

ABSTRACT

Title of Dissertation: **SOCIAL STRUCTURE OF ASIAN ELEPHANTS (*ELEPHAS MAXIMUS*) IN SRI LANKA**

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Asian elephants (*Elephas maximus*) are critically endangered and live in fragmented populations spread across 13 countries. Yet in comparison to the African savannah elephant (*Loxodonta africana*), relatively little is known about the social structure of wild Asian elephants because the species is mostly found in low visibility habitat. A better understanding of Asian elephant social structure is critical to mitigate human-elephant conflicts that arise due to increasing human encroachments into elephant habitats. In this dissertation, I examined the social structure of Asian elephants at three sites: Yala, Udawalawe, and Minneriya National Parks in Sri Lanka, where the presence of large open areas and high elephant densities are conducive to behavioral observations. First, I found that the size of groups observed at georeferenced locations was affected by forage availability and distance to water, and the effects of these environmental factors on group size depended on site.

Second, I discovered that while populations at different sites differed in the prevalence of weak associations among individuals, a core social structure of individuals sharing strong bonds and organized into highly independent clusters was present across sites. Finally, I showed that the core social structure preserved across sites was typically composed of adult females associating with each other and with other age-sex classes. In addition, I showed that females are social at all life stages, whereas males gradually transition from living in a group to a more solitary lifestyle. Taking into consideration these elements of Asian elephant social structure will help conservation biologists develop effective management strategies that account for both human needs and the socio-ecology of the elephants.

**SOCIAL STRUCTURE OF ASIAN ELEPHANTS (ELEPHAS MAXIMUS) IN
SRI LANKA**

by

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Dedication

To my family with all my love, to Nikini for always inspiring me in moments of doubt, and to Professor Bertrand Deputte for always believing in me and my dream of studying wild elephants.

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List of Abbreviations

MNP	Minneriya National Park
UNP	Udawalawe National Park
YNP	Yala National Park
HEC	Human-Elephant Conflict
NDVI	Normalized Difference Vegetation Index
SNA	Social Network Analysis
AI	Association Index
HWI	Half-Weight association Index
SD	Standard Deviation
SE	Standard Error
AIC	Akaike Information Criterion
LRT	Likelihood Ratio Test
AF	Adult Female
AM	Adult Male
SF	Sub-adult Female
SM	Sub-adult Male
JF	Juvenile Female
JM	Juvenile Male
CA	Calf

Introduction

Asian elephants (*Elephas maximus*) are one of three extant members of the Order Proboscidae and are endangered (Haynes 1991, Choudhury et al. 2008). Fewer than 50,000 wild individuals live in fragmented populations dispersed across the species' range (Leimgruber et al. 2003, Blake and Hedges 2004, Choudhury et al. 2008). Elephants are found in the Indian sub-continent and Southeast Asia with half of the wild population residing in India (Sukumar 1989). Throughout its range, the most significant threats to Asian elephant survival result from habitat loss and fragmentation (Sukumar 1992, Leimgruber et al. 2003). Unlike for African elephants, ivory poaching is of minor importance for Asian elephants as only males carry tusks (Fernando et al. 2005).

Due to increasing human densities and resulting land use change, almost every Asian elephant habitat is surrounded by human settlements. As a result, conflicts between humans and elephants frequently arise at the edges of these habitats (Sukumar 1992). Elephants often raid crops and are responsible for important economic losses as well as human casualties (Sukumar 1992, Fernando et al. 2005). Furthermore, elephants risk being shot, poisoned, hit by trains and trucks, or captured for domestication (Sukumar and Santiapillai 1996, Leimgruber et al. 2008). Currently, active mitigation of human-elephant conflict (HEC) happens only in response to crises and management of wild elephants to reduce HEC is often ineffective (Fernando 1997, Fernando et al. 2012).

Not only are Asian elephants endangered, but they are also a keystone species that plays a crucial role in maintaining ecosystem function and biodiversity (Campos-

Arceiz 2009, Campos-Arceiz and Blake 2011). As ecosystem engineers and “megagardeners of the forests” (Campos-Arceiz and Blake 2011) elephants modify landscapes, affect vegetation regeneration, and influence the distribution and abundance of wildlife (Wright and Jones 2006, Pringle 2008, Campos-Arceiz and Blake 2011). Therefore, with Asian elephants on the edge of extinction, entire ecosystems may be at risk. In tropical forests of Congo, for instance, several species of trees are solely dependent on elephants for seed dispersal (Beaune et al. 2013).

Asian elephants have an extended history of association with humans and have been extensively studied in captivity (Sukumar 1992, 2006). However, in comparison to the well-documented African savannah elephants (*Loxodonta africana*) living in open areas of Eastern Africa, our knowledge of Asian elephant’s ecology and behavior in the wild is limited. Studies of wild Asian elephants have been hampered by habitat visibility: Asian elephants tend to occupy densely vegetated areas (Sukumar 1992). As a result, only two detailed studies based on individual identifications have been conducted for wild Asian elephants (Fernando and Lande 2000, de Silva et al. 2011).

Asian elephants inhabit a variety of habitats such as grasslands, scrub forests, dry deciduous forests, moist evergreen forests, swamps, and mangroves (Sukumar 2006). The extent of their past and present ranges suggests that Asian elephants have been able to adapt to a wide variety of environmental conditions. Behavioral plasticity likely contributes to this adaptability, and to the persistence of elephants in areas populated by humans, which escalates HEC. Thus, the socio-ecology of Asian elephants should be examined across habitats in order to better preserve this

endangered species by developing management strategies that account for both human needs and elephant biology.

Wild Asian elephants display a fission-fusion social structure (Fernando and Lande 2000, de Silva et al. 2011). Fission-fusion describes a flexible group behavior in which the changing balance between costs and benefits of association can result in increases or decreases in group associations. When costs of association outweigh the benefits, groups will fission into subgroups. On the other hand, when benefits of association outweigh costs, fusion occurs – subgroups rejoin each other. Fission-fusion dynamics are regulated by the combined effects of patchy and temporally variable access to mates, food resources, and predation pressure (Kummer 1968, Wittemyer et al. 2005, Couzin and Laidre 2009). For instance, chimpanzees form smaller subgroups when access to food resources require long travel time and the proportion of males in these subgroups is higher when food density is high (Chapman et al. 1995). Thus, examining group size, group membership, and association stability can offer insight into the social structure of a species (Whitehead 1997). This provides crucial information on the biology of a species, as social structure can affect mortality, fitness (reproductive success), dispersal (gene flow), and population dynamics and persistence (Hamilton 1964, Wilson 2000). Therefore, studies of animal social structure are critical for effective management and conservation efforts of endangered species (Sutherland 1998).

Sri Lanka, where I conducted my research, is one of the few places in Asia conducive to behavioral observations of wild Asian elephants because of the presence of large open areas in combination with high densities of elephants (Fernando et al.

2011). Throughout Sri Lanka, wild elephants are found alone as well as in groups that greatly vary in size, encompassing from two to hundreds of individuals. Because group size could reflect behavioral adaptations to local ecological conditions, in chapter 1, I examined the relationship between environmental predictors of resource availability and the size of groups at georeferenced locations in three national parks in Sri Lanka. I used open metapopulation *N*-mixture models, which did not require individual identification and accounted for detection error. I quantified the availability of forage and water at a location using the normalized difference vegetation index (NDVI) and distance to water, respectively. I found that NDVI and distance to water impacted group size in Asian elephants, but the effects of these two variables were dependent on the site.

The groups I observed could have reflected enduring social relationships or short-term aggregations of individuals. To examine the nature of the groupings at different sites, in chapter 2, I used social network analysis (SNA) to compare the social relationships of the elephants at Yala and at Minneriya National Parks. I investigated associations among individually identified elephants. While at Yala elephants were organized into highly independent social clusters, at Minneriya no clusters were apparent until weak dyadic associations were removed. Thus, a core social structure common to both sites was revealed by filtering associations: there were subsets of individuals with strong bonds that formed small, highly independent clusters. This information is critical for the management of wild populations. In cases of disease outbreaks, knowledge of how individuals are connected to one another at a site can influence which management strategy would be most effective in limiting

spread of disease (Ortiz-Pelaez et al. 2006). It is also important that management decisions consider social structure because there are several examples in African elephants of conservation strategies that overlooked the biology of the species and resulted in unforeseen detrimental outcomes (Slotow et al. 2000, Slotow and Van Dyk 2001). For example, juvenile male African elephants introduced in places without mature bulls, entered musth at an early age and killed a large number of rhinoceroses. After, introducing mature bulls musth was suppressed in the juveniles and rhinoceros mortality decreased.

Determining which age-sex class of individuals associate with one another can improve understanding of population social structure. In chapter 3, I investigated the effects of age and sex on group size, space use, and strength of association at Minneriya National Park. I focused on this population because all age and sex classes were well represented. I found that solitary individuals were frequently adult males while sub-adult males exhibited a gregarious behavior intermediate between that of juvenile and adult males. Females of all ages were social. My results show that while associations among adult females were important, those between adult females and other age and sex classes formed the core of Asian elephant social structure.

Chapter 1: Environmental determinants of group size in Asian elephants (*Elephas maximus*)

Abstract

In many species, individuals form groups in response to social and ecological conditions. Asian elephants are mega-herbivores with a fission-fusion social structure and individuals observed together can represent either transient aggregations or social units. To determine the relationship between environmental predictors of resource availability and group size in Asian elephants, I observed groups of elephants at georeferenced locations in three sites, Yala (YNP), Udawalawe (UNP), and Minneriya (MNP) National parks in Sri Lanka. I used the normalized difference vegetation index (NDVI) and distance to water as proxies for forage and water availability. I then used open metapopulation N -mixture models that account for detection errors and do not require individual identification to predict group size. A model that included site-specific variation in environmental conditions fit the data best. Thus, the relative effects of NDVI and distance to water on group size in Asian elephants vary depending on site. These results reveal important ecological features that should be considered when developing conservation strategies for these endangered animals.

