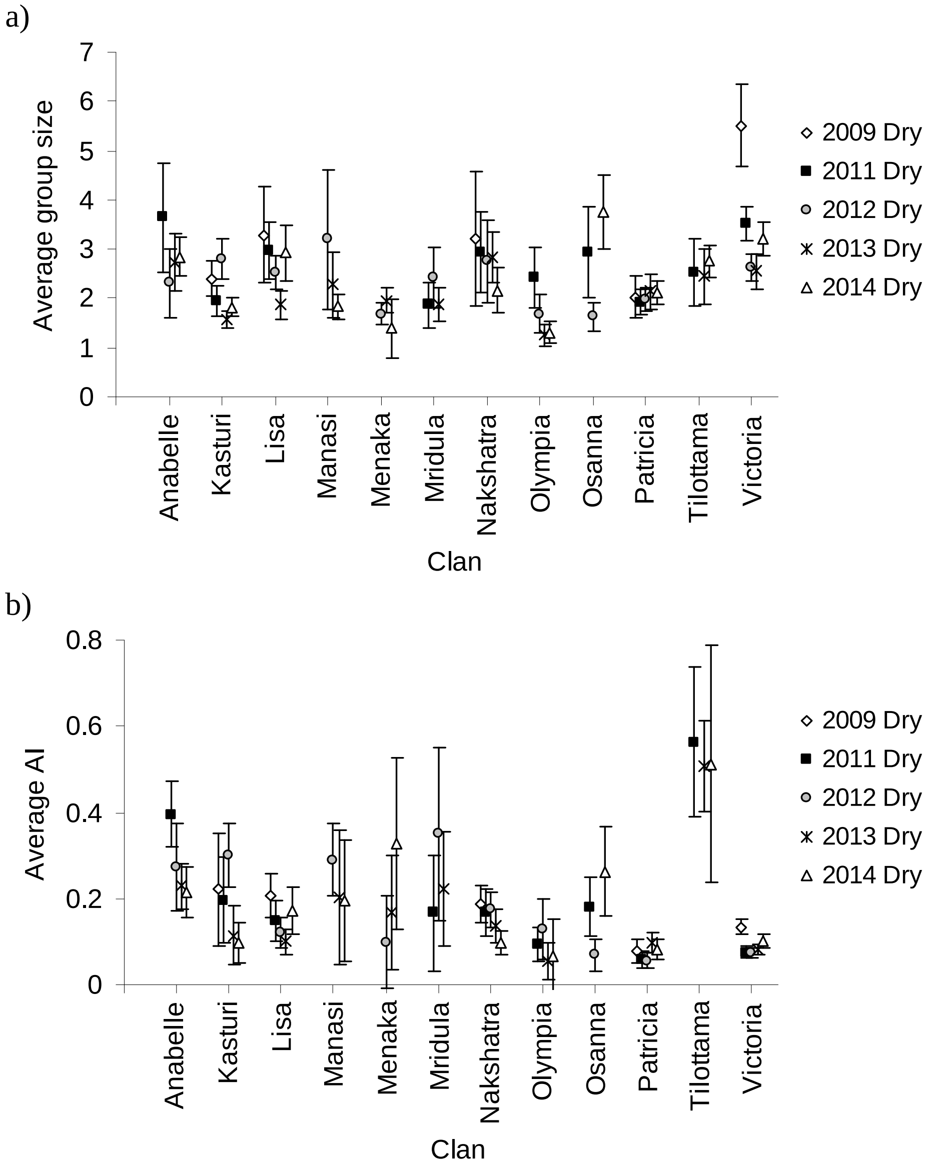


Figure 7. Average (±1.96 SE) group sizes (a) and average (±1.96 SE) AI (b) for focal clans across dry seasons of different years. Only those clans that were seen at least ten times in a

particular dry season are included here. Only the seven clans represented here in all four years from 2011-2014 were used for the repeated measures ANOVA. Data from 2009 are also, however, shown here in these graphs.

Repeated measures ANOVA on group sizes of clans during dry seasons of different years showed no significant effect of year on group size ($F_{3,18}$=2.9129, P=0.063, also see Figure 7a), although the lack of significance was borderline. There was also no effect of year on average within-clan AI ($F_{3,18}$=1.8503, P=0.174, see Figure 7b).

Discussion

Population-level versus clan-level differences in seasonal effects on social structure and group size

Our results showed some effects of seasonality on social structure at the population level but not at the clan level. Results of the population-level analysis were in the direction that we expected, with larger group sizes during the dry season than in the wet season. There were also a greater number of connections in the social network, as reflected by the higher proportions of non-zero AIs and higher degree, during the dry season compared to the wet season if all females were included in the analysis. This higher level of connectedness during the dry season probably stemmed from the larger number of rarer individuals seen during this season, and the difference in degree disappeared when only common females seen in both seasons were analysed. We also did not find uniformly higher connection strengths during the dry season. The shift in knot towards higher linkage distance (lower AI value) in the cumulative bifurcation curve of the dry season compared to the wet season, and the network structure curve of the wet season being right-shifted compared to the dry season, indicated a relatively greater number of stronger connections during the wet season and a relatively greater number of weaker connections during the dry season. The observation of a greater number of weaker connections in the wet season was not an outcome of pooling data from different years. When we constructed cumulative bifurcation curves for individual years, the proportion of cumulative number of bifurcations at lower linkage distance (higher AI) was higher in the wet season compared to the dry season in each year from 2010-2014, and was the same in both seasons during 2009.

Although there were significant differences in group size and in cumulative bifurcation and network structure curves between the two seasons, there was no significant difference in network statistics such as clustering coefficient, path length, density, number of shortest paths, or average degree (mentioned above) based on females common to both seasons. All the network statistics compared, with the exception of modularity, are based on the presence or absence of a connection but are insensitive to edge weight (AI values in the case of our association networks), whereas the cumulative bifurcation curve and network structure curves are based on AI values. As with seasonal differences based on the cumulative bifurcation curve and network structure curve, we found significant differences in the skew and kurtosis of AI, which are also based on actual AI values. Therefore, the different analyses performed provide different kinds of information about social structure. Our results suggest no population-level seasonal difference in social network structure based on the presence or absence of associations between females, but seasonal differences based on association strengths.

In contrast to the significant difference in group size found at the population level, there was no significant difference in within-clan group sizes between seasons. There was no consistently significant difference in network statistics that clans showed between the two seasons, similar to the population-level results. However, unlike the population level results, there was no consistent pattern across clans in social structure based on association strengths either. The network structure curves of focal clans did not show consistent patterns between seasons. The network structure curve based on the wet season data was right-shifted compared to that for the dry season in four clans, the network structure curve for the dry season was right-shifted compared to that for the wet season in two clans, and the network structure curves were not very different between seasons in three clans (Supplementary Material 15). Similarly, the cumulative number of bifurcations (in the cumulative bifurcation curve) was smaller in the dry season compared to that in the wet season in two clans, smaller in the wet season compared to the dry season in one clan, larger initially in the wet season and then larger in the dry season at higher linkage distances in two clans, larger initially in the dry season and then larger in the wet season at higher linkage distances in one clan, and not different between the seasons in three clans (Supplementary Material 16). There was also no consistently significant difference across clans in the skew or kurtosis of AI between seasons, while there had been a significant seasonal difference in the skew and kurtosis of AI at the population level.

Therefore, population-level results may be misleading because they arise as a combination of results from different social units, which may be sighted different numbers of times and show different patterns individually. This has important implications in terms of findings from other studies that have examined only population-level changes. For instance, Sukumar (2003) reported larger group sizes during the second wet season and dry season than in the first wet season in a different southern Indian elephant population. However, it is not clear how groups were defined in that study (as an aggregation in an area or as a social unit that showed coordinated activities) and, even if they were distinct social units and did not include multiple clans, since clans were not identified or demarcated clearly, it is possible that there were no clan-level seasonal differences in that study either. Elephants utilizing the Kabini Reservoir during the dry season in Nagarahole-Bandipur National Parks were also described as large groups with opportunities for social interactions among groups (Sukumar 2003), while we actually found many discrete clans that did not interact positively with members of other clans and did not change in group size across seasons. It is thus important to discriminate between congregations of animals that might share the same resource and female-bonded social groups, as the social environment that a female experiences in these two circumstances can be very different.

Since we do not know of any other comprehensive clan-level analysis of group size and social structure in Asian elephants, we have no other population to compare our clan-level results with. Based on a single clan, Baskaran and Desai (1996) had suggested differences between dry and wet season group sizes, with the former being smaller, in Mudumalai, southern India. However, in a subsequent analysis at the population level, the average group size was not found to vary significantly across seasons or habitats (Ashokkumar *et al*. 2010). Based on population-level data, de Silva *et al*. (2011) had found similar group sizes across seasons. Smaller group sizes from population-level data during the dry season compared to the wet season were found in a study in Ruhuna National Park, Sri Lanka (Katugaha *et al*. 1999), but the seasonal effect in that study was confounded by data collected over 23 years during a 30-year period, with the number of field days in years when data were collected varying from 1-17. McKay (1973) did not find population-level group sizes to be affected seasonally in Sri Lanka. In the light of our finding that group sizes at the population-level and clan-level can show different seasonal patterns, and that population-level group size data are likely to be confounded by unequal representation of different clans, it might be worth re-examining past findings of seasonal differences in group sizes at the population level by investigating their within-clan group sizes.

Similarly, it is also important to examine social structure at the clan/community level in other populations. de Silva *et al*. (2011) carried out the only previous detailed analysis of Asian elephant female social structure, in Uda Walawe, Sri Lanka. They found no clear seasonal difference in network-structure curves, and lower average ego-network (network comprising a female and her direct associates) statistics in the wet season compared to the dry season, with larger degree and two-step reach during the dry season (although density was found to be lower in the dry season). It is not clear whether there were contrasting results at the population and ego-network levels because network structure curves (which depend on AI values) could be constructed only at the population, and not the ego-network, level and the network statistics calculated for ego-networks (which are insensitive to edge weight) were not reported at the population level for the different seasons. In the Uda Walawe population also, the population-level social network could be divided into communities (de Silva *et al*. 2011), based on modularity, which probably correspond to what we describe as clans. The communities were not as disconnected as our clans because of a 500-m distance cutoff being used to detect sightings in that study. Nevertheless, since ego-network statistics are averaged across females (as opposed to clan-level statistics being calculated for and averaged across communities), if there was a seasonal difference in a network statistic in a few large communities, it could potentially give rise to significant seasonal differences in average ego-network statistics because of the large communities comprising many females. It would be interesting to examine whether network statistics of communities formed in the Uda Walawe social network are also different across seasons.

Temporal stability in social structure and group size

As explained above, there was no seasonal difference at the clan-level in group size or social network or AI statistics. We also found, based on Mantel tests, that associations between females were correlated to a moderate extent between successive seasons and years. We also found no effect of year on group size or average within-clan AI. Therefore, there was some temporal stability in clan social structure and group size. It is possible that there are specific pair-wise differences in AIs that change over time, but because group sizes are small, even with thousands of sightings overall, it will be difficult to detect such differences or the lack thereof.

Seasonal effects on group size and social structure have been described in African savannah elephants and related to resource availability (Leuthold 1976, Western and Lindsay 1984, Wittemyer *et al*. 2005), although these were also not analysed clan-wise. If these group size differences hold when analysed separately for different clans, there are at least two directions of enquiry that can be pursued to explain the lack of seasonal effects on clan-level social structure in our population. One reason for the lack of a seasonal effect on group size or social network structure could be the absence of meaningful changes in resources across seasons. While there are apparently distinct seasons in our study area, seasonal differences in food plants that elephants feed on need to be quantified in order to infer meaningful seasonal differences in resources. In a study in Mudumalai Wildlife Sanctuary, which is part of the larger Nilgiris-Eastern Ghats landscape in which Nagarahole-Bandipur are located, Baskaran *et al*. (2010) found differences in grass biomass available and the percentage of grass versus browse consumed by elephants across seasons. Availability of browse was not quantified.

A second possible reason for the lack of seasonal effects on clan-level social structure in our population is that even if resources that elephants use change seasonally, in the form of resource patch size changes, resource dispersion may limit group size. If resource patches are depleting (increasing group size increases the rate of patch depletion) and uniform, patch density is likely to strongly affect group size, with larger groups being found when patch density is high and smaller groups being found when patch density is low (Chapman *et al*. 1995, Chapman and Chapman 2000). This is expected irrespective of patch size being small or large because the costs of travelling between patches restricts group size. On the other hand, if patches are depleting but clumped rather than uniform, group sizes are expected to be large irrespective of patch density or size as the travel cost between patches is expected to be low (Chapman *et al*. 1995, Chapman and Chapman 2000). Therefore, if resources were uniformly distributed and patch density were low in Asian elephant habitat, small group sizes would be expected. It would, therefore, be illuminating to investigate the dispersion and density of resource patches, and to find out whether patches are depleting or not, in different areas of Asia and Africa. It is possible that elephant food resources are generally widely dispersed in rain forests compared to savannahs (Powell 1997, Blake 2002, Sukumar 2003), although heterogeneity at different scales and patchiness of elephant food plants has been shown only by Blake (2002) (in African forest elephant range), and we do not know of any study that has quantified patch sizes with respect to elephant food plants or shown that patches are depleting. As mentioned earlier, no seasonal differences in visitations to the Dzanga Bai or social networks were found in African forest elephants, whose resources are widely dispersed and which also show small group sizes (Turkalo *et al*. 2013, Schuttler *et al*. 2014). We speculate that populations with group sizes constrained to small numbers are less likely to show seasonal differences in group sizes, while recognizing the fact that larger sample sizes would be required to find significant differences in group sizes in such populations (compared to populations with large group sizes).

Within-clan group sizes and associations and fission-fusion dynamics

Our finding that average group sizes are not different between clans of different sizes suggests that there is a constraint on group size. The similarity in group sizes across clans resulted in a larger number of sightings of larger clans being required for females to meet their clan-mates. A trade-off between the number of associates of individual females and their average AIs had been seen in elephants in Uda Walawe, Sri Lanka (de Silva *et al*. 2011), which suggests that constraints on sociality might be greater in larger than in smaller clans in that population too if clan-level analyses were carried out. Although larger clans showed higher maximum group sizes in our study, the proportion of sightings in which large group sizes were seen was very small (proportion of sightings with group size of more than five females: average (SD) = 0.055 (0.050), range: 0-0.147, based on the 15 focal clans) and, therefore, larger group sizes did not substantially decrease the number of sightings required for females to meet clan-mates (Supplementary Material 13). Since AIs were mostly low, despite some temporal stability, social structure was fluid rather than consisting of fixed, small groups (on average, group size was one-fourth of the clan size, average (SD)=0.265 (0.198), range=0.081-0.790) in the 15 focal clans; percentage of clan-members who did not meet, averaged across clans=10%).

Fission-fusion dynamics are thought to alter the cost-benefit ratio in response to varying resource availability, with groups fusing together when resources are abundant and fissioning when within-group competition for resources is high (Kummer 1971, Dunbar 1988, Strier 1992, Chapman 1990, Chapman *et al*. 1995, Wittemyer *et al*. 2005, Aureli *et al*. 2008, Asensio *et al*. 2009). Resource availability and/or aggregation have been shown to affect grouping in non-Elephantid species with high fission-fusion dynamics such as spider monkeys (Symington 1988, Asensio *et al*. 2009), chimpanzees (Wittiger and Boesch 2013), brown hyaenas (Owens and Owens 1978), and spotted hyaenas (Smith *et al*. 2008). However, in our population, fission-fusion dynamics primarily allowed for clan-mates to meet, while maintaining similar group sizes, rather than changing group sizes seasonally. Thus, when there is a constraint on group size, fission-fusion dynamics may be a means of associating with different individuals while holding group size relatively constant, rather than a means of increasing or decreasing the group size itself. A constraint on group size can, possibly, change a society from one that is apparently multitiered and hierarchical to one that is apparently multileveled (see chapter 2). In the latter, combinations of individuals without all the individuals from a tier being present would allow for increased sociality without increasing the group size, which would not occur in the former.

That there is a turnover of groups rather than small, fixed groups despite a constraint on group size suggests benefits from interacting with other individuals. Therefore, while small group sizes may be related to the costs of traveling (for example, Wrangham *et al*. 1993, Chapman and Chapman 2000, Lehmann *et al*. 2007, Asensio *et al*. 2009), it also seems important for females in our population to associate with other females beyond the small group. A primary benefit of group living in elephants is cooperative care of offspring (Lee 1987, Lee and Moss 2011, Moss and Lee 2011) and benefits such as exploiting an ephemeral resource or feeding efficiency are thought to be unimportant (Fernando and Lande 2000). Since Asian elephants show allomothering (Gadgil and Nair 1984, Vidya 2014), one of the functions of fission-fusion dynamics in the face of limited group sizes in Asian elephants may be to associate with allomothers when required. Benefits of sociality may also include the acquisition and exchange of ecological and social knowledge as in the African savannah elephant (Mc Comb *et al*. 2001, 2011, Mutinda *et al*. 2011, Chiyo *et al*. 2012) and, possibly, African forest elephant (see Fishlock and Lee 2013).

In summary, we find significant seasonal effects on social structure and group size at the population level and a contrasting lack of such effects at the clan level in female Asian elephants in the Kabini population. We caution against the use of population-based statistics as applied to clans. We find relatively stable clan group sizes and social structure across seasons and years, but low overall association strengths between females within clans, suggesting a turnover of females within groups. Similar average group sizes irrespective of clan size indicates a constraint on group size, affecting larger clans to a greater extent. We find that fission-fusion seems to serve as a means of interacting with more individuals outside the group, while retaining a relatively small group size. It would be interesting to study the benefits of such interactions in the future.

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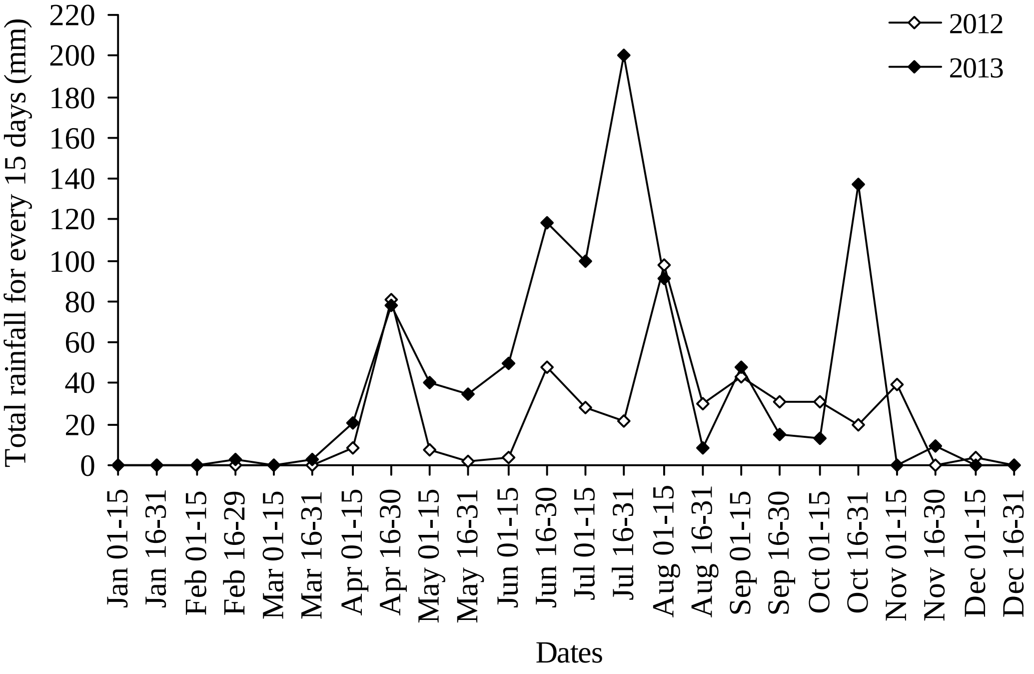
Supplementary Material

Supplementary Material 1. Rainfall data and dates for wet and dry season sampling.

The date of onset of the southwest monsoon is determined by the India Meteorological Department based on 60% of selected weather stations along the southwestern coast of India receiving $\geq$2.5 mm of rainfall for two consecutive days, along with wind conditions and outgoing longwave radiation criteria. We considered the wet season to begin one week from the date of onset of the southwest monsoon (data available from http://www.imd.gov.in/section/nhac/dynamic/Monsoon_frame.htm) because the study area is very close to the southwestern coast of India, and it only takes about a week for the effect of the monsoonal rains to be reflected in the vegetation (due to pre-monsoon showers in the previous two months). As mentioned in the main text, periods with pre-monsoon showers were not included in the wet season as these showers occur in the otherwise dry and hot months of April and May, resulting in little availability of surface water. The dry season was determined as beginning two weeks after the end of the northeast monsoon rains (or three weeks after the midpoint date between the last fortnight of heavy rain, October 16-31, 2013, in Figure 1 below, and the following fortnight with no rain, November 1-15, 2013, in Figure 1 below).



Supplementary Material 1, Figure 1. An example of rainfall patterns recorded at one weather station (Beechanahalli, which is situated in between Bandipur and Nagarahole National Parks) in the study area (rainfall data, courtesy, H.D. Kote Taluka office) plotted every fortnight for the years 2012 and 2013. The beginning of the wet season for 2013 was 8-Jun-2013 and the beginning of the dry season was 1-Dec-2013 (the end of the northeast monsoon was 15-Nov-2013 and there were two days of sporadic rain after that during the second half of November). The year 2012 was a drought year in the study area.

We used photos taken of the forest at different times of the year (for example, see Figure 2 below) to confirm the appropriateness of the start and end dates for each dry and wet season. The average rainfall the study area receives ranges from 625 mm per year in the east of Bandipur (AERCC 1998) to about 1500 mm per year in the west of Nagarahole (Karanth and Sunquist 1992). The dates used to demarcate wet and dry seasons are shown below (Table 1).

Supplementary Material 1, Figure 2. Photos in roughly the same area after the onset of the southwest monsoon (3-Jun-2010) and just before the beginning of the dry season (29-Nov-2013).

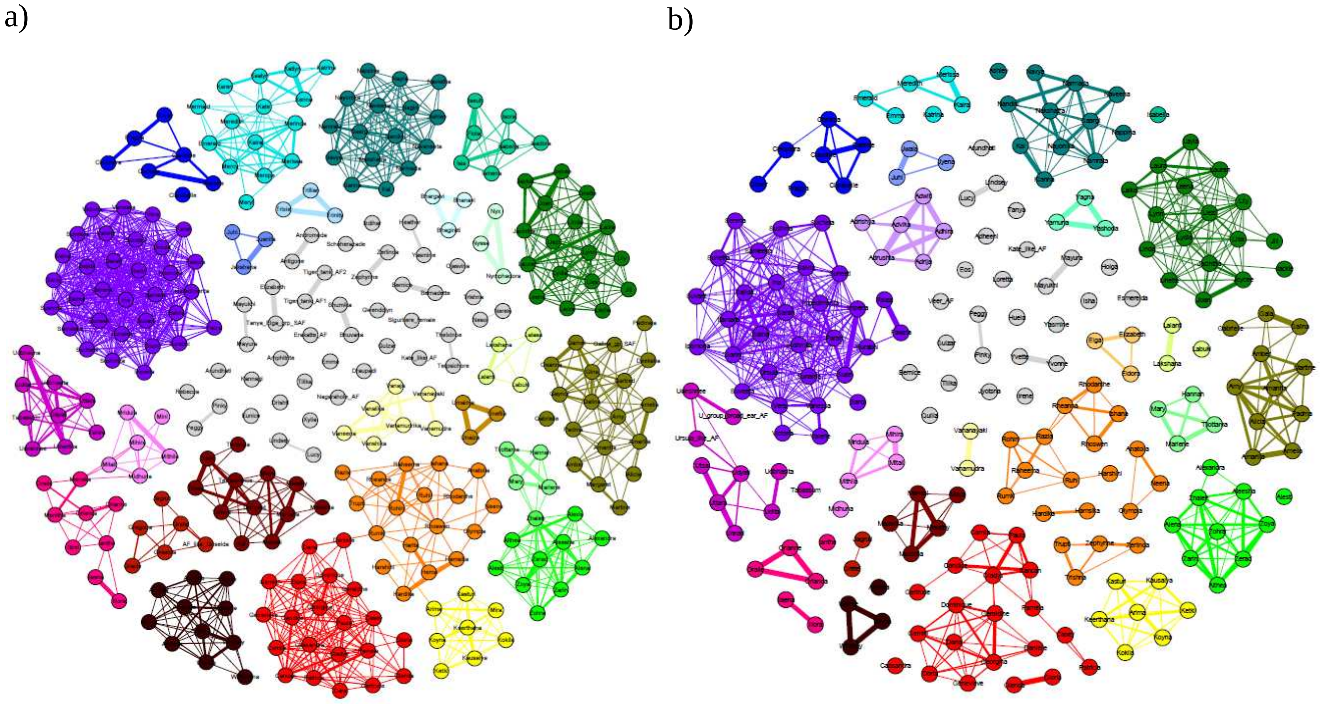
Supplementary Material 1, Table 1. Dates of the onset of the southwest monsoon and end of the northeast monsoon, and dates marking the beginning of the wet and dry seasons from 2008-2014.

Year	Date of onset of SW monsoon	Start of the wet season	Date of end of NE monsoon	Start of the dry season
1	31-May-08	07-Jun-08	15-Nov-08	01-Dec-08
2	23-May-09	30-May-09	15-Dec-09	01-Jan-10
3	31-May-10	07-Jun-10	15-Dec-10	01-Jan-11
4	29-May-11	05-Jun-11	15-Dec-11	01-Jan-12
5	5-Jun-12	12-Jun-12	30-Nov-12	16-Dec-12
6	1-Jun-13	08-Jun-13	15-Nov-13	01-Dec-13
7	6-Jun-14	13-Jun-14	15-Nov-14	01-Dec-14

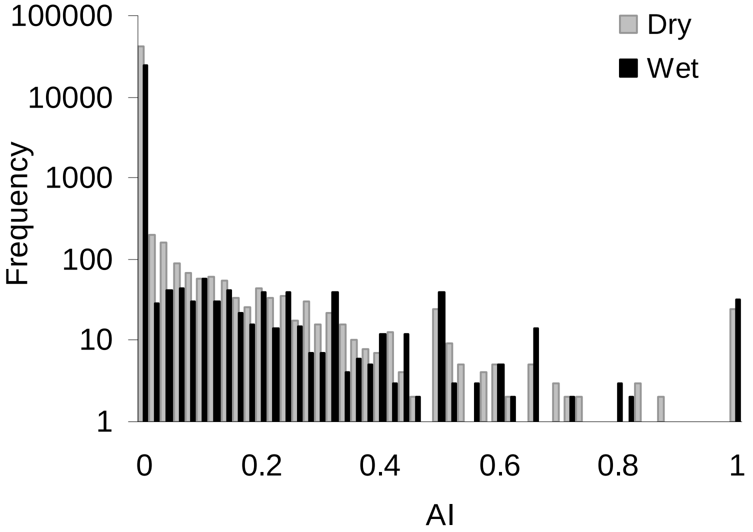
References:

1. AERCC (1998) The Asian elephant in southern India: A GIS database for conservation of Project Elephant Reserves. Asian Elephant Research and Conservation Centre, Bangalore.
2. Karanth KU, Sunquist ME (1992) Population structure, density and biomass of large herbivores in the tropical forests of Nagarahole, India. *Journal of Tropical Ecology* 8: 21-35.

Supplementary Material 2. Social networks based on the entire a) dry and b) wet season datasets. Colours of nodes indicate different clans. Most of the solitary nodes towards the centre are females that were seen only once or a few times. There were only a few connections across clans (discussed in chapter 2).



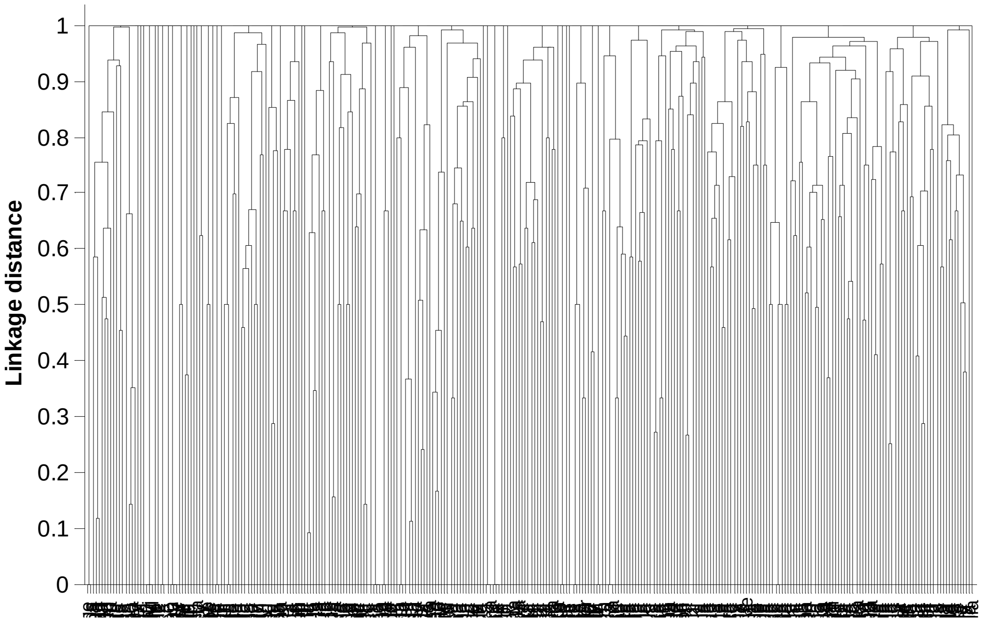
Supplementary Material 3. AI distributions during the dry and wet seasons based on the entire datasets.



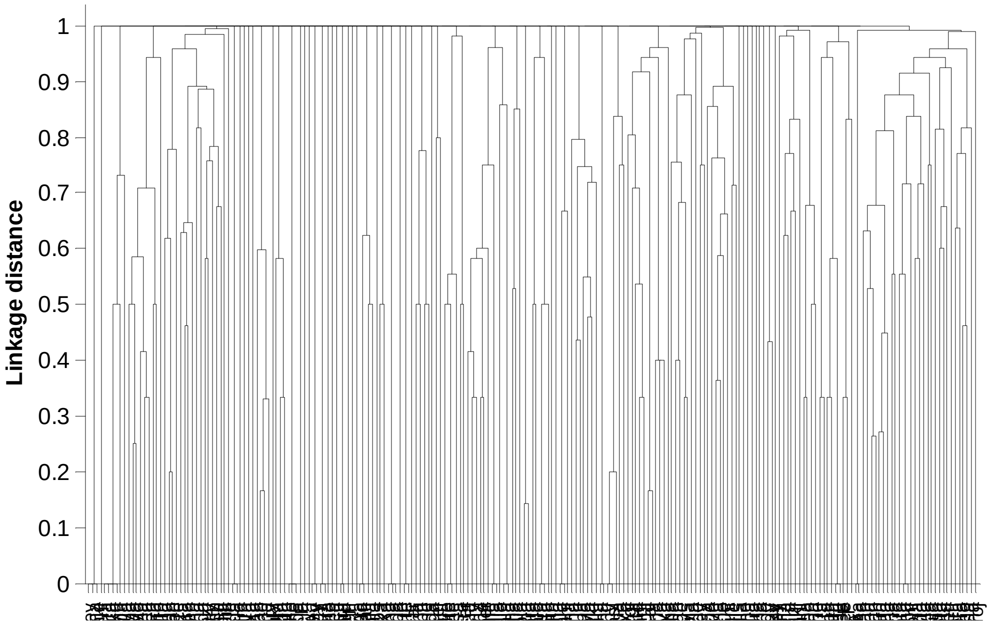
The proportion of non-zero AIs was 2.9% during the dry season and 2.5% during the wet season based on the entire datasets for these seasons.

Supplementary Material 4. Average linkage dendrograms for the a) entire dry season dataset, b) entire wet season dataset, and c) and d) dry and wet season datasets, respectively, based on the same 103 females.

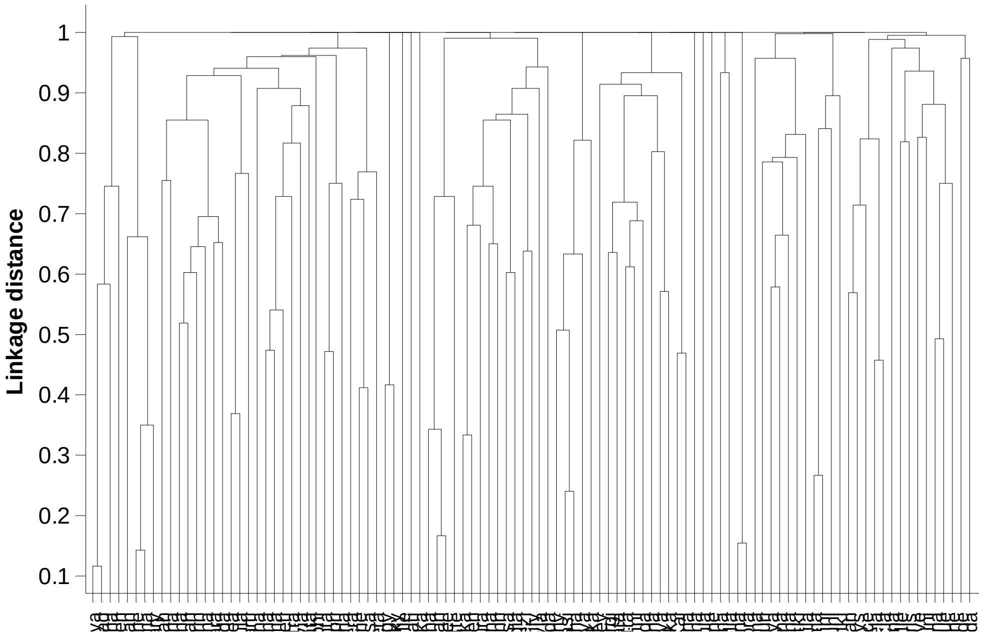
a) Entire dry season dataset



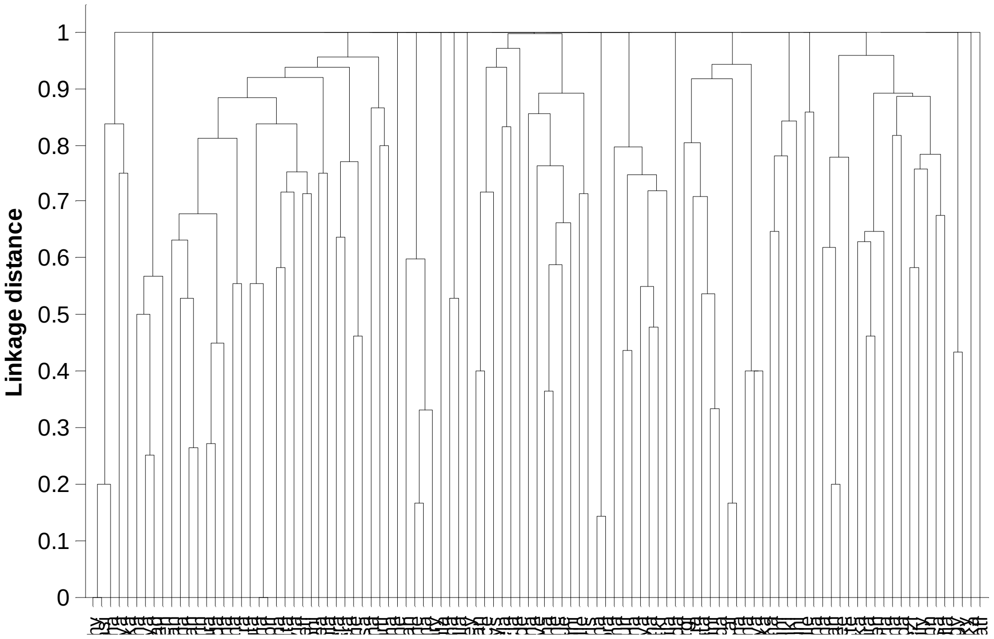
b) Entire wet season dataset



c) Dry season based on 103 common females



d) Wet season based on 103 common females



Supplementary Material 5. AI and network statistics for nine focal clans, and averages of these statistics based on the two-sample permutation test with 10,000 permutations. *P* values from the two-sample permutation test to test for differences across seasons are shown and the significant ones are in bold.