Introduction

Individuals of the same species are often found together in groups that either represent fleeting aggregations due to a common response to environmental conditions or social units in which animals are attracted to particular conspecifics (Krause and Ruxton 2002). The size of these groups can range from several to thousands of individuals (Lott 1991, White et al. 2012). Species with a fission-fusion social system demonstrate dynamic group sizes, adaptively changing group membership in response to shifting environmental conditions (Couzin and Laidre 2009). Two particularly important environmental factors that influence group size are predation risk (Alexander 1974, Jarman 1974, Van Hoof and Van Schaik 1983, Brashares and Arcese 2002) and resource distribution (Krause and Ruxton 2002). Examining group size, group composition, and stability of associations can offer important insights into the evolution of animal social systems (Whitehead 2008) and the conservation of endangered species (Caro 1998).

Studying the size of groups composed of individuals with unknown social affinities can provide information that is not easily obtained from studies focused either on animal population density or on composition of social units. While population density provides information on how populations respond to environmental conditions on a regional scale (Pettorelli et al. 2005, Morellet et al. 2007), group size in fission-fusion species reflects adaptive responses to environmental characteristics acting within and among populations (Aureli et al. 2008, Silk et al. 2014).

Asian elephants (*Elephas maximus*) have a fission-fusion social system with groups varying greatly in size, and encompassing a few animals to hundreds of individuals (Kurt 1974, Fernando and Lande 2000, Sukumar 2006, de Silva et al. 2011). Asian elephants occupy a diversity of habitats representing a range of ecological conditions with respect to vegetation and water availability (McKay 1973, Seidensticker 1984, Sukumar 1989, Santiapillai and Jackson 1990, Leimgruber et al. 2003). Elephants in Sri Lanka have no natural predators (Fernando and Lande 2000), and therefore represent a simplified system in which group size should more directly reflect adaptations to local resource conditions.

As exceptionally large herbivores (Owen-Smith 1988), adult elephants consume massive amounts of forage (250 kg) and water (180 L) daily (Laws 1970). Consequently, I expected forage availability and proximity to water to positively influence group size. While elephant occurrence and density across habitats is positively correlated with vegetation availability (Marshall et al. 2011, Duffy and Pettorelli 2012) and access to surface water (Stokke and Toit 2002, Chamaillé-Jammes et al. 2007, 2008, Gaugris and Van Rooyen 2010), no study has yet examined the relationship between local environmental conditions and group size in Asian elephants. When resources are clumped, larger groups should be observed compared to when resources are dispersed (Clutton-Brock and Harvey 1977, Isbell 1991). For elephants, surface water always constitutes a clumped resource (Chamaillé-Jammes et al. 2008), while good quality forage can either be dispersed or concentrated (Osborn 2004). Because the distributions of vegetation and water are not necessarily

correlated, these factors may have additive, synergistic or antagonistic effects on group size depending on the location.

For this study, I examined the relationship between the size of Asian elephant groups and estimates of forage and water availability derived from satellite images. I used NDVI, an index of vegetation greenness as a measure of forage availability, and I calculated the distance in meters between elephant locations and closest surface water sources. When studying the size of populations or groups, accounting for detection error is necessary to prevent bias and increase the accuracy of conclusions (Walsh et al. 2001, Kappeler and Van Schaik 2002, Kéry et al. 2005, Wenger and Freeman 2008). For this reason, I used open metapopulation *N*-mixture models (Dail and Madsen 2011) that were developed and are appropriate for studying unmarked individuals in imperfect detection conditions.

Methods

Study sites

I observed elephants at three sites in Sri Lanka: Yala (YNP) Udawalawe (UNP), and Minneriya (MNP) National parks. YNP is located in the semi-arid dry zone of southeastern Sri Lanka. Observations in YNP were restricted to Block I (6°22'N 81°31'E), which covers 140 km². The predominant vegetation type at this site is mature scrub forest, with patches of evergreen forest and a few short-grass clearings (Mueller-Dombois 1968, 1972). Annual rainfall varies between 500 and 775 mm (de Silva et al. 1994). Drinkable water is present in reservoirs, natural waterholes, and the Menik River. During the driest months of the year (August-

September), most natural waterholes dry out and water becomes less abundant (Mueller-Dombois 1968, de Silva et al. 1994).

UNP spans 308 km² and is situated 99 km west of YNP in the southern dry zone of Sri Lanka (6°26'N 80°53'E). The predominant vegetation type at this site is savannah, though some residual teak plantations, dry-scrubs, and tall-dry evergreen forests also occur (Fernando and Lande 2000, de Silva et al. 2011). UNP receives 1,486 mm of mean annual rainfall (de Silva et al. 2011). Permanent water is available in two reservoirs and a river, while seasonal water is present in streams and waterholes (de Silva et al. 2011).

MNP extends over 88 km² in the dry zone of the North Central province of Sri Lanka (7°58'N 80°50'E). This site contains grasslands surrounded by dry-mixed evergreen and scrub forests (Green 1990, Nekaris and Jayewardene 2004). Annual rainfall varies between 1,500 and 2,000 mm. Permanent water is present in a large reservoir that receives water from both the Amban River and the Elahera Canal. This reservoir shrinks in the dry season, which allows for short grass to grow around the remaining water. The park borders the Maradankadawala-Habarana Thirukhondaiadimalu highway and wildlife can move in and out of the park because it is unfenced.

Data collection

Observation periods. I collected data on elephant group size at YNP during 25 days from June to September 2007, at UNP during 17 days in August 2007, and at MNP during 25 days from June to September 2010.

Census routes. At each site, I observed elephants from a vehicle following a circumscribed route during typical park hours (YNP and UNP: 0600-1830, MNP: 1200-1830). The vehicle included a scientist, a driver, and a tracker who had knowledge of the park roads and helped locate elephants. In YNP and UNP, I traversed a well-established system of roads once a week, on average. In MNP, roads were only present in forested areas, and I drove off-road in grassland areas surrounding the reservoir and covered all accessible parts of the park once a week.

Group size counts. Because most adult males are solitary (Eisenberg and Lockhart 1972, McKay 1973) I focused my observations on females and mixed-sex groups that usually included more than one individual and varied in size (Wittemyer et al. 2005, de Silva et al. 2011).

In all three parks, I spotted elephants using binoculars, and when an aggregation of individuals was detected, I recorded the date, time, and GPS location. During each census I observed elephants as long as possible until all moved out of sight. I defined a “group” as an aggregation of individuals at a specific location and time with no individual at a distance from its nearest neighbor farther than the group diameter at its widest point (Archie et al. 2006). A particular group was considered to exist as long as its membership remained stable. When individuals joined or left the focal group, I recorded the time and considered the aggregation as a new group. The total duration of observation for each encounter varied between 5 and 240 minutes, with each distinct group observed between 1 and 184 minutes.

Environmental variables

Forage availability. The normalized difference in vegetation index (NDVI) represents the ratio of red to near infrared reflection captured by remote sensing (Carlson and Ripley 1997, Pettorelli et al. 2005). NDVI is a good indicator of vegetation quantity and quality in a range of ecosystems and is often used as a measure of above-ground biomass (Box et al. 1989, Van Soest 1994, Pettorelli et al. 2011). Because elephants are considered generalists that consume a variety of plant species (Owen-Smith 1988, Stokke and du Toit 2000, Owen-Smith and Chafota 2012), I followed Rasmussen et al. (2006) in using NDVI as a proxy for forage availability.

NDVI measurements were obtained from Moderate Resolution Imaging Spectroradiometer (MODIS) images. For all three national parks, I used a *16-Day L3 Global 250m SIN Grid V005* product, which is a composite MODIS NDVI image with a 250 m resolution compiled over 16-day intervals. Composites help correct for molecular scattering, aerosols, and absorption from the ozone, and are calculated by taking the maximal NDVI value recorded during a 16-day period for each pixel in an image (Gallo et al. 2004).

For each national park, I downloaded MODIS NDVI images from the NASA website (www.modis.gsfc.nasa.gov) to cover the entire period of observation. I stacked images and extracted NDVI values for GPS locations corresponding to each encounter using packages *raster* and *rasterVis* in R (Lamigueiro and Hijmans 2014, Hijmans 2015). For each location where elephants were encountered, I used the NDVI value that was closest in time to when group size data were collected.

Water availability. For each national park, I digitized contours of all water sources using the best cloud free images from Landsat 5 TM (Thematic Mapper) and Landsat 8 LDCM (Landsat Data Continuity Mission) with 30m resolution, downloaded from the GLOVIS website (www.glovis.usgs.gov) loaded into ArcGIS. I applied the function *Near* in ArcGIS to calculate the distance in meters between each GPS location at which elephants were encountered and the closest water source to quantify water availability.

Model structure

To predict group size from environmental factors I used hierarchical *N*-mixture models, which were originally developed to estimate species abundance and distribution (Royle 2004). Hierarchical *N*-mixture models account for uncertainty and measurement error due to imperfect detection by simultaneously modeling latent abundance as well as detection probability (Dodd and Dorazio 2004, Royle 2004, Fiske and Chandler 2011).

I used group size as a proxy for latent abundance. The models do not require information on individual identity. Instead, the models utilize repeated counts at spatially defined and independent locations. The models are referred to as “metapopulation design” models in which a metapopulation typically represents a set of separated populations with some level of interaction (Fiske and Chandler 2011). For this study I considered groups at a GPS location to be analogous to populations.

To assess the effects of environmental variables on group size and account for fluctuating associations that are characteristic of Asian elephants, I chose an extension of the Royle (2004) model, i.e. the dynamic open metapopulation *N*-

mixture model (Dail and Madsen 2011). Instead of assuming a constant group size at each location, in the open metapopulation N -mixture models, latent group size at a specific location i and time t can vary from time $t-1$ due to addition of individuals by birth (B) and immigration (I) or deletion by death (D) and emigration (E), i.e.

$$N_{it} = N_{it-1} + B + I - D - E$$

Because data were collected within a three month period in each park, I ignored births and deaths and used immigration and emigration as proxies for individuals leaving or joining a group.

Open metapopulation N -mixture models are appropriate for predicting the size of elephant groups as they allow the dynamic of fission-fusion to differ among groups and for individuals to move between locations and groups. In N -mixture models, animals are detected and counted at i spatially distinct and independent locations $\{i = 1, \dots, I\}$ during t sampling occasions $\{t = 1, \dots, T\}$. All animals at a given location and time have the same detection probability (p_{it}). The number of individuals counted at location i at time t (n_{it}) depends on the latent number of individuals present at that location and time (N_{it}) and their detection probability (p_{it}). The probability density function of group size at location i and time t , N_{it} , $f(N_{it}, N_{it-1}, \theta)$, is the sum of two random variables- survival (S_{it}) or animals remaining, and recruitment (G_{it}) or animals joining. N_{it+1} is related to N_{it} through survival and recruitment. Thus, latent group size at location i and time t (N_{it}) has an inherent Markov property in that N_{it} for $t \geq 2$ depends on both the initial group size at that location (N_{i1}) as well as the group size at an immediately prior time step (N_{it-1}).

In N -mixture models, N_{it} , S_{it} , G_{it} , and p_i are modeled separately in sub-models and the parameters that describe their distributions could either be constants or functions of environmental or observation covariates (Kéry et al. 2005). I estimated N_{it} , S_{it} , G_{it} , and p_{it} , using maximum likelihood and the function *PcountOpen* from the package *unmarked* (Fiske and Chandler 2011). All analyses were performed in R version 3.2.2 (R Core Team 2015).

Model fit and selection

If group size remained unchanged at a location, I recorded one group size as the response variable. If group size varied at a location due to the arrival or departure of individuals, I recorded each different group size. In both cases the duration of observation for each group was recorded and included as a covariate in the model as explained below.

To examine the relationship between group size, NDVI, and distance to water across sites, I modeled the *group size* parameter as a function of these predictor variables in several types of models. In the models, site was always included as an additive or interactive effect, and I either included or excluded additive or interactive effects of NDVI and distance to water (Table 1). NDVI and distance to water values were not highly correlated ($r = 0.38$), therefore we did not expect any problems due to multi collinearity. Including models with interactions between site and other predictors allowed us to examine effects of different ranges of NDVI and distance to water values observed within each site.

In all models, I assumed the *survival* and *recruitment* parameters were constants. I hypothesized that accuracy of group size estimates was likely to increase

with observation duration. Therefore, to take into account sampling effort at each location, I modeled *detection probability* either as a constant or as a linear or logarithmic function of observation duration (Table 1). To best optimize convergence of the optimization algorithms, I standardized all covariates by subtracting the arithmetic mean and dividing by the standard deviation. The models assumed that the distribution of latent group sizes followed a Poisson distribution.

For a set of candidate models I used AIC model selection to choose the best model and subsequently performed hypothesis tests with that model. I considered the best model to be the one with the lowest AIC unless there was a simpler model with a delta AIC (ΔAIC) less than two (Burnham and Anderson 2002). To test additive and interactive effects of predictors I used likelihood ratio tests (LRTs), and to test for differences among factor levels (sites) I employed Wald z tests.

I examined effects of predictors on group size using the best model and a dataset that preserved the properties of the original data (i.e. ranges of NDVI and distance to water values specific to each site) (Fiske and Chandler 2011).

Non-spatial models such as the open metapopulation N -mixture models assume no spatial autocorrelation. Comparisons between spatial and non-spatial models of species distribution shows little difference in coefficient estimates and model inference for Poisson data (Dormann et al. 2007). However, in ecological studies, spatial autocorrelation can occur when environmental determinants induce spatial structure in the response variable (Besag 1974). To determine if spatial autocorrelation influenced my results, I used Moran's I to test for spatial

autocorrelation in the residuals from the best model, averaging residuals for each location.

Results

The best model included interactions between site and NDVI and site and distance to water as predictors for group size, and detection probability was estimated as a function of the log of observation duration (Table 2, 3). The interaction between site and distance to water was significant ($X^2=13.35$, $df=2$, $P=0.001$) because group size decreased as distance to water increased at MNP and UNP (both $P<0.001$) but was not affected by distance to water at YNP ($P=0.53$, Figure 1). The interaction between site and NDVI was also significant ($X^2=10.46$, $df=1$, $P=0.005$) because group size decreased with increasing NDVI at UNP ($P<0.001$) but was not affected by NDVI at YNP ($P=0.77$) or MNP ($P=0.12$) (Figure 1). Based on the Moran I test I found no significant spatial autocorrelation in the residuals of the best model ($P=0.35$).

Groups at MNP were significantly larger than at YNP and at UNP but did not differ between YNP and UNP, based on 95% confidence intervals of model predictions for the sites (Figure 2).

Discussion

I applied open metapopulation N -mixture models to investigate how group size in Asian elephants is affected by environmental variables while taking into account imperfect detection. Group size estimates integrated potential arrivals and departures of individuals at a location and were appropriate for species like Asian

elephants in which individuals frequently separate and reunite (Fernando and Lande 2000, de Silva et al. 2011).

Group size estimates were significantly larger at MNP than at YNP and at UNP. While elephants could have been observed at similar distances from water in all three sites, parks differed with respect to forage and water availability. Consequently, the best-fitting model, included a site-specific relationship between group size and both NDVI and distance to water.

NDVI likely affected group size because it relates to food availability and quality (Pettorelli et al. 2007, 2011). NDVI values positively correlate with green leaf density and leaf chlorophyll density (Tucker et al. 1985), therefore larger NDVI values indicate greener vegetation and greater canopy coverage (Pettorelli et al. 2011). The entire range of NDVI values observed in my study encompassed different habitat types as well as different vegetation cover. NDVI values in vegetated areas could be summarized as follows: low NDVI values indicated sparse vegetation such as grass, intermediate NDVI values denoted areas with a mixture of herbaceous and woody plants, and high NDVI values corresponded to dense vegetation such as forests (Nemani and Running 1997, Pettorelli et al. 2005). NDVI values likely translated into different levels of food availability for herbivores, thus explaining the relationship with group size I observed.

Elephants are generalists but, like other ungulates (Jarman 1974), they selectively consume plant species and plant parts that are less fibrous and contain more proteins and digestible carbohydrates (McCullagh 1969, Sukumar 1990). Young grasses have low NDVI values (Pettorelli et al. 2011) and are a preferred food source

because they have higher soluble carbohydrates and lower lignin and secondary compounds compared to woody vegetation (McNaughton and Georgiadis 1986, Sukumar 1990). Grasses are more digestible than woody plants and require little handling time (Bryant et al. 1991). Grass patches represent homogenous concentrations of high quality resources for elephants (Osborn 2004). Woody vegetation such as scrub or evergreen forests has higher NDVI values (Nemani and Running 1997) compared to young grass and, typically, is not a preferred food source for elephants despite its higher protein content (Jarman 1974, Sukumar 1990). Woody plants require longer handling time compared to grass because their chemical defenses vary substantially among plant parts and plant growth stages (Bryant et al. 1991). Therefore, as NDVI increases and woody plants become more abundant, good quality food will be more dispersed. This should result in smaller group sizes because individuals will have to move more to harvest sufficient high quality browse and spread out more to avoid competition. Conversely, at low NDVI values where good quality resources are more concentrated, larger groups should be favored because animals would be less likely to disperse when foraging.

Like most mammals, elephants are dependent on water for survival and adults drink on average 180 liters of water per day (Laws 1970). Unlike foraging, which takes up 12 to 18 hours per day depending on individual's age and reproductive status (Sukumar 1989, 1992, Joshi and Singh 2008), less than 2-3 hours of the day are devoted to drinking and bathing (Joshi and Singh 2008). Water is not only a vital resource but it also facilitates social interactions by promoting play behavior (Joshi 2009). Water and high quality food sources may not be close to one another. As a

result, elephants may have to travel long distances to switch between feeding and drinking activities (Sukumar 1989). All members of a social unit would be more likely to synchronously switch between feeding and drinking activities to avoid costs of separation imposed on all members of a group (Conradt and Roper 2000). When harvesting water rather than food elephants can remain closer to each other because resource depletion is less likely. As a result, I would expect elephants to be observed in larger groups when close to water. Furthermore, when water is limited to a few locations, very large aggregations of animals could be expected near water (Chamaillé-Jammes et al. 2007) and these may correspond to ephemeral gatherings of multiple social units.

Minneriya National Park

I observed the largest groups at MNP where vegetation is mostly comprised of grasslands surrounded by dry-mixed evergreen and scrub forests. African forest elephants form small groups when in the forest but gather by hundreds at clearings (Fishlock and Lee 2013, Turkalo et al. 2013). Similarly, Asian elephants at MNP formed large groups near water in open grass areas or at the edges between grasslands and forests (Figure 3). Distance to water clearly impacted group size in the model specific to MNP with larger groups observed closer to water. In contrast, group size was not predicted by NDVI at MNP. This likely is because NDVI exhibited little variation at MNP relative to the other sites (Figure 3). Most of the available habitat consisted of high quality grass with low NDVI.