Season	Average AI (SD)	Skew in AI	Kurtosis of AI	Average degree (SD)	Average clustering coefficient (SD)	Average path length (SD)	Modu-larity	Density	No. of shortest paths
Kasturi									
Dry observed	0.147 (0.1325)	0.691	2.45	7.0 (0.00)	1.00 (0.000)	1.00 (0.000)	0.163	1.000	56
Dry permuted	0.154 (0.1230)	0.459	2.31	6.8 (0.23)	0.99 (0.013)	1.03 (0.051)	0.104	0.974	56.0
Wet observed	0.290 (0.1167)	1.050	3.22	6.0 (0.00)	1.00 (0.000)	1.00 (0.000)	0.017	1.000	42
Wet permuted	0.164 (0.1367)	0.751	3.11	5.4 (1.30)	0.93 (0.095)	1.20 (0.370)	0.108	0.800	51.8
P value	1.000	0.606	0.632	0.877	0.877	0.267	**<0.001**	0.877	0.256
Lisa									
Dry observed	0.105 (0.1612)	2.223	8.09	12.2 (2.68)	0.87 (0.093)	1.24 (0.426)	0.424	0.765	272
Dry permuted	0.104 (0.1490)	2.208	8.53	12.4 (2.72)	0.88 (0.081)	1.22 (0.418)	0.385	0.777	272.0
Wet observed	0.100 (0.1307)	2.134	9.14	10.6 (3.83)	0.86 (0.116)	1.37 (0.542)	0.277	0.662	272
Wet permuted	0.107 (0.1584)	2.224	8.72	9.6 (3.01)	0.84 (0.135)	1.45 (0.578)	0.384	0.606	264.5
P value	0.290	0.407	0.662	0.782	0.811	0.290	**0.026**	0.766	1.000
Manasi									
Dry observed	0.136 (0.2272)	2.208	7.24	6.8 (2.29)	0.83 (0.120)	1.52 (0.749)	0.469	0.621	132
Dry permuted	0.140 (0.2381)	2.099	6.66	6.0 (2.08)	0.87 (0.119)	1.40 (0.608)	0.483	0.559	108.8
Wet observed	0.382 (0.343)	0.876	2.02	4.0 (0.00)	1.00 (0.000)	1.00 (0.000)	0.057	1.000	20
Wet permuted	0.199 (0.2943)	1.510	4.26	3.9 (1.36)	0.96 (0.060)	1.11 (0.194)	0.424	0.470	46.6
P value	0.992	0.059	**0.033**	0.614	1.000	0.534	0.067	0.946	0.075

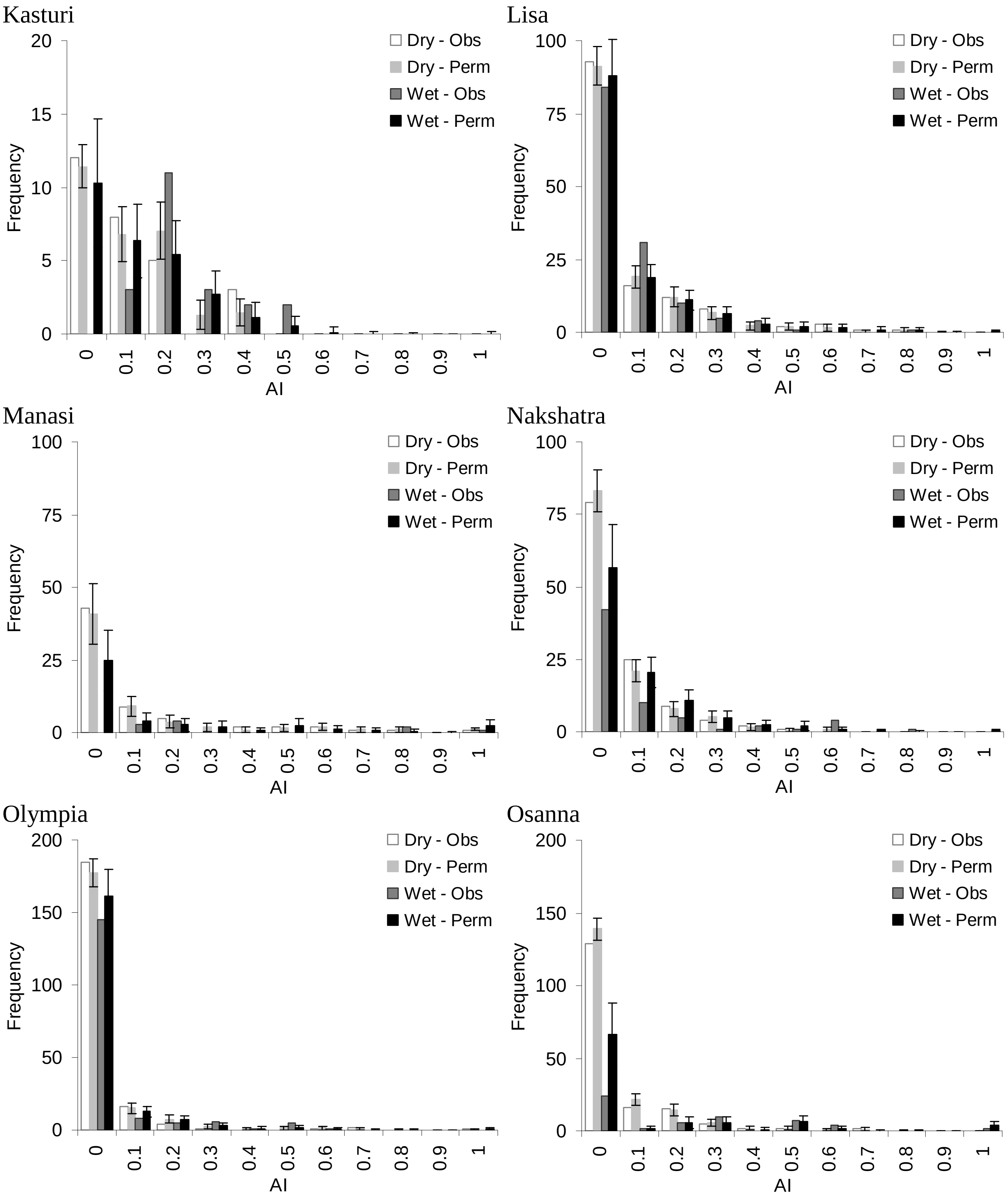
Supplementary Material 5 Contd.

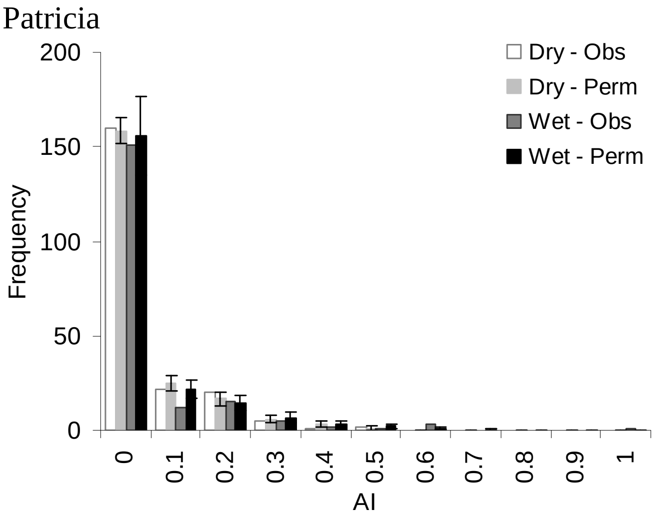
Season	Average AI (SD)	Skew in AI	Kurtosis of AI	Average degree (SD)	Average clustering coefficient (SD)	Average path length (SD)	Modu-larity	Density	No. of shortest paths
Nakshatra									
Dry observed	0.098 (0.1030)	1.885	6.67	12.6 (2.36)	0.90 (0.060)	1.16 (0.367)	0.185	0.842	240
Dry permuted	0.094 (0.1079)	2.137	8.31	12.2 (2.59)	0.89 (0.066)	1.18 (0.390)	0.207	0.816	239.9
Wet observed	0.126 (0.1915)	1.958	6.17	6.2 (2.89)	0.85 (0.163)	1.33 (0.474)	0.334	0.561	110
Wet permuted	0.113 (0.1479)	1.895	7.67	7.5 (3.10)	0.81 (0.156)	1.46 (0.568)	0.250	0.553	186.9
P value	0.644	0.695	0.585	0.184	0.668	0.274	0.881	0.450	**0.018**
Olympia									
Dry observed	0.040 (0.1187)	5.302	35.58	5.3 (3.26)	0.70 (0.207)	1.82 (0.736)	0.535	0.267	308
Dry permuted	0.041 (0.1073)	4.075	23.14	5.0 (2.57)	0.70 (0.230)	2.07 (0.921)	0.591	0.252	330.1
Wet observed	0.048 (0.1253)	2.850	10.56	3.1 (1.35)	0.90 (0.184)	1.73 (0.891)	0.724	0.170	110
Wet permuted	0.045 (0.1221)	4.039	22.85	3.9 (2.23)	0.73 (0.244)	2.11 (1.003)	0.589	0.208	240.0
P value	0.660	**0.005**	**0.006**	0.136	0.960	0.389	0.975	0.164	0.177
Osanna									
Dry observed	0.072 (0.1325)	2.626	10.98	7.5 (3.64)	0.77 (0.153)	1.63 (0.656)	0.354	0.415	306
Dry permuted	0.073 (0.1301)	2.594	11.15	8.0 (3.65)	0.77 (0.173)	1.65 (0.616)	0.388	0.425	370.4
Wet observed	0.240 (0.2670)	0.972	3.39	5.6 (1.96)	0.81 (0.17)	1.55 (0.69)	0.179	0.564	110
Wet permuted	0.137 (0.2551)	2.002	6.53	3.7 (2.17)	0.85 (0.210)	1.56 (0.625)	0.405	0.285	107.8
P value	0.993	**0.011**	0.102	0.912	0.240	0.553	0.074	0.989	0.851

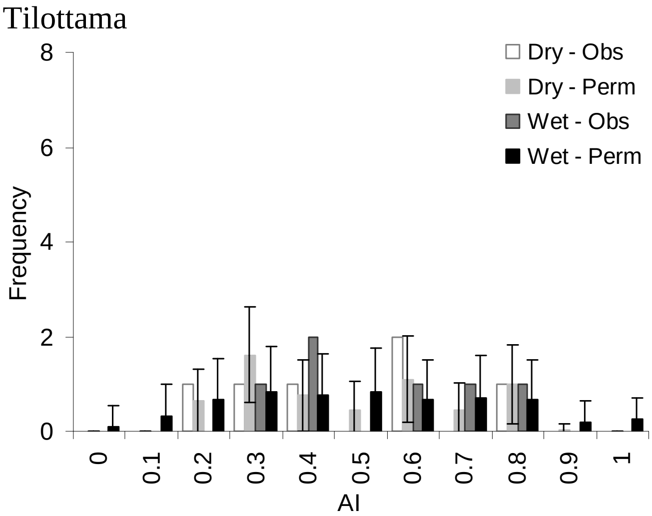
Supplementary Material 5 Contd.

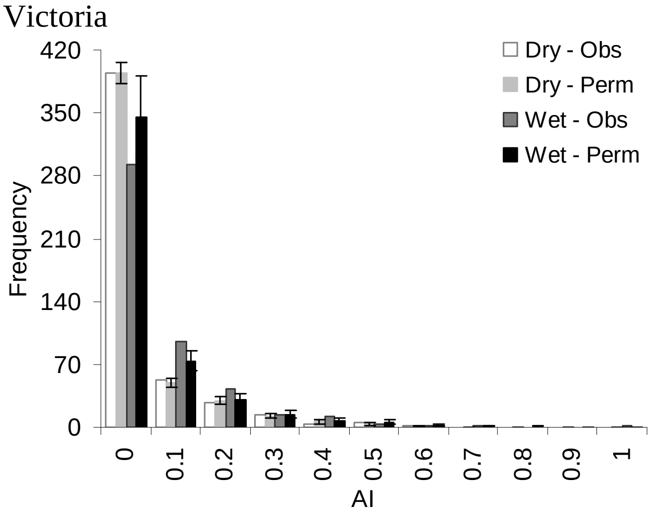
Season	Average AI (SD)	Skew in AI	Kurtosis of AI	Average degree (SD)	Average clustering coefficient (SD)	Average path length (SD)	Modu-larity	Density	No. of shortest paths
Patricia									
Dry observed	0.063 (0.1034)	2.064	7.21	13.5 (4.31)	0.84 (0.067)	1.35 (0.525)	0.346	0.676	420
Dry permuted	0.066 (0.1066)	1.977	6.56	13.0 (4.33)	0.84 (0.082)	1.38 (0.533)	0.398	0.649	419.4
Wet observed	0.061 (0.1421)	3.240	16.05	4.6 (2.74)	0.74 (0.277)	2.30 (1.178)	0.568	0.242	274
Wet permuted	0.068 (0.1179)	2.274	8.80	8.1 (3.73)	0.85 (0.137)	1.66 (0.725)	0.403	0.412	335.1
P value	0.394	0.949	0.941	**<0.001**	**0.016**	0.996	1.000	**0.001**	0.111
Tilottama									
Dry observed	0.528 (0.2286)	0.256	1.64	3.0 (0.00)	1.00 (0.000)	1.00 (0.000)	0.000	1.000	12
Dry permuted	0.533 (0.2223)	0.305	1.64	3.0 (0.00)	1.00 (0.000)	1.00 (0.000)	0.000	1.000	12.0
Wet observed	0.563 (0.1898)	0.298	1.54	3.0 (0.00)	1.00 (0.000)	1.00 (0.000)	0.000	1.000	12
Wet permuted	0.532 (0.2378)	0.365	1.83	3.0 (0.02)	1.00 (0.005)	1.00 (0.008)	0.001	0.994	12.0
P value	0.628	0.580	0.421	1.000	1.000	0.985	0.974	1.000	1.000
Victoria									
Dry observed	0.074 (0.0992)	2.597	10.60	27.6 (3.85)	0.92 (0.028)	1.11 (0.312)	0.323	0.891	992
Dry permuted	0.076 (0.0981)	2.524	10.06	28.4 (3.46)	0.94 (0.023)	1.08 (0.275)	0.308	0.918	992.0
Wet observed	0.095 (0.138)	2.571	12.88	16.3 (7.60)	0.86 (0.091)	1.54 (0.643)	0.255	0.544	930
Wet permuted	0.164 (0.1367)	0.751	3.11	5.4 (1.30)	0.93 (0.095)	1.20 (0.370)	0.108	0.800	51.8
P value	0.914	0.612	0.773	0.780	0.999	0.363	0.063	0.804	0.455

Supplementary Material 6. Observed AI distributions during the dry and wet seasons for nine focal clans, and averages (±SD) of AI distributions (for each season) based on the two-sample permutation test with 10,000 permutations.




Patricia
Dry - Obs
Dry - Perm
Wet - Obs
Wet - Perm
Frequency
200
150
100
50
0
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
AI

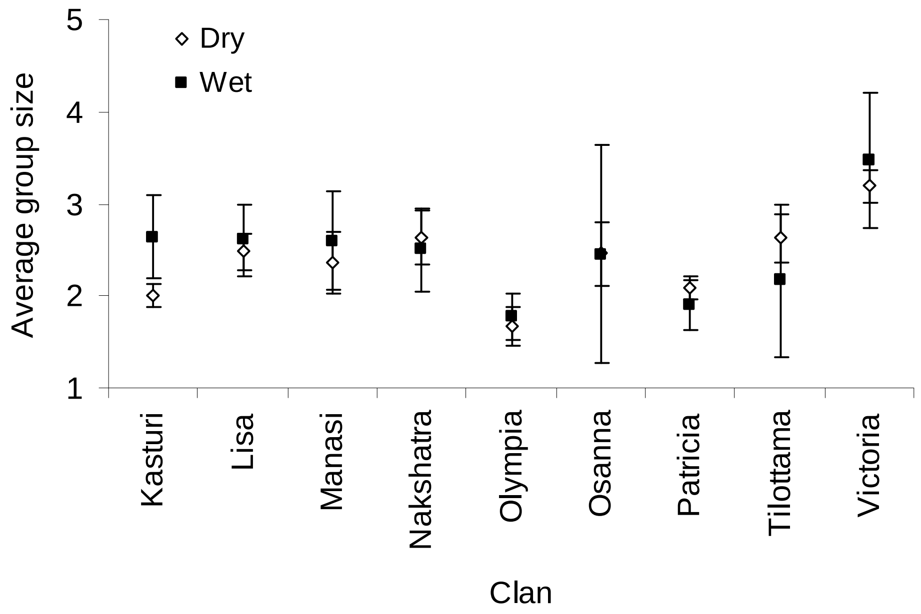

Tilottama
Dry - Obs
Dry - Perm
Wet - Obs
Wet - Perm
Frequency
8
6
4
2
0
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
AI


Victoria
Dry - Obs
Dry - Perm
Wet - Obs
Wet - Perm
Frequency
420
350
280
210
140
70
0
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
AI

Supplementary Material 7. *P* values from the two-sample permutation (with 10,000 permutations) test to assess differences in AI distributions (using frequencies in different AI bins as shown in Supplementary Material 6) between seasons for each of nine focal clans.

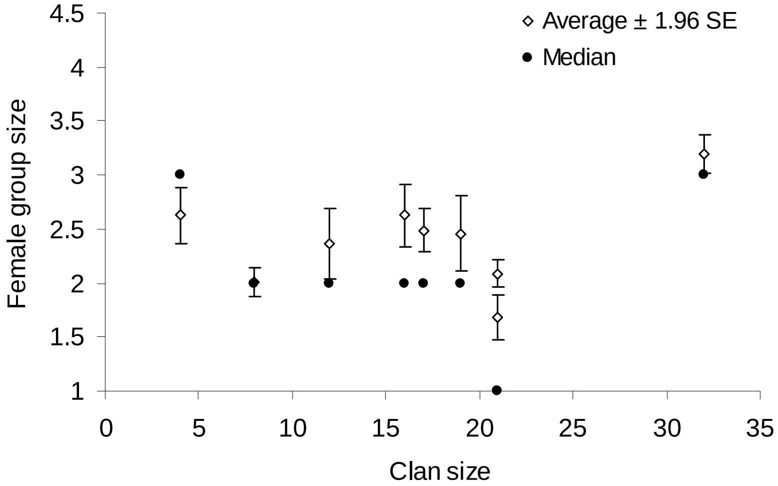
	AI range										
Clan	0-<0.1	0.1-<0.2	0.2-<0.3	0.3-<0.4	0.4-<0.5	0.5-<0.6	0.6-<0.7	0.7-<0.8	0.8-<0.9	0.9-<1.0	1.0
Kasturi	**0.003**	0.073	1.000	0.845	0.497	0.992	0.886	0.980	0.996	1.000	0.984
Lisa	0.244	0.997	0.464	0.258	0.972	0.341	0.053	0.119	0.859	0.909	0.773
Manasi	**0.018**	0.614	0.612	0.633	0.206	0.201	0.308	0.459	0.972	0.884	0.382
Nakshatra	0.257	**0.036**	0.065	0.216	0.484	0.274	1.000	0.743	0.991	0.997	0.751
Olympia	0.115	0.191	0.665	0.971	0.804	0.995	0.732	0.080	0.823	0.998	0.123
Osanna	0.071	0.948	0.564	0.902	0.425	0.640	0.946	0.255	0.935	1.000	0.322
Patricia	0.256	0.122	0.348	0.484	0.756	0.160	0.998	0.896	0.982	0.999	1.000
Tilottama	0.933	0.784	0.481	0.844	0.906	0.531	0.547	0.829	0.866	0.861	0.750
Victoria	**0.049**	0.867	0.969	0.483	0.974	0.078	0.243	0.935	0.731	0.980	0.990

Supplementary Material 8. Average (±1.96 SE) group sizes of nine focal clans in the dry and wet seasons.

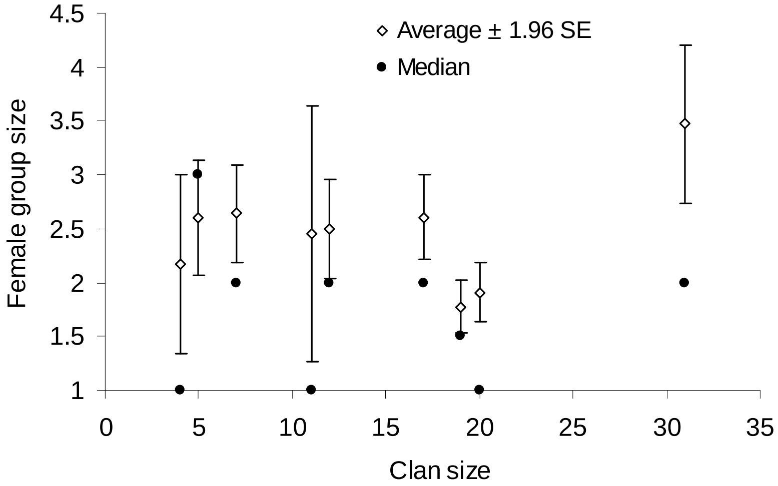


Supplementary Material 9. Average (±1.96 SE) and median group size plotted against clan size for the a) dry and b) wet seasons.

a)



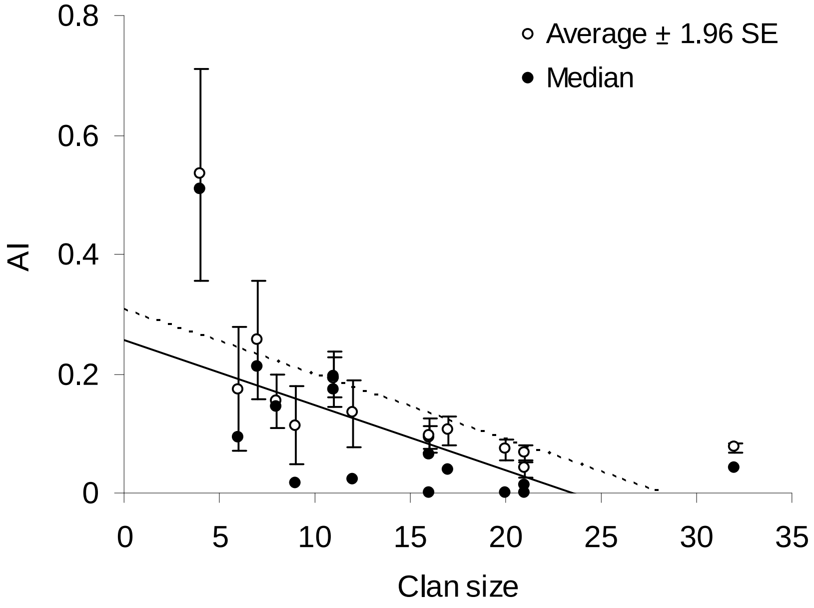
b)



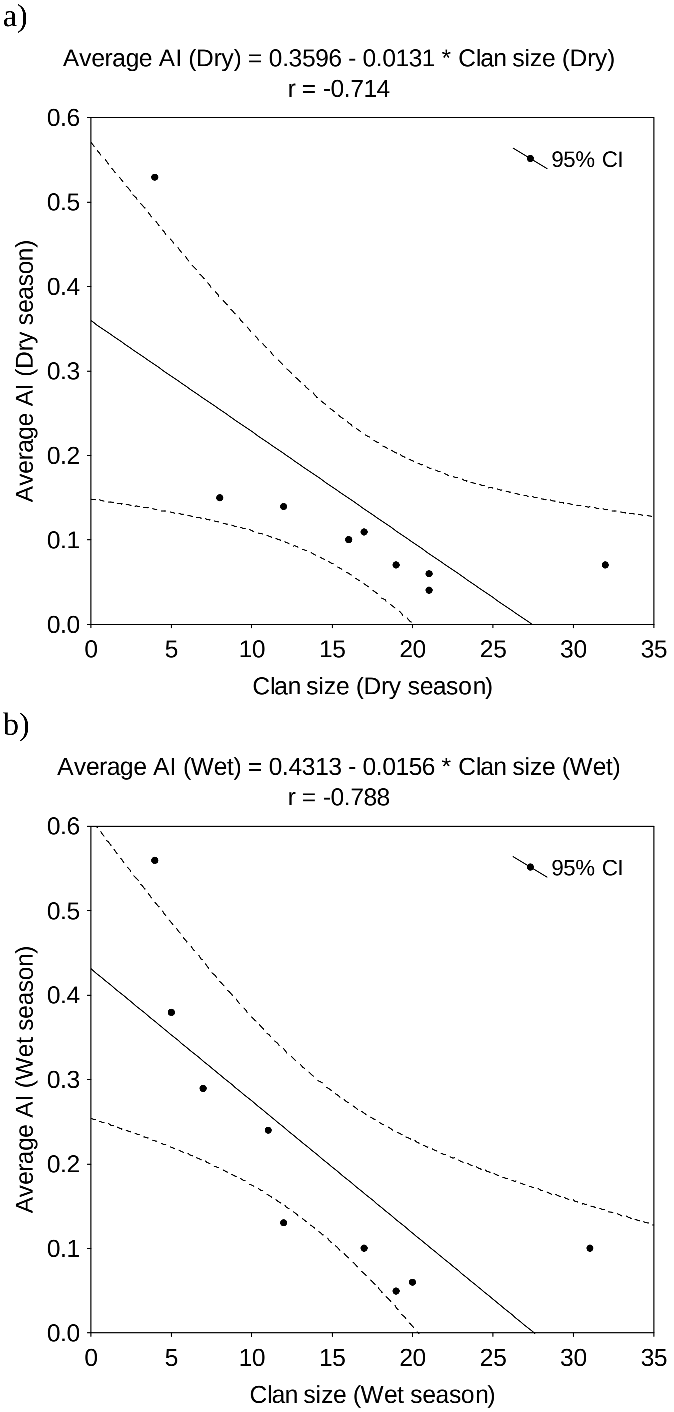
There was no relationship between group size and clan size. The clan sizes used here are the numbers of females seen during the wet or dry seasons, hence they are different in some clans because of not sighting the entire clan in a season. However, the results do not change if the overall clan sizes are used in both cases.

Supplementary Material 10. Regressions of AI on clan size.

In the main text, regression of clan size on average AI had been shown to be significant (R = -0.669, R^2=0.447, P<0.006). Since there could be pairs of individuals that we had never seen together in larger clans, such clans could have zero AI values, which might affect the results. The analysis was, therefore, repeated on the non-zero AIs also, and was also found to give similar results (R = -0.706, R^2=0.498, P<0.003). We also carried out the analysis using median AI instead of average AI and found similar results (R = -0.600, R^2=0.360, P<0.018).



Supplementary Material 10, Figure 1: Average (±1.96 SE) (open circles) and median (solid circles) AI plotted against clan size for 15 focal clans based on the entire data. While the averages had already been shown in the main text, they are repeated here for visual comparison with the medians. The regression lines based on average AI and median AI are shown as dotted and solid lines, respectively.



Supplementary Material 10, Figure 2: Regressions of clan size on average AI during the a) dry (R^2=0.509, $F_{1,7}$=7.264, P<0.031) and b) wet (R^2=0.621, $F_{1,7}$=11.471, P<0.012) seasons.

Supplementary Material 11. Details of permutation tests using SOCPROG.

Permutations were carried out in SOCPROG 2.4 using 14-day sampling periods. Association data for each focal clan were randomly permuted in order to find out whether the observed average AI was significantly lower than random and whether the observed SD and CV of AI were significantly higher than random. We used 5000 permutations with 1000 flips per permutation for this test because we found that increasing the number of permutations or flips further did not change the results (shown below).

Supplementary Material 11, Table 1: *P* values for different numbers of permutations carried out on the largest clan, using 1000 and 10000 flips per permutation. Statistically significant values are marked in bold.

Number of permutations	Statistic	Observed value	Ave. random value using 1000 flips	*P* (1000 flips)	Ave. random value using 10000 flips	*P* (10000 flips)
1000	Mean AI	0.1669	0.2205	**0.001**	0.2233	**0.001**
	SD of AI	0.1527	0.1195	**0.999**	0.1181	**0.999**
	CV of AI	0.9146	0.5430	**1.000**	0.5288	**1.000**
	Mean non-zero AI	0.1804	0.2268	**0.001**	0.2286	**0.001**
	SD of non-zero AI	0.1509	0.1152	**1.000**	0.1143	**0.999**
	CV of non-zero AI	0.8363	0.5089	**0.999**	0.5002	**1.000**
5000	Mean AI	0.1669	0.2230	**<0.001**	0.2234	**<0.001**
	SD of AI	0.1527	0.1178	**1.000**	0.1178	**1.000**
	CV of AI	0.9146	0.5284	**1.000**	0.5276	**1.000**
	Mean non-zero AI	0.1804	0.2282	**<0.001**	0.2283	**<0.001**
	SD of non-zero AI	0.1509	0.1140	**1.000**	0.1143	**1.000**
	CV of non-zero AI	0.8363	0.4997	**1.000**	0.5006	**1.000**
10000	Mean AI	0.1669	0.2235	**<0.001**	0.2234	**<0.001**
	SD of AI	0.1527	0.1183	**1.000**	0.1178	**1.000**
	CV of AI	0.9146	0.5293	**1.000**	0.5273	**1.000**
	Mean non-zero AI	0.1804	0.2284	**<0.001**	0.2282	**<0.001**
	SD of non-zero AI	0.1509	0.1148	**1.000**	0.1144	**1.000**
	CV of non-zero AI	0.8363	0.5025	**1.000**	0.5011	**1.000**

Number of permutations	Statistic	Observed value	Ave. random value using 1000 flips	*P* value (1000 flips)	Ave. random value using 10000 flips	*P* value (10000 flips)
15000	Mean AI	0.1669	0.2232	**<0.001**	0.2234	**<0.001**
	SD of AI	0.1527	0.1178	**1.000**	0.1180	**1.000**
	CV of AI	0.9146	0.5279	**1.000**	0.5280	**1.000**
	Mean non-zero AI	0.1804	0.2280	**<0.001**	0.2284	**<0.001**
	SD of non-zero AI	0.1509	0.1144	**1.000**	0.1144	**1.000**
	CV of non-zero AI	0.8363	0.5016	**1.000**	0.5012	**1.000**
20000	Mean AI	0.1669	0.2233	**<0.001**	0.2235	**<0.001**
	SD of AI	0.1527	0.1181	**1.000**	0.1178	**1.000**
	CV of AI	0.9146	0.5289	**1.000**	0.5271	**1.000**
	Mean non-zero AI	0.1804	0.2284	**<0.001**	0.2283	**<0.001**
	SD of non-zero AI	0.1509	0.1145	**1.000**	0.1143	**1.000**
	CV of non-zero AI	0.8363	0.5014	**1.000**	0.5008	**1.000**

Supplementary Material 12. Permutation test results for focal clans based on all data, and only dry and wet seasons. Only focal clans with at least 20 sightings in the dataset being considered were used in the permutation tests.