Disturbance by humans may have contributed to the large average group size at MNP. Group size increases with predation pressure and habitat openness (Jarman

1974, Brashares and Arcese 2002) and human disturbance is perceived as predator risk (Frid and Dill 2002, Beale and Monaghan 2004). Hence, variation in the number of tourists present may have affected the size of the groups observed and encouraged the formation of groups composed of several social units.

Areas with abundant water and forage should contain higher densities of animals (Clutton-Brock and Harvey 1977). However, the extent to which animals are aggregated may depend on selective associations among individuals. African forest elephants (*Loxodonta cyclotis*) stay in small groups of two to three individuals in the forest and sometimes gather by hundreds at clearings (Turkalo et al. 2013). Female African forest elephants are selective in their associations and individual identity and familiarity among conspecifics could influence whether or not social units fuse (Fishlock and Lee 2013). Hence, differences in association strength between specific individuals or groups could have accounted for the range of group sizes observed for similar combinations of NDVI and distance to water values at MNP.

Udawalawe National Park

Group size was best explained by additive effects of NDVI and distance to water at this site. Group size decreased with distance to water and increased with NDVI. Water was available in two reservoirs as well as middle size ponds and vegetation at this site had intermediate NDVI values compared to the other two sites.

Small scale fires were a common occurrence in this park, generating patches of lush grass scattered across the entire landscape (de Silva et al. 2013, Peiris and Padmalal 2014) that should exhibit lower NDVI values than surrounding savannah areas (Pettorelli et al. 2011). In these patches of regenerating vegetation which

constituted high quality and clustered food sources, elephants were often observed in large groups. Locations in the low range of NDVI values, close to water, and where large groups were observed may just reflect attraction to water. However, locations far from water, in low NDVI conditions where large groups were present may correspond to burnt patches with good quality forage. Hence, accounting for proximity to water, NDVI at this site may be able to provide the most accurate information on forage quality and resource availability compared to the two other sites in this study.

Yala National Park

Neither NDVI nor distance to water were significantly related to group size at YNP. Elephants were observed at locations with similar NDVI values compared to UNP and average group size did not differ from UNP but was significantly lower than at MNP.

Water was spread throughout the landscape in the form of small water ponds and habitat was the densest of the three sites (Mueller-Dombois 1972, de Silva et al. 1994). The distribution of water in this landscape may have contributed to the non-significant relationship between water and group size.

The absence of a relationship between group size and NDVI at YNP may indicate that forage quality is low regardless of NDVI in the scrub forest habitat that dominates this site. Alternately or in addition, the dense structure of scrub forest may impose space constraints that prevent the formation of large groups. Elephants are social animals and non-random associations among individuals are expected.

However, high environmental constraints may not permit gatherings of several social units at this site.

Conclusion

In this study I examined the effects of NDVI and distance to water, respectively used as proxies for forage and water availability, on the size of wild Asian elephant groups at three sites. I found that both NDVI and distance to water were important predictors of group size and that their relative importance varied among sites. Along with information about group composition and association stability among individuals, these results could reveal important aspects of a population social structure that could be used to develop efficient conservation strategies.

Table 1. Parameters used in candidate set of N -mixture models. Subscripts correspond to possible covariates for each parameter with a dot indicating a parameter held constant. Environmental covariates for the parameter describing *group size* (λ) were NDVI and distance to water (Water); Parameters *recruitment rate* (γ) and *survival rate* (ω) were held constant; and *detection probability* (ρ) was either constant, a function of duration of observation (Dur) or its logarithm (LogDur). Models tested correspond to combinations of each of the possible effects on initial group size and detection probability. I considered all possible models nested within a three way interaction between site, NDVI, and water.

Model parameters	Description
Effects on initial group size (λ)	
λ_{Site}	λ varies with site
λ_{NDVI}	λ varies with NDVI
λ_{Water}	λ varies with distance to water
Effects of survival (ω) and recruitment	
$\omega.$	ω is a constant
$\gamma.$	γ is a constant
Effects on detection probability (ρ)	
$\rho.$	ρ is a constant
ρ_{Dur}	ρ varies with observation duration
$\rho_{\text{Log (Dur)}}$	ρ varies with the log of observation

Table 2. Candidate N -mixture models ranked by AIC and Δ AIC. In the table “nPars” indicates the number of parameters in a model. Only the top 9 models along with the null model (all parameters constant) are presented in the table. When parameters for *group size* (λ), *animals surviving* (ω), *animals recruited* (γ), and *detection error* (ρ), potential covariates are indicated in parentheses. A dot denotes a parameter held constant, a “+” indicates an additive effect, and an “*” indicates an interaction between two covariates. Environmental covariates for initial *group size* are NDVI and distance to water (Water). *Detection probability* could be a constant or a function of observation duration (Dur) or its logarithm (LogDur).

Rank	Model	AIC	Δ AIC	nPars
1	λ (Site+Water+NDVI+ Site:Water+ Site:NDVI) $\gamma(.)$ $\omega(.)$ ρ (LogDur)	3836.6	0.00	13
2	λ (Site+Water+NDVI+ Site:Water+ Site:NDVI+ NDVI:Water) $\gamma(.)$ $\omega(.)$ ρ (LogDur)	3838.3	1.64	14
3	λ (Site+Water+NDVI+ Site:Water+ NDVI:Water) $\gamma(.)$ $\omega(.)$ ρ (LogDur)	3840.4	3.76	12
4	λ (Site*Water*NDVI) $\gamma(.)$ $\omega(.)$ ρ (LogDur)	3842.2	5.52	16
5	λ (Site*Water+NDVI) $\gamma(.)$ $\omega(.)$ ρ (LogDur)	3843.1	6.46	11
6	λ (Site*NDVI+Water) $\gamma(.)$ $\omega(.)$ ρ (LogDur)	3846.0	9.35	11
7	λ (Site+NDVI*Water) $\gamma(.)$ $\omega(.)$ ρ (LogDur)	3851.1	14.42	10
8	λ (Site+Water) $\gamma(.)$ $\omega(.)$ ρ (LogDur)	3853.6	16.96	8
9	λ (Site+NDVI+Water) $\gamma(.)$ $\omega(.)$ ρ (LogDur)	3854.3	17.62	9
10	$\lambda(.)$ $\gamma(.)$ $\omega(.)$ $\rho(.)$	4517.3	680.6	4

Table 3. Parameter estimates with standard errors (SE) for the best model. P values indicate the probability that each estimate deviates from zero and correspond to Wald z tests.

		Estimate	SE	Z	P
Group size	MNP	2.6878	0.2533	10.612	<0.001
	UNP	3.5473	0.3103	11.431	<0.001
	YNP	1.8291	0.2815	6.498	<0.001
	MNP:Water	-0.5094	0.1065	-4.783	<0.001
	UNP:Water	-0.2481	0.0604	-4.105	<0.001
	YNP:Water	0.0701	0.1112	0.630	0.529
	MNP:NDVI	-0.4666	0.3000	-1.555	0.120
	UNP:NDVI	-1.2511	0.3985	-3.139	0.002
	YNP:NDVI	0.0504	0.1790	0.281	0.778
Recruitment	Constant	1.08	0.0807	13.4	<0.001
Survival	Constant	14.4	94.8	0.152	0.879
Detection	Intercept	0.333	0.0964	3.46	<0.001
	LogDur	0.341	0.0326	10.46	<0.001

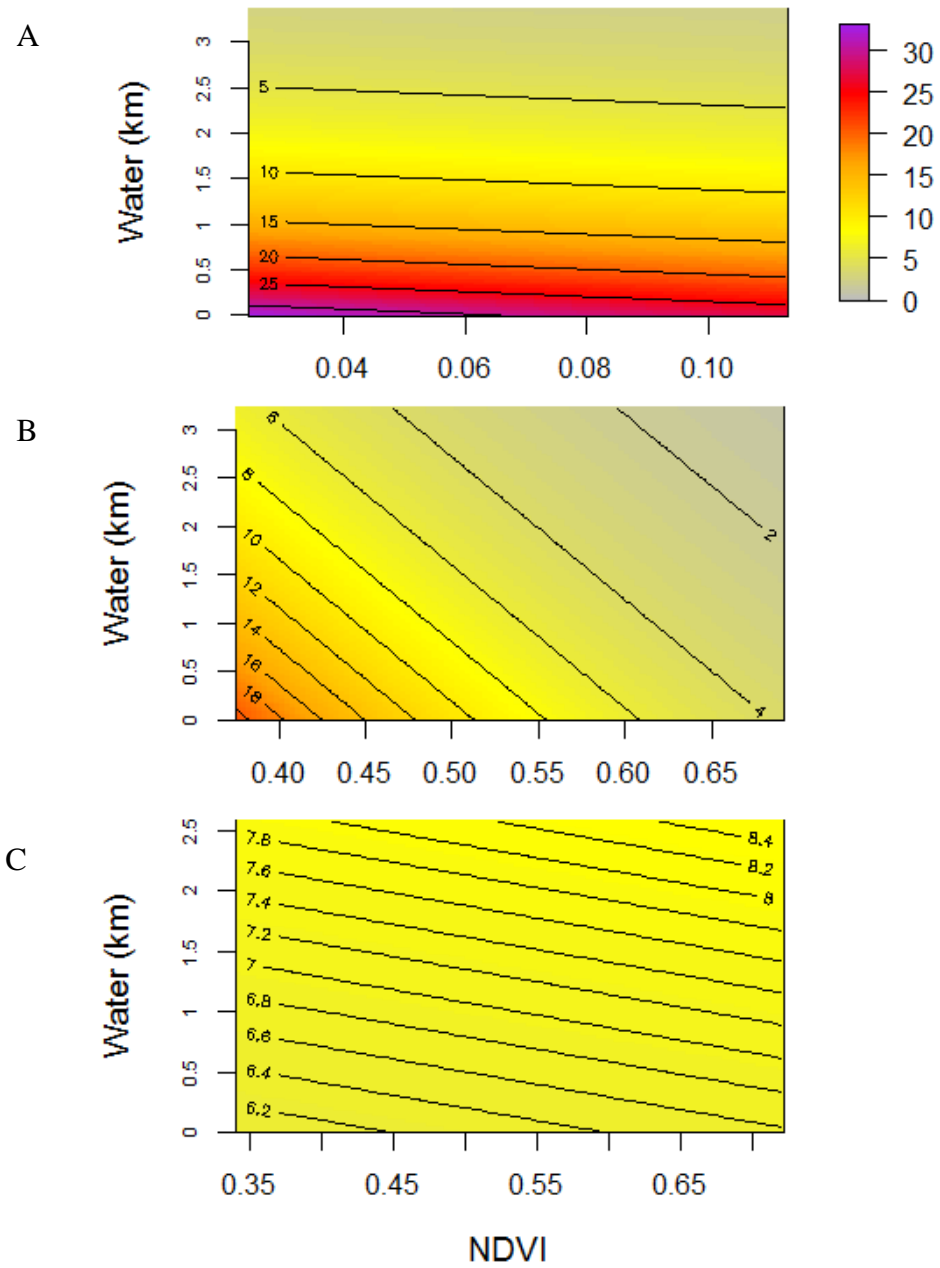


Figure 1. Effects of NDVI and distance to water on group size. Each figure is site-specific: MNP (A), UNP (B), and YNP (C). Colors indicate predicted group sizes which range from 1 to 32.

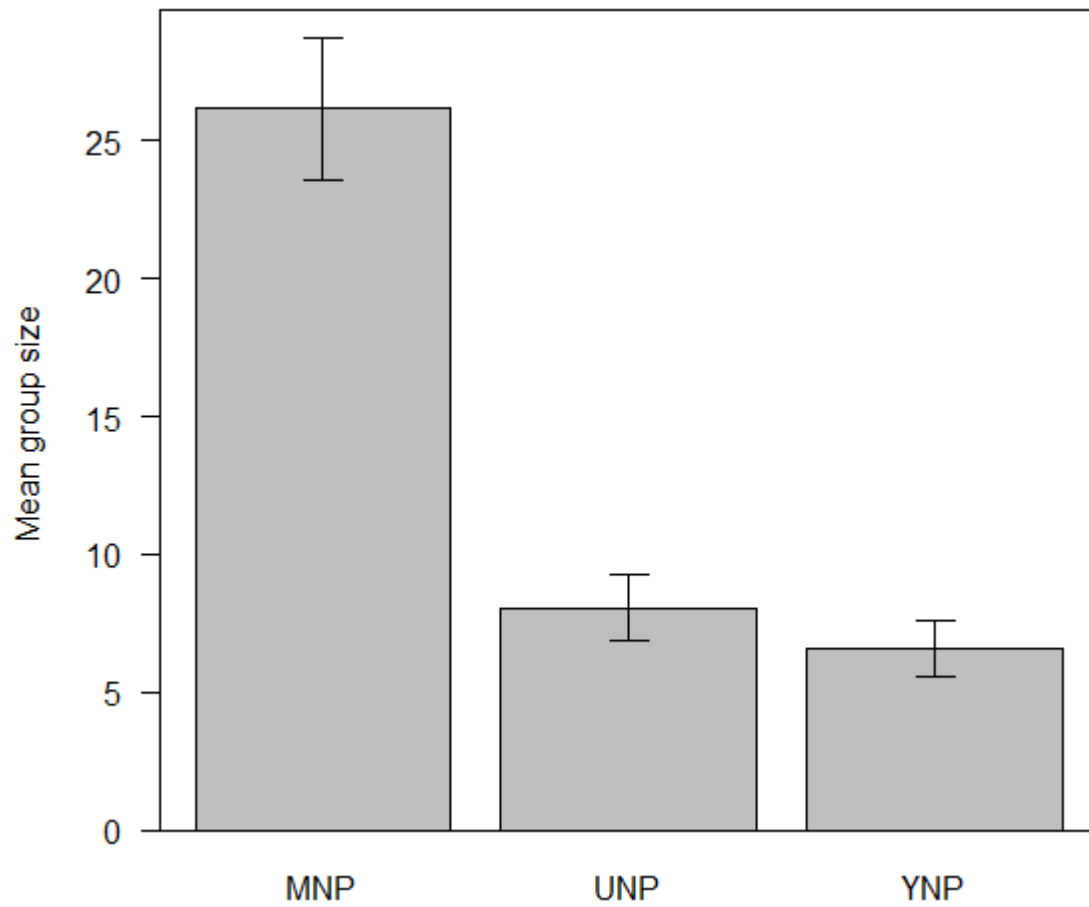


Figure 2. Group size predictions for each site from the best model. Error bars represent 95% confidence intervals.

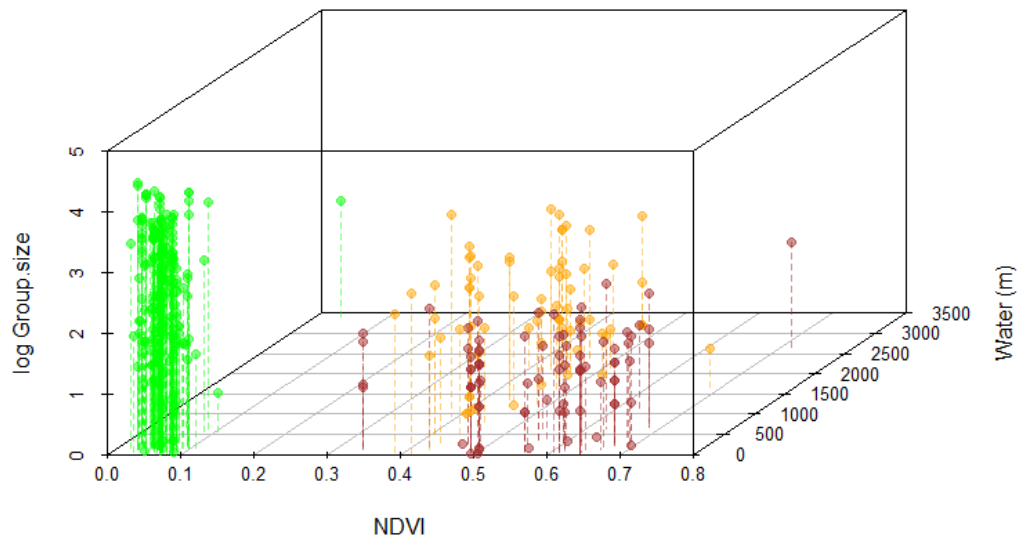


Figure 3. Observed group sizes in relation to NDVI and distance to water. X and Y axes respectively represent the NDVI and distance to water (m) characteristic of each of the locations at which elephants were observed. The Z axis represents the log of group sizes. The dotted lines correspond to the vertical projection of each point onto the X/Y plane. Point color indicates which site it belongs to: MNP (green), UNP (orange), and YNP (brown).

Chapter 2: Social network structure in two wild Asian elephant (*Elephas maximus*) populations

Abstract

Social Network Analysis (SNA) provides a powerful analytical framework to quantify how individuals associate with each other at different levels from dyads to populations. I applied SNA to compare the social networks of Asian elephants (*Elephas maximus*) across two different environments. Previous studies of Asian elephants suggest that environmental differences may result in different social structures, but direct comparisons of sites are hampered by the lack of analogous observational and analytical approaches. Using 50 days of observations over two years I quantified pairwise associations between 208 individually identifiable elephants at two national parks. I found that at one site individuals formed highly independent social clusters whereas, at the other site no social clusters were apparent. By gradually removing low strength dyadic associations I discovered that individuals with strong ties formed small isolated social clusters of tightly associated members at both sites. This study demonstrates how similarities in social structure can be masked by differences in gregariousness caused by environmental conditions.

Introduction

Animal societies are the result of recurrent interactions and inter-attractions among conspecifics (Chauvin 1968, Deputte 2000, Wilson 2000). Why and how associations are formed and maintained remains unclear (Couzin 2006). Studies of social dynamics can provide insight into the costs and benefits of individual associations (Aureli et al. 2008). Examining the social structure of different populations within the same species can identify potential social differences or similarities (Krause et al. 2007) and assess whether an underlying social structure is preserved across different environmental conditions. This information has consequences for interpretation of potential adaptations for group living as well as for devising management strategies for endangered species (Caro 1998).

Some societies, like those of elephants (African elephants: Wittemyer et al. 2005; Asian elephants: de Silva et al. 2011) exhibit a fission-fusion system in which the changing balance between the costs and benefits of staying together regulates increased (fusion) or decreased (fission) associations among individuals (Kummer 1971, Dunbar 1992, Van Schaik 1999, Couzin 2006). Because the dynamic of associations varies among social systems, more than just a label is needed to characterize animal social structure (Aureli et al. 2008). Instead, quantitative measures of the strength and number of associations among individuals over time make it possible to detect changes or measure differences among social systems (Kappeler and Van Schaik 2002, Aureli et al. 2008).