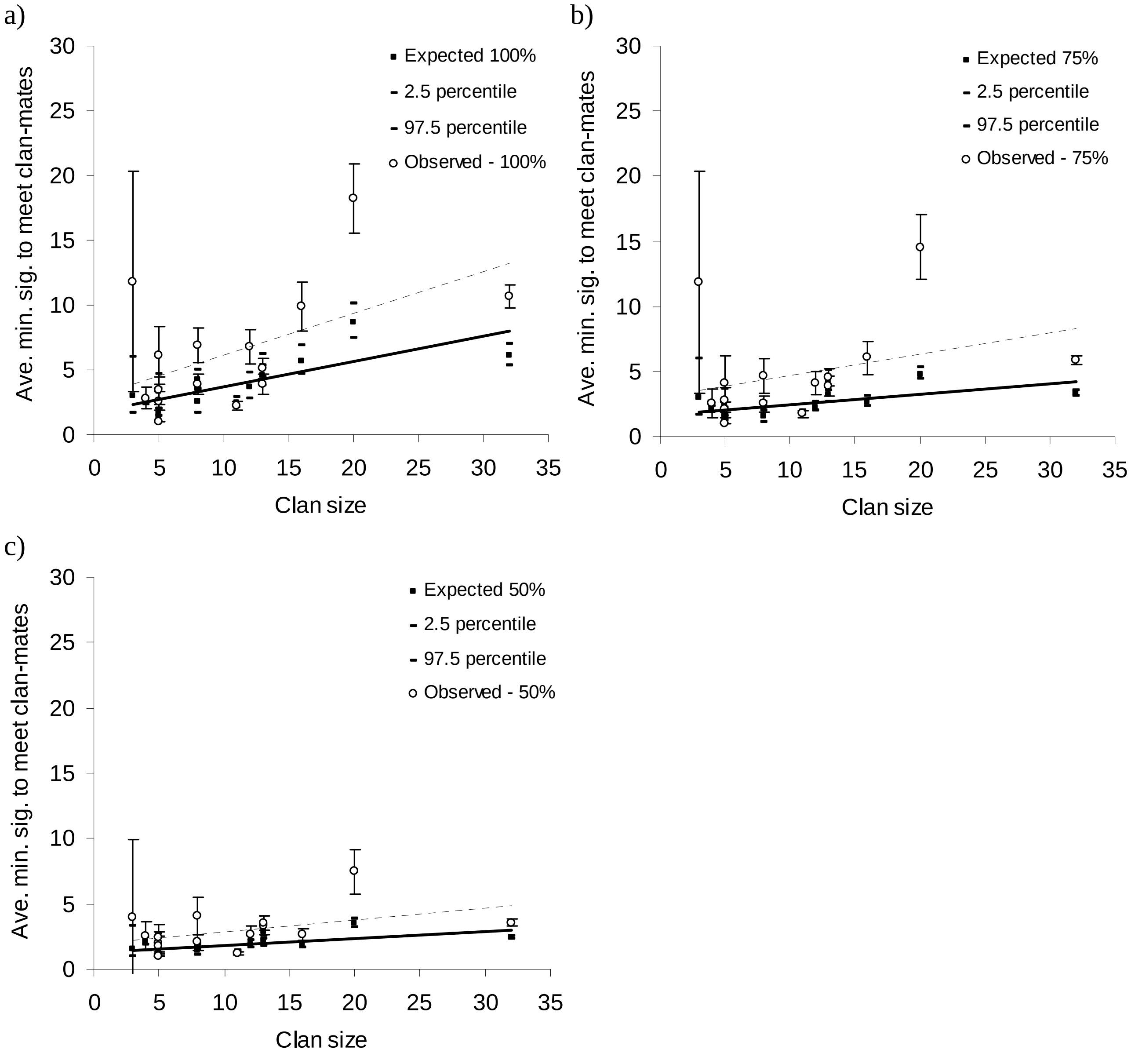
Clan	Season	Mean AI (*P* value)	SD for AI (*P* value)	CV for AI (*P* value)
Alexandra	All	0.210 (**<0.001**)	0.146 (0.252)	0.693 (0.923)
	Dry	0.238 (<**0.001**)	0.167 (0.049)	0.705 (0.767)
	Wet	–	–	–
Anabelle	All	0.282 (**<0.001**)	0.180 (**1.000**)	0.638 (**1.000**)
	Dry	0.290 (<**0.001**)	0.184 (**1.000**)	0.635 (**1.000**)
	Wet	–	–	–
Fiola	All	0.237 (0.070)	0.200 (0.931)	0.846 (0.932)
	Dry	0.251 (0.067)	0.213 (0.934)	0.849 (0.932)
	Wet	–	–	–
Kasturi	All	0.317 (**<0.001**)	0.218 (**1.000**)	0.688 (**1.000**)
	Dry	0.313 (<**0.001**)	0.233 (**1.000**)	0.744 (**1.000**)
	Wet	0.434 (**0.005**)	0.121 (0.785)	0.279 (0.881)
Katrina	All	0.105 (0.898)	0.177 (0.884)	1.679 (0.602)
	Dry	0.117 (0.206)	0.193 (0.607)	1.648 (0.657)
	Wet	–	–	–
Lisa	All	0.147 (**<0.001**)	0.175 (**1.000**)	1.196 (**1.000**)
	Dry	0.153 (<**0.001**)	0.192 (**1.000**)	1.256 (**1.000**)
	Wet	0.127 (<**0.001**)	0.145 (**1.000**)	1.140 (**1.000**)
Manasi	All	1.150 (**0.026**)	0.232 (**1.000**)	1.550 (**1.000**)
	Dry	0.152 (**0.005**)	0.229 (**1.000**)	1.511 (**1.000**)
	Wet	0.373 (**0.017**)	0.351 (**0.984**)	0.939 (**0.984**)
Menaka	All	0.117 (0.987)	0.195 (**1.000**)	1.669 (0.937)
	Dry	0.108 (0.976)	0.178 (**1.000**)	1.655 (**0.991**)
	Wet	–	–	–
Mridula	All	0.220 (0.070)	0.220 (**1.000**)	1.001 (**1.000**)
	Dry	0.226 (0.089)	0.235 (**1.000**)	1.036 (**1.000**)
	Wet	–	–	–

Clan	Season	Mean AI (*P* value)	SD for AI (*P* value)	CV for AI (*P* value)
Nakshatra	All	0.131 (**<0.001**)	0.138 (**1.000**)	1.051 (**1.000**)
	Dry	0.141 (<**0.001**)	0.141 (**0.999**)	0.997 (**1.000**)
	Wet	0.144 (**0.048**)	0.218 (**1.000**)	1.514 (**1.000**)
Olympia	All	0.047 (0.835)	0.104 (**1.000**)	2.227 (**1.000**)
	Dry	0.048 (0.797)	0.118 (**1.000**)	2.458 (**1.000**)
	Wet	0.052 (0.838)	0.134 (**1.000**)	2.575 (**1.000**)
Osanna	All	0.090 (**<0.001**)	0.145 (**1.000**)	1.622 (**1.000**)
	Dry	0.087 (<**0.001**)	0.150 (**0.989**)	1.710 (**1.000**)
	Wet	–	–	–
Patricia	All	0.104 (**<0.001**)	0.150 (**1.000**)	1.442 (**1.000**)
	Dry	0.107 (**<0.001**)	0.154 (**1.000**)	1.444 (**1.000**)
	Wet	0.070 (0.998)	0.152 (**1.000**)	2.187 (**1.000**)
Tilottama	All	0.626 (0.237)	0.142 (**0.999**)	0.226 (**0.999**)
	Dry	0.669 (0.192)	0.134 (**0.999**)	0.200 (**0.999**)
	Wet	–	–	–
Victoria	All	0.167 (**<0.001**)	0.153 (**1.000**)	0.915 (**1.000**)
	Dry	0.172 (<**0.001**)	0.168 (**1.000**)	0.978 (**1.000**)
	Wet	0.146 (<**0.001**)	0.184 (0.783)	1.261 (**1.000**)

* The values of mean AI in this table are different from clan AIs shown in the main text because a two week sampling period was used for this randomisation analysis.

Supplementary Material 13. Waiting time to meet clan-mates.

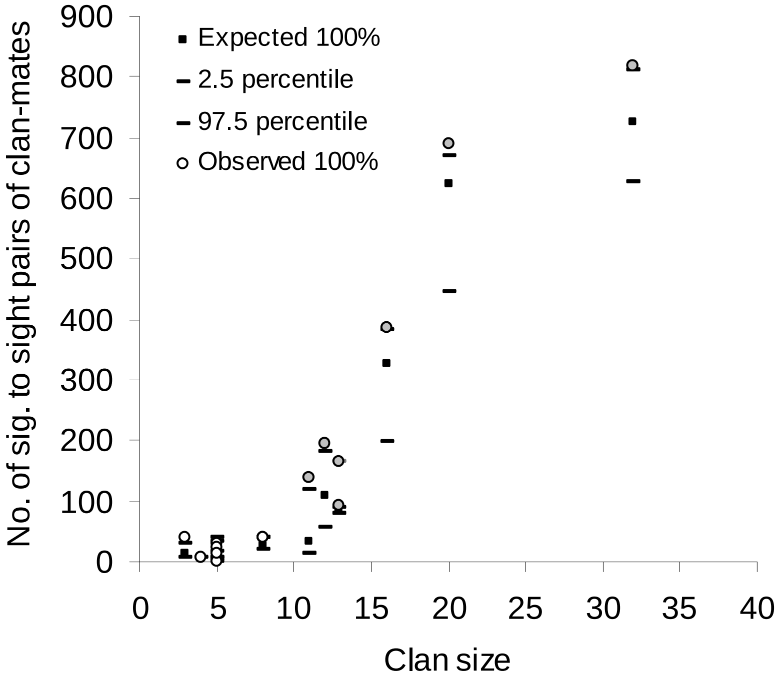
As explained in the main text, we examined the waiting time for females in clans of different sizes to meet their clan-mates. Figure 7 in the main text shows the average of the minimum number of sightings of females in the 15 focal clans to meet all their clan-mates (shown below again as Expected and Observed 100%). Also shown below, are the average of the minimum number of sightings of females in different clans to meet 75% of their clan-mates and 50% of their clan-mates.



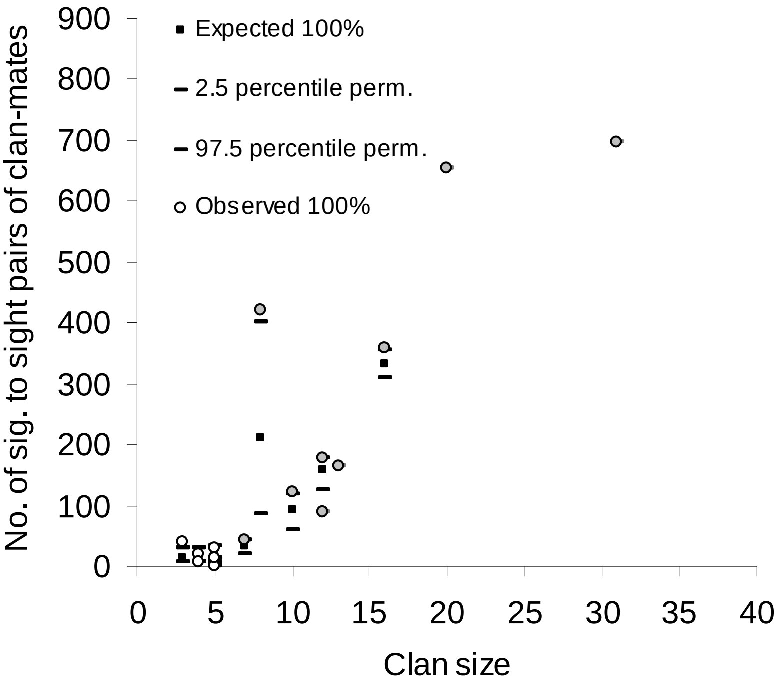
Supplementary Material 13, Figure 1: Average observed and expected minimum number of sightings of females in the 15 focal clans to meet a) 100% (also shown in the main text,

Figure 7), b) 75%, and c) 50% of their clan-mates. The expected values were obtained by permuting the sighting data, and 2.5 and 97.5 percentiles of the expected values are also shown. Error bars for the observed data are 1.96 SE of the mean. Trendlines for the average observed (dotted lines) and average expected (solid lines) values are shown. It must be noted that some of the females did not meet all their clan-mates during the entire period of observation.

We also calculated the waiting time to meet clan-mates in another manner. In the analysis above, the minimum number of sightings that each female took to meet each of the other females was recorded and this matrix of the minimum number of sightings was averaged to obtain the observed or expected values (depending on the original or permuted datasets). We also calculated the minimum number of sightings that were required for us to sight all pairs of females within sightings and used this as the waiting time to meet clan-mates. This was carried out for the original and permuted data (Figure 2 below).



Supplementary Material 13, Figure 2: Observed and average expected minimum number of sightings of the clan required for us to sight all pairs of females within clans. The expected values were obtained by permuting the sighting data, and 2.5 and 97.5 percentiles of the expected values are also shown. In several clans, all pairs of females were not sighted together, despite hundreds of sightings of the clan, and the observed values shown here are one number higher than the number of sightings of that clan. Such observed values are shown as grey circles instead of white circles. All pairs of females were also not seen in the permuted data for one clan and the expected number of sightings in this case is also one number higher than the number of sightings of that clan (Olympia, clan size=13, number of sightings=165).



Supplementary Material 13, Figure 3: Observed and average expected minimum number of sightings of the clan required for us to sight all pairs of females within clans. The difference between this and the previous figure is that this was generated by using only those sightings in which the group size was five females or fewer. As in the previous figure, in several clans, all pairs of females were not sighted together, despite hundreds of sightings of the clan, and the observed values shown here are one number higher than the number of sightings of that clan. Such observed values are shown as grey circles instead of white circles. All pairs of females were also not seen in the permuted data for several clans in this case and the expected numbers of sightings in these cases are also one number higher than the number of sightings of those clans. Therefore, there are several points with the observed value lying at the upper end of the expected values.

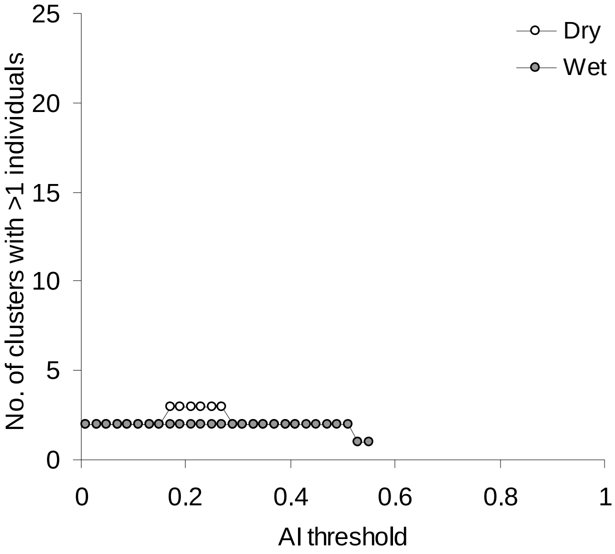
Supplementary Material 14. Results of Mantel tests to examine correlations between AI matrices across time. Since sightings during the wet season were limited, clans sighted at least 15 times during the particular wet season dataset being compared, and at least 20 times in all the other datasets were used for this analysis.

Clan	Comparison	No. of sightings	No. of individuals	Correlation *r*	R^2	*P*
	Consecutive seasons					
Kasturi	Dry 2012, Wet 2012	69, 27	6	0.647	0.419	**0.043**
	Wet 2012, Dry 2013	27, 133	6	0.832	0.692	**0.003**
Lisa	Dry 2011, Wet 2011	34, 22	14	0.699	0.489	**<0.001**
	Wet 2011, Dry 2012	22, 94	14	0.729	0.532	**<0.001**
	Dry 2012, Wet 2012	94, 27	15	0.638	0.408	**<0.001**
	Wet 2012, Dry 2013	27, 94	15	0.519	0.270	**0.001**
	Dry 2013, Wet 2013	94, 20	11	0.464	0.215	**0.009**
	Wet 2013, Dry 2014	20, 52	11	0.473	0.223	**0.002**
Olympia	Dry 2013, Wet 2013	27, 16	8	0.369	0.136	0.102
Patricia	Dry 2009, Wet 2009	33, 34	22	0.636	0.405	**<0.001**
	Dry 2011, Wet 2011	96, 17	12	0.778	0.605	**<0.001**
	Wet 2011, Dry 2012	17, 154	12	0.548	0.301	**<0.001**
	Dry 2012, Wet 2012	154, 22	14	0.741	0.550	**<0.001**
	Wet 2012, Dry 2013	22, 110	15	0.632	0.400	**<0.001**
	Dry 2013, Wet 2013	110, 19	10	0.465	0.216	**0.031**
	Wet 2013, Dry 2014	19, 154	10	0.431	0.186	**0.025**
	Dry 2014, Wet 2014	154, 17	8	0.702	0.493	**0.004**
Victoria	Dry 2009, Wet 2009	69, 29	23	0.646	0.417	**<0.001**
	Dry 2014, Wet 2014	209, 15	13	0.763	0.582	**<0.001**
	Consecutive dry seasons					
Anabelle	2011-2012	31, 26	8	-0.081	0.007	0.524
	2012-2013	26, 27	7	0.124	0.015	0.268
	2013-2014	27, 46	8	0.521	0.272	**0.011**

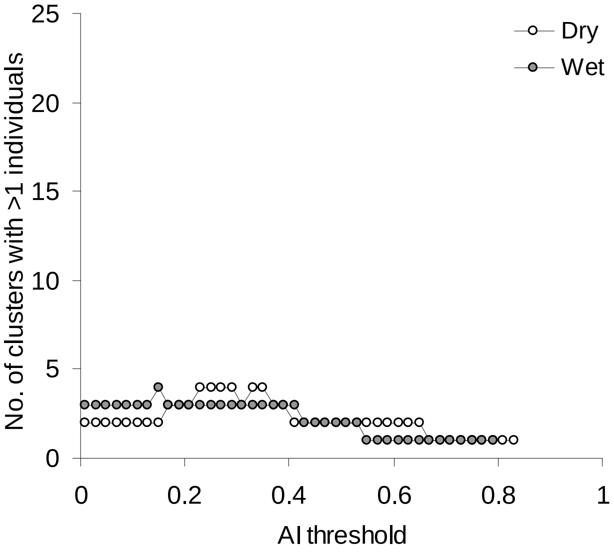
Clan	Comparison	No. of sightings	No. of individuals	Correlation *r*	R^2	*P*
	Consecutive dry seasons					
Kasturi	2011-2012	60, 69	7	0.257	0.066	0.163
	2012-2013	69, 133	7	0.665	0.442	**<0.001**
	2013-2014	133, 85	7	0.640	0.410	**0.005**
Lisa	2011-2012	34, 94	16	0.857	0.734	**<0.001**
	2012-2013	94, 94	16	0.729	0.532	**<0.001**
	2013-2014	94, 52	16	0.740	0.548	**<0.001**
Nakshatra	2011-2012	20, 24	12	0.295	0.087	**0.016**
	2012-2013	24, 47	13	0.203	0.041	0.054
	2013-2014	47, 43	13	0.354	0.125	**0.010**
Olympia	2012-2013	28, 27	9	0.683	0.466	**0.010**
Patricia	2011-2012	96, 154	20	0.663	0.439	**<0.001**
	2012-2013	154, 110	18	0.530	0.280	**<0.001**
	2013-2014	110, 154	18	0.768	0.590	**<0.001**
Victoria	2011-2012	125, 199	28	0.588	0.346	**<0.001**
	2012-2013	199, 136	26	0.710	0.504	**<0.001**
	2013-2014	136, 209	26	0.697	0.486	**<0.001**

Supplementary Material 15. Network structure curves of the nine focal clans that were analysed for dry-wet season differences. The name of the clan and the differences that the network structure curves showed between seasons are written against each plot.

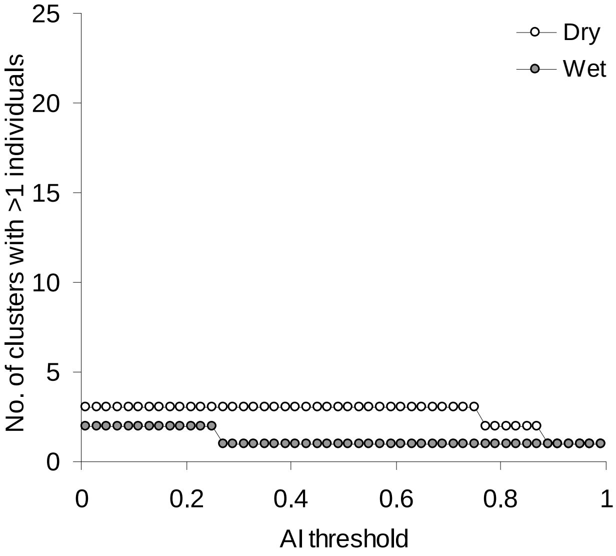
Kasturi: wet slightly right-shifted



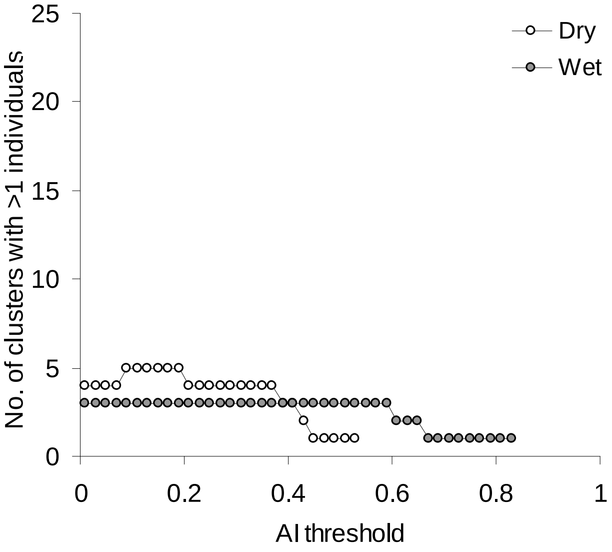
Lisa: dry slightly right-shifted



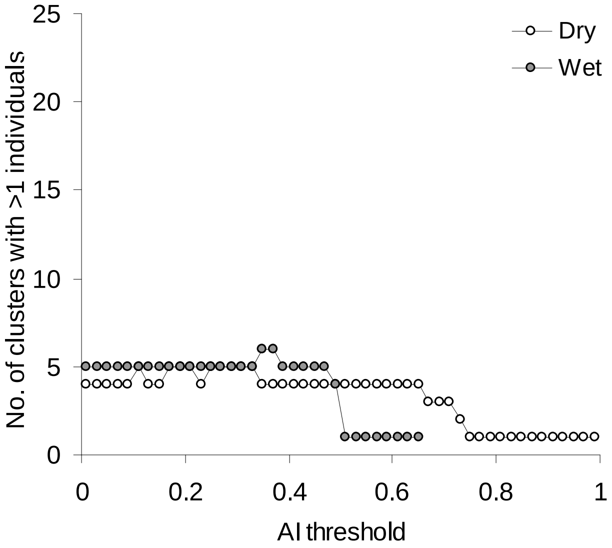
Manasi: dry and wet not very different in shape



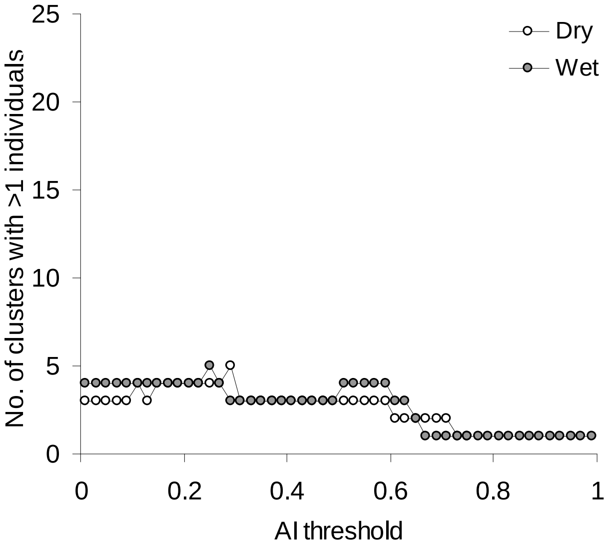
Nakshatra: wet right-shifted



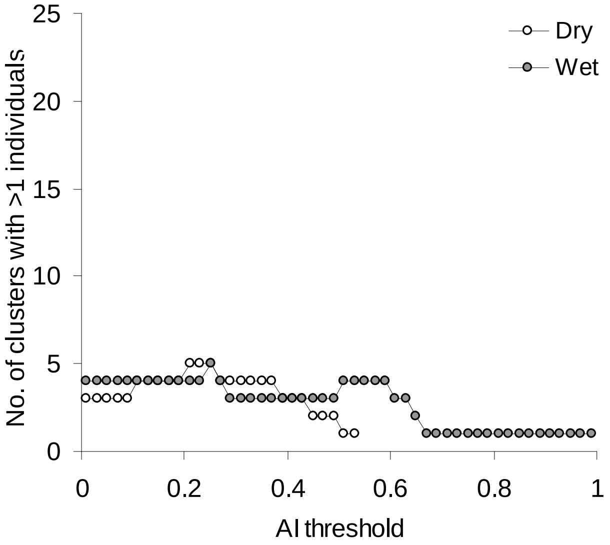
Olympia: dry right-shifted



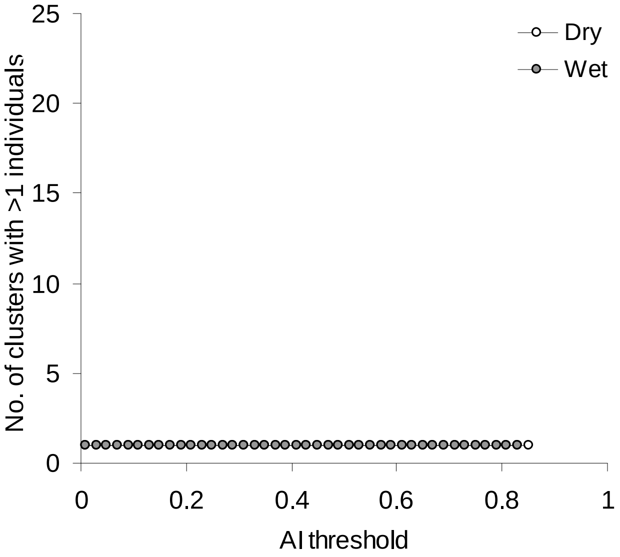
Osanna: dry and wet not very different



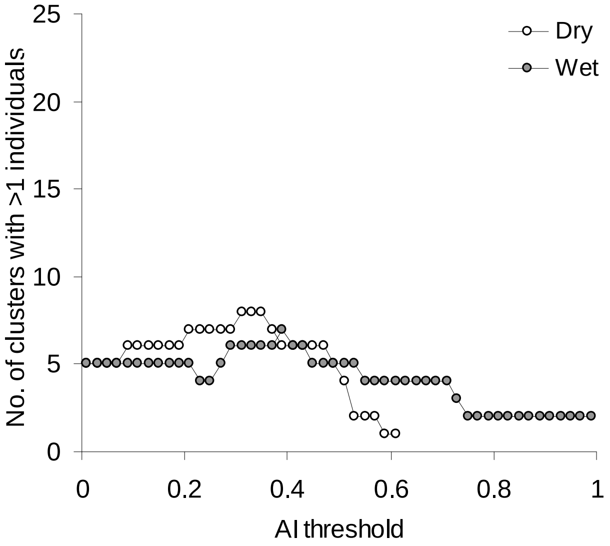
Patricia: wet right-shifted



Tilottama: dry and wet almost identical

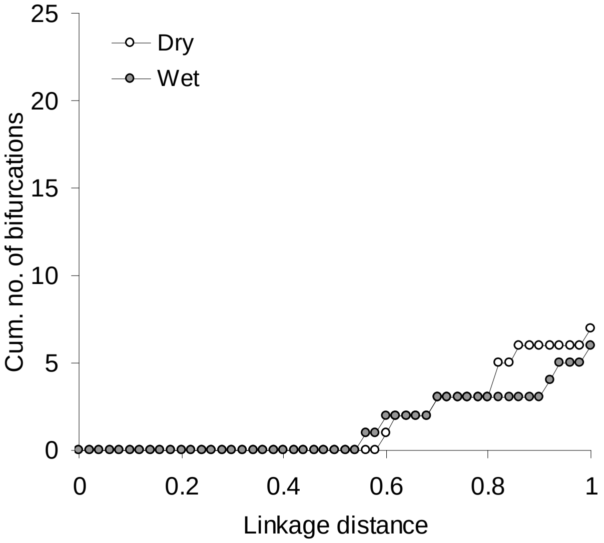


Victoria: wet right-shifted

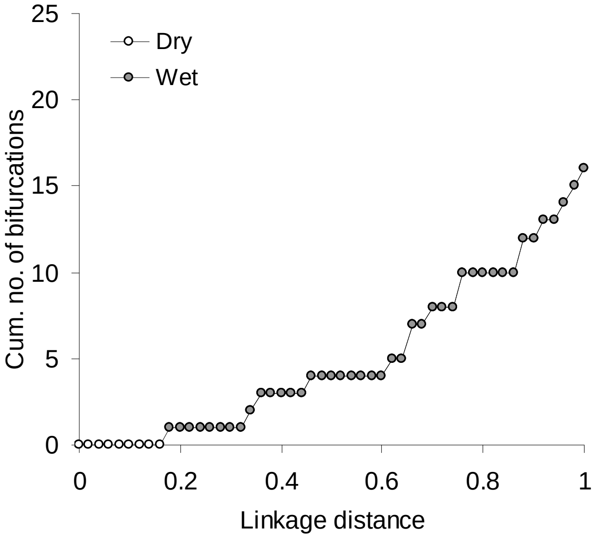


Supplementary Material 16. Cumulative bifurcation curves of the nine focal clans that were analysed for dry-wet season differences. The name of the clan and the differences that the cumulative bifurcation curves showed between seasons are written against each plot

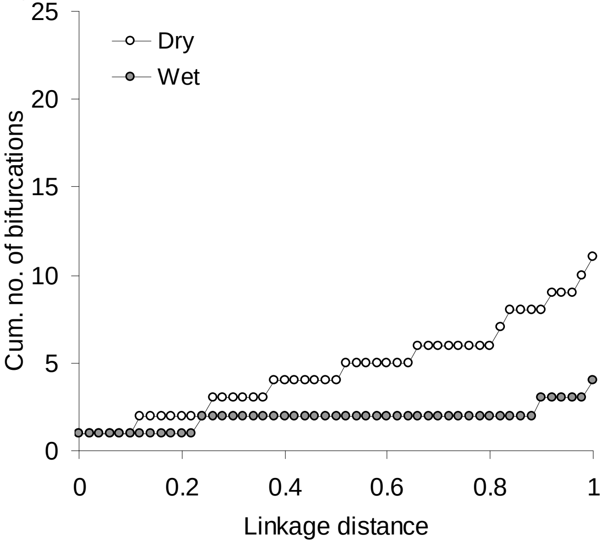
Kasturi: cum. no. of bifur. mostly not different between seasons



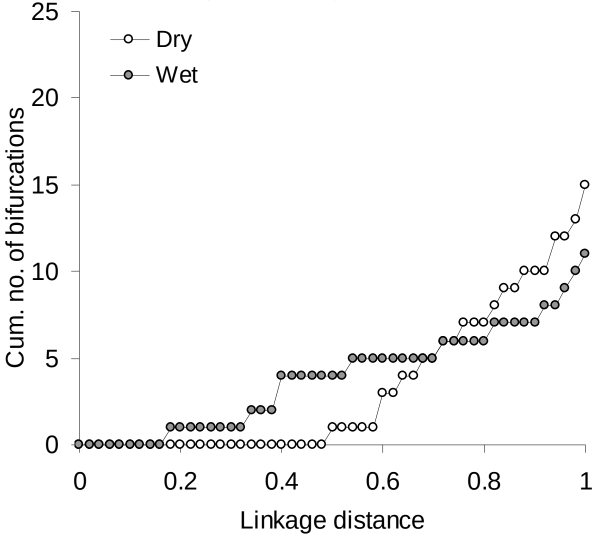
Lisa: cum. no. of bifur. almost identical between seasons

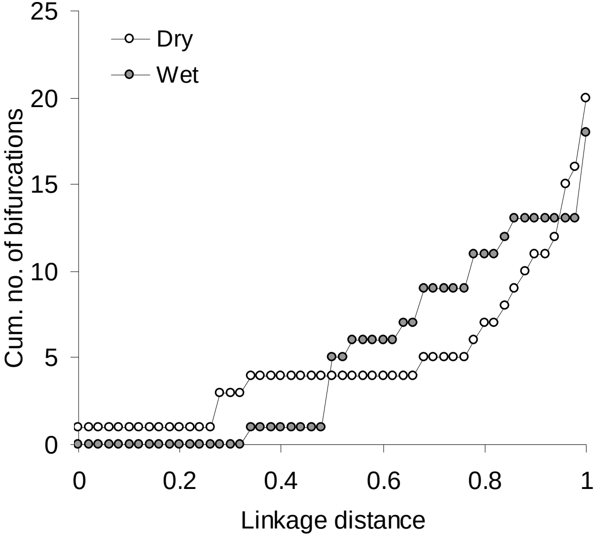


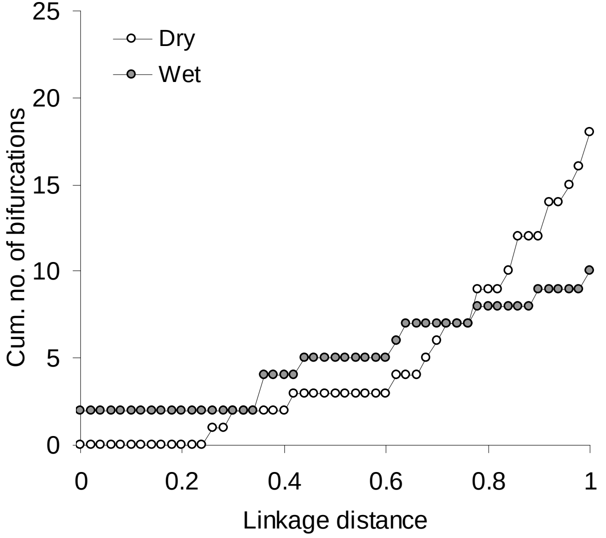
Manasi: cum. no. of bifur. smaller in the wet than in the dry season

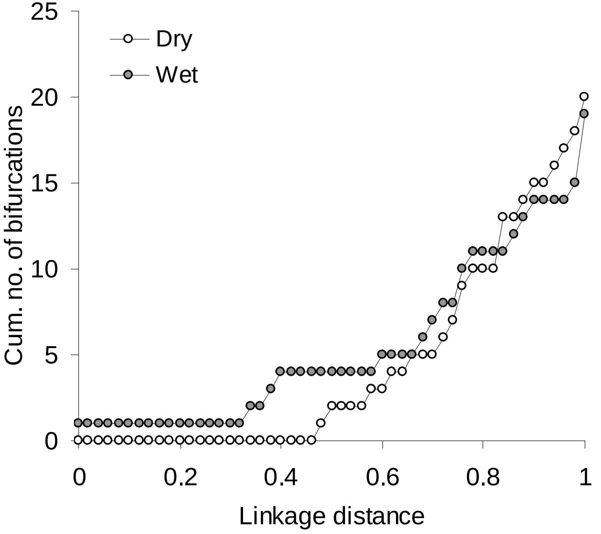


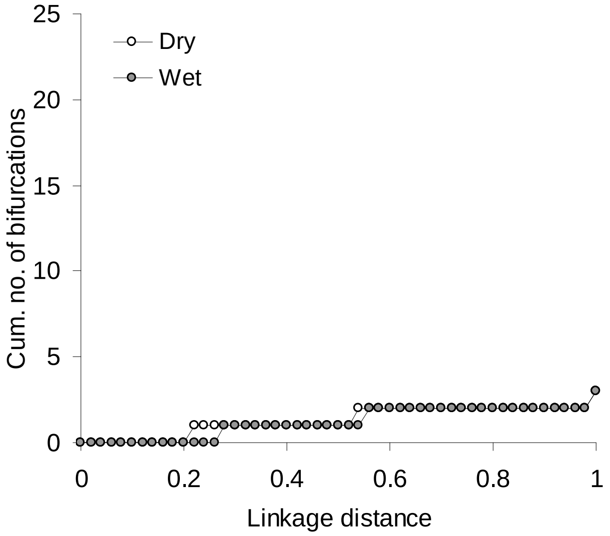
Nakshatra: cum. no. of bifur. larger initially in the wet season and then larger in the dry season

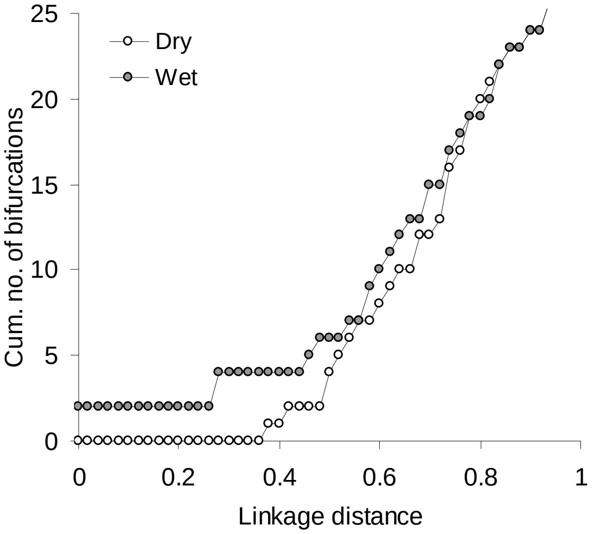



Olympia: cum. no. of bifur. larger initially in the dry season and then larger in the wet season


Osanna: cum. no. of bifur. larger initially in the wet season and then larger in the dry season


Patricia: cum. no. of bifur. smaller in dry than in wet season mostly


Tilottama: cum. no. of bifur. almost identical between seasons


Victoria: cum. no. of bifur. smaller in dry than in wet season

CHAPTER 4

Genetic Relatedness and Associations in Female Asian Elephants in Nagarahole-Bandipur, Southern India

Title: Genetic relatedness and associations in female Asian elephants in Nagarahole-Bandipur, southern India

Authors: Nandini Shetty, Manan Gupta, P. Keerthipriya, T.N.C. Vidya

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

Abstract

Associations amongst kin may provide opportunities for inclusive fitness benefits through offspring care or coalitionary support in the defense of resources. In species showing high fission-fusion dynamics, in which there is a constraint on group sizes, kinship may form an important axis along which a community might fission into smaller groups. We describe here, a study of genetic relatedness in relation to female social relationships in female Asian elephants, which show high fission-fusion dynamics. Based on field sampling in Nagarahole and Bandipur National Parks, southern India, and genotyping elephants at 14 nuclear microsatellite loci from dung-extracted DNA, we examined whether female Asian elephant social structure was based on kinship. The relationship between associations and genetic relatedness was analysed at the level of the clan, which is the most inclusive unit of female social organisation, at the level of first-level communities within clans, and at the level of top associates of individuals. The average relatedness within first-level communities was high, suggesting that such communities probably comprised first- and second-order relatives. The oldest females of first-level communities within clans were also related on average. Females showed high average pair-wise genetic relatedness values with their top associate and were significantly more related to their top and second associates than to the average associate. These results indicate that close associations were based on genetic relatedness between females. However, although the average pair-wise relatedness amongst females within clans was significantly greater than zero, suggesting that clans also comprised related females, less than half the clans individually showed average within-clan relatedness values that were significantly greater than zero. Similarly, less than half the focal clans showed significant correlations between genetic relatedness and association strength. Occasionally, even first-level communities within clans had unrelated females. These findings suggest that genetic relatedness between females was not the only prerequisite for bonding amongst them. It is possible that direct fitness benefits are important at the clan level.