Social Network Analysis (SNA) is a powerful analytical tool for investigating the structural properties of a society (James et al. 2009). While an array of techniques

and measures have been used in studies of animal social structure (Whitehead and Dufault 1999), the advantages of SNA is that the same conceptual framework can be used to describe and quantify how close and connected individuals are to each other at different organizational levels- from a dyad, to a group, or to a population (Croft et al. 2008, James et al. 2009). In comparison to more standard measures of social structure, such as mating patterns or group size (Whitehead and Dufault 1999), SNA takes into account relationships between multiple individuals at the same time (Whitehead 2008). With SNA, it is also possible to filter out specific classes of individuals or levels of associations to reveal higher order structures that might otherwise be masked (Lusseau 2003, James et al. 2009). Hence, SNA offers both a coarse and detailed approach to the study of associations among individuals.

The endangered Asian elephant (*Elephas maximus*) (Choudhury et al. 2008) occupies diverse habitats but is often found in dense forests, making visual observations of elephant behavior difficult, if not impossible (Sukumar 1992, de Silva et al. 2011). Consequently, it has been challenging to characterize Asian elephant social organization. Previous field studies of Asian elephants in Sri Lanka, where high elephant density and the presence of open habitats are conducive to behavioral observations, reached different conclusions regarding the size and stability of social groups. Using behavioral observations, radio telemetry, and population genetic data in Yala National Park (YNP), Fernando & Lande (2000) described independent matrilineal social units composed of adult and sub-adult females and juveniles that exhibited low levels of association and no intergroup transfer of females. Conversely, based on behavioral observations de Silva et al. (2011) reported that associating adult

females in Udawalawe National Park (UNP) were not always together but formed larger social units than reported for YNP. In UNP social units were also stable across years. Some individuals formed persistent associations, and females occasionally moved between social units (de Silva et al. 2011). These studies suggest that differences in association patterns exist between populations in YNP and UNP. However, because the methods used were different, direct comparison is difficult. To confirm whether intraspecific variation in social structure exists in Asian elephants or any other species, similar behavioral and analytical tools are required.

Thus, for this study I used SNA to describe and compare association patterns between wild Asian elephants at two ecologically different sites in Sri Lanka. I hypothesized that differences in associations at both dyadic and site levels would be consistent with the social system previously reported. However, to determine if the elephants at both sites shared common core social groupings, I conducted an iterative SNA using different association thresholds. This procedure reveals the existence of social units that otherwise would have been hidden.

Methods

Study sites

The study was conducted at two national parks in Sri Lanka. At YNP I conducted observations in Block I (6°22'N 81°31'E) which spans 140 km² in the semi-arid dry zone in the southeast. The predominant vegetation type at this site is scrub forest, with patches of evergreen forest and a few short-grass clearings (Mueller-Dombois 1968, 1972). Annual rainfall varies between 500-1,000 mm (Chandimala and Zubair 2007). At YNP drinkable water is limited to the Menik

River, reservoirs, and natural waterholes. In the driest months of the year (August-September) water becomes a limited resource as most natural waterholes dry out (de Silva et al. 1994).

I also conducted observations at Minneriya National Park (MNP), which covers 88 km² in the north central province (7°58'N 80°50'E). MNP is dominated by grasslands (Nekaris and Jayewardene 2004) surrounded by dry-mixed evergreen and scrub forests (Green 1990). Annual rainfall at MNP ranges between 1,500 and 2,000 mm (Chandimala and Zubair 2007) with a dry season from May to September and a wet season from October to January (Perera et al. 2012). The main source of water is a reservoir that shrinks in the dry seasons and allows for short grass to grow around the remaining water.

Data collection

Observation periods. Data were collected in YNP during 25 days from June to September 2007 and in MNP during 25 days from June to September 2010. At both YNP and MNP, the elephants were habituated to human presence due to frequent visits by tourists, which facilitated my behavioral observations.

Census routes. At each site, data were collected from a vehicle while following a circumscribed census route during typical park hours (YNP: 0600-1830, MNP: 1200-1830). The vehicle contained a scientist, a driver, and a tracker who had knowledge of the park roads and helped locate elephants. In YNP a well-established system of roads was traversed on average once a week. In MNP roads were present in forested areas but not in the open grasslands that surrounded the reservoir.

Consequently, I drove off-road in grassland areas but still covered all accessible parts of the park once a week.

Elephant identification. Whenever elephants were spotted, I recorded the date, time, and GPS location. When an elephant was seen alone I observed until it moved out of sight or up to 101 minutes, after which I continued along the census route. I defined a group as a temporary aggregation of individuals at a specific location and time with no individual at a distance from its nearest neighbor farther than the group diameter at its widest point (Archie et al. 2006). I recorded whenever individuals moved in or out of the gathering place, and I defined a new group whenever the aggregation composition changed. I observed groups until all individuals moved out of sight. Duration of group observations varied between 1 and 184 min.

I individually identified all elephants encountered using distinctive physical features derived from digital photographs (Fernando and Lande 2000). I created an identification card for each individual (see Appendix 1), using unique features, such as ear lobe shape, ear folds (primary and secondary), back shape, tail length and tuft pattern, depigmentation pattern, tears and cuts, as well as the animal's approximate height and sex. I then used the cards to confirm identities in subsequent photographs. I identified 168 individuals in YNP and 1,317 individuals in MNP.

Data analysis

Estimating associations. I defined associations based on the gambit of the group: individuals found in the same group were considered associated (Whitehead and Dufault 1999). I used group composition to derive a measure of association

strength for pairs of individuals. I used the half weight association index (HWI) to estimate the proportion of time that a pair of individuals was observed together (Cairns and Schwager 1987). This index is most appropriate when not all associates of an individual are identified and when groups are weighted by the duration of observation (Whitehead 2008). I calculated HWI as $X / (X + Y_{AB} + \frac{1}{2} (Y_A + Y_B))$ where X is the number of minutes for which individuals A and B were associated, Y_{AB} is the number of minutes in sampling periods in which A and B were identified but not associated, Y_A is the number of minutes in sampling periods for which only individual A was identified and Y_B is the number of minutes in sampling periods in which only individual B was identified. To calculate association indices (AI) and network statistics, I used SOCPROG version 2.3 (Whitehead 2009), Gephi (Bastian et al. 2009), and sna (Butts 2014), network (Butts 2008, 2015) and igraph (Csárdi and Nepusz 2006) packages for R (R Core Team 2015). I only included individuals that were seen ≥ 2 times at different locations over the course of the entire study period (see Appendix 2) to avoid bias due to individuals associating only once (Croft et al. 2008). As a result, I considered 116 groups in YNP and 167 in MNP corresponding to a sample size of 57 individuals in YNP and 151 individuals in MNP.

Testing association pattern. I tested the null hypothesis of no preferred companionship by assuming that individuals should associate with any other individual in the population with a fixed probability. For each site, I generated 1,000 random SNA graphs that had the same number of nodes and edges as the original graph and used randomization techniques to distinguish between social preferences and arbitrary gregariousness (Whitehead et al. 2005, Whitehead 2009). To create each

random graph, I reassigned randomly chosen individuals to groups using 1,000 conservative “flips.” For each flip, a sampling period (a day) was randomly chosen and only two individuals were swapped between groups (Bejder et al. 1998, Whitehead 1999, 2008, 2009). Every 100 flips, percentage and mean of non-zero association indices, and standard deviation of all association indices were calculated (Whitehead et al. 2005, Whitehead 2009). I compared statistics from the observed data to a distribution of values generated after data randomization (Whitehead 2009). Conducting flips within sampling periods accounts for the possibility that not all individuals might be present in each sampling period (Whitehead 1999). Moreover, preserving the number of individuals in each group and the total number of groups in which each individual was observed during each sampling period (Bejder et al. 1998) accounts for the possibility that individuals seen in many groups were grouped together by chance (Whitehead 2008).

If individuals associate non-randomly with a selected number of conspecifics from the pool of individuals available, the percentage of non-zero AI should be significantly lower and the standard deviation of all AI significantly higher in observed than in random datasets (Whitehead et al. 2005, Whitehead 2009). If elephants form permanent bonds then all non-zero AI will be equal to 1.0. If elephants live in a fission-fusion society in which individuals separate and reunite then mean of non-zero AI will be greater than 0.0 and less than 1.0.

Comparing associations between sites. I tested the null hypothesis that the distributions of association indices at YNP and MNP were not significantly different from one another using a 2-sample permutation test with 10,000 permutations, using

percentage of non-zero AI, mean of non-zero AI, and skewness of the AI distribution as test statistics (de Silva and Wittemyer 2012). The percentage of non-zero AI represents the proportion of individuals from a population that associate, while the mean of non-zero AI measures on average how strongly associated pairs of individuals are. The skewness of non-zero AI distribution indicates whether associations are overall loose or strong.

Connectedness. In a network, individuals are represented by nodes and an association by the link (or edge) between two nodes (Wey et al. 2008). An edge carries information about the strength of an association and is directly proportional to the association index between two individuals (Lusseau et al. 2008). I built a weighted, undirected network, where edges are association indices based on co-occurrence of individuals (Lusseau et al. 2008).

To compare the connectedness of individuals in the two populations I used three SNA metrics (see Table 4 for formulae) - Strength (S), Reach (R), and Clustering coefficient (C) (Newman 2004, Barthelemy et al. 2005, Flack et al. 2006, Holme et al. 2007). Strength measures an individual's gregariousness or direct connectedness (Barthelemy et al. 2005), Reach is a measure of indirect connectedness (2 or more steps away) (Flack et al. 2006, Whitehead 2008), and Clustering coefficient indicates the extent to which the associates of an individual are connected to each other (Barthelemy et al. 2005).

I estimated standard errors for each network statistic by creating bootstrap replicates and resampling with replacement 1,000 times (Efron and Tibshirani 1994, Whitehead 2008). I inferred that observed statistics significantly differed from

random if they were greater than 95% of the values from 1,000 randomly generated datasets.