Keywords: Asian elephant, relatedness, association, fission-fusion, social structure, direct and indirect fitness benefits, Kabini, Nagarahole-Bandipur.

Introduction

Social organisation may arise as a complex response to ecological factors and individual relationships with conspecifics (Crook and Gartlan 1966, Clutton-Brock and Harvey 1977, Wrangham 1980). The patterning and quality of interactions with conspecifics, while often constrained by ecological and demographic circumstances, may also be strongly influenced by kinship (Clutton-Brock 2002). Therefore, apart from ecological and demographic factors, societies may be structured based on inclusive fitness benefits (inclusive fitness is an individual's personal reproductive success plus the indirect reproductive success contributed by relatives, who share the individual's genes, as a result of the individual's intervention in their reproductive activities, Hamilton 1964), direct fitness benefits (Cameron *et al*. 2009), and/or conflict from conspecifics (Kummer 1978, Walters and Seyfarth 1987). Associations amongst kin have been recorded in many species of social mammals (Silk *et al*. 2006) and such associations may allow for food sharing (Holekamp *et al*. 1997), coalitionary support during dominance (Holekamp and Smale 1990, Silk *et al*. 2004, Perry *et al*. 2008), and increased offspring care and survival (Owens and Owens 1984, Packer *et al*. 1990, Pusey and Packer 1994, Cant 2000, Silk *et al*. 2003, Eberle and Kappeler 2006). Kinship may be especially important in species that show high fission-fusion dynamics (see Aureli *et al*. 2008), in which group compositions and size change frequently over time by the fission and fusion of subgroups, depending upon resource-risk distributions (Kummer 1971). Such flexible organisation is thought to reduce the costs of group-living, while also providing the benefits of sociality (Kummer 1971, Dunbar 1988, Strier 1992, Chapman 1990, Chapman *et al*. 1995, Connor *et al*. 2000, Wittemyer *et al*. 2005, Lehman *et al*. 2007, Aureli *et al*. 2008, Smith *et al*. 2008, Asensio *et al*. 2009). It is interesting to examine whether fissioning of groups occurs along the lines of genetic relatedness, thereby providing an opportunity for kin selection. Social associations are based on kinship in some species showing high fission-fusion dynamics, such as spotted hyaenas (Holekamp *et al*. 1997), cetaceans (see Connor *et al*. 2000), bats (Kerth *et al*. 2002), and geladas (Johnson *et al*. 2013, Snyder-Mackler *et al*. 2014).

Female elephants also show high fission-fusion dynamics (Moss and Poole 1983, Wittemyer *et al*. 2005, de Silva *et al*. 2011, chapter 2 of this thesis). Female Asian elephants usually form small, fluid groups of 2-3 adult females, along with their offspring, but they may occasionally form larger groups, and the most inclusive unit of social structure is the clan (see McKay 1973, Sukumar 1989, Vidya and Sukumar 2005, de Silva *et al*. 2011, chapter 2 of this thesis). Clans may be further structured and associations between females are non-random even within clans. However, females almost never interact positively between clans (this thesis). Female African savannah elephants form a more nested multilevel society than female Asian elephants. The hierarchical levels include mother-offspring units, family groups or core groups, kinship groups or bond groups, and clans (Douglas-Hamilton 1972, Moss and Poole 1983, Wittemyer *et al*. 2005, Archie *et al*. 2006). African forest elephants show nuclear families of single adult females and her offspring, although they may form larger associations in forest clearings (Turkalo and Fay 1995, Fishlock and Lee 2013, Turkalo *et al*. 2013). The potential benefits of sociality in female elephants include cooperative offspring care and allomothering (Dublin 1983, Gadgil and Nair 1984, Lee 1987, Lee and Moss 2011, Vidya 2014), and the opportunity to associate with older females who are thought to be repositories of ecological and social knowledge (Mc Comb *et al*. 2001, 2011, Foley 2002, Mutinda *et al*. 2011). Indirect fitness benefits were thought to be important in the Amboseli African savannah elephant population (Archie *et al*. 2006). Adult females within core groups were closely related to one another, first-order maternal relatives remained together during temporary group fission, and related groups were more likely to fuse (Archie *et al*. 2006). In Samburu and Sengwa, two African savannah elephant populations that had faced more poaching than Amboseli, females within bond groups and clans did not always share the same mitochondrial DNA haplotypes, and direct benefits were thought to be important in the formation of hierarchical social structure (Charif *et al*. 2005, Wittemyer *et al*. 2009).

We wanted to examine the extent to which female Asian elephant society is based on kinship. Asian elephants show female philopatry (Fernando and Lande 2000, Vidya and Sukumar 2005, Vidya *et al*. 2005a) and male locational dispersal (Desai and Johnsingh 1995, Vidya and Sukumar 2005). Based on sampling groups of 2-3 adult females in Mudumalai, southern India, it was known that such groups were related as first- and second-order relatives and were thought of as family groups (Vidya and Sukumar 2005). Related females in small groups were also inferred in Lao PDR and in Alur, southern India, through genotyping of closely-spaced dung piles (Ahlering *et al*. 2011, Chakraborty *et al*. 2014). However, the relatedness between females beyond such small groups had not been examined previously. As mentioned above, the most inclusive unit of social structure was called the clan and this was based on social network modularity (chapter 2). Some clans were further structured and first-level communities could be detected within clans using the Louvain algorithm (Blondel *et al*. 2008). Our aim was to find out whether a) clans were composed of related females, b) first-level communities within clans comprised close relatives, c) the strength of association between females was based on genetic relatedness, and d) the relationship between associations and genetic relatedness varied between the dry and wet seasons.

Methods

Field data collection

The study was carried out between March 2009 and July 2014 in Nagarahole National Park and Tiger Reserve (Nagarahole) and the adjoining Bandipur National Park and Tiger Reserve (Bandipur), in the Nilgiris-Eastern Ghats landscape, southern India (see Vidya 2014, chapter 2 of this thesis for more details about the study area). Nagarahole and Bandipur are separated by the Kabini reservoir, created by the Beechanahalli Dam on the river Kabini. The reservoir is a source of water and forage during the dry season and sustains a high density of elephants and other herbivores. Elephants tended to use the area around the Kabini reservoir during the dry season (December to mid-June) and were more scattered in the forest during the wet season (mid-June to November, see chapter 3 of this thesis). We sampled elephants from about 6:30 AM to 6:00-6:45 PM (depending on daylight hours and permits) by driving along pre-selected routes in both habitats, but concentrated more towards the reservoir. As mentioned previously (chapter 2 of this thesis), we identified female groups as a collection of female elephants and their young that moved in a coordinated manner, especially towards the water or forest edge, or showed affiliative behaviour. These females were usually within 50-100 m of one another and would also vocalize in response to one another or huddle together if disturbed by another elephant group or by humans (although they were largely habituated to vehicles in the tourism zone of the parks). Individuals were aged, sexed, and identified using various natural physical characteristics (see Vidya *et al*. 2014).

We collected data on associations between females that were at least ten years old, which we simply refer to as females in the rest of the chapter. All females within a group were said to be associating with one another. Sightings of the same group at least 2.5 hours apart were considered to be independent based on preliminary work on how often groups changed in composition (see chapter 2). As it is logistically difficult to collect blood or tissue samples from free ranging elephants, dung samples were collected as the source of DNA. Tissue samples were occasionally collected if a female was found dead. Dung samples were collected from identified females upon observed defecation. The outer-most layer of dung, which is rich in endothelial cells, was collected into about 9 ml of 95% ethanol. Collected samples were stored at ambient temperature in the field station for up to a few months and at 4ºC in our laboratory at Bengaluru thereafter. During the sample collection, the identity of the animal, time of defecation, time of collection, GPS readings, and names of observers collecting the dung were noted down. Since the area around the Kabini reservoir could have a large number of elephants present at the same time, or could have a group defecating and then feeding in the same area till the time we had to leave the forest (because of permits), it would often not be possible to collect the dung sample (even though we had observed animals defecate) without disturbing too many animals. In these cases, we did not collect the sample. Occasionally, because of a large number of previous dung piles lying in the area, there was a small doubt about the correct identity of the observed female's dung pile, in which case also, the dung was not collected. Moreover, we tried to collect multiple samples from the same females on different days in order to further reduce sampling error.

Genetic analysis

We digested approximately 0.5 g of dung sample using 1.5 mL of Tris-EDTA-SDS buffer and 20 µL Proteinase K overnight at 55ºC. We extracted DNA using 800 µL phenol/chloroform/isoamyl alcohol in 400 µL of the digest and purified it using 1 mL of QIAGEN solubilisation buffer and QIAGEN gel purification columns (for details, see Fernando *et al*. 2003). DNA extracts were stored in 1.5 mL microcentrifuge tubes at -20°C. We carried out digestions and extractions very carefully, keeping in mind that dung is a sub-optimal source of DNA. We also used aerosol resistant barrier tips to further reduce cross-contamination. We amplified 14 microsatellite loci from the extracts using the Polymerase Chain Reaction (PCR). These loci included the tetra-nucleotide repeat locus, EMX-4, the tri-nucleotide repeat loci, EMX-1 and EMX-2 (all three isolated from *Elephas maximus*, Fernando *et al*. 2001), the dinucleotide repeat loci, EMU03, EMU04, EMU12, EMU14, EMU15, and EMU17, isolated from *Elephas maximus* (Kongrit *et al*. 2008), and the dinucleotide repeat loci, LafMS02, LafMS03, LafMS05, FH60, and FH94, isolated from *Loxodonta africana* (Nyakaana and Arctander 1998, Comstock *et al*. 2000). We carried out the PCRs in 12.5 µL reactions, using 2 µL DNA extract, 9 µL of PCR mix (containing dNTPs, Tris buffer, $MgCl_2$, KCl, and BSA), 0.25 µL each of 10 µM forward and reverse primers, 0.1 µL Taq polymerase, and 0.9 µL of autodaved MilliQ water. All PCR sets included a negative control in which the DNA extract was substituted with water. PCRs were usually carried out following initial denaturation at 94°C for 3 minutes, 40-42 cycles of denaturation at 93°C for 1 minute, annealing at the specific annealing temperature for 1 minute, and extension at 72°C for 1 minute, and a final extension at 72°C for 15 minutes (details of loci and their annealing temperatures are shown in Supplementary Material 1). Amplified samples were stored at -20ºC and electrophoresed in an Applied Biosystems 3730 DNA Analyzer at the JNCASR Sequencing Facility. We scored genotypes (see Supplementary Material 2) using the GeneMapper software v4.0 (Applied Biosystems, Foster City, CA). In order to confirm genotypes, if only one dung sample had been sampled from a female, we carried out three separate PCRs if it was homozygous at the locus, and carried out two PCRs if the same heterozygous genotype was obtained at the locus. If more than one dung sample had been collected from a female, we carried out a total of three PCRs for homozygotes and two PCRs for heterozygotes, using extracts from two different dung samples. If PCRs occasionally showed mismatches, allelic dropouts, or poor amplification (allele peaks <1500 in the electropherogram), they were repeated until the same genotype was obtained at least three times. This was rarely the case because dung samples were collected fresh and we obtained 100% amplification success (also see Fernando *et al*. 2003). We used dedicated instruments and work benches for pre- and post-PCR work to reduce laboratory error. We could not use mitochondrial DNA (mtDNA) to examine maternal lineages because a previous study had shown that a single mtDNA haplotype is fixed across the Nilgiris-Eastern Ghats landscape, in which our study area falls (Vidya *et al*. 2005b).

Data analysis

All the loci were checked for Hardy-Weinberg equilibrium and all pairs of loci for linkage disequilibrium, and gene diversities were calculated, using Genepop v.4.2.1 (Rousset 2008). All the loci were checked for null alleles using Microchecker v.2.2.3 (Van Oosterhout *et al*. 2004). The probability of identity (P_{ID}) (Paetkau and Strobeck 1994), which is the probability that two randomly chosen individuals from the population have the same genotypes, and P_{ID}(sib) (Evett and Weir 1998), which is the probability that two randomly chosen siblings having the same genotypes, were calculated for the 14 loci using the software IDENTITY v.1.0. (Wagner and Sefc 1999). Genetic relatedness between individuals was calculated using the Queller and Goodnight (1989) measure of relatedness, using the software Coancestry v.1.0.1.5 (Wang 2011). We calculated the average genetic relatedness for known mother-offspring pairs and checked their genotypes for mismatches to identify non-Mendelian inheritance or genotyping problems. We then calculated the average relatedness between females within the first-level communities within clans, as identified by the Louvain method (Blondel *et al*. 2008) of community detection (see chapter 2). We also calculated the average genetic relatedness between females within clans.

We used the association data shown in chapter 2 of this thesis to examine the relationship between association strength and genetic relatedness. The strength of association was measured using the association index (AI; Ginsberg and Young 1992). This was calculated between pairs of females, as the ratio of the number of times two females A and B were seen together (N_{AB}) to the number of times either A or B was observed (N-D, where N is the total number of sightings and D the number of times neither A nor B was seen). Only sightings in which all females had been identified were used to calculate AI. There were 3922 such sightings, of which 3264 sightings were from the dry seasons and 658 sightings were from the wet season (see chapter 3). These sightings comprised 330 unique females, 298 of which were seen during the dry season and 223 during the wet season. Genetic relatedness was examined in 17 clans, but only 15 clans were used as the focal clans because the other two had only two females each. To examine whether relatedness between females was correlated with their levels of association, Mantel tests (Mantel 1967) were carried out between pair-wise AI and relatedness matrices. Mantel tests were performed at the population level, which comprised females from the 17 clans, and at the focal clan level. Matrix correlations were also performed in focal clans based on dry and wet season data separately. Seven focal clans with at least 15 sightings during the wet season were used to examine the AI-relatedness correlation in the wet season. We also compared the relatedness values of the individuals' top, second, and third associates with the relatedness values averaged across all their associates using Wilcoxon's matched-pairs tests to find out whether these preferred associates were more related than the average associate. Data analysis of associations and Mantel tests were carried out in MATLAB 7 R2004a (The MathWorks, Inc, 1984-2011, www.mathworks.com).

Results

A total of 346 samples, including 337 dung and 9 tissue samples, were collected from 174 unique females (see Supplementary Material 3). Of these 174 females (53% of the identified females in the population), 73 were sampled once and the remaining 101 were sampled more than once. From the 15 focal clans, 71% of the females were sampled on average (Supplementary Material 3).

All the 14 loci were in Hardy-Weinberg equilibrium and exhibited moderate to high heterozygosity (Table 1). All pairs of loci were in linkage equilibrium, except for one pair, EMX-4 and EMU-17 (Supplementary Material 4). Therefore, we carried out the analyses using all 14 loci and also using 13 loci after excluding the locus EMX-4, to check if the results changed (no result changed significantly). None of the loci used showed null alleles and the combined P_{ID} and $P_{ID}(sib)$ were very small (based on 14 loci: $P_{ID} = 1.34\times10^{-10}$, $P_{ID}(sib) = 1.48\times10^{-4}$; based on 13 loci: $P_{ID} = 5.96\times10^{-10}$, $P_{ID}(sib) = 2.77\times10^{-4}$). The average genetic relatedness (mean ± 1.96 SE) between mother-offspring pairs was 0.542 ± 0.040 (n = 32 pairs; based on 13 loci, mean ± 1.96 SE = 0.538 ± 0.042) and there was no allelic mismatch between these pairs.

Table 1. Number of alleles, observed heterozygosity (H_O), *P* value for the Hardy-Weinberg equilibrium test (HWE *P*), and allele sizes and their frequencies for the 14 microsatellite loci used. The flat Bonferroni corrected *P* was 0.0036.

Locus	No. of alleles	H_O	HWE *P*	Allele size/frequency						
EMX-1	2	0.583	0.123	134	151					
				0.523	0.477					
EMX-2	2	0.450	0.359	219	225					
				0.433	0.567					
EMX-4	3	0.673	0.900	262	286	298				
				0.341	0.214	0.445				
EMU03	4	0.708	0.625	134	136	138	140			
				0.383	0.45	0.079	0.087			
EMU04	4	0.496	0.039	97	99	103	105			
				0.05	0.655	0.122	0.172			
EMU12	4	0.678	0.533	139	141	147	151			
				0.445	0.242	0.284	0.03			
EMU14	6	0.574	0.516	127	129	131	133	137	145	
				0.013	0.07	0.078	0.591	0.022	0.226	
EMU15	5	0.746	0.678	144	146	152	154	156		
				0.351	0.004	0.268	0.092	0.285		
EMU17	7	0.765	0.657	120	122	124	126	128	132	134
				0.151	0.189	0.462	0.05	0.101	0.034	0.013
LafMS02	4	0.731	0.408	133	135	137	141			
				0.069	0.343	0.394	0.194			
LafMS03	5	0.647	0.822	137	139	149	151	155		
				0.525	0.214	0.202	0.008	0.05		
LafMS05	4	0.592	0.631	144	150	152	156			
				0.125	0.113	0.571	0.192			
FH60	6	0.809	0.420	148	152	154	156	158	162	
				0.183	0.083	0.365	0.243	0.078	0.048	
FH94	5	0.585	0.269	214	216	220	222	228		
				0.242	0.644	0.03	0.047	0.038		

Genetic relatedness within first-level communities within clans

We identified lower-level communities within clans using the Louvain method (Blondel *et al.* 2008) in ten focal clans. The average (± SD) size of these communities was 6.46 (± 5.479; range: 2-26). The average pair-wise genetic relatedness (mean ± 1.96 SE) within first-level communities was 0.215 ± 0.082 (n = 20 first-level communities from 10 focal clans; mean ± 1.96 SE = 0.214 ± 0.084 based on 13 loci; there were totally 26 first-level communities in ten focal clans but six first-level communities had either only a single female sampled or no female sampled). The average pair-wise AI (average ± SD) of females within these communities was 0.278 ± 0.197. Therefore, first-level communities within clans were units of closely related individuals, probably as first-order and second-order relatives. The average genetic relatedness within first-level communities of individual clans are shown in Table 2. Ten first-level communities from seven clans had average pair-wise relatedness that were significantly greater than zero, while the average pair-wise relatedness values in four first-level communities from four clans were not significantly greater than zero (the remaining six first-level communities had only two females each sampled), suggesting that close associations also occurred amongst unrelated females. The average pair-wise genetic relatedness between the oldest females of first-level communities within clans was 0.131 ± 0.124 (n = 12 pairs; six oldest females could not be sampled; based on 13 loci, mean ± 1.96 SE = 0.153 ± 0.112).

Genetic relatedness within clans

The average pair-wise relatedness amongst females within clans was 0.079 ± 0.044 (n = 15 focal clans; based on 13 loci, mean ± 1.96 SE = 0.074 ± 0.038), which was significantly greater than zero (frequency distributions of within-clan pair-wise *r* shown in Figure 1). Among 15 focal clans, only five clans (four clans when 13 loci were used) had average pair-wise genetic relatedness values that were significantly greater than zero, indicating the presences of unrelated females in many clans. The average pair-wise genetic relatedness values for the focal clans are shown in Table 3. The average pair-wise genetic relatedness within clans increased slightly when only females at least 15 years old were considered (mean ± 1.96 SE = 0.097 ± 0.047, n = 15 focal clans; based on 13 loci, mean ± 1.96 SE = 0.091 ± 0.041).

Table 2. Average AI and average genetic relatedness between females within first-level communities in ten focal clans. For each first-level community, the size of the community, followed by the number of females genotyped are shown. Values of *r* that were significantly greater than zero are marked in bold. Actual values of relatedness are shown for those communities in which only two females had been sampled. Results based on 13 loci are shown in Supplementary Material 5.

Clan (size/no. of communities)	First-level communities (size/no. sampled)	Average AI (SD)	Average *r* (1.96 SE)
Katrina (16/2)	Community 1 (6/2)	0.250	0.061
	Community 2 (10/2)	0.400	0.124
Lisa (17/2)	Community 1 (5/4)	0.357 (0.164)	**0.391** (0.073)
	Community 2 (12/11)	0.160 (0.121)	0.006 (0.074)
Manasi (12/3)	Community 1 (5/4)	0.333 (0.244)	**0.163** (0.115)
	Community 2 (3/0)	_	_
	Community 3 (4/1)	_	_
Menaka (9/2)	Community 1 (7/4)	0.127 (0.191)	-0.051 (0.193)
	Community 2 (2/2)	0.846	0.529
Mridula (6/2)	Community 1 (4/3)	0.313 (0.024)	**0.272** (0.140)
	Community 2 (2/1)	_	_
Nakshatra (16/2)	Community 1 (14/9)	0.167 (0.110)	-0.003 (0.065)
	Community 2 (2/2)	0.614	0.622
Olympia (21/6)	Community 1 (3/3)	0.159 (0.106)	**0.413** (0.215)
	Community 2 (5/3)	0.158 (0.100)	**0.277** (0.121)
	Community 3 (3/2)	0.059	0.472
	Community 4 (2/0)	_	_
	Community 5 (4/1)	_	_
	Community 6 (4/0)	_	_
Osanna (20/2)	Community 1 (11/7)	0.067 (0.078)	**0.178** (0.081)
	Community 2 (9/4)	0.461 (0.172)	**0.263** (0.194)
Patricia (21/3)	Community 1 (11/9)	0.218 (0.097)	0.034 (0.063)
	Community 2 (8/8)	0.131 (0.118)	**0.080** (0.078)
	Community 3 (2/2)	0.368	0.170
Victoria (32/2)	Community 1 (27/26)	0.090 (0.105)	**0.037** (0.025)
	Community 2 (5/5)	0.284 (0.129)	**0.266** (0.126)

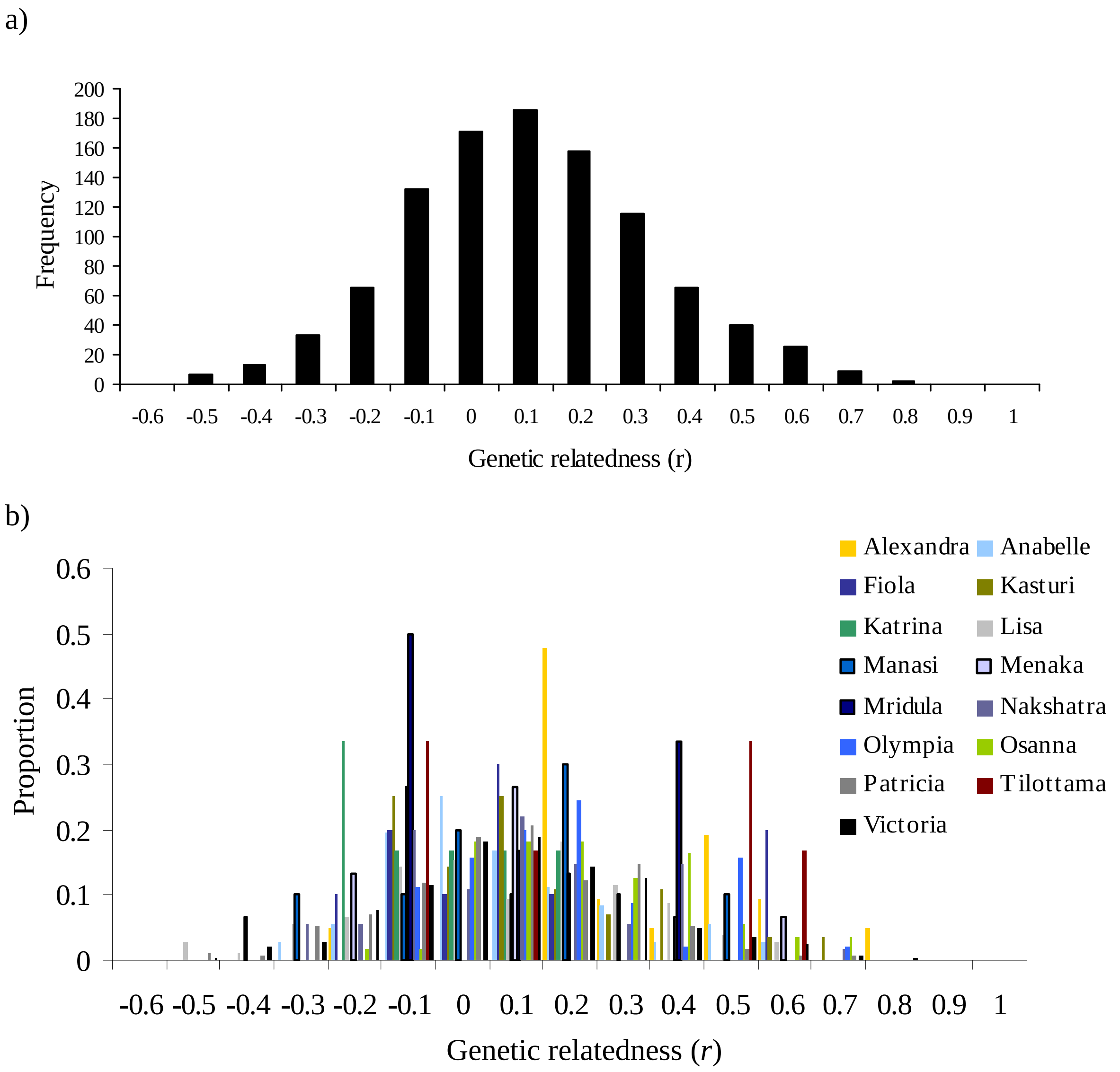


Figure 1. Frequency distributions of within-clan pair-wise genetic relatedness (n = 1025 pairs from 15 clans). All the clans are shown together in a) and individually in b). The frequency distribution based on 13 loci is shown in Supplementary Material 6. As should be the case, the average genetic relatedness across adult females at the level of the entire population was not much larger than zero.

Table 3. Average pair-wise AI and average pair-wise genetic relatedness, and Mantel test correlation *r*, R^2, and *P* values for the focal clans. For each clan, the clan size and the number of females sampled are shown. Values of *r* that were significantly greater than zero are marked in bold, as are significant *P* values. A similar table based on 13 loci is in Supplementary Material 7.

Clan (clan size/ no. of females sampled)	Average AI (SD)	Average *r* (1.96 SE)	Correlation *r*	R^2	*P* value
Alexandra (11/7)	0.283 (0.134)	**0.277 (0.088)**	0.023	0.001	0.465
Anabelle (11/9)	0.187 (0.145)	0.033 (0.067)	-0.022	0.000	0.513
Fiola (7/5)	0.393 (0.244)	0.076 (0.158)	0.633	0.401	0.069
Kasturi (8/8)	0.154 (0.123)	**0.084 (0.079)**	0.673	0.453	**0.005**
Katrina (16/4)	0.129 (0.162)	-0.081 (0.107)	0.947	0.897	**0.033**
Lisa (17/15)	0.111 (0.133)	0.038 (0.047)	0.357	0.128	**<0.001**
Manasi (12/5)	0.200 (0.250)	0.062 (0.123)	0.377	0.142	0.127
Menaka (9/6)	0.115 (0.240)	-0.012 (0.117)	0.501	0.251	0.070
Mridula (6/4)	0.219 (0.111)	0.070 (0.177)	0.772	0.596	0.259
Nakshatra (16/11)	0.140 (0.123)	0.037 (0.057)	0.229	0.052	0.068
Olympia (21/9)	0.034 (0.069)	**0.132 (0.063)**	0.518	0.269	**<0.001**
Osanna (20/11)	0.087 (0.154)	**0.180 (0.053)**	0.240	0.057	0.055
Patricia (21/19)	0.074 (0.111)	0.028 (0.031)	0.163	0.027	**0.021**
Tilottama (4/4)	0.533 (0.222)	0.209 (0.226)	0.849	0.721	0.254
Victoria (32/31)	0.076 (0.100)	**0.046 (0.020)**	0.216	0.047	**<0.001**

Genetic relatedness and associations

At the population level, relatedness between individuals was significantly correlated with the strength of their associations, but the correlation was small (Mantel test: based on 14 loci: correlation $r = 0.115$, $R^2 = 0.013$, $P < 0.001$; based on 13 loci: correlation $r = 0.112$, $R^2 = 0.013$, $P < 0.001$) (see Figure 2). At the clan level, six of the 15 focal clans showed a significant correlation between AI and relatedness matrices (Table 3). Three of these six clans were among the clans that had an average within-clan relatedness greater than zero, while the other three showed an overall low within-clan relatedness, but showed significant

Mantel test correlations (Table 3). Seven clans did not show either an average within-clan relatedness greater than zero or a correlation between relatedness and associations (Table 3). We also carried out the Mantel tests separately on seasonally partitioned data and found that the same pattern of results was obtained based on the dry season data, and clans that showed a significant correlation based on these data also showed a significant correlation based on the wet season data wherever it was possible to perform the tests (we used clans that were seen at least 15 times in the wet season; Supplementary Material 8, 9). An additional clan showed average within-clan relatedness significantly greater than zero in the wet season compared to the dry season and the entire dataset.

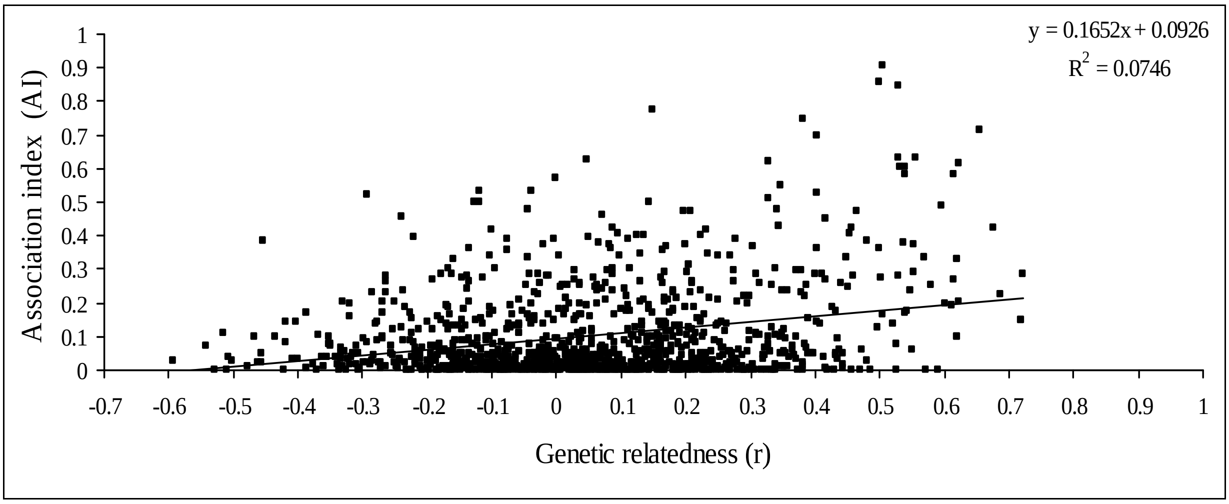


Figure 2. Linear regression of pair-wise AI on genetic relatedness at the population level (n = 1029 pairs, 17 clans; $R^2 = 0.081$, P <0.001 when based on 13 loci).

When we examined the dyads with AI>0.5 in the focal clans, their average (± 1.96 SE) pair-wise genetic relatedness was 0.336 ± 0.116 (n= 21 pairs from ten focal clans, the other clans did not have any AIs>0.5). The average pair-wise relatedness between individuals and their top associates was 0.254 ± 0.046 (n = 124 pairs, 15 focal clans, Figure 3), suggesting that their top associates were their first- or second-order relatives. The average pair-wise relatedness between individuals and their top associates was significantly greater than zero in 11 of the 14 clans for which relatedness with the top associates could be estimated (Supplementary Material 10). The average (± 1.96 SE) pair-wise AI with the top associate was 0.418 (± 0.183). The average pair-wise genetic relatedness between individuals and their second associates was 0.139 ± 0.044 (n = 128 pairs, 15 focal clans, Figure 3) and their average (± 1.96 SE) AI was 0.281 (± 0.139). In five of the 15 focal clans, the average pair-wise relatedness with the second associate was significantly greater than zero and corresponded to second-, third-, and, perhaps, even first-, order relatives (Supplementary Material 10). The average pair-wise genetic relatedness with individuals' third associates was 0.072 ± 0.040 (n = 122 pairs, 14 focal clans) and the average pair-wise AI with the third associate was 0.215 ± 0.109. Females from all the focal clans showed generally low relatedness values with their third associates. Wilcoxon's matched pairs' tests showed that females were significantly more related to their top and second associates than to the average associate (top associate: n = 123, T = 1139.0, Z = 6.749, $P < 0.001$; second associate: n = 126, T = 2969.0, Z = 2.511, P = 0.012). The test was also carried out using only females with at least seven associates, of which at least six had been genotyped, and averaging only across the top seven. The pattern of results remained the same for the top associate (n = 80, T = 647.0, Z = 4.667, $P < 0.001$) but the second associate was not significantly more related than the average associate (n = 82, T = 1357.0, Z = 1.593, P = 0.111) unless the top associate was excluded (n = 82, T = 2969.0, Z = 2.511, P = 0.012). The third associate was not significantly more related than the average associate (n = 116, T = 3246.0, Z = 0.405, P = 0.686), even after excluding the top and second associates (n = 93, T = 2134.0, Z = 0.197, P = 0.844).

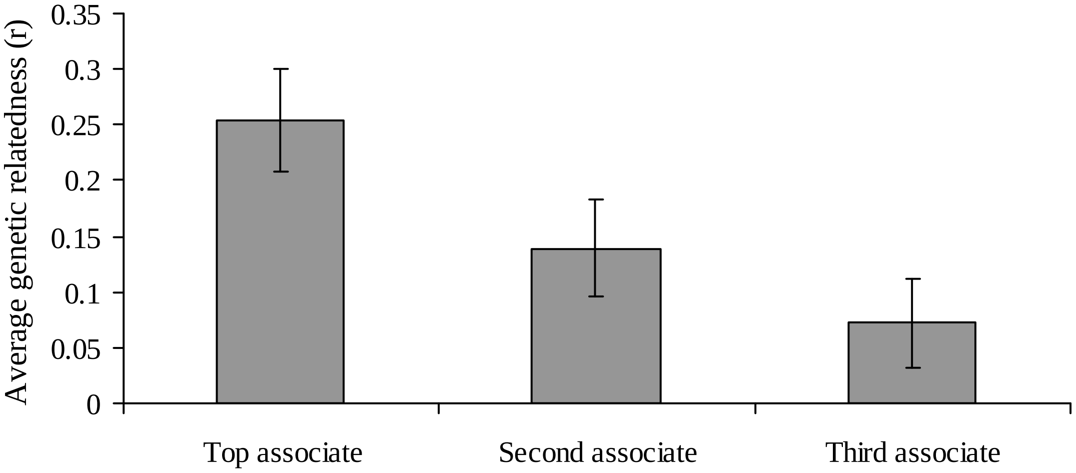


Figure 3. Average pair-wise genetic relatedness of females with their top associates, second associates, and third associates. Error bars are 1.96 SE.

Discussion

Relatedness between females within first-level communities within clans and with top associates

We found high average pair-wise relatedness (0.215 ± 0.082) within first-level communities within clans, indicating that females in these communities were closely related as first-, second-, and third-order relatives. This was in keeping with the results of Vidya and Sukumar (2005), although our first-level communities did not strictly correspond to their family groups, which were just small groups of females seen in the field. Our first-level communities could be larger than the typical groups seen in the field. Not surprisingly, females from those smaller groups seemed to have a slightly higher relatedness (0.365 ± 0.159; n = 13 groups) than females from the first-order communities we sampled. The relatively high average AI (0.278 ± 0.197) seen within first-order communities, in comparison to the low average AI seen within clans (chapter 2), suggests that females tend to limit their limited social time to relatives.

Females that showed strong associations were closely related to one another. The small number of dyads with unusually high AIs (21 dyads from ten focal clans with AI>0.5) were mostly first- and second-order relatives (average pair-wise genetic relatedness = 0.336 ± 0.116). Moreover, in all the focal clans, the average pair-wise relatedness of females with their top associates (0.254 ± 0.046) was of the level expected from first- and second-order relatives. The average pair-wise relatedness with the second associate was about the level of second- and third-order relatives in many of the focal clans. These associates were more closely related than the average associate. Thus, close associations were based on genetic relatedness between females. These associates could be combinations of mother-daughters, full-sisters, half-sisters, aunt-nieces, and grandmother-granddaughters. It might be possible to gain indirect fitness benefits, in the form of protection of calves against predators (Dublin 1983, McComb 2011) and allomothering (Gadgil and Nair 1984, Lee 1987) through such associates. Tigers occasionally prey on calves in our study area and we have observed calves with wounds suggesting tiger attacks. Protection of calves might be an important benefit of living with relatives.

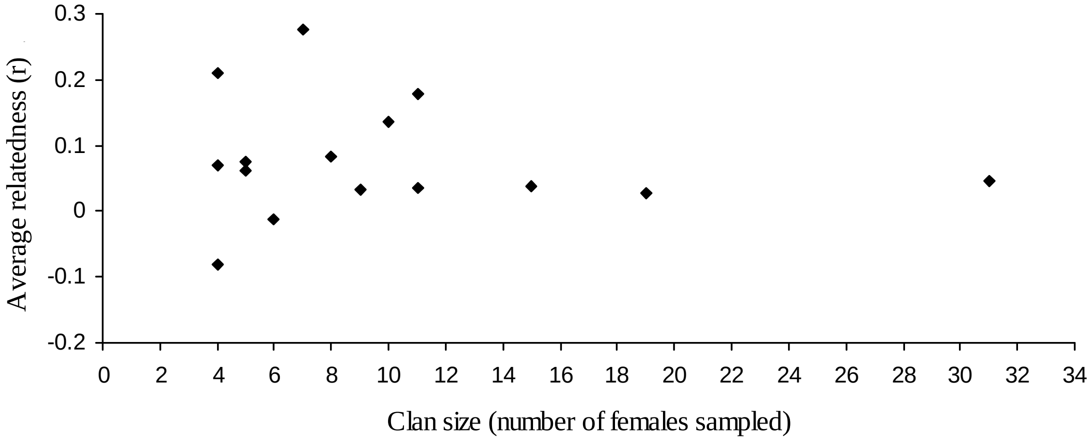


Figure 4. Relationship between the number of females sampled from each clan and the average within-clan pair-wise relatedness.

Relatedness between females within clans

The average genetic relatedness at the clan-level was significantly greater than zero, suggesting that clans comprise related females. The average pair-wise relatedness between the oldest females of the first-level communities within clans corresponded to third-order relatives demonstrating that clans comprised communities of related females. However, unlike in the first-level communities within clans, genetic relatedness between females at the level of the entire clan was low. Upon inspection of relatedness within individual clans, many of the focal clans did not have average pair-wise relatedness significantly greater than zero. Thus, there were many unrelated or distantly related females within clans. A speculation for the low within-clan average relatedness values is the possible death of older, related females. As younger females learnt about their associates from their mothers, they may have continued associating with less-related or unrelated females in the clan. Goldenberg *et al*. (2016) found that social networks in the Samburu elephants were robust in this manner, with daughters filling their mothers' social network roles after their mothers had been poached. Elephants are known to exhibit fidelity to their groups (Moss and Lee 2011) and this continued association may help them acquire valuable knowledge about resource distributions or gain access to resources by associating with other older females (Moss 1988, Foley 2002). Such individuals might continue to show nonrandom associations with their clan members based on familiarity rather than relatedness. On the other hand, heavily poached or disturbed populations have shown a breakdown of social structure, with unrelated females from surviving groups joining together to form social groups (Eltringham and Malpas 1980, Nyakaana *et al*. 2001, Vidya *et al*. 2007). Poached elephant groups with few or no closely related associates showed less cohesion (Gobush and Wasser 2009), were more stressed, and showed reduced reproductive output compared to females with kin-bonded groups (Gobush *et al*. 2008).

Although elephants in southern India have not been exposed to the magnitude of historical disturbance that their counterparts in Sri Lanka faced during the 1800s and early 1900s (Sanderson 1879, pp. 68-69, see McKay 1973, Lorimer and Whatmore 2009), southern Indian populations are by no means completely undisturbed. There was sport-hunting and capture of elephants in southern India also, although the population size is not thought to have declined (Sanderson 1879, pp. 68-69). *Kheddahs* (Sanderson 1879, pp. 70-73) were used for capturing female groups in Nagarahole National Park and the last *kheddah* took place in 1971. Although this is supposed to have been used to capture entire groups, in which case female social structure would not be affected very much, we cannot rule out the possibility of there having been disruptions to social structure. It is possible that the entire clan was not captured and a few individuals escaped or that not all first-level communities of a clan were caught. Another possibility is that some of the females, not necessarily the older ones, may have died of disease. Since mortality records have been maintained actively only in recent times, we do not know if there was any large outbreak several decades ago. Deaths of females would also explain the large differences in clan size despite a large number of sightings of some of the clans. Low within-clan relatedness amongst females may also arise from increasing clan sizes. As a clan increases in size and spans a greater number of generations, the relatedness is expected to decrease (for example, see Leukas *et al*. 2005). This decline in relatedness would be marked especially if different males sired the females born into a clan. At present, we do not know what the patterns of male reproductive success in our population are. However, a plot of the number of females we had sampled from different clans and average within-clan relatedness did not show a clear declining trend (Figure 4). The presence of immigrant females in clans would also reduce average relatedness levels. However, this is unlikely as we find that different clans either do not interact or interact negatively. Although it is possible that orphan females might join and integrate into unrelated clans when they are still young, it is unlikely that this would be widespread across clans. Another possibility for low within-clan relatedness could be the presence of paternal relatives across clans. Since relatedness is calculated in a relative manner, by subtracting the baseline allele frequencies from the allele frequencies in the groups of interest (Queller and Goodnight 1989), if there were paternal relatives of females across different clans, the within-clan relatedness would decrease. This would be plausible if a few males were dominant and garnered many matings across clans in specific years. Under this scenario, one would not expect synchrony of births within clans as that would likely result in full-sisters in the clan, increasing the average relatedness.

Sociality and direct versus indirect fitness

As mentioned previously, kinship was a strong predictor of associations in Amboseli but not in the Samburu African savannah elephant population (Archie *et al*. 2006, Wittemyer *et al*. 2009). In Amboseli, the average relatedness between females that spent 90% of their time together was 0.42 (Archie *et al*. 2006). Such high levels of association and relatedness were extremely rare in our population. We found that first-level communities were genetically based and could offer opportunities for indirect fitness benefits. Moreover, as closest associates were also close kin, females could possibly gain indirect fitness benefits. However, relatedness was low at the level of the clan. Even in the case of first-level communities, the average pair-wise relatedness within four such communities was not significantly greater than zero. This indicates the presence of unrelated individuals even at this otherwise cohesive level. Third associates of individuals were also not more related than a randomly chosen associate. These findings suggest that genetic relatedness between females was not the only prerequisite for bonding amongst them and it is possible that direct fitness benefits are important at the level of the clan. Direct benefits could include reduced predation risk (Dublin 1983, Moss 1988), increased foraging efficiency or resource defense (Moss 1988). In our study area, there is a high frequency of between-clan contests and group size seems to be important in the outcome of these interactions (chapter 5). Thus, benefits from cooperative resource defense might maintain bonds between females that are not closely related.

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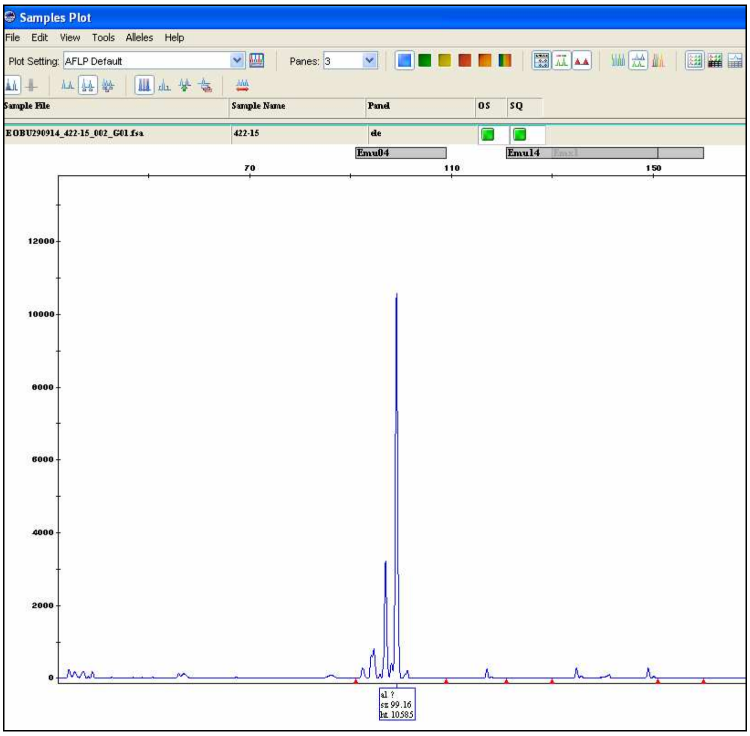
Supplementary Material

Supplementary Material 1. Details of the 14 microsatellite loci used in the study. Details of the repeat unit and primer sequences are from Fernando *et al*. (2001), Kongrit *et al*. (2008), Nyakaana and Arctander (1998), and Comstock et al. (2000).

Locus	Repeat unit	Primer sequence (5' - 3')	Label	T_a (°C)	Ann. time (min)	Allele size (bp)	N_a
EMX-1	(GTT)$_{14}$	F: AGGACTTATTTGCTTAGATGG	FAM	59	1	134-151	2
		R: AGGCAATGTTTCGTTCTGT					
EMX-2	(GTT)$_{5}$	F: CCCATGAGTCGGAATCCACTT	FAM	62	1	219-225	2
		R: CCATAGGGTTGCCAAGGAATG					
EMX-4	(GGAA)$_{3}$A (GA)$_{3}$A(GGAA)$_{3}$	F: AGTTCGTGTCTCGGTGCTGTA	NED	59	1	262-298	3
		R: ACTTGAGGGCAGGGGAAGGTCCACA					
EMU03	(GT)$_{6}$GC(GT)$_{8}$	F: AGAAGCAAAACCCATGAAGC	NED	63	1	134-140	4
		R: TTGAAACTTGCCAGCCTCTT					
EMU04	(TG)12	F: TGACTCTCCCTCTTCTGCATC	6-FAM	63	0.5	97-105	4
		R: GGCTGAGAGGGAAAGAAATTG					
EMU12	(AC)8	F: CCAAAGAAGACCCATGTTCC	VIC	61	1	139-151	4
		R: CTGACTATGGGGGAGACTGC					
EMU14	(GT)15	F: GCCTACATGCAGGGTTTGC	6-FAM	61	1	127-145	6
		R: TGAGCCTCTGGCATTTATGA					
EMU15	(AC)14	F: TTCGGGATGTTCTCTTCTGT	PET	57	1	144-156	5
		R: GGGGCTTAACTAATAGGCTTCA					
EMU17	(GT)16	F: CACTCAGAGTTCCAAGAAGCAG	PET	58	1	120-134	7
		R: TGCCAGCCATTTCCTCTC					
LafMS02	(AC)$_{16}$	F: GAAACCACAACTTGAAGGG	VIC	62	1	133-141	4
		R: TCGCTTGTAAGAAGGCGTG					
LafMS03	(TG)$_{15}$	F: CATATGAACATACCGGAAC	VIC	54	1	137-155	5
		R: GAAACTCCTCGAGTAGTAGAA					
LafMS05	(AC)$_{11}$	F: CCTTAGGCTGGGTTGTAT	VIC	58	1	144-156	4
		R: AATGGACTTGGGACTTGCCAAAATGT					
FH60	(CA)$_{13}$	F: CAAGAAGCTTTGGGATTGGG	NED	61	1	148-162	6
		R: CCTGCAGCTCAGAACACCTG					
FH94	(CA)16	F: TTCCTCCCACAGAGCAGC	NED	63	0.5	214-228	5
		R: ATTGGTTAATTTGCCAGTCCC					

T_a is the annealing temperature and Ann. time is the annealing time after our standardization. N_a is the number of alleles. Allele size ranges are based on our data after the standardization, and allele sizes for loci EMX-2, LafMS02, and LafMS03 correspond to the sizes shown in Vidya *et al*. (2005). Five pairs of loci, EMX-1 and EMX-4, FH60 and EMU14, EMU17 and LafMS05, EMU04 and FH94, and EMX-2 and LafMS02 were amplified using multiplex PCRs. The 14 loci were genotyped in six panels: EMX-1-EMX-4, FH60-EMU14, EMU17-LafMS05, EMU03-LafMS03, EMU04-FH94-EMU12, and EMX-2-LafMS02- EMU15.

Supplementary Material 2. Sample electropherograms from GeneMapper software.



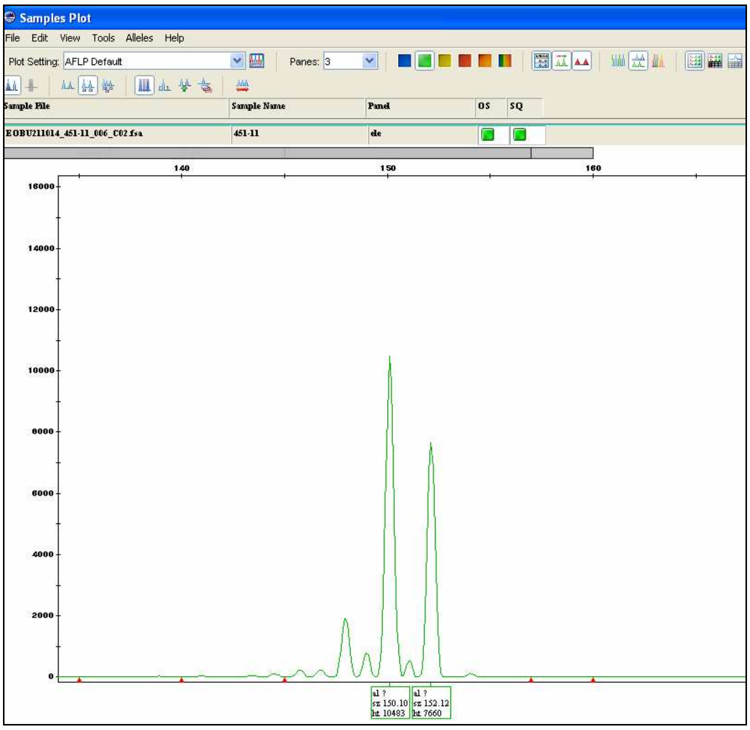
Plot Setting: AFLP Default

Panes: 3

Sample File	Sample Name	Panel	OS	SQ
EOBU290914_422-15_002_G01.fsa	422-15	ele	🟩	🟩

al ?
sz 99.16
ht 10585

Supplementary Material 2, Figure 1. Electropherogram of a homozygous individual at the locus EMU04. The forward primer was fluorescently labeled with 6-FAM (blue) dye. The individual’s genotype at this locus is 99/99.



Plot Setting: AFLP Default

Panes: 3

Sample File	Sample Name	Panel	OS	SQ
EOBU211014_451-11_006_C02.fsa	451-11	ele	🟩	🟩

al ?
sz 150.10
ht 10483

al ?
sz 152.12
ht 7660

Supplementary Material 2, Figure 2. Electropherogram of a heterozygous individual at the locus LafMS05. The forward primer was fluorescently labeled with VIC (green) dye. The individual's genotype at this locus is 150/152.

Supplementary Material 3. Details of the samples collected.

Supplementary Material 3, Table 1. Females with different samples collected.

Category	Number
Total samples collected	346
Females with one sample	73
Females with more than one sample	101
Total dung samples collected	337
Females with only one dung sample	73
Females with more than one dung sample	98
Total tissue samples collected	9
Females with only tissue samples	3

Supplementary Material 3, Table 2. Percentage of females sampled in the 15 focal clans.

Clan	Clan size	No. females sampled	% females sampled
Alexandra	11	7	64
Anabelle	11	9	82
Fiola	7	5	71
Kasturi	8	8	100
Katrina	16	4	25
Lisa	17	15	88
Manasi	12	5	42
Menaka	9	6	67
Mridula	6	4	67
Nakshatra	16	11	69
Olympia	21	9	43
Osanna	20	11	55
Patricia	21	19	90
Tilottama	4	4	100
Victoria	32	31	97
Average			71

Supplementary Material 4. Test for linkage disequilibrium between pairs of the 14 loci used. The pair of loci and *P* values are shown. The value of *P* after a flat Bonferroni correction was 0.0005.

Locus 1	Locus 2	*P* Value	Locus 1	Locus 2	*P* Value	Locus 1	Locus 2	*P* Value
Emu 12	Emx 1	0.943	Emu 04	Emu 15	0.148	Laf 5	Emu 17	0.291
Emu 12	Emx 2	0.061	Emu 04	Emu 17	0.291	Emu 17	Emx 4	**0.000**
Emu 12	Emx 4	0.022	Emu 04	Laf 5	0.608	Emu 17	Laf 3	0.286
Emu 12	Laf 3	0.518	Emu 04	Emu 14	0.944	Emu 17	Emu 3	0.281
Emu 12	Emu 3	0.709	Emu 04	Fh 60	0.994	Emu 17	Laf 2	0.548
Emu 12	Laf 2	0.661	Fh 60	Emx 1	0.887	Emu 17	Emu 15	0.137
Emu 12	Emu 15	0.502	Fh 60	Emx 2	0.728	Emu 17	Emx 1	0.471
Emu 12	Emu 17	0.004	Fh 60	Emx 4	0.496	Emu 17	Emx 2	0.381
Emu 12	Laf 5	0.523	Fh 60	Laf 3	0.587	Emu 15	Emx 1	0.308
Emu 12	Emu 14	0.918	Fh 60	Emu 3	1.000	Emu 15	Emx 2	0.356
Emu 12	Fh 60	0.284	Fh 60	Laf 2	0.808	Emu 15	Emx 4	0.367
Emu 12	Emu 04	0.126	Fh 60	Emu 15	0.953	Emu 15	Laf 3	0.035
Emu 12	Fh 94	0.374	Fh 60	Emu 17	0.747	Emu 15	Emu 3	0.008
Fh 94	Emx 1	0.840	Fh 60	Laf 5	0.916	Emu 15	Laf 2	0.728
Fh 94	Emx 2	0.788	Fh 60	Emu 14	0.136	Laf 2	Emx 1	0.944
Fh 94	Emx 4	0.194	Emu 14	Emx 1	0.796	Laf 2	Emx 2	0.536
Fh 94	Laf 3	0.588	Emu 14	Emx 2	0.937	Laf 2	Emx 4	0.914
Fh 94	Emu 3	0.756	Emu 14	Emx 4	0.148	Laf 2	Laf 3	0.068
Fh 94	Laf 2	0.004	Emu 14	Laf 3	0.413	Laf 2	Emu 3	0.891
Fh 94	Emu 15	0.823	Emu 14	Emu 3	0.496	Emu 3	Emx 1	0.785
Fh 94	Emu 17	0.274	Emu 14	Laf 2	0.523	Emu 3	Emx 2	0.280
Fh 94	Laf 5	0.991	Emu 14	Emu 15	0.173	Emu 3	Emx 4	0.979
Fh 94	Emu 14	0.249	Emu 14	Emu 17	0.114	Emu 3	Laf 3	0.479
Fh 94	Fh 60	0.099	Emu 14	Laf 5	0.994	Laf 3	Emx 1	0.342
Fh 94	Emu 04	0.444	Laf 5	Emx 1	0.401	Laf 3	Emx 2	0.081
Emu 04	Emx 1	0.049	Laf 5	Emx 2	0.319	Laf 3	Emx 4	0.047
Emu 04	Emx 2	0.842	Laf 5	Emx 4	0.101	Emx 4	Emx 1	0.775
Emu 04	Emx 4	0.225	Laf 5	Laf 3	0.711	Emx 4	Emx 2	0.498
Emu 04	Laf 3	0.466	Laf 5	Emu 3	0.294	Emx 2	Emx 1	0.389
Emu 04	Emu 3	0.348	Laf 5	Laf 2	0.190			
Emu 04	Laf 2	0.963	Laf 5	Emu 15	0.023			

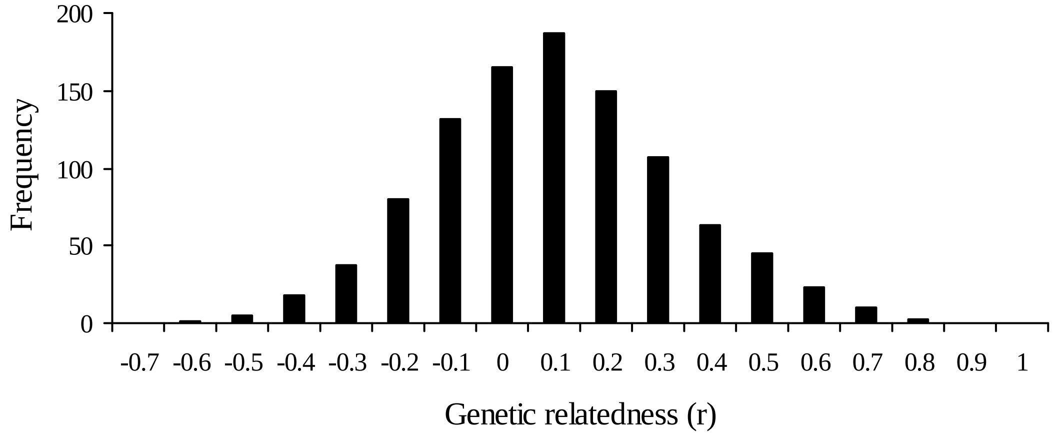
Supplementary Material 5. Average AI and average genetic relatedness between females within first-level communities in ten focal clans. For each first-level community, the size of the community and the number of females genotypes are shown. Values of *r* that were significantly greater than zero are marked in bold. Actual values of relatedness are shown for those communities in which only two females had been sampled. These are results based on 13 loci (results based on 14 loci are in Table 2 of the main chapter).

Clan (size/no. of communities)	First-level community	Average AI (SD)	Average *r* (1.96 SE)
Katrina (16/2)	Community 1 (6/2)	0.250	0.046
	Community 2 (10/2)	0.400	0.148
Lisa (17/2)	Community 1 (5/4)	0.357 (0.164)	**0.418** (0.041)
	Community 2 (12/11)	0.160 (0.121)	0.004 (0.073)
Manasi (12/3)	Community 1 (5/4)	0.333 (0.244)	**0.175** (0.117)
	Community 2 (3/0)	_	_
	Community 3 (4/1)	_	_
Menaka (9/2)	Community 1 (7/4)	0.127 (0.191)	-0.026 (0.183)
	Community 2 (2/2)	0.846	0.540
Mridula (6/2)	Community 1 (4/3)	0.313 (0.024)	**0.259** (0.151)
	Community 2 (2/1)	_	_
Nakshatra (16/2)	Community 1 (14/9)	0.167 (0.110)	0.003 (0.069)
	Community 2 (2/2)	0.031	0.374
Olympia (21/6)	Community 1 (3/3)	0.159 (0.106)	**0.437** (0.225)
	Community 2 (5/3)	0.158 (0.100)	**0.234** (0.080)
	Community 3 (3/2)	0.059	0.487
	Community 4 (2/0)	_	_
	Community 5 (4/1)	_	_
	Community 6 (4/0)	_	_
Osanna (20/2)	Community 1 (11/7)	0.067 (0.078)	**0.152** (0.091)
	Community 2 (9/4)	0.461 (0.172)	0.211 (0.234)
Patricia (21/3)	Community 1 (11/9)	0.218 (0.097)	0.039 (0.066)
	Community 2 (8/8)	0.131 (0.118)	0.076 (0.084)
	Community 3 (2/2)	0.368	0.152
Victoria (32/2)	Community 1 (27/26)	0.090 (0.105)	0.023 (0.026)
	Community 2 (5/5)	0.284 (0.129)	**0.254** (0.130)

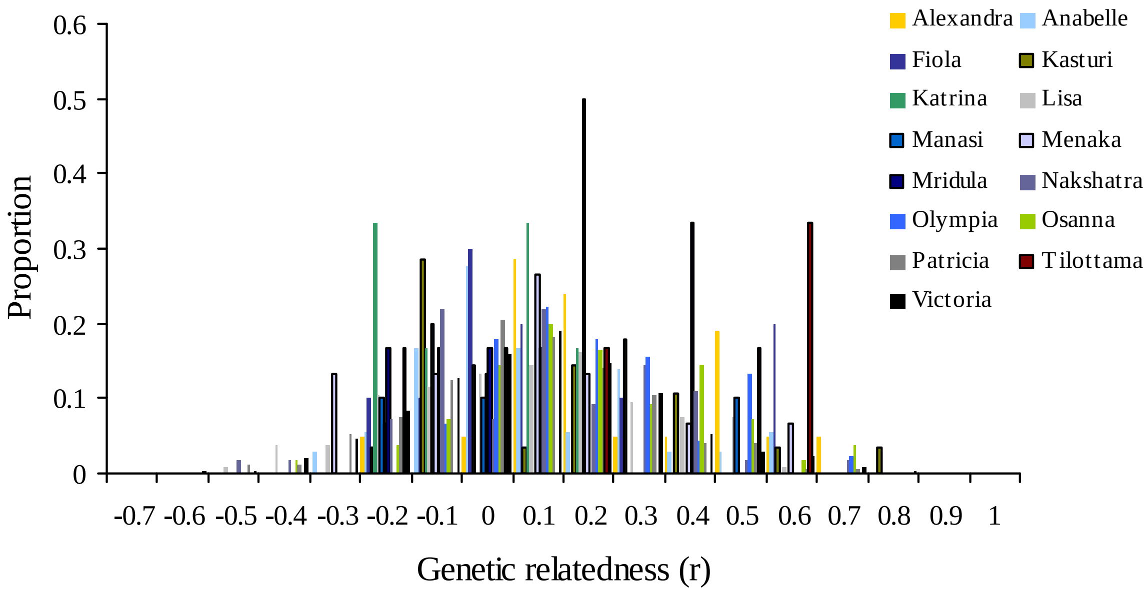
Based on data from 13 loci, seven first-level communities from six clans had average pair-wise relatedness that was significantly greater than zero, while the average pair-wise relatedness values in the other seven communities, from six clans, were not significantly greater than zero.

Supplementary Material 6. Frequency distributions of within-clan pair-wise genetic relatedness (n = 1025 pairs from 15 clans). All the clans are shown together in a) and individually in b). A similar figure based on data from 14 loci is shown as Figure 1 in the main chapter.

a)



b)



Supplementary Material 7. Average pair-wise AI and average pair-wise genetic relatedness, and Mantel test correlation *r*, R^2, and *P* values for the focal clans, based on 13 loci. For each clan, the clan size and the number of females sampled are given. Values of *r* that were significantly greater than zero are marked in bold, as are significant *P* values. The values based on 14 loci are shown in Table 3 in the main chapter. The same pattern as in this table were seen when only data from the dry seasons were analysed using 13 loci. *P* values alone from the Mantel tests based on wet season data (using 13 loci) are shown in the last column. Mantel tests were done only for those clans seen at least 15 times in that season.

Clan (clan size/ no. of females sampled)	Average AI (SD)	Average *r* (1.96 SE)	Correlation *r*	R^2	*P* value	*P* value, wet season
Alexandra (11/7)	0.283 (0.134)	**0.209 (0.096)**	0.114	0.013	0.323	_
Anabelle (11/9)	0.187 (0.145)	0.046 (0.068)	-0.008	0.000	0.495	_
Fiola (7/5)	0.393 (0.244)	0.083 (0.154)	0.654	0.427	0.063	_
Kasturi (8/8)	0.154 (0.123)	0.082 (0.088)	0.662	0.439	**<0.001**	**0.017**
Katrina (16/4)	0.129 (0.162)	-0.076 (0.122)	0.870	0.756	**0.043**	_
Lisa (17/15)	0.111 (0.133)	0.036 (0.048)	0.379	0.144	**0.003**	**0.002**
Manasi (12/5)	0.200 (0.250)	0.071 (0.119)	0.417	0.174	0.138	0.794
Menaka (9/6)	0.115 (0.240)	-0.006 (0.125)	0.502	0.252	**0.045**	_
Mridula (6/4)	0.219 (0.111)	0.056 (0.184)	0.695	0.483	0.239	_
Nakshatra (16/11)	0.140 (0.123)	0.046 (0.060)	0.211	0.045	0.080	0.216
Olympia (21/9)	0.034 (0.069)	**0.148 (0.061)**	0.445	0.198	**0.005**	**0.014**
Osanna (20/11)	0.087 (0.154)	**0.143 (0.059)**	0.202	0.041	0.070	_
Patricia (21/19)	0.074 (0.111)	0.022 (0.033)	0.186	0.035	**0.015**	**0.024**
Tilottama (4/4)	0.533 (0.222)	0.215 (0.231)	0.852	0.726	0.223	_
Victoria (32/31)	0.076 (0.100)	**0.030 (0.021)**	0.233	0.055	**<0.001**	**<0.001**

Supplementary Material 8. Average pair-wise AI and average pair-wise genetic relatedness, and Mantel test correlation *r*, R^2, and *P* values for the focal clans, based on 14 loci, but only using data from the dry seasons. For each clan, the clan size and the number of females sampled are given. Values of *r* that were significantly greater than zero are marked in bold, as are significant *P* values.

Clan (clan size/ no. of females sampled)	Average AI (SD)	Average *r* (1.96 SE)	Correlation *r*	R^2	*P* value
Alexandra (11/7)	0.271 (0.162)	**0.277 (0.088)**	0.014	0.000	0.482
Anabelle (11/9)	0.188 (0.146)	0.033 (0.067)	-0.021	0.000	0.529
Fiola (7/5)	0.398 (0.245)	0.076 (0.158)	0.649	0.421	0.062
Kasturi (8/8)	0.147 (0.132)	**0.084 (0.079)**	0.672	0.451	**0.005**
Katrina (16/4)	0.137 (0.170)	-0.081 (0.107)	0.957	0.915	**0.036**
Lisa (17/15)	0.111 (0.146)	0.038 (0.047)	0.346	0.12	**0.001**
Manasi (12/5)	0.215 (0.263)	0.062 (0.123)	0.414	0.171	0.135
Menaka (9/6)	0.116 (0.239)	-0.012 (0.117)	0.500	0.25	0.061
Mridula (6/4)	0.222 (0.119)	0.070 (0.177)	0.741	0.549	0.263
Nakshatra (16/11)	0.144 (0.117)	0.037 (0.057)	0.211	0.044	0.069
Olympia (21/9)	0.024 (0.044)	**0.132 (0.063)**	0.381	0.145	**0.017**
Osanna (20/10)	0.094 (0.173)	**0.177 (0.055)**	0.253	0.064	0.055
Patricia (21/19)	0.070 (0.108)	0.028 (0.031)	0.145	0.021	**0.032**
Tilottama (4/4)	0.528 (0.229)	0.209 (0.226)	0.840	0.706	0.251
Victoria (32/31)	0.075 (0.101)	**0.046 (0.020)**	0.212	0.045	**<0.001**

Supplementary Material 9. Average pair-wise AI and average pair-wise genetic relatedness, and Mantel test correlation *r*, R^2, and *P* values for the focal clans, based on 14 loci, but only using data from the wet seasons. For each clan, the clan size and the number of females sampled are given. Mantel test results are shown only for the clans with at least 15 sightings each. Values of *r* that were significantly greater than zero are marked in bold, as are significant *P* values.