Network statistics are dependent on graph properties (e.g. number of nodes and node degree), and while they capture essential features of a network, no statistical tests exist for direct comparisons of networks that differ in size and connectedness (Croft et al. 2008). However, by normalizing the mean of each network metric [i.e. dividing the mean by its maximum expected value ($n-1$ for Strength, $(n-1)*(n-2)$ for Reach, and 1 for Clustering coefficient, with n being the number of individuals], values for each metric will lie between 0.0 and 1.0 which makes comparison of networks possible (Croft et al. 2008).

Population structure. I measured modularity Q , which describes the degree to which a population is homogenous or divided into social units or clusters (Newman 2004, 2006, Newman and Girvan 2004, Whitehead 2008). The modularity coefficient is the difference between the proportion of total association indices within clusters and the expected proportion if dyads were associating at random. Q varies between 0.0 (random associations) and 1.0 (no associations between clusters) (Whitehead 2008). A modularity greater than 0.3 indicates significant social divisions (Whitehead 2008). I calculated Q in Gephi (Bastian et al. 2009) based on an algorithm that can be implemented for large networks and that maximizes the number and weight of edges within clusters and minimizes the number and weight of edges between clusters (Blondel et al. 2008, Bastian et al. 2009). The best network division is the one that maximizes Q (Blondel et al. 2008).

Edge filtering. Given that individuals were considered to be associated when they co-occurred in a group, populations that have high gregariousness and in which large groups can be observed will have more individuals associating as compared to populations in which small groups are more common (Lusseau et al. 2008). When associations are averaged within a population, a large number of loose associations can mask underlying strong associations that might occur within subsets of individuals (Croft et al. 2008). By filtering the network and only leaving associations that are above a given threshold, higher order structures and core components will emerge. Hence, to examine whether pairs of individuals that associate strongly exhibit comparable connectedness patterns in both YNP and MNP, I repeatedly filtered edges in increasing 0.1 increments for AI cut-off values. For each AI filtering step, I examined network fragmentation by calculating the modularity, number of clusters, and average size of clusters.

Results

Association strength and pattern

The percentage of non-zero AI was lower in the observed data than in randomly generated datasets for both YNP and MNP, and the standard deviation of all AI was higher in the observed dataset ($P < 0.001$, Table 5). This indicates that associations were non-random and individuals exhibited preferred companionship. In both parks, non-zero AI were greater than 0.0 and less than 1.0 indicating that different dyads associated to differing degrees (Figure 4).

Average non-zero AI for YNP differed from that observed in MNP (2 sample-permutation test with 10 000 permutations, $P < 0.001$). In YNP the percentage of non-

zero AI was lower than in MNP (Table 5). However, the mean non-zero AI was higher in YNP and the distribution of non-zero AI was left skewed for YNP and right skewed for MNP, indicating that, on average, individuals associations were stronger in YNP than in MNP (Figure 4).

Connectedness

All network metrics were significantly different from randomly generated values ($P < 0.01$, Table 6). Individual gregariousness and sociality measured by node Strength was, on average, high in MNP and low in YNP. Indirect connectedness, as measured by Reach, was high for MNP and low for YNP, while average Clustering coefficient was high for YNP and low for MNP (Table 6).

Community structure

With an AI cut-off value of 0.0, the modularity index value indicates that YNP forms differentiated groups ($Q=0.78$) and was subdivided into several well-defined social clusters while MNP had lower modularity ($Q=0.45$) and more homogeneity. For YNP, edge filtering from 0.1 to 0.9 had little effect on network fragmentation (Figure 5) or modularity, and the number of clusters increased by a factor of 3 (Figure 6). In MNP, edge filtering from 0.1 to 0.9 resulted in an increase in the number of clusters by a factor of 100, a decrease in the average size of clusters by a factor of 100, and a decrease in the size of the largest cluster by a factor of 37 (Figure 6). Even though the unfiltered network formed one large cluster, several clusters appeared at an AI cut-off value of 0.3 (Figure 5). For AI cut-off values greater than or equal to 0.8, modularity and average cluster size was similar for YNP

and MNP (Figure 6). I examined different network statistics as I applied gradual edge filtering, for AI values ranging from 0.0 to 0.9 (Figure 7). For all network statistics, the median, upper quartile and lower quartile values for MNP and YNP became comparable at high AI cut-off values (≥ 0.8). In both populations, individuals that engaged in strong associations had a few partners that were themselves strongly associated (Figure 7).

Discussion

In this study I applied analytical methods derived from Social Network Analysis to characterize association and connectedness in two populations of wild Asian elephants in ecologically distinct sites. My findings confirmed previous results (Fernando and Lande 2000, de Silva et al. 2011) indicating that elephants form non-random associations and interact with a selected number of companions in a preferred and flexible manner congruous with a fission-fusion social system. Additionally, elephants at the two sites exhibited apparent differences in patterns of association. Associations can, however, arise from either social relationships or transient aggregations due to clumped resources (Krause and Ruxton 2002). Once formed, transient aggregations provide an opportunities for social interactions, which might mask similarities in the core social structure of different sites (Lusseau et al. 2006). Using edge filtering (Croft et al. 2008) I show that the apparent differences in social structure implied by the unfiltered networks are due to differences in the prevalence of weak connections. At high AI thresholds both populations exhibited similar core social structures. Similar core social structures within large aggregations were

observed in migrant sparrows, where SNA revealed social units that were maintained across years within large flocks (Shizuka et al. 2014).

In contrast with previous studies, which reported loose associations at YNP (McKay 1973, Fernando and Lande 2000), my analysis revealed highly independent social clusters in which each individual had a few partners that were themselves strongly associated. This difference may have resulted from the use of dissimilar methodologies. For species with a fission-fusion social system, observation length can affect how social structure is represented. For example, short observation sessions are likely to miss fission and fusion events. In a previous study conducted in YNP, observers detected all elephants present during each encounter (Fernando and Lande 2000), but they did not specify details, such as how long groups were observed, whether observations were interrupted once individuals were identified, or whether observations continued until all elephants went out of sight. Furthermore, they averaged data over a three-year period, in contrast to focusing on a single season, which could also contribute to differences in associations. For species with a fission-fusion social system, different seasons might produce different ecological constraints on associations (Chapman et al. 1994, Doran 1997).

Using all observations at MNP, I failed to identify discrete social groups because individuals had many weak or non-existent associations with each other. However, edge filtering revealed that some individuals shared strong ties (AI up to 1.0) and connections existed between females in different social units, similar to reports from Udawalawe National Park (de Silva et al. 2011). A community-type structure with clusters of individuals more closely associated to one another than with

the rest of the population became evident when I filtered out weak links below an AI value of 0.3. Hence, after applying edge filtering, the MNP network fragmented into well-defined social units with increased modularity and decreased average cluster size.

Causes of similarities & differences in social structure

The social stability I observed at both sites suggests that there are benefits associated with small social clusters across populations of Asian elephants. Below I discuss possible reasons for the similarities and differences between populations in light of ecological conditions at both sites. More data would be necessary to tease apart competing hypotheses that I propose.

Predation pressure. Asian elephant sociality might reflect antipredator behavior. In Sri Lanka, the top predator, the leopard (*Panthera pardus*) is not a threat to adult elephants nor calves (Fernando and Lande 2000). However, tigers (*Panthera tigris*) may have inhabited Sri Lanka and become extinct during the Holocene (Kitchener and Dugmore 2000). Because tigers can attack adult elephants they may be responsible for the evolution and maintenance of group living in this species. Comparing the strength of association and the size of social clusters in populations from Sri Lanka to those in India, where there is a high risk of tiger predation, would help clarify the impact of animal predation pressure on social structure in this species (Fernando and Lande 2000).

Studies across taxa indicate that some animals respond to humans as to predators (Frid and Dill 2002, Beale and Monaghan 2004). Human disturbance is likely to contribute to differences in aggregation patterns and association strength

observed between YNP and MNP. In Sri Lanka, elephants have cohabited with humans for centuries (Fernando et al. 2011). In this country, elephants are considered by some to be a nuisance, responsible for severe damage to human habitat, cultivated land, and human lives. To others elephants represent an economic asset, attracting tourists to national parks (Bandara and Tisdell 2003, Fernando et al. 2005).

One of the most well-known antipredator strategies is the tendency to aggregate when predation risk is high (Pulliam and Caraco 1984), especially in open environments (Jarman 1974, Caro et al. 2004). In YNP, where elephants occupy a scrub forest habitat, human presence is limited to a well-established system of roads, and small groups of tightly associated individuals probably provide sufficient protection from predators. By contrast, in open areas surrounding the MNP reservoir, there are no established roads, so tourist vehicles routinely get close to elephants (personal observations). Observations conducted in areas where both elephants and humans live indicated that elephants moved into large open areas at dusk and stayed together in large groups (personal observations). Large aggregations observed in MNP might thus reflect elephants being exposed to higher rates of human disturbance than in YNP.

Resource abundance and distribution. Aggregation size may also be influenced by resource abundance and distribution (Chapman et al. 1994). Chaverri (2010) reported an effect of resource availability on the social network of leaf roosting bats, *T. tricolor*. In this species, individuals associated closely with one another and formed stable social units. While only small isolated clusters were observed when resources were abundant, one large cluster and a few small clusters

were reported when resources were limited and clumped. In Asian elephants, I observed that groups were larger when near water (Chapter 1). Therefore, the high level of gregariousness and low average AI in MNP could be due to individual attraction to surface water (Sukumar 1992, Fernando et al. 2008, Pastorini et al. 2010). By contrast in YNP, where several small water ponds were present, large groups were not observed.