Clan (clan size/ no. of females sampled)	Average AI (SD)	Average *r* (1.96 SE)	Correlation *r*	R^2	*P* value
Alexandra (11/7)	0.390 (0.159)	**0.277 (0.088)**	_	_	_
Anabelle (11/4)	0.500 (0.548)	-0.094 (0.076)	_	_	_
Fiola (7/1)	_	_	_	_	_
Kasturi (8/7)	0.290 (0.117)	**0.104 (0.099)**	0.58	0.337	**0.013**
Katrina (16/1)	_	_	_	_	_
Lisa (17/15)	0.112 (0.119)	0.038 (0.047)	0.326	0.106	**<0.001**
Manasi (12/4)	0.286 (0.260)	**0.163 (0.115)**	-0.248	0.061	0.836
Menaka (9/3)	0.286 (0.495)	0.189 (0.272)	_	_	_
Mridula (6/4)	0.250 (0.387)	0.070 (0.177)	_	_	_
Nakshatra (16/10)	0.141 (0.198)	0.050 (0.065)	0.153	0.023	0.156
Olympia (21/9)	0.044 (0.108)	**0.132 (0.063)**	0.492	0.242	**0.001**
Osanna (20/7)	0.199 (0.262)	**0.157 (0.082)**	_	_	_
Patricia (21/19)	0.067 (0.148)	0.028 (0.031)	0.154	0.024	**0.032**
Tilottama (4/4)	0.563 (0.190)	0.209 (0.226)	_	_	_
Victoria (32/30)	0.092 (0.138)	**0.039 (0.021)**	0.179	0.032	**<0.001**

Supplementary Material 10. Average pair-wise AI and average pair-wise genetic relatedness with the top (first), second and third associates.

Clan	Associate's rank	Average AI (SD)	Average *r* (1.96 SE)
Alexandra	First	0.482 (0.024)	**0.261 (0.137)**
	Second	0.405 (0.092)	**0.323 (0.206)**
	Third	0.315 (0.089)	0.144 (0.156)
Anabelle	First	0.413 (0.216)	0.101 (0.240)
	Second	0.311 (0.159)	-0.007 (0.084)
	Third	0.181 (0.098)	-0.077 (0.159)
Fiola	First	0.684 (0.236)	**0.425 (0.208)**
	Second	0.522 (0.019)	-0.121 (0.006)
	Third	0.274 (0.127)	-0.054 (0.146)
Kasturi	First	0.332 (0.070)	**0.317 (0.178)**
	Second	0.217 (0.121)	0.140 (0.157)
	Third	0.164 (0.105)	0.101 (0.149)
Katrina	First	0.366 (0.118)	_
	Second	0.350 (0.087)	**0.103 (0.041)**
	Third	0.210 (0.119)	_
Lisa	First	0.394 (0.150)	**0.322 (0.122)**
	Second	0.289 (0.140)	**0.189 (0.096)**
	Third	0.248 (0.108)	0.065 (0.162)
Manasi	First	0.648 (0.215)	**0.173 (0.049)**
	Second	0.278 (0.122)	0.008 (0.152)
	Third	0.273 (0.128)	0.161 (0.199)
Menaka	First	0.564 (0.299)	0.117 (0.333)
	Second	0.077 (0.036)	-0.047 (0.125)
	Third	0.115 (0.045)	_
Mridula	First	0.328 (0.021)	**0.179 (0.157)**
	Second	0.272 (0.054)	0.232 (0.264)
	Third	0.091 (0.003)	-0.114 (0.013)

Clan	Associate’s rank	Average AI (SD)	Average *r* (1.96 SE)
Nakshatra	First	0.400 (0.132)	0.154 (0.175)
	Second	0.237 (0.093)	0.016 (0.104)
	Third	0.201 (0.099)	0.055 (0.111)
Olympia	First	0.232 (0.088)	**0.489 (0.087)**
	Second	0.127 (0.073)	**0.331 (0.159)**
	Third	0.083 (0.081)	0.096 (0.122)
Osanna	First	0.400 (0.259)	**0.334 (0.184)**
	Second	0.264 (0.204)	0.187 (0.192)
	Third	0.207 (0.107)	0.217 (0.158)
Patricia	First	0.351 (0.122)	**0.186 (0.112)**
	Second	0.246 (0.099)	0.067 (0.093)
	Third	0.182 (0.103)	0.090 (0.080)
Tilottama	First	0.706 (0.207)	**0.326 (0.282)**
	Second	0.558 (0.160	**0.327 (0.324)**
	Third	0.335 (0.055)	-0.026 (0.121)
Victoria	First	0.403 (0.130)	**0.270 (0.095)**
	Second	0.292 (0.085)	**0.172 (0.114)**
	Third	0.208 (0.098)	0.061 (0.093)

CHAPTER 5

Dominance Relationships amongst Female Asian Elephants in Nagarahole-Bandipur, Southern India

Title: Dominance relationships amongst female Asian elephants in Nagarahole-Bandipur, southern India

Authors: Nandini Shetty, P. Keerthipriya, T.N.C. Vidya

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

Abstract

We describe here, the first study of dominance relationships in female Asian elephants. We collected data on agonistic interactions in social groups of individually identified Asian elephants in Nagarahole and Bandipur National Parks from 2009 - mid 2012. We recorded 2104 agonistic interactions over several hundred hours of observation. Dominance was seen both within and between clans, which is the most inclusive female social unit in this population. Based on 530 independent agonistic interactions within clans, we found low rates of agonistic interactions. No linear dominance hierarchy could be detected although there was unidirectionality in interactions, and interactions almost always had clear winners. There was an effect of age on dominance, with initiators tending to be older than recipients. However, the clan's matriarch (oldest adult female) was not the single most dominant animal in the clan, unlike in African savannah elephants, nor the most central animal based on social networks. Social association was not correlated strongly with dominance. We observed 516 independent interactions involving individuals from different clans, as part of 152 clan-level interactions. Competition was more intense between than within clans, and only about half the between-clan interactions resulted in a clear winning clan. There were bidirectional interactions between clans and no dominance hierarchy amongst clans. We speculate that the Kabini reservoir, built in the 1970s and currently a large point resource for elephants in the dry season, could have altered patterns of resource availability in the study area, giving rise to strong between-clan interactions and tolerance within clans.

Keywords: Asian elephant, dominance, agonistic interaction, within-clan, between-clan, matriarch, contest, Kabini reservoir.

Introduction

Socioecological theory posits that social systems are a balance between the costs and benefits of group living (Kummer 1968, Dunbar 1992) and predicts that spatio-temporal patterns of female dispersion in polygynous mammals relate to resource-risk distributions (Wrangham 1980, Clutton-Brock 1989, van Schaik 1983, 1989, Terborgh and Janson 1986). Food resource-based limitation of female reproductive success may lead to the transition from egalitarian societies with female transfer between groups to more socially structured, female-bonded groups with varying inter- and intra- group competition/dominance relationships (Wrangham 1980, van Schaik 1989, Isbell 1991, Sterck *et al*. 1997, Isbell and Young 2002). Egalitarian societies with poorly differentiated dominance relationships within groups and female transfer between groups are expected when food resources do not limit female reproductive success (Isbell 1991). On the other hand, when food resources limit female reproductive success, societies are expected to be more socially structured, with no female transfer between groups, and with between-group and within-group competition (Isbell 1991). Food competition may occur through scramble (non-interference) or contest (interference) competition (Nicholson 1954). If important resources are widely dispersed and cannot be monopolised by single females, scramble competition occurs and dominance relationships within groups are expected to be weakly differentiated, while if such resources are clumped and can be monopolised by single females, there is contest competition, and despotic societies are expected to arise, with strong dominance hierarchies within groups (Wrangham 1980, van Schaik 1989, Isbell 1991, van Hooff and van Schaik 1992, Sterck *et al*. 1997, Isbell and van Vuren 1996, Isbell and Young 2002). The nature of the dominance hierarchy within groups may be individualistic or nepotistic, the occurrence of which is likely to depend on the role of kinship in social organisation.

Dominance relationships are especially interesting to study in Asian elephants because of three contradicting predictions about the nature of dominance relationships in this species (as in African savannah elephants, see Archie *et al*. 2006). Elephants are considered generalist bulk feeders and resources are presumed to be widely distributed (Owen-Smith 1988). The primary food of Asian elephants is believed to be grasses (Baskaran *et al*. 2010), which is also a widely distributed resource. The widely-distributed, low quality resources fed upon by elephants would predict primarily scramble competition and, therefore, egalitarian relationships within, and possibly between, groups. However, in the African savannah elephant, age/size-based hierarchies have been observed (Archie *et al.* 2006, Wittemyer and Getz 2007). In African savannah elephants, the matriarch (oldest adult female) that heads each family group (Douglas-Hamilton 1972) is often the most dominant animal (Dublin 1983, Wittemyer and Getz 2007), and also plays an important role in between-family group dominance (Wittemyer and Getz 2007). Dominance relationships between matriarchs of different family groups were found to be based on matriarch age, and those between non-matriarchs of different groups were found to be based on the ranks of their respective matriarchs (Wittemyer and Getz 2007). It must be pointed out here that African savannah elephants show a nested multilevel organisation and family groups are not the most inclusive unit of social organisation. Family groups may associate together to form bond groups, which may associate to form clans (Moss and Poole 1983, Wittemyer *et al.* 2005). Since their closest living relatives (the African savannah elephants) show age/size based hierarchies, it might be expected that Asian elephants would show such hierarchies too rather than an egalitarian society. However, age/size based hierarchies are expected to be more common in species in which grouping is not genetically based (Wrangham 1980, van Schaik 1989, Isbell 1991, Isbell and van Vuren 1996, Sterck *et al.* 1997, Isbell and Young 2002). The most inclusive level of female social grouping in the Asian elephant is the clan (chapter 2). Female Asian elephants show high fission-fusion dynamics (*sensu* Aureli *et al.* 2008) and are usually found in small groups, which are subsets of a clan (chapter 2). Females in these groups, which may be thought of as ‘family groups’ are closely related to one another (Vidya and Sukumar 2005), and females within the entire clan are also more related to one another on average compared to the rest of the population (previous chapter). Therefore, there might be opportunity for inclusive fitness benefits, which might then predict nepotistic dominance relationships (Wrangham 1980, van Schaik 1989, Isbell 1991, Isbell and van Vuren 1996).

Dominance relationships have not been previously studied in the Asian elephant. Since there is no support for female transfer in the species (Fernando and Lande 2000), except as a consequence of social breakdown due to habitat loss (Vidya *et al.* 2007), it is likely that female reproductive success is limited to some extent by resources, resulting in at least a low level of dominance between clans. We, therefore, wanted to examine the nature of dominance relationships in Asian elephants to find out whether female relationships within clans are egalitarian or whether there is a linear dominance hierarchy, and whether there is an effect of age/size on dominance relationships within clans. Since the matriarch is the oldest female in a clan, we also wanted to find out whether the matriarch is the most dominant animal. Since dominance is expected to be affected by resource availability, we also examined seasonal difference in within-clan dominance. We had observed that there were multiple groups using the area around the Kabini backwaters without showing any affiliative behaviour towards one another. Therefore, we also wanted to find out if there were agonistic interactions between clans.

Methods

Field data collection

Field data were collected in Nagarahole National Park and Tiger Reserve (Nagarahole) and the adjoining Bandipur National Park and Tiger Reserve (Bandipur) in southern India under the Kabini Elephant Project (see Vidya *et al*. 2014, chapter 2 of this thesis for more details about the study area). Both these parks are part of the Nilgiris-Eastern Ghats landscape in southern India, and harbour high elephant densities (~2-4 elephants/km^2, AERCC 1998). Nagarahole and Bandipur primarily consist of deciduous forests and are separated by the Kabini reservoir on the river Kabini, providing a large point resource with water and grass during the dry season to elephants and other herbivores. The dry season lasts from about December to mid-June, when the wet season begins (chapter 2 of this thesis). Elephants tended to use the area around the Kabini reservoir during the dry season and were more scattered in the forest during the wet season. Because of low visibility and the scattered nature of groups in the forest, most of the behavioural data on dominance come from areas centred around the Kabini reservoir.

Field data were collected from March 2009 to June 2012, between about 6:30 AM to 6:00-6:45 PM (depending on daylight hours and field permits). As mentioned previously (chapter 2), female elephant “groups” were identified as a set of female elephants and their young that showed coordinated movement (especially to or from a water source) or affiliative behaviour, and were within 50-100 m of one another. All elephants within groups were aged, sexed, and individually identified (see Vidya *et al*. 2014). Ageing was done based on skull size, body size, the top fold of the ear, and other body characteristics, using the Forest Department’s semi-captive elephants of known ages in the area as a reference (see Vidya *et al*. 2014). Females were broadly categorized as calves (<1 year), juveniles (1-<5 years), subadults (5-<10 years), or adults ($\geq$10 years; although individuals older than 15 years have been referred to as adults in Vidya *et al*. 2014, since we subsequently found that females were often sexually mature at 10 years of age, we have used 10 years here). Adult females were further placed into 5- (up to about 20 years of age) or 10-year age intervals.

Data on dominance behaviours were obtained through *ad libitum* and focal group sampling (see Altmann 1974). The latter was part of behavioural sampling carried out in half-hour cycles, consisting of a scan (5 minutes), group position pictures (5 minutes), focal sampling (15 minutes), and a 5-minute break. Behaviours such as charges, chases, pushes, shoves, displacements, supplants, lashing out with trunk, kicking, trunk wrestling, pulling tail, and placing trunk over the head of another animal with some force, were recorded as agonistic behaviours. Subordinate behaviours included walking backwards, turning away and walking or running, cowering down and tilting head up slightly, and looking backwards and walking. In dominance between individuals, the initiator of the interaction was considered the winner if the other individual physically retreated in some way, by either walking away, being supplanted, cowering down or flinching. There was no winner if the recipient ignored the initiator or retaliated, but ineffectually. Occasionally, the recipient would retaliate in such a manner as to make the initiator walk away hurriedly, in which case, the recipient was considered the winner. All the focal sampling and most of the *ad libitum* sampling were recorded on a Sony HDR-XR100E video camera. Although scoring was done in the field, we also went through all the video footage to confirm the behaviours and identities of animals engaged in such agonistic behaviours. All occurrences of agonistic interactions, both within and between clans, were recorded and this was done irrespective of whether the participants in the interaction were adult females or not.

Data Analysis

An agonistic interaction was said to be independent of another agonistic interaction involving the same animals only if the individuals fed or interacted with another individual between the two interactions. Agonistic interactions between two clans were usually considered independent only if they occurred on different days. We analysed non-independent and independent interactions to use their ratio as a measure of the intensity of dominance. All interactions were considered dyadic. Therefore, an individual simultaneously winning against more than one individual (such as during displacements) was scored as multiple dyadic interactions (see Archie *et al*. 2006). However, such interactions were not common.

Dominance data were tested for linearity of dominance using Landau’s index *h* (Landau 1951) and de Vries’ corrected index *h*' (de Vries 1995). Linear dominance hierarchies are obtained when triadic relationships are transitive (if A dominates B and B dominates C, A also dominates C) and not circular (A dominates B, B dominates C, and C dominates A). Linear dominance hierarchies also show largely unidirectional interactions within dyads (if A dominates B, B usually does not dominate A). Reciprocity (retaliation) of agonistic interactions was calculated through a Mantel Z test by comparing the dominance matrix with its inverse. These analyses were carried out using SOCPROG 2.4 (Whitehead 2009), which runs on MATLAB, and statistical tests were carried out using Statistica 8 (StatSoft 2007). Other data manipulation and analyses were carried out in MATLAB 7 R2004a (The MathWorks, Inc, 1984-2011, www.mathworks.com). The rate of dominance between pairs of individuals was calculated by dividing the number of agonistic interactions observed between those individuals by the amount of time the two individuals were sighted together. This was then averaged across all pairs of individuals seen together within each group. We examined the effect of age on dominance by carrying out Wilcoxon’s matched-pairs tests on the ages of the initiators and recipients. We also calculated the average dominance index (see Hemelrijk *et al*. 2005) for adult females within clans and ranked them using this index. We examined if older females showed higher ranks. We also carried out Mantel tests (Mantel 1967) to find out whether individuals that were farther apart in age interacted to a greater extent than those of similar ages. We examined the correlation between the absolute age differences of initiators and recipients and the total amount of dominance (given and received) between them. In addition, *t*-tests were carried out to examine the difference in ages between individuals that were part of an agonistic interaction and those that were not.

We also calculated centrality measures of females in order to find out how important a female was in her clan’s association network. Association data were already available from previous work (chapter 2). Degree centrality (the number of associates a focal female has, or the number of nodes a focal node is connected to in the network), closeness centrality (a measure of how close a female, or node in the network, is to others, calculated as the inverse of the sum of path lengths from a focal node to all the other nodes), and betweenness centrality (a measure of how important a female is in the connectedness of the network, calculated as the proportion of all shortest paths between all other pairs of nodes that go through the focal node) were calculated using Gephi 0.7 (Bastian *et al*. 2009). Dominance networks were created using NetDraw (Borgatti 2002). We examined whether dominance networks were random by comparing the in-degree (dominance received) and out-degree (dominance given) distributions of the observed network against Poisson expectations that would arise from an Erdös-Rényi random network (Erdös and Rényi 1960) using chi-square tests.

We also examined the relationship between the strength of association between adult females within clans and the number of agonistic interactions between them. The strength of association was measured using the association index (AI) between pairs of adult females, as the ratio of the number of times two females A and B were seen together (N_{AB}) to the number of times either A or B was observed (N-D, where N is the total number of sightings and D the number of times neither A nor B was seen) (Ginsberg and Young 1992). This was based on previously collected association data (chapter 2). Since we were not sure if resource availability differed between the dry and wet seasons in our study area, we also examined agonistic interactions across seasons, with season as a proxy for resource availability. An ANCOVA was carried out with the number of agonistic interactions/hour as the dependent variable, season as the categorical predictor, and average group size as a continuous predictor.

We analysed between-clan dominance at the individual level and at the clan level. There could be multiple individual-level interactions that occurred during a single clan-level interaction. Therefore, we examined the effect of age separately in individual-level interactions, and examined the effect of age and group size in clan-level interactions. One clan had to displace or supplant the other from its feeding patch in order to be deemed the winner of the clan-level interaction. Therefore, it was possible to have individual-level winners but no clan-level winner in between-clan interactions.

Results

We recorded a total of 2104 (independent plus non-independent) agonistic interactions, of which 1511 were collected *ad libitum* and 593 during 121 focal sampling sessions (of a total duration of 105.2 hours; 26 of the focal sampling sessions were less than half an hour long as the elephants moved away).

Within-clan dominance relationships

A total of 739 agonistic interactions were observed within groups, of which 530 were independent interactions. There were clear winners in 98% of the independent interactions, and the initiator of the agonistic interaction was the final winner of the interaction 96.6% of the time, across all independent, within-group interactions. The types of agonistic interactions and their frequencies are shown in Table 1, and the proportions of different agonistic interactions across five different clans are shown in Figure 1. Although within-group agonistic interactions were recorded in 18 different clans, we analysed interactions from only the five clans for which at least 30 independent agonistic interactions had been recorded because the other clans showed low numbers of agonistic interactions (Table 2). Most of the five clans showed similar proportions of displacements and pushes, which were the two most common types of agonistic interactions. However, Kasturi’s clan showed a larger number of pushes (Figure 1), largely because of one individual.

Based on the focal sampling sessions, the rate of independent agonistic interactions within clans, including all clan members, was 0.054 ± 0.020 per min (3.2 interactions per hour) and the same involving only females was 0.022 ± 0.015 per min (1.3 interactions per hour). The rates appear to be even lower when the total time a clan is observed is considered (Table 2), but that was because there were many sightings of short duration during which a dominance event would not be likely to occur because of the low dominance rate. We did examine whether the number of interactions/hour changed with the duration of the observation bout and found that it did not appear to (Figure 2), but the CI was very large for 10 minute observations. The average (± 95% CI) pair-wise dominance/hour for pairs of adult females within clans was found to be low but variable (0.035 ± 0.032 in Kasturi’s clan, 0.023 ± 0.014 in Lisa’s clan, 0.095 ± 0.090 in Patricia’s clan, 0.209 ± 0.098 in Unnati’s clan, and 0.050 ± 0.021 in Victoria’s clan).

Table 1. Agonistic behaviours within clans and their absolute and relative frequencies. Interactions that were similar have been grouped together. Abbreviations: CHS – chase, CHR – charge, PSH – push (with head), POK – poke with tusks (by young males that were part of female groups), HIT – hit (head on head), KIC – kick, SHO – shove (with body), LSH – lash out with trunk, PUL – pull tail with trunk, SUP – supplant, PSP – push slightly and supplant, DIS – displace, AVO – avoid, AVB – turn away, WBW – walk backwards, BLK – block (but not through physical contact), NDG – nudge, TCH – touch face/mouth roughly, not in a gesture of placation, TRH – place trunk on head, again not in an affiliative manner, PTR – pulling/holding the trunk and preventing the animal from feeding, CHK – checking the genitalia of another female (but roughly).

Type of dominance	Absolute frequency	Relative frequency
CHS/CHR	26	0.035
PSH/POK/HIT	183	0.248
KIC	47	0.064
SHO	26	0.035
LSH/PUL	38	0.051
SUP/PSP	68	0.092
DIS/AVO/AVB/WBW/BLK	252	0.340
NDG/TCH/TRH/PTR	61	0.083
CHK	38	0.051

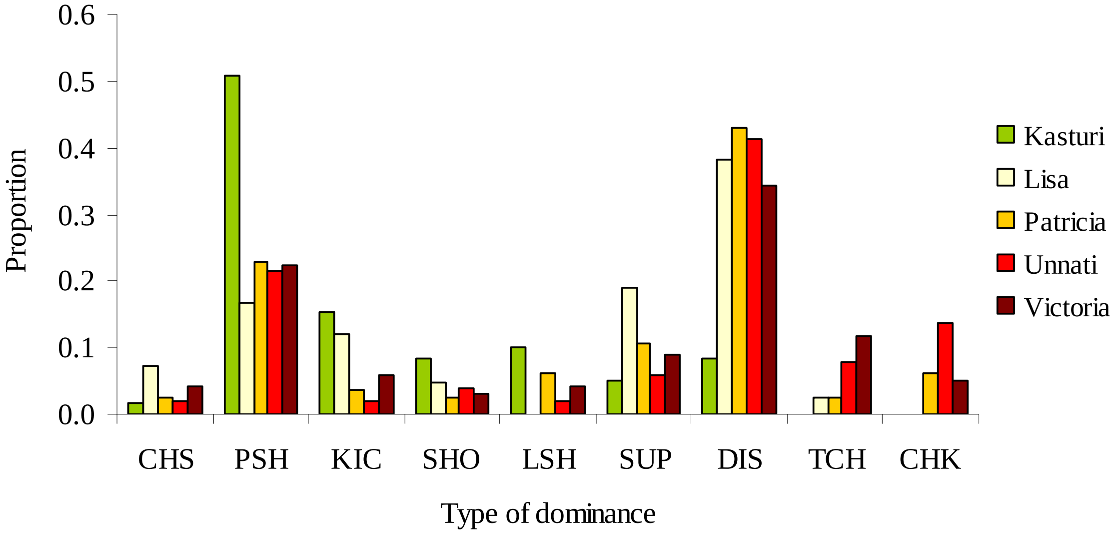


Figure 1. Proportions of different types of agonistic interactions across five clans.

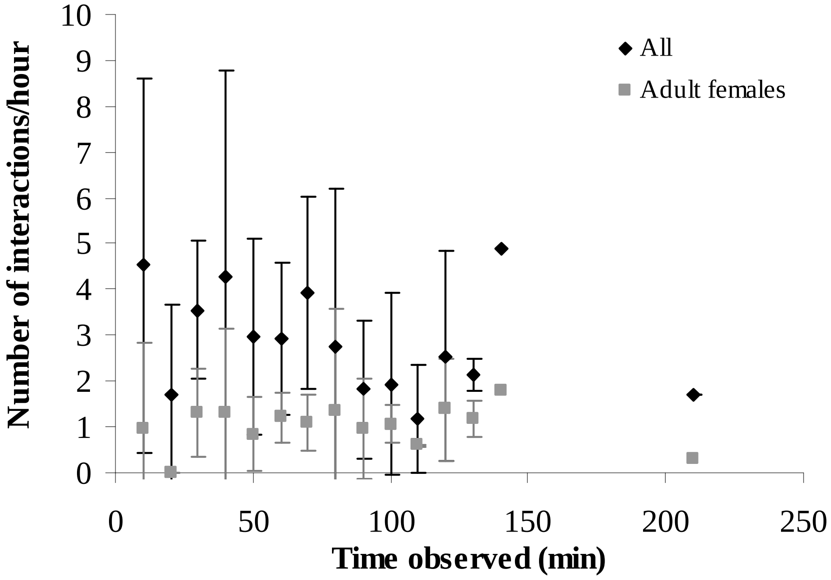
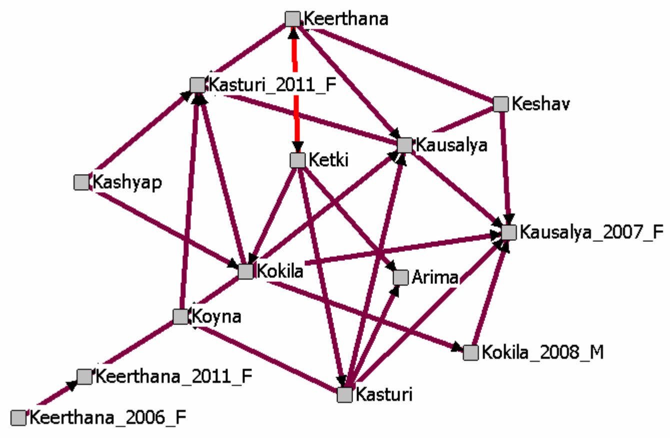


Figure 2. Rate of independent agonistic interactions plotted against observation duration for interactions by all individuals and for those involving only adult females. Error bars are 95% CI.

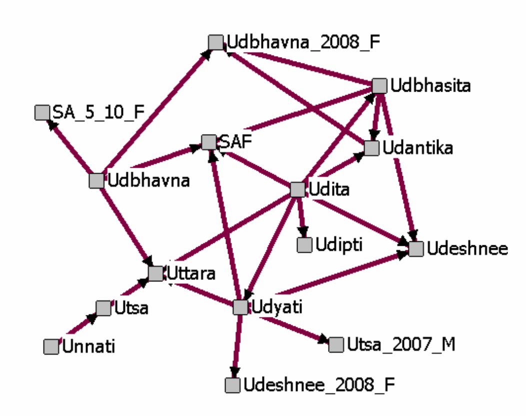
We found no linear dominance hierarchy within any of the five clans tested (Kasturi’s clan: Landau’s *h*=0.114, expected random value=0.200; de Vries’ *h*'=0.257, test for linearity *P*=0.288; Lisa’s clan: Landau’s *h*=0.020, expected random value=0.120; de Vries’ *h*'=0.129, test for linearity P=0.442; Patricia's clan: Landau's h=0.016, expected random value=0.079; de Vries' h'=0.088, test for linearity P=0.364; Unnati's clan: Landau's h=0.130, expected random value=0.188; de Vries' h'=0.277, test for linearity P=0.217; Victoria's clan: Landau's h=0.012, expected random value=0.043; de Vries' h'=0.052, test for linearity P=0.205). The test for reciprocity (retaliation), however, showed unidirectionality in Kasturi's clan (Mantel Z-test for absolute reciprocity, Z=-0.088, P=0.944, Hemelrijk Rr-test for relative reciprocity, Rr=-0.006, P=0.495), Patricia's clan (Mantel Z-test for absolute reciprocity, Z=-0.038, P=1.000, Hemelrijk Rr-test for relative reciprocity, Rr=-0.043, P=0.974), Unnati's clan (Mantel Z-test for absolute reciprocity, Z=-0.103, P=1.000, Hemelrijk Rr-test for relative reciprocity, Rr=0.009, P=0.442), and Victoria's clan (Mantel Z-test for absolute reciprocity, Z=-0.023, P=0.981, Hemelrijk Rr-test for relative reciprocity, Rr=-0.024, P=0.953). The relative, but not absolute, reciprocity test was significant in Lisa's clan (Mantel Z-test for absolute reciprocity, Z=0.038, P=0.223, Hemelrijk Rr-test for relative reciprocity, Rr=0.136, P=0.004). Thus, although there was unidirectionality in agonistic interactions, with little retaliation between individuals, we were not able to detect a linear dominance hierarchy in any of the clans. This was not so much because of intransitivity (in which A is dominant over B, B over C, and C over A, which contributes to a lack of linearity) in triads, but because many individuals did not interact (in a dominance relationship) with one another at all (Figures 3, 4).

Analysis of degree distributions of the focal clans' dominance networks showed that the observed distributions of in-degree were random (P>0.05, df<5) in all clans except Victoria's clan (all individuals: χ^2=72.801, df=11, P<0.001; only adult females: χ^2=20.874, df=7, P=0.004). This could be a result of small sample size of degrees in the other clans. The out-degree distributions of Kasturi's and Lisa's clans were random based on chi-square tests (P>0.05, df<5), non-random based on Patricia's and Unnati's clans only when all individuals were included (Patricia's clan: all individuals: χ^2=120.955, df=7, P<0.001; only adult females: χ^2=2.758, df=3, P=0.430; Unnati's clan: all individuals: χ^2=79.833, df=6, P<0.001; only adult females: χ^2=8.966, df=4, P=0.062), and non-random in Victoria's clan when either all individuals (χ^2=635064.021, df=8, P<0.001) or only adult females were included (χ^2=126.397, df=9, P<0.001).

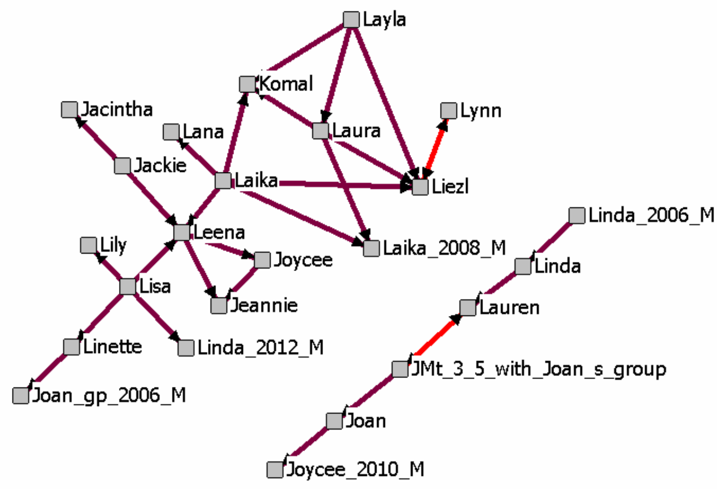
Kasturi’s clan



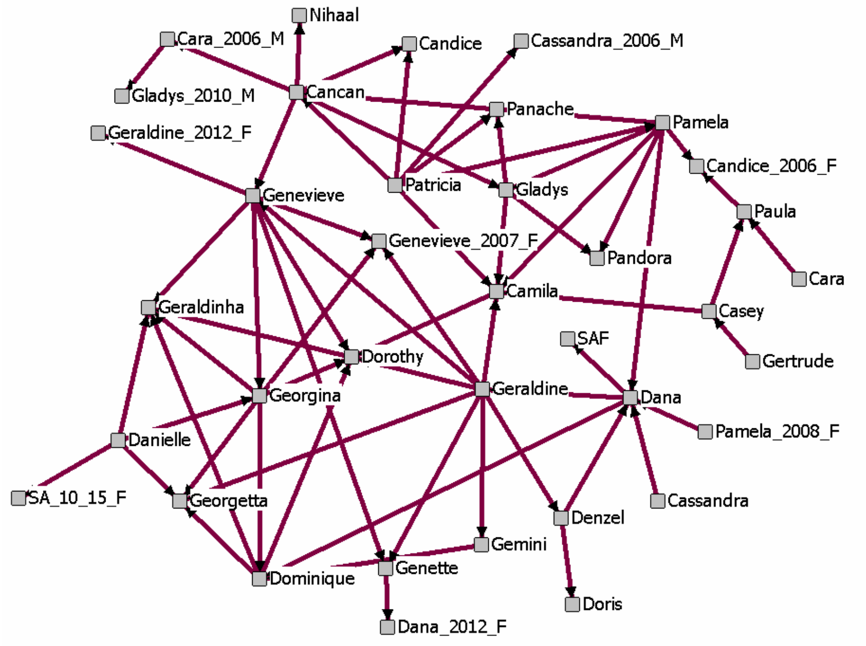
Unnati’s clan



Lisa’s clan



Patricia's clan



Victoria's clan

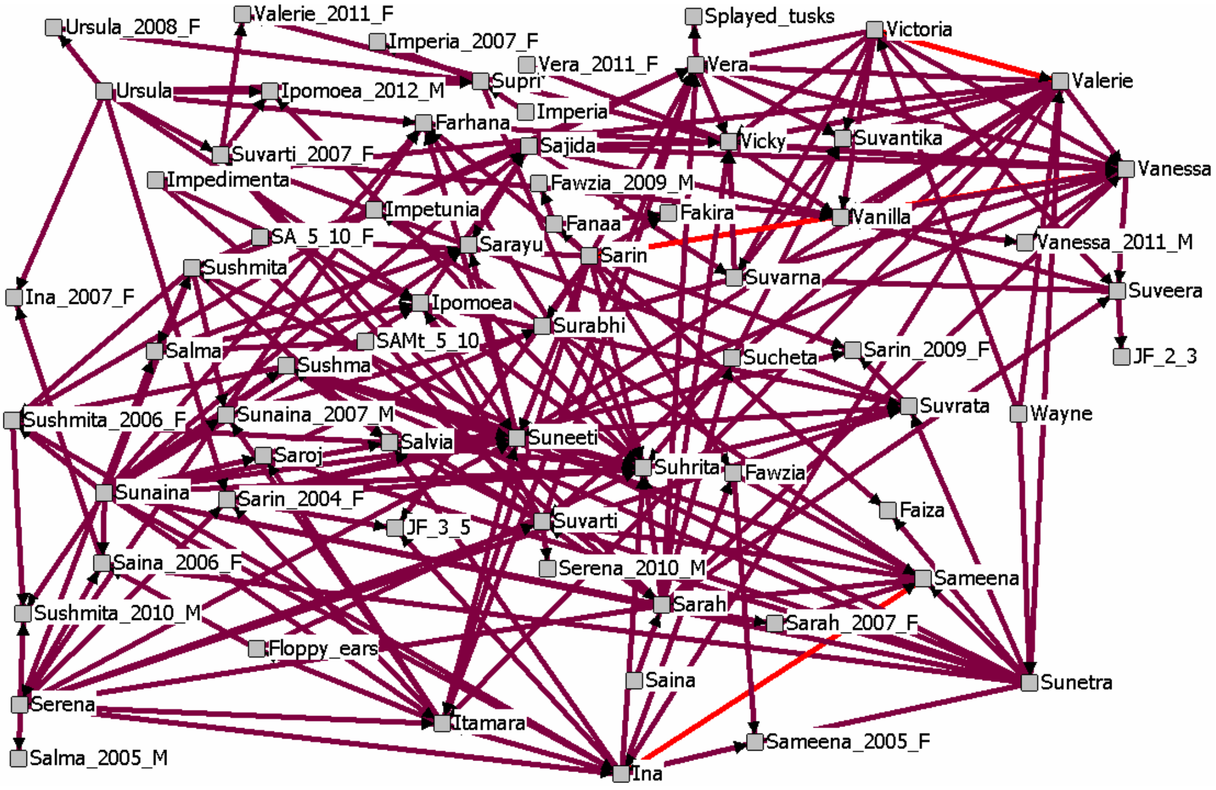
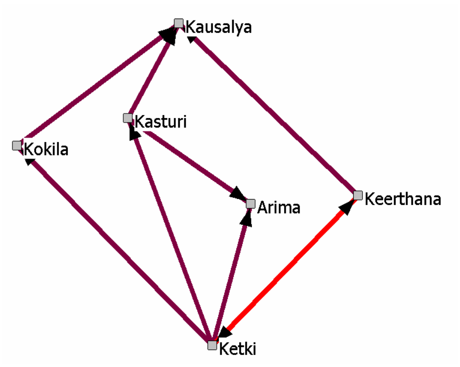
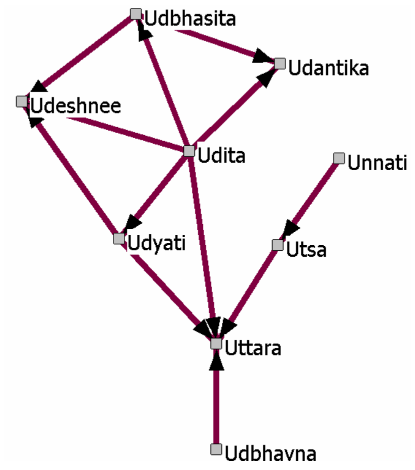


Figure 3. Within-group dominance networks for the five focal clans based on all individuals. Each node is an individual and lines indicate agonistic interactions in the directions the arrows point towards. Maroon lines are unidirectional relationships and red lines are bidirectional relationships.

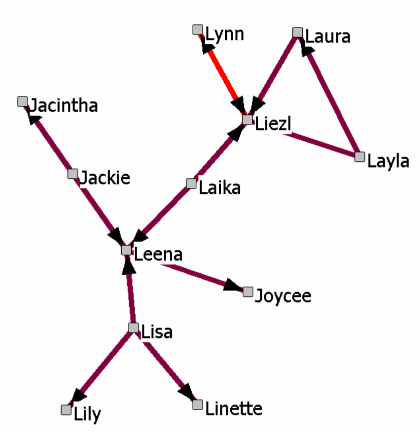
Kasturi's clan



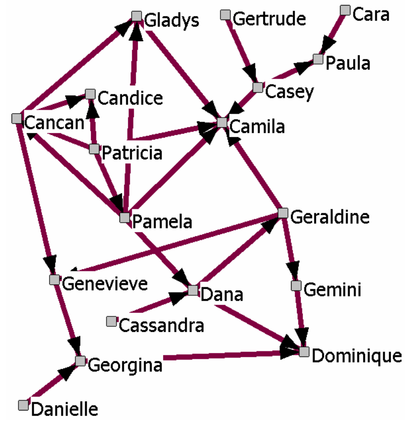
Unnati's clan



Lisa's clan



Patricia's clan



Victoria's clan

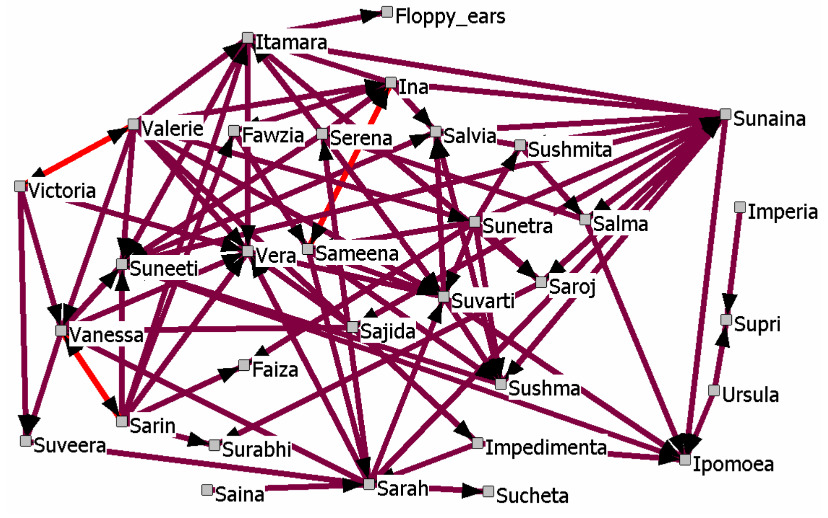


Figure 4. Within-group dominance networks for the five focal clans based on only adult females. Nodes are adult females and lines indicate directional agonistic interactions. Maroon lines are unidirectional relationships and red lines are bidirectional relationships.

a) Kasturi’s clan

	Kasturi	Keerthana	Kausalya	Kokila	Ketki	Arima	Koyna
Kasturi	*	0	1	0	0	1	0
Keerthana	0	*	1	0	1	0	0
Kausalya	0	0	*	0	0	0	0
Kokila	0	0	1	*	0	0	0
Ketki	1	1	0	1	*	1	0
Arima	0	0	0	0	0	*	0
Koyna	0	0	0	0	0	0	*

b) Unnati’s clan

	Unnati	Udantika	Utsa	Udita	Udbhavna	Udeshnee	Udbhasita	Udyati	Uttara
Unnati	*	0	1	0	0	0	0	0	0
Udantika	0	*	0	0	0	0	0	0	0
Utsa	0	0	*	0	0	0	0	0	1
Udita	0	2	0	*	0	1	2	2	3
Udbhavna	0	0	0	0	*	0	0	0	1
Udeshnee	0	0	0	0	0	*	0	0	0
Udbhasita	0	2	0	0	0	1	*	0	0
Udyati	0	0	0	0	0	1	0	*	2
Uttara	0	0	0	0	0	0	0	0	*

c) Victoria’s clan

	Victoria	Valerie	Imperia	Salma	Impedimenta	Faiza	Farah	Sucheta	Saina	Ursula	Sunetra	Vanessa	Sunaina	Fawzia	Sameena	Suveera	Sushmita	Serena	Ina	Suvarti	Sarah	Ipomoea	Itamara	Sarin	Surabhi	Suneeti	Vera	Supri	Sushma	Salvia	Sajida	Saroj	Floppy_ears	Impetunia	Sarayu
Victoria	*	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
Valerie	1	*	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0
Imperia	0	0	*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Salma	0	0	0	*	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Impedimenta	0	0	0	0	*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Faiza	0	0	0	0	0	*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Farah	0	0	0	0	0	0	*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sucheta	0	0	0	0	0	0	0	*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Saina	0	0	0	0	0	0	0	0	*	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ursula	0	0	0	0	0	0	0	0	0	*	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	1	0	0	0	0	0	0	0
Sunetra	0	0	0	0	0	1	0	0	0	0	*	0	5	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	3	0	0	1	0	0	0
Vanessa	0	0	0	0	0	0	0	0	0	0	0	*	0	0	0	2	0	0	0	0	0	0	0	1	0	1	2	0	0	0	0	0	0	0	0
Sunaina	0	0	0	2	0	0	0	0	0	0	0	0	*	0	0	0	3	0	1	0	0	1	3	0	0	2	0	0	2	1	1	4	0	0	0
Fawzia	0	0	0	0	0	0	0	0	0	0	0	0	0	*	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sameena	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0	0	0	1	2	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Suveera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sushmita	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	*	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Serena	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	1	1	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0
Ina	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	*	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0
Suvarti	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0
Sarah	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	2	0	2	0	1	*	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Ipomoea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0	0	0	1	0	0	0	0	0	0	0	0	0
Itamara	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0	0	2	1	0	0	0	0	1	1	0	0
Sarin	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	2	*	1	1	1	0	0	0	0	0	0	0	0
Surabhi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0	0	0	0	0	0	0	0	0	0
Suneeti	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0	0	0	3	0	0	0	0	0
Vera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0	0	0	0	0	0	0	0
Supri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0	0	0	0	0	0	0
Sushma	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	*	1	0	0	0	0	0
Salvia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0	0	0	0	0
Sajida	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	*	0	0	0	0
Saroj	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	*	0	0	0
Floppy_ears	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0	0
Impetunia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0
Sarayu	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*

d) Lisa's clan

	Lisa	Joan	Laika	Layla	Linda	Jackie	Jill	Lucy	Laura	Lindsey	Lydia	Leena	Jacintha	Liezl	Linette	Lily	Lynn	Joycee	Lauren
Lisa	*	0	0	0	0	0	0	0	0	0	0	2	0	0	3	1	0	0	0
Joan	0	*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Laika	0	0	*	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Layla	0	0	0	*	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0
Linda	0	0	0	0	*	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jackie	0	0	0	0	0	*	0	0	0	0	0	1	1	0	0	0	0	0	0
Jill	0	0	0	0	0	0	*	0	0	0	0	0	0	0	0	0	0	0	0
Lucy	0	0	0	0	0	0	0	*	0	0	0	0	0	0	0	0	0	0	0
Laura	0	0	0	0	0	0	0	0	*	0	0	0	0	1	0	0	0	0	0
Lindsey	0	0	0	0	0	0	0	0	0	*	0	0	0	0	0	0	0	0	0
Lydia	0	0	0	0	0	0	0	0	0	0	*	0	0	0	0	0	0	0	0
Leena	0	0	0	0	0	0	0	0	0	0	0	*	0	0	0	0	0	1	0
Jacintha	0	0	0	0	0	0	0	0	0	0	0	0	*	0	0	0	0	0	0
Liezl	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0	0	1	0	0
Linette	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0	0	0	0
Lily	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0	0	0
Lynn	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	*	0	0
Joycee	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0
Lauren	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*

e) Patricia's clan

	Patricia	Danielle	Pamela	Geraldine	Cara	Casey	Gertrude	Gladys	Genevieve	Dana	Gloria	Cancan	Camila	Glenda	Georgina	Doris	Cassandra	Candice	Dominique	Gemini	Paula
Patricia	*	0	1	0	0	0	0	0	0	0	0	2	2	0	0	0	0	1	0	0	0
Danielle	0	*	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Pamela	0	0	*	0	0	0	0	3	0	2	0	1	2	0	0	0	0	0	0	0	0
Geraldine	0	0	0	*	0	0	0	0	1	0	0	0	4	0	0	0	0	0	0	1	0
Cara	0	0	0	0	*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Casey	0	0	0	0	0	*	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Gertrude	0	0	0	0	0	1	*	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gladys	0	0	0	0	0	0	0	*	0	0	0	0	1	0	0	0	0	0	0	0	0
Genevieve	0	0	0	0	0	0	0	0	*	0	0	0	0	0	3	0	0	0	0	0	0
Dana	0	0	0	1	0	0	0	0	0	*	0	0	0	0	0	0	0	0	1	0	0
Gloria	0	0	0	0	0	0	0	0	0	0	*	0	0	0	0	0	0	0	0	0	0
Cancan	0	0	0	0	0	0	0	1	1	0	0	*	0	0	0	0	0	1	0	0	0
Camila	0	0	0	0	0	0	0	0	0	0	0	0	*	0	0	0	0	0	0	0	0
Glenda	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0	0	0	0	0	0	0
Georgina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0	0	0	2	0	0
Doris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0	0	0	0	0
Cassandra	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	*	0	0	0	0
Candice	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0	0	0
Dominique	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0	0
Gemini	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	*	0
Paula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*

Figure 5. Numbers of agonistic interactions between adult females in the five focal clans. The rows represent the aggressors and the columns represent the recipients of dominance.

Females are ordered by age, decreasing from left to right, and from top to bottom. Therefore, if dominance was based on age, one would expect to see most of the dominance in the upper triangles. Such instances when the older female won the majority of agonistic interactions are coloured in black, and those when the younger female won the majority of agonistic interactions are coloured in grey. White squares represent either no agonistic interaction or an equal number of aggressive interactions shown by both individuals.

Effect of age on within-clan dominance and the role of the matriarch

As mentioned above, we did not find clear evidence for a linear dominance hierarchy; tests for detecting hierarchies were not significant but almost all interactions had clear winners and bidirectional interactions were rare. We examined the effect of age on dominance and found, based on the entire dataset of agonistic interactions within clans, that the ages of the initiators and recipients were significantly different (Wilcoxon's matched-pairs test, N=529, Z=15.92, P<0.001), with the initiators tending to be older than recipients (mean ± 1.96 SE age of initiators: 32.3 ± 1.39, of recipients: 15.1 ± 1.17). The dataset of only adult females also showed a significant difference between the ages of the initiators and recipients of agonistic interactions (Wilcoxon's matched-pairs test, N=238, Z=9.51, P<0.001), with initiators being older on average than recipients (mean ± 1.96 SE age of initiators: 37.6 ± 1.76, of recipients: 24.7 ± 1.61). The percentage of independent agonistic interactions in which older individuals won was 85.55% when all individuals within clans were considered, and this was 77.73% when only adult females were considered. The significant difference between the ages of initiators and recipients (of all ages included) remained when each of the five focal clans was tested individually including all individuals (Wilcoxon's matched-pairs tests: Kasturi's clan: N=33, Z=3.17, P=0.002; Lisa's clan: N=35, Z=4.08, P<0.001; Patricia's clan: N=87, Z=6.96, P<0.001; Unnati's clan: N=31, Z=3.66, P<0.001; Victoria's clan: N=272, Z=11.41, P<0.001) and largely remained when only interactions involving adult females were analysed (Wilcoxon's matched-pairs tests: Kasturi's clan: N=11, Z=1.20, P=0.230; Lisa's clan: N=17, Z=3.55, P<0.001; Patricia's clan: N=39, Z=4.83, P<0.001; Unnati's clan: N=19, Z=1.85, P=0.064; Victoria's clan: N=118, Z=6.46, P<0.001). The effect of age can be seen in Figure 5, in which most of the agonistic interactions are found above the diagonal. However, there were also several instances of younger individuals dominating older individuals in four of the five clans (Figure 5).

Mantel tests (Mantel 1967) to check for correlations between the absolute age differences of initiators and recipients and the total amount of dominance (given and received) between them showed no significant correlation in four clans (Kasturi's clan: R=-0.141, one-tailed P=0.318; Patricia's clan: R=0.031, one-tailed P=0.331; Unnati's clan: R=0.042, one-tailed P=0.406; Victoria's clan: R=-0.061, one-tailed P=0.089), and a small but significant correlation in Lisa's clan (R=0.167, one-tailed P=0.018). Therefore, individuals of similar and different ages did not interact agonistically at different rates. Similarly, when *t*-tests were carried out to examine the difference in ages between individuals that were part of an agonistic interaction and those that were not, only Lisa's clan showed a significant difference (N_{no_dom}=159, N_{dom}=12, t=-2.046, P=0.042), with the set showing no dominance being closer aged than the set showing dominance. None of the other clans showed a significant difference in this *t*-test (Kasturi's clan: N_{no_dom}=13, N_{dom}=8, t=0.890, P=0.384; Patricia's clan: N_{no_dom}=184, N_{dom}=26, t=0.488, P=0.626; Unnati's clan: N_{no_dom}=24, N_{dom}=12, t=0.175, P=0.862; Victoria's clan: N_{no_dom}=512, N_{dom}=83, t=1.511, P=0.131) and seemed to show different patterns qualitatively. None of the *F*-ratios (for variances) were significantly different from one (P>0.2).

While there was some effect of age on dominance, the clan's matriarch (oldest adult female) was the single most dominant adult female in only one clan (Figure 6). When we looked at the proportions of other adult females within clans to which dominance was shown, the highest proportion (of clan-mate adult females) was dominated by the matriarch only in Lisa's clan and was dominated by non-matriarchs in other clans (Figure 7). A non-matriarch dominated a greater proportion of individuals even in Lisa's clan if the proportion of all individuals in the clan and not just adult-females that were dominated were examined. Based on dominance ranks, the matriarch was not the single most dominant female in any clan (Figure 8). Centrality measures calculated based on the association network of all adult females showed that the matriarch did not have the highest degree centrality in any of the five clans. The matriarch shared the highest closeness and betweenness centrality with another individual in one clan, and did not have the highest closeness or betweenness centrality in the other clans (Figure 9). Spearman rank order correlations using centrality measures and ages of all the individuals in the association network showed significant positive correlations between degree centrality, closeness centrality, and betweenness centrality (degree and closeness centrality: R=0.766, P<0.05; degree and betweenness centrality: *R*=0.696, *P*<0.05; closeness centrality and betweenness centrality: *R*=0.743, *P*<0.05). There was no clear relationship between dominance and centrality measures, although the highest dominance seemed to correspond to intermediate degree centrality.

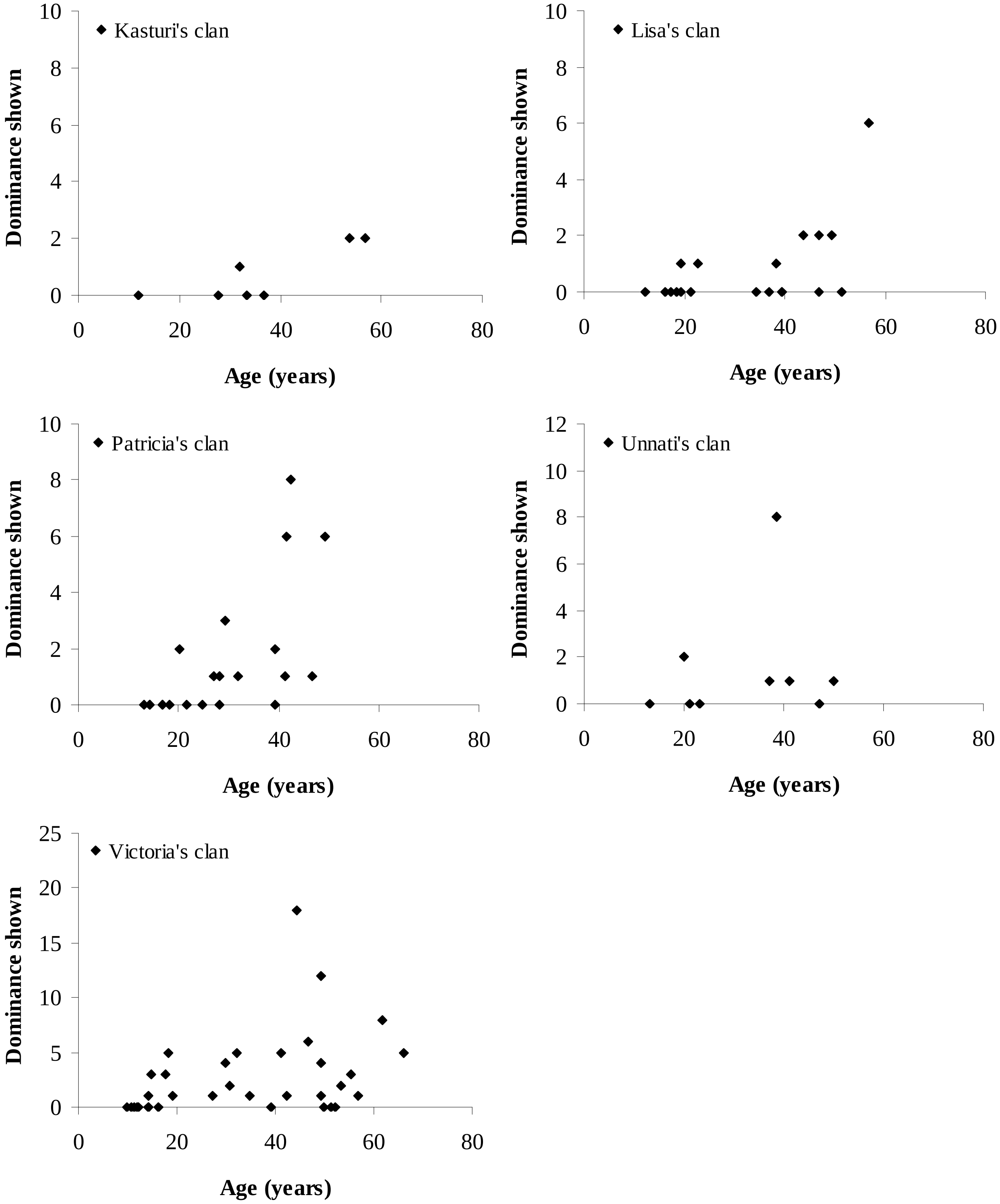


Figure 6. Dominance shown by adult females of different ages in the five clans. The oldest

animal is the matriarch.

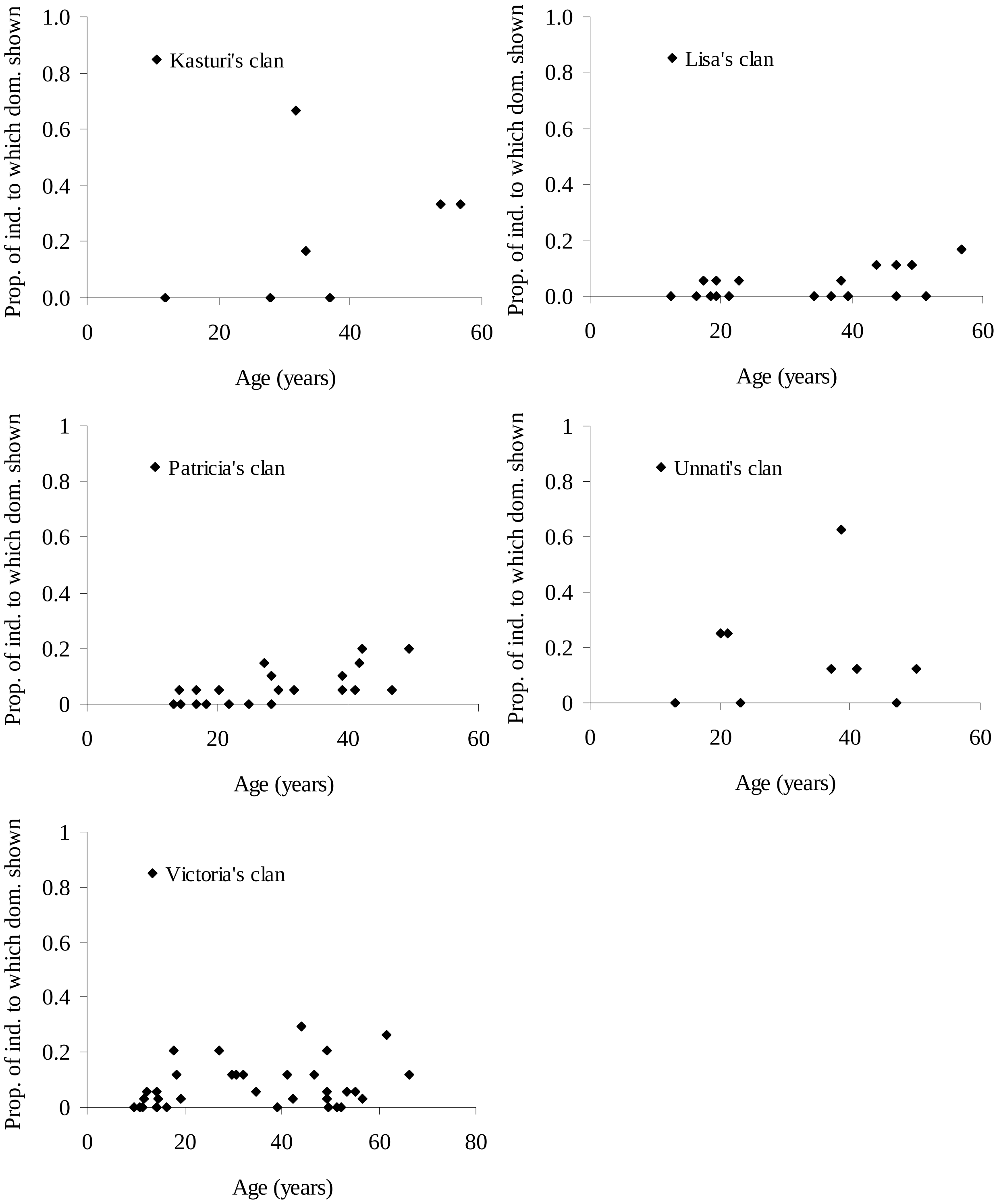


Figure 7. Proportion of clan-mates (adult females) to which dominance was shown, by adult females, plotted against age.

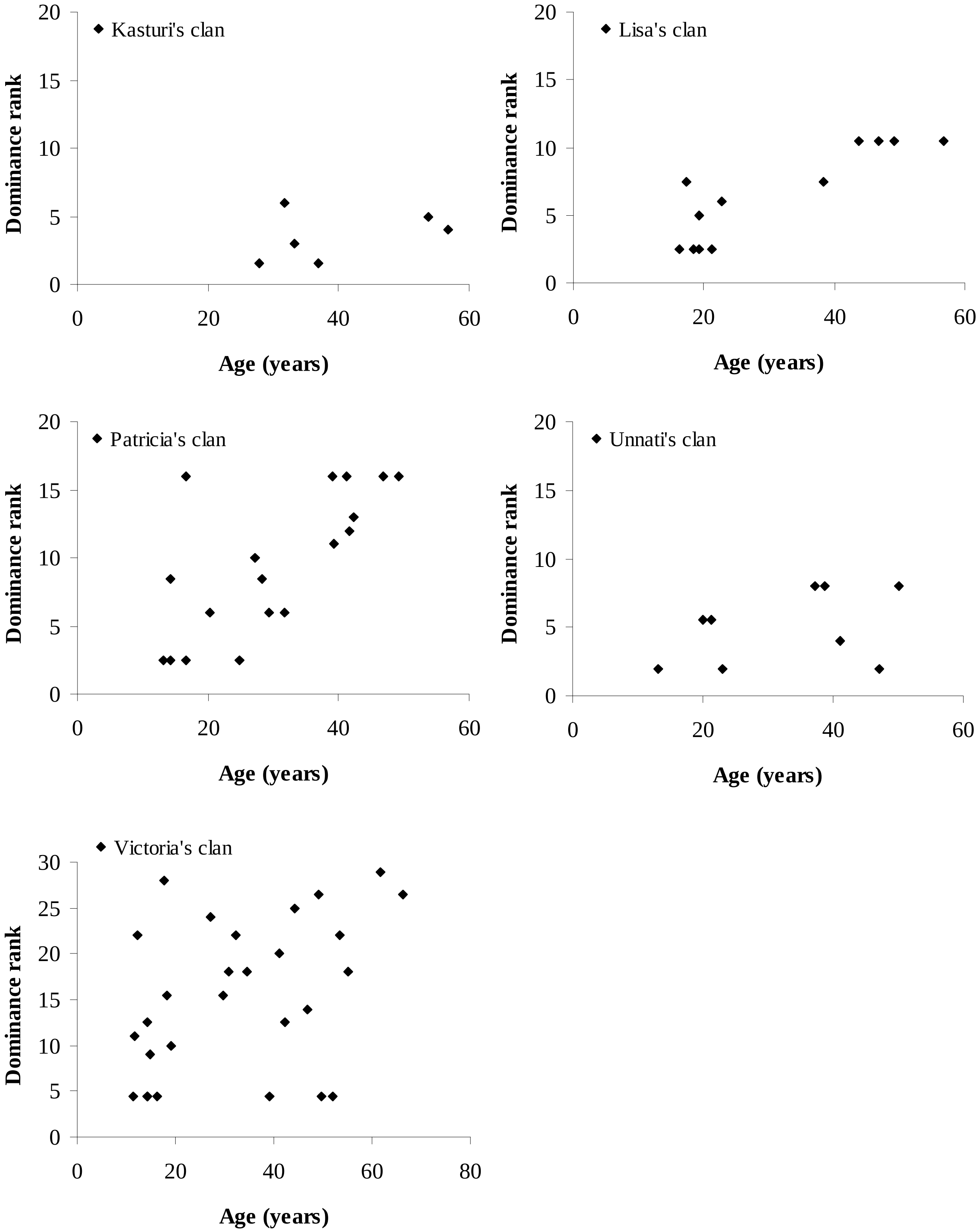
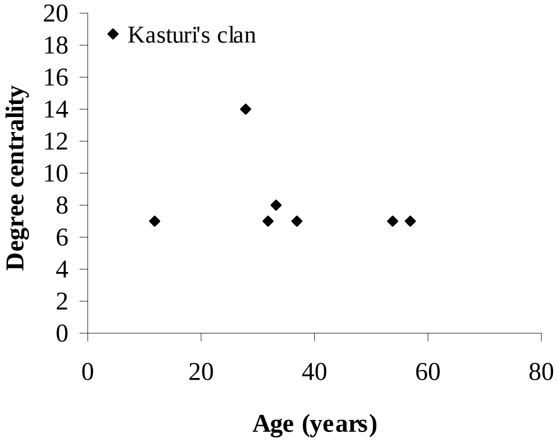
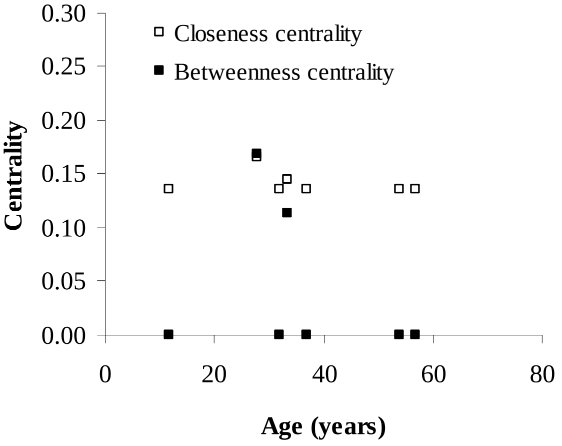
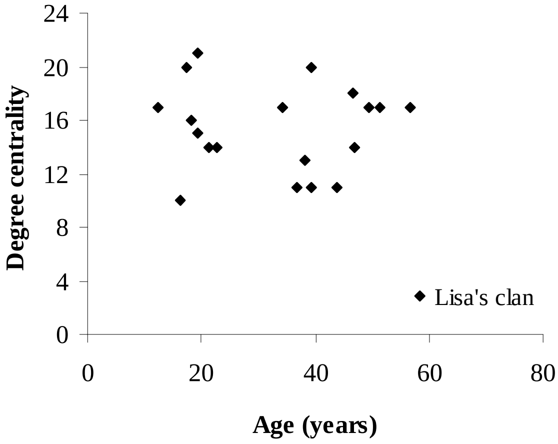
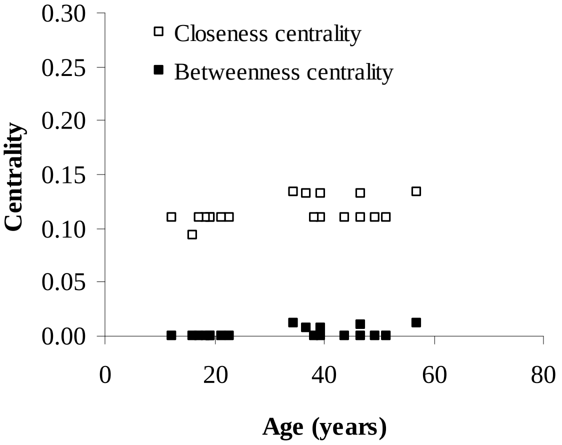


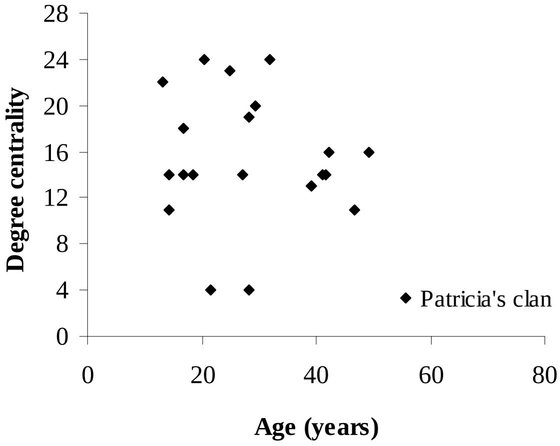
Figure 8. Dominance rank of adult females within clans, plotted against age. Here, the highest dominance rank corresponds to the most dominant female.

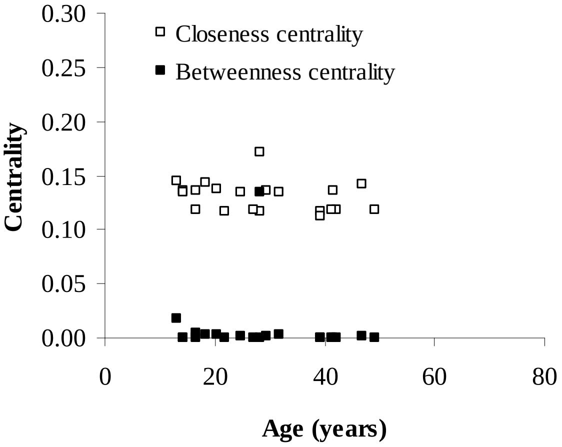

Kasturi's clan
Degree centrality
20
18
16
14
12
10
8
6
4
2
0
0
20
40
60
80
Age (years)

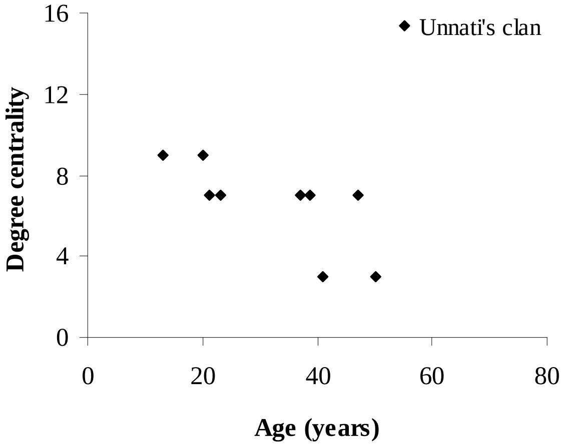

Closeness centrality
Betweenness centrality
Centrality
0.30
0.25
0.20
0.15
0.10
0.05
0.00
0
20
40
60
80
Age (years)

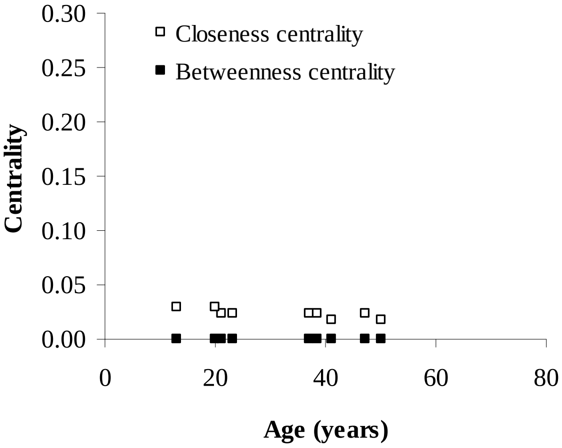

Lisa's clan
Degree centrality
24
20
16
12
8
4
0
0
20
40
60
80
Age (years)


Closeness centrality
Betweenness centrality
Centrality
0.30
0.25
0.20
0.15
0.10
0.05
0.00
0
20
40
60
80
Age (years)


Patricia's clan
Degree centrality
28
24
20
16
12
8
4
0
0
20
40
60
80
Age (years)


Closeness centrality
Betweenness centrality
Centrality
0.30
0.25
0.20
0.15
0.10
0.05
0.00
0
20
40
60
80
Age (years)


Unnati's clan
Degree centrality
16
12
8
4
0
0
20
40
60
80
Age (years)


Closeness centrality
Betweenness centrality
Centrality
0.30
0.25
0.20
0.15
0.10
0.05
0.00
0
20
40
60
80
Age (years)

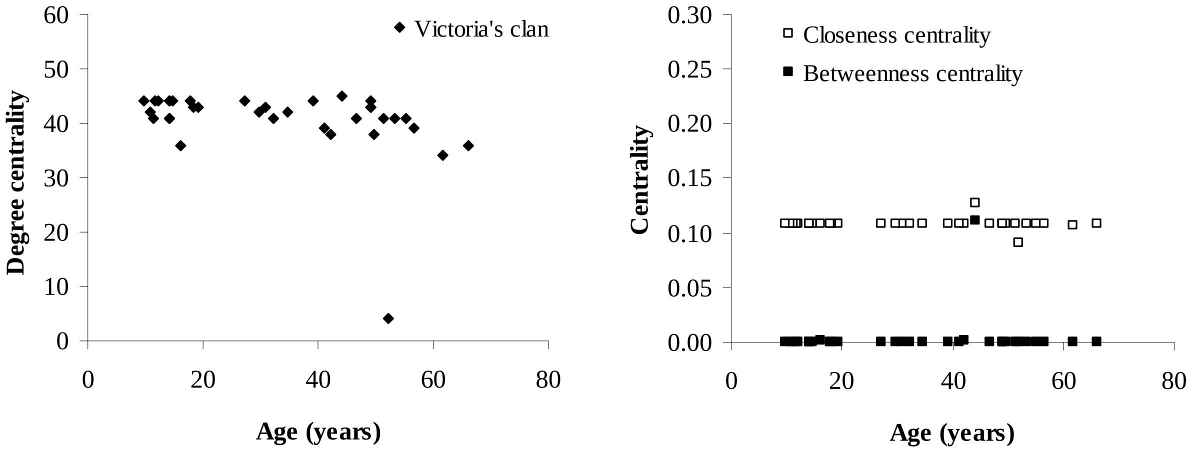


Figure 9. Centrality measures of adult females in different clans plotted against age.

Association index, seasonality, and within-clan dominance

There was no relationship between association index (mean AI ± 95% CI: Kasturi’s clan: 0.26 ± 0.068, Lisa’s clan: 0.10 ± 0.024, Patricia’s clan: 0.07 ± 0.016, Unnati’s clan: 0.22 ± 0.075, Victoria’s clan: 0.09 ± 0.009) and the total amount of dominance (number of agonistic interactions) given or received in Kasturi’s clan (Mantel test: *R*=0.146, one-tailed *P*=0.259), Lisa’s clan (*R*=0.142, one-tailed *P*=0.056), or Unnati’s clan (*R*=0.327, one-tailed *P*=0.026), but there was a small but significant correlation in Patricia’s clan (*R*=0.248, one-tailed P=0.004) and Victoria’s clan (*R*=0.299, one-tailed *P*=0.001) (Figure 10). This could be due to the last two being larger clans than the others and, therefore, having a greater number of combinations of AIs and levels of dominance.

An ANCOVA carried out with the number of agonistic interactions/hour as the dependent variable, season as the categorical predictor, and average total group size (including animals of all ages in the group) as a continuous predictor showed an effect of total group size, but no effect of season on the rate of dominance (Table 2 for details of clans used, Table 3).

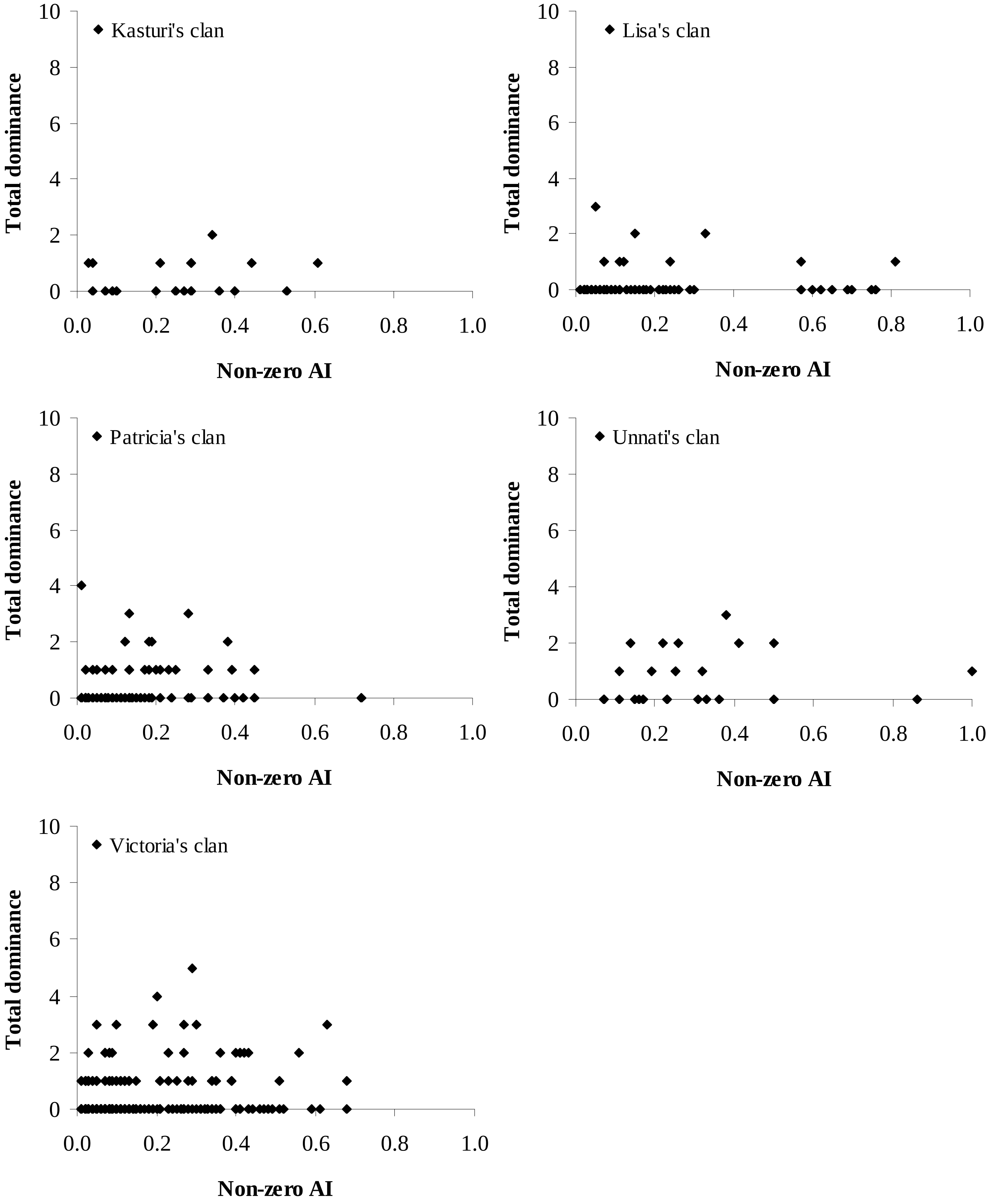


Figure 10. Association index versus total dominance (dominance shown and received) between adult females in five clans. Only pairs that were ever seen together (and, therefore, have a non-zero AI) are considered here.

Table 2. Clan name, number of hours of observation, and the number of independent agonistic interactions seen involving all individuals, during the dry and wet seasons.

	Dry season		Wet season	
Clan	Hours of observation	No. of independent agonistic interactions	Hours of observation	No. of independent agonistic interactions
Alexandra	2.1	0	0.7	0
Anabelle	43.9	13	0.6	0
Cleopatra	5.2	0	4.9	0
Elizabeth	2.0	0	2.8	0
Fiola	3.6	0	0.0	0
Gregoria	9.1	1	1.5	0
Ianthe	7.5	0	0.0	0
Ilaena	15.2	7	0.0	0
Isabella	12.2	0	0.0	0
Kasturi	142.5	33	2.3	0
Katrina	21.8	5	1.9	0
Lalanti	3.8	0	0.0	0
Lisa	128.8	34	15.5	1
Loganayaki	1.1	1	0.0	0
Manasi	27.0	4	0.3	0
Menaka	38.6	4	0.4	0
Mira	10.8	0	0.0	0
Nakshatra	64.7	8	7.2	0
Olympia	44.2	3	13.7	1
Osanna	65.4	7	6.3	2
Patricia	249.0	87	18.0	0
Peggy	102.0	6	4.7	0
Tanya	0.0	0	2.9	0
Thamarai	2.5	1	0.7	0
Tilottama	12.5	4	6.8	4
Unnati	17.2	31	2.2	0
Victoria	387.4	271	15.3	1
Yasmine	3.9	0	1.4	0

Table 3. Results from the ANCOVA with the number of agonistic interactions/hour as the dependent variable, season as the categorical predictor, and average total group size as a continuous predictor.

Effect	SS	df	MS	F	P
Average group size	0.392	1	0.392	4.535	0.039
Season	0.151	1	0.151	1.747	0.193

Between-clan dominance

We observed 516 independent interactions between individuals from different clans. The number of non-independent interactions per independent interaction was much higher in between-clan dominance (1.53) than in within-clan dominance (0.39). In between-clan, individual-level agonistic interactions, 91.2% of the interactions had clear winners at the level of individuals, as opposed to 98% of the interactions showing clear winners in within-clan interactions. However, despite the high proportion of individual-level winners, only 79 of the 152 between-clan interactions that were independent at the level of clan, had a clear winning clan that displaced the other clan from its feeding area. In keeping with this, we found no linear dominance hierarchy amongst groups (Landau's h=0.167, expected random value=0.200; de Vries' h'=0.281, test for linearity P=0.177). The test for reciprocity showed retaliatory interactions between clans (Mantel Z-test for absolute reciprocity, Z=0.473, P<0.001, Hemelrijk Rr-test for relative reciprocity, Rr=0.140, P=0.012) (see Figure 11).

In the independent, individual-level interactions between clans (N=516), the initiator was significantly older than the recipient (average ± 1.96 SE, initiator age: 32.2 ± 1.39, recipient age: 23.0 ± 1.39; Wilcoxon's matched-pairs test, Z=9.590, P<0.001, Figure 12). When we examined only the first (independent) interactions of between-clan interactions, the average (1.96 SE) initiator age was 35.2 (2.37) and the average (1.96 SE) recipient age was 27.8 (2.50) (Figure 12). We then examined the first (independent) interactions at the level of clans under situations when there was a winning clan and when there was no clear winner. When there was a clear winner, the initiator was older than the recipient (average ± 1.96 SE, initiator age: 34.7 ± 3.61, recipient age: 27.6 ± 3.57; Wilcoxon's matched-pairs test, Z=3.013, P=0.003), the winning clan's matriarch was older than the losing clan's matriarch (average ± 1.96 SE, winning clan's matriarch's age: 57.5 ± 1.71, losing clan's matriarch's age: 53.1 ± 2.20; Wilcoxon’s matched-pairs test, *Z*=2.483, *P*=0.013), and the winning clan’s oldest adult female present at the time of the interaction was older than the losing clan’s oldest adult female present (average ± 1.96 SE, winning clan: 48.3 ± 2.42, losing clan: 38.5 ± 2.86; Wilcoxon’s matched-pairs test, *Z*=4.371, *P*<0.001). When there was a clear winning clan, the total group size (average ± 1.96 SE, winning clan’s group: 8.29 ± 1.090, losing clan’s group: 4.80 ± 0.870; Wilcoxon’s matched-pairs test, *Z*=4.158, *P*<0.001; the total group size includes all individuals, including dependent offspring and subadults of both sexes who may be part of the group at the time of the interaction) and the number of adult females in the group (average ± 1.96 SE, winning clan’s group: 3.70 ± 0.485, losing clan’s group: 2.39 ± 0.361; Wilcoxon’s matched-pairs test, *Z*=3.646, *P*<0.001) of the winning clan were also larger than those of the losing clan (Figure 13).

When there was no clear winning clan, while the initiator was older than the recipient (average ± 1.96 SE, initiator age: 35.7 ± 3.06, recipient age: 27.5 ± 3.54; Wilcoxon’s matched-pairs test, *Z*=3.503, *P*<0.001), the initiator’s clan’s matriarch was not significantly different in age from the recipient’s clan’s matriarch (average ± 1.96 SE, initiator’s clan’s matriarch’s age: 57.4 ± 1.81, recipient’s clan’s matriarch’s age: 55.1 ± 1.77; Wilcoxon’s matched-pairs test, *Z*=1.346, *P*=0.178), and the oldest adult female present at the time of the interaction in the initiator’s clan was not significantly different in age from her counterpart in the recipient’s clan (average ± 1.96 SE age, initiator’s clan: 45.9 ± 2.58, recipient’s clan: 42.6 ± 3.16; Wilcoxon’s matched-pairs test, *Z*=1.489, *P*=0.136). The total group sizes (average ± 1.96 SE, initiator’s group: 6.94 ± 1.220, recipient’s group: 6.50 ± 1.106; Wilcoxon’s matched-pairs test, *Z*=0.102, *P*=0.919) and the number of adult females (average ± 1.96 SE, initiator’s group: 3.21 ± 0.562, recipient’s group: 3.14 ± 0.460; Wilcoxon’s matched-pairs test, *Z*=0.368, *P*=0.713) were also not different between the initiators’ and recipients’ groups when there was no winning clan (Figure 13).

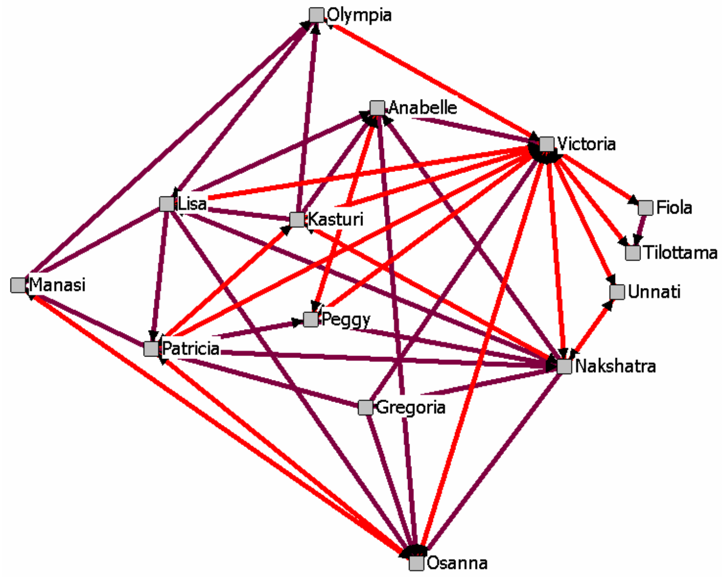


Figure 11. Between-clan dominance network. Each node here represents a clan and is named with the clan’s oldest adult female. Lines indicate agonistic interactions in the directions the arrows point towards. Maroon lines are unidirectional relationships and red lines are bidirectional relationships.

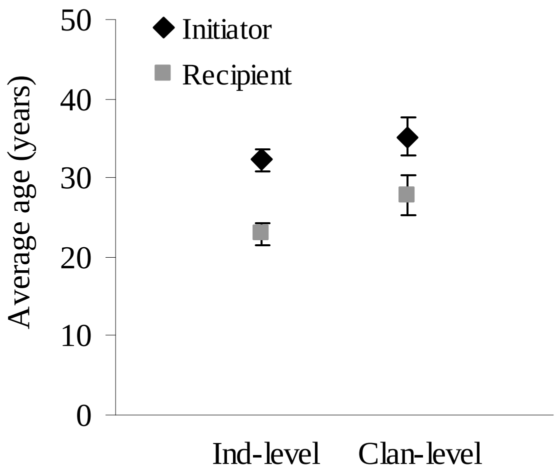


Figure 12. Average ages of the initiator and recipient in between-clan interactions, at the individual-level and during the first individual-level interaction of a between-clan interaction (subset of the former). Error bars are 1.96 SE of the mean.

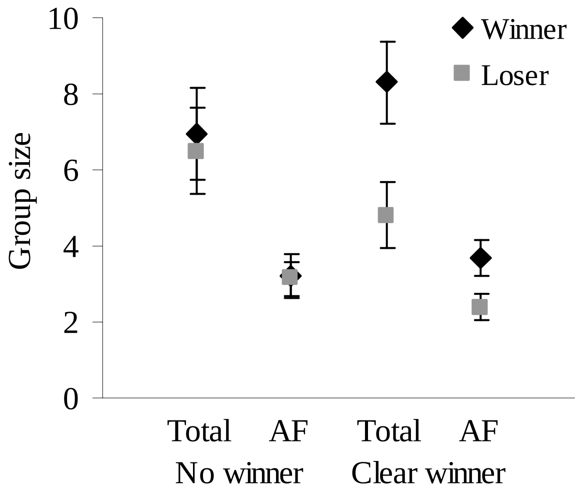


Figure 13. Group sizes of the winning and losing group during between-clan interactions when there was no winning clan and when there was a clear winning clan. Winner and loser correspond to initiator and recipient when there was no clear winner. The total number of individuals in the participating groups (Total) and the number of adult females (AF) are shown. Error bars are 1.96 SE of the mean.

Discussion

This is the first study of dominance relationships in female Asian elephants. We recorded agonistic interactions within and between clans, and found 530 independent agonistic interactions within clans, and 516 at the individual-level between clans. Since most of our time was spent observing single clans, between-clan agonistic interactions seem to be more frequent than within-clan agonistic interactions. The within-clan rate of dominance was low but variable across clans, ranging from an average of 0.023 (± 0.014) agonistic interactions between pairs of adult females per hour to an average of 0.209 (± 0.098). The corresponding rates of dominance/hour (mean ± SE) in African savannah elephants in Amboseli had been found to be 0.14 ± 0.02 amongst mother-daughter pairs, 0.14 ± 0.03 amongst maternal sisters, and 0.05 ± 0.01 amongst non-first-order maternal relatives (Archie *et al.* 2006). Therefore, it appeared that there was a correlation between the time spent in association and the frequency of dominance in Amboseli. We did not find any correlation at least between AI and total dominance in three of the five clans examined, and there was only a small correlation in the other two clans. Whether the variation across clans in the frequency of agonistic interactions arises from variation in personality, demography, or ecology remains to be seen.

We found no linear dominance hierarchy within clans as tested using Landau's *h* or de Vries' *h*'. However, there was a significant effect of age on dominance, with initiators tending to be older than recipients. The effect of age was lower than that seen in the Amboseli African savannah elephant population, in which older adult females won 94% of the agonistic interactions observed. In our population, older females won 78% of the interactions, and the initiator of the agonistic interaction was found to be the final winner nearly all the time. The percentage of reversals (younger females winning against older females; 22%, but varied across clans from 0-33%) was much higher though than in the Amboseli population, where it was 4-6%. The absence of linear dominance hierarchies within clans was not a result of intransitivity, but because many individuals did not show agonistic behaviours to one another at all, despite these clans being observed for long periods of time. Although a linear dominance hierarchy based on age was reported in African savannah elephants (Archie *et al*. 2006), that was also not based on Landau's *h* or de Vries' *h*', and was, instead, based on the consistency in direction of aggression between individuals and transitivity, on the argument that these were better at measuring competition (Rutberg 1986, Isbell and Pruetz 1998, Isbell and Young 2002, Koenig *et al*. 2004). If we were also to use only transitivity and unidirectionality as criteria, our population might also show a linear dominance hierarchy. However, we do not think it is really appropriate to do this because several pairs of individuals had been seen interacting only once.

Although there was an effect of age on within-clan dominance, the matriarch, which was defined as the oldest adult female in the clan, was not the single most dominant animal. In African savannah elephants, the matriarch was the most dominant animal in the family group and the dominance status of non-matriarchs in between-family group encounters was correlated with the dominance ranks of matriarchs in their respective groups (Wittemyer and Getz 2007). While a strong leadership role of the matriarch has been postulated in the latter (McComb *et al*. 2001, Wittemyer and Getz 2007, Mutinda *et al*. 2011), which could relate to the matriarch's high dominance (Dublin 1983), it is possible that decision-making may be less centralized in the Asian elephant over the short term. When we measured centrality in the association network, we did not find the matriarch to be the most central animal in the clan. This may stem from the differences in social structure between the two species, with smaller groups in Kabini despite similar clan sizes (see chapter 2) and, therefore, the absence of the matriarch on a day-to-day basis.

With seasonality as a proxy for resource availability, we found that there was no significant effect of season, but a significant effect of group size, on within-clan dominance rates. Sampling was low during the wet season simply because elephants could not be spotted. Radiocollaring of animals in order to find them and obtain observations during the wet season might allow for a better understanding of how seasonality affects dominance. It is also very important to quantify resource (elephant food plants) availability and distribution, and monopolisability of these resources. We suggest that resource availability may be driving between-clan dominance even if not within-clan dominance. As mentioned above, we found a large number of between-clan agonistic interactions and these interactions were more intense than within-clan interactions; the number of non-independent interactions per independent interaction was several times higher in between-clan than within-clan interactions. These interactions occurred around the Kabini reservoir backwaters, which appears to be a large point resource (offering water and grass) during the dry season. Elephant densities in Kabini are very high in the dry season near the backwaters, and the intense competition between clans may have reduced within-group dominance, leading to between-group contest with weak within-group interactions (see van Schaik 1989). Large, clumped point resources are required for between-group contests to be profitable to the winning group (Wrangham 1980, van Schaik 1989, Isbell 1991). Areas around the backwaters may actually be defended by groups, although grass is usually thought of as a non-defendable resource. On the other hand, typical defendable resources such as fruiting trees, which can be defended by single individuals, are rare in our study area. This is consistent with the absence of a clear dominance hierarchy within clans.

We also found that only about half the independent agonistic interactions at the clan level had a clear winning clan, and there was no dominance hierarchy amongst clans, with retaliatory interactions instead. This, along with the intensity of competition, suggests that the between-clan dominance here may be recent, with not enough time having passed for different clans to settle down to a pattern. The Kabini reservoir was created by the construction of the Beechanahalli Dam across the River Kabini in 1974. The creation of the reservoir could have led to loss of habitat for some clans (with over 60 km^2 of forest being submerged) but also the creation of the large point resource that was previously unavailable, thus effecting changes in resource distribution for elephants traditionally using the area. Whether this large point resource has given rise to the high between-clan competition or whether this is the natural kind of competition amongst elephant clans in the larger area needs to be examined in the future. Surface water availability is known to drive elephant distribution in southern Africa (Chamaille-Jammes *et al.* 2007, de Beer and van Aarde 2008), and artificial water sources can affect elephant movement and, consequently, the pressure on vegetation (Loarie *et al.* 2009). Whether the Kabini reservoir has led to unnatural aggregations of females, which has, in turn led to strong between-group dominance between clans can be examined by radiocollaring elephants and examining between-clan dominance across their home ranges, in areas away from the Kabini reservoir. In the absence of collared animals, the areas that these identified elephants range across are not known. Although there has been no previous study on Asian elephant between-clan dominance, other populations in southern India do not seem to show high levels of between-clan dominance (TNCV, personal observations, and Baskaran 1998). During a study following three radiocollared clans of elephants in Mudumalai Wildlife Sanctuary, in the Nilgiris-Eastern Ghats landscape, southern India, Baskaran (1998) observed one independent between-clan agonistic interaction, with one clan shifting its range considerably the next day, and had inferred the role of a dominance hierarchy between clans in space use. No other physical aggression between clans was observed during that entire study, while we have observed 152 such interactions between clans. This high frequency of between-clan interactions suggests that the reservoir could be playing a role in between-clan dominance. In Samburu, dominant groups had smaller home ranges, were closer to permanent water sources during the dry season, and travelled less than low ranking groups (Wittemyer *et al.* 2007). The Kabini population has probably not had enough time to respond to the change in resource, resulting in high-intensity agonistic interactions without clear winners.

There was an effect of age on between-clan interactions also, with the ages of the initiator, the winning clan’s matriarch, and the winning clan’s oldest adult female present in the group being important. Group size was also important in deciding the winning clan, as expected (Wrangham 1980, Isbell *et al.* 1990, Packer *et al.* 1990, Sugiura *et al.* 2000). According to the socioecological framework, between-group contest is usually associated with tolerance within groups because group members benefit by excluding other groups (de Waal 1989, Sterck *et al.* 1997). Between-group contest is, therefore, expected to produce resident egalitarian or resident nepotistic tolerant societies (van Schaik 1989). The Samburu

African elephant population had shown clear dominance hierarchies both between and within groups and was thought to be a resident-nepotistic-tolerant society with nepotism suppressed. The Kabini population seems to show more tolerance within clans than the Samburu population and could almost be classified as egalitarian within clans if it were not for the effect of age on winning dominance interactions. However, resident-nepotistic-tolerant and resident-egalitarian societies are modal types, when societies in fact fall along a continuum. Studies on resource use by individuals within clans and the role of within-clan dominance in obtaining access to these resources would be important in order to understand the importance or lack thereof, of within-clan dominance in the Kabini population.

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CHAPTER 6

Conclusions

Conclusions

This is the first quantitative study of the social structure of female Asian elephants in India. We found that female Asian elephants in the Kabini population showed a multilevel fission-fusion society that was not fully nested. Female groups sighted in the field were usually small, but were connected into larger communities in association networks. The clan, identified through network methods, was the most inclusive level of social organisation. There was almost no association between clans and there was a high frequency of between-clan dominance. The average relatedness between females within clans was significantly greater than zero but many clans individually had unrelated females. Associations at the level of the clan were, therefore, likely to be based on direct rather than indirect fitness benefits. Since group size and the presence of old females were important in between-clan agonistic interactions, between-clan interactions is an example wherein associations at the level of the clan might be beneficial through direct fitness benefits.

Females showed nonrandom associations within clans. Hierarchical communities could be detected in the larger clans, with one of them showing three levels of hierarchical clustering and the remaining showing two levels of clustering. We compared female associations in the Kabini population, with suitably modified data to match sampling methods, with those of the Uda Walawe Asian elephant population and Samburu African savannah elephant population. The Samburu association network was more connected and cohesive when compared to both the Asian elephant populations, and the Kabini population was intermediate in network connectedness and cohesiveness. Surprisingly, the average sizes of first-level communities and second-level communities detected through network methods were not different across populations, suggesting some basic similarities in social structure. Moreover, in all the three populations, second level communities were formed in a similar manner, with similar relationships between second-level community sizes and the number of first-level communities within second-level communities. However, significantly larger average group size was seen in Samburu compared to the Asian elephant populations, and the average group size in Samburu matched the average first-level community size, whereas the average group sizes in the Asian elephant populations were smaller than the average first-level community sizes. This difference in group sizes probably resulted in the differences in AI and network statistics observed between the Samburu and Kabini populations. We thus showed how underlying similarities in social structure may be masked by differences in group sizes. The Asian elephant populations possibly face a constraint in group size compared to the Samburu population due to ecological differences. Food is likely to be more sparsely distributed in forests compared to the savannah. Between the Asian elephant populations, the Kabini population exhibited more cohesiveness compared to Uda Walawe, and we speculate that this could be a result of the extensive historic anthropogenic disturbance to elephant populations in Sri Lanka, with several thousand elephants having been killed (Sanderson 1879, Lorimer and Whatmore 2009). Differences in sampling methods have also resulted in some differences across studies in Asian and African savannah elephants.

We also found some support for a constraint on group size when we examined different clans within the Kabini population. Average group sizes were similar across clans, irrespective of clan size. This resulted in females in larger clans showing a longer waiting time to meet all their clan-mates, and weaker associations between clan-mates. However, rather than forming small, fixed groups, females maintained associations with clan-mates through changing group compositions. Within-clan group size, AI, and network statistics did not change across seasons and fission-fusion dynamics, therefore, seemed to enable a meeting of more individuals while keeping the group size constant, rather than increasing and decreasing group sizes seasonally. It would be interesting to see if this is the pattern found in other populations facing constraints on group sizes as well.

Although there was no effect of seasonality on within-clan sociality, there were differences between the dry and wet season at the population level. At the population level, average group size was larger in the dry season and there were stronger associations during the wet season. We caution that population-level results may be misleading as they arise from a combination of the patterns seen in different clans. As the clans contribute asymmetrically to the population-level results due to the placement of the study area with respect to the home ranges of different clans, the combined result seen at the population level may either represent patterns seen frequently in only a few clans with more sightings or may represent a combined pattern which is not seen in any of clans. The stability in associations amongst females within clans might result from unchanging resource availability and distribution between seasons, or from changing resource availability but uniform distribution of resources with low patch density. Differences in grass biomass availability (Baskaran *et al.*

2010) and differences in feeding patterns by elephants across habitats and seasons (Sukumar 1989, Baskaran *et al*. 2010) have previously been reported in another area in the Nilgiris-Eastern Ghats landscape, in which Kabini also lies. Therefore, it would be important to quantify resource availability and distribution and feeding patterns in this area also to find out if the aseasonality in female associations arises because of unchanging resources in this area or despite changing resources.

A significant anthropogenic modification in our study area is the creation of the Kabini reservoir itself, around which our study area was centred. The Kabini reservoir was created in 1974 by the construction of the Beechanahalli Dam across the River Kabini. The reservoir submerged forest habitat but created a large point resource that was previously unavailable, thus effecting changes in resource distribution for elephants traditionally using the area. Large point resources are required for between-group contests to be profitable to the winning group (Wrangham 1980, van Schaik 1989, Isbell 1991). It is possible that the high level of between-clan agonistic interactions that we found are a result of this resource. Feeding areas around the backwaters may actually be defended by groups, although grass is usually thought of as a non-defendable resource. This needs to be investigated in the future. About half of the between-clan interactions were undecided, with no clear winner and the intensity of aggressive interactions between clans was also high, suggesting that the between-clan dominance here may be recent. Whether the reservoir has given rise to the high between-clan competition observed or whether this is prevalent in the larger area should be examined in the future. There have been no previous studies of dominance relationships in Asian elephants, but personal observations and field researcher accounts suggest that this level of dominance interactions are rare in other populations in southern India at least. If females are radiocollared, one can examine between-clan dominance across their home ranges, in areas away from the Kabini reservoir. Several elephant populations around the world, including the Uda Walawe population, inhabit such modified habitats. Surface water availability is known to drive elephant distribution in southern Africa (Chamaille-Jammes *et al*. 2007, de Beer and van Aarde 2008), and artificial water sources can affect elephant movement, which may then affect the pressure on vegetation (Loarie *et al*. 2009). We wonder if the Kabini reservoir has similarly led to unnatural aggregations of females, which has, in turn led to strong between-group dominance between clans.

Agonistic interactions within-clans were infrequent and low-intensity in nature. There was no linear dominance hierarchy, but almost all agonistic interactions had clear winners, and initiators of the interactions were almost always the winners. It is possible that the strong between-clan competition suppressed within-clan dominance. Unlike on the African savannah, resources that could be defended by single females, such as fruiting trees, were rare in the study area, and this could also explain the absence of a linear dominance hierarchy. There was an effect of age on within-clan dominance, but the matriarch, who is the oldest female in the clan, was not the single most dominant female in any clan studied. The matriarch was also not the most central female in clans based on association networks. Given the small group sizes and fluid nature of groups, it is possible that the matriarch is not as important on a day-to-day basis in the Asian elephant, unlike in the African savannah elephant (Dublin 1983, McComb *et al*. 2001, Wittemyer and Getz 2007, Mutinda *et al*. 2011).

As mentioned above, there were non-random associations within clans. First-level communities identified within clans showed high average pair-wise relatedness indicating that these communities comprised first- and second-order relatives. Females' top and second associates were also more related than the average associate. These results suggest that females' close associates are mostly their close relatives and each female may have her own daughters and/or siblings as close associates. Such close associations with relatives may offer indirect fitness benefits to individuals. One such benefit might be through allomothering (Gadgil and Nair 1984). However, both first-level communities within clans as well as entire clans sometimes did not have related females, and direct fitness benefits might also be important. Continued associations of younger females with less related or unrelated females after older females have died may help them acquire valuable knowledge about resource distributions (Foley 2002, see Goldenberg *et al*. 2016). The role of relatedness in within- and between-clan dominance is yet to be examined in the Kabini population.

In summary, this thesis provides new information on female Asian elephant social organisation by illuminating the female social structure of the species, examining the effects of seasonality and genetic relatedness on social structure, and presenting the first study of dominance relationships in the species. All of this has been carried out using information from a large number of individually identified females. The findings also raise new questions about sociality in this population and species, such as the role of the matriarch, the role of allomothering in fission-fusion dynamics, and the role of natural resources and anthropogenic modification in between-clan dominance. Additionally, the database that has been created so far on individually identified females would offer enormous possibilities for the study of other themes in the future.

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