Strong associations might also play a role in resource defense and monopolization in low and clumped resource conditions. Resource defense has rarely been documented in Asian elephants (de Silva et al. 2011). However, in one instance at YNP I observed that a group located near a pond moved away after expressing clear signs of acoustic perception (i.e. head raised, body immobile, ears spread) and was immediately replaced by a larger group at the same location. Acoustic monitoring (Payne et al. 1986) of the types of vocalizations emitted (i.e. threats, greetings) near scarce resources are needed to clarify how resource defense occurs in Asian elephants.

Increased reproductive success. Strong associations between old and young females could influence reproductive success through knowledge transfer and cooperative offspring care. Animal social structure is influenced by information transfer (Goodale et al. 2010), and Hansen (1999) suggested a positive relationship between tie strength and the complexity of knowledge transferred. In African elephants, groups led by an older matriarch exhibit a higher per capita reproductive success as these older females are better at discriminating known from unknown individuals and gauging danger accurately (McComb et al. 2001). Hence, strong ties

between younger and older more experienced females might prove useful in conflict situations.

Alloparental care, which represents care provided to young by individuals other than the parents, has been reported in elephants and other mammals (Riedman 1982, Lee 1987, Roulin 2002). In vervet monkeys *Cercopithecus aethiops sabaesus*, females derived reciprocal benefits from allomothering (Fairbanks 1990). Females with helpers were able to spend more time away from their infant without leaving it alone and exhibited a shorter inter-birth interval than females without helpers. Also, females that were once allomothers had a higher success rate in raising their first offspring (Fairbanks 1990). In African elephants allomothering is crucial for infant survival (Douglas-Hamilton 1972, Dublin 1983) and allomothers are usually nulliparous females (Lee 1987). Strong associations between mothers, infants, and allomothers might be favored in elephants, because to obtain sufficient food for lactation, adult females spend more than 12-18 hours/day feeding (Sukumar 1992, Joshi and Singh 2008). Because Asian and African elephants have similar life expectancy, gestation duration, and inter-birth interval, strong associations between mothers, infants, and their allomothers should have energetic benefits for infant survival and female reproductive success in both species.

Conclusion

My study indicates that Asian elephants at two different sites have core social structures that are similar, but this similarity is masked by superficial differences due to ecological conditions. These patterns were revealed by SNA, which is an important tool for elucidating differences in social structure within and among species and

gaining insight into the evolution of social systems. Additional studies that use SNA to compare social structures of closely related species and populations have considerable potential to reveal the ecological and social determinants of social structure. I anticipate that SNA will prove particularly useful for revealing cases where gregariousness masks social structure, when hundreds or thousands of individuals gather such as in caribou (Russell et al. 1996) and Mongolian gazelles (Zhaowen et al. 1998, Olson et al. 2009).

Table 4. Network terminology.

Network terms

Social graph or network: individuals are represented by dots (nodes) connected by lines (edges). An edge corresponds to an association (type and strength) between two nodes.

Nodes: network component that represents individuals.

Edges: network component that represents an association between two nodes.

Social unit: collection of individuals more closely associated to each other than with rest of the population.

Network metrics

Degree: number of neighbors directly connected to an individual.

Strength: individual's gregariousness and direct connectedness. Strength is the sum of a node's association indices.

$SI = \sum_{I \neq J} AI_{IJ}$ where AI is the association index between individual I and J

Reach: measure of indirect connectedness based on the number of nodes two or more steps away from a given node. Reach is the sum over other individuals B of the sum of products of all pairs of association indices linking A and B through C.

$$RI = \sum_J AI_{IJ} \times S_J$$

Clustering coefficient: degree to which the associates of an individual are associated to one another. Clustering coefficient takes into consideration the weights on the edges of a triad involving a given node. High clustering coefficients are measured in societies composed of tight and closed social clusters while low values indicate that the partners of an individual may not associate with each other.

$$C_{IJ} = \frac{\sum_J \sum_K AI_{IJ} \cdot AI_{IK} \cdot AI_{JK}}{\max(AI_{JK}) \cdot \sum_J \sum_K AI_{IJ} \cdot AI_{JK}}$$

Modularity: measures the community structure of a network and how well a population can be divided into independent social units.

Table 5. Summary statistics describing AI values at YNP and MNP.

	Non-zero % AI		Mean non-zero AI (SD)	SD all AI		Skewness
	<i>Observed</i>	<i>Random</i>		<i>Observed</i>	<i>Random</i>	
YNP	0.109	0.213	0.616 (0.300)	0.216	0.004	-0.199
MNP	0.250	0.327	0.351 (0.246)	0.195	0.006	0.862

Table 6. Strength, Reach, and Clustering coefficient values for YNP and MNP.

	YNP			MNP		
	<i>Calculated</i>	<i>Random</i>	<i>Normalized</i>	<i>Calculated</i>	<i>Random</i>	<i>Normalized</i>
Strength	3.8 (2.5) [0.2]	0.1 (0.06)	0.07	13.1 (6.9) [0.9]	0.4 (0.24)	0.08
Reach	20.6 (19.8) [3.3]	0.01 (0.01)	6e-3	221.3 (146.7) [38.7]	0.2 (0.2)	0.01
Clustering coefficient	0.7 (0.3) [0.04]	0.3 (0.2)	0.7	0.4 (0.2) [0.03]	0.06 (0.02)	0.4

For each statistic, the calculated mean, random mean, and normalized mean values are represented with their standard deviation in brackets. Random values are averaged over a 1,000 random graphs generated using the same number of edges and vertices as the original dataset. The normalized values are obtained by dividing the calculated value by its maximum possible given each network features (number of nodes and possible edges). In square brackets are the standard errors obtained from 1000 bootstraps obtained by resampling sampling periods with replacement.

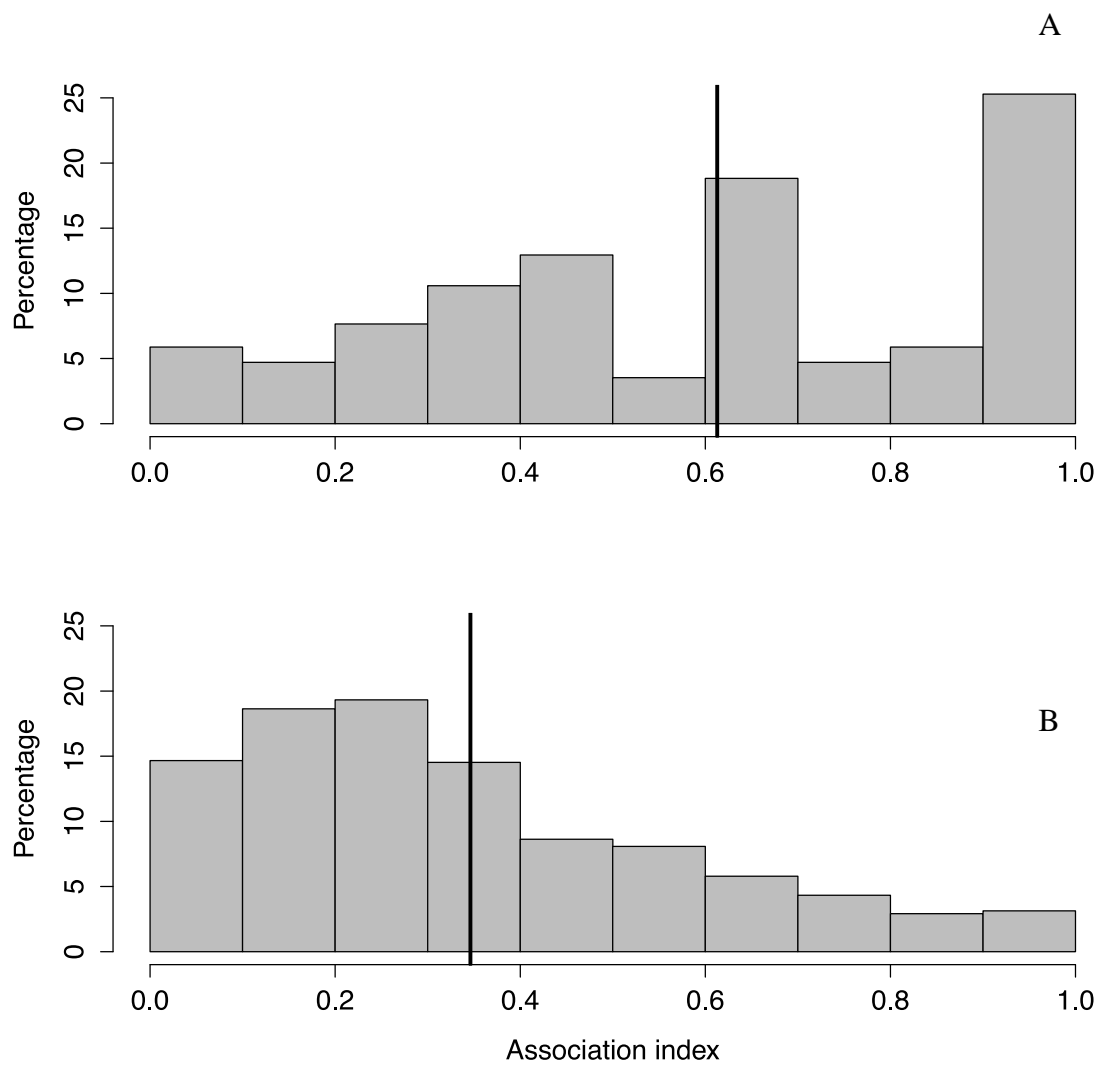


Figure 4. Percentage of non-zero AI. Each panel represents a specific site YNP (A) and MNP (B). The vertical lines denote the means.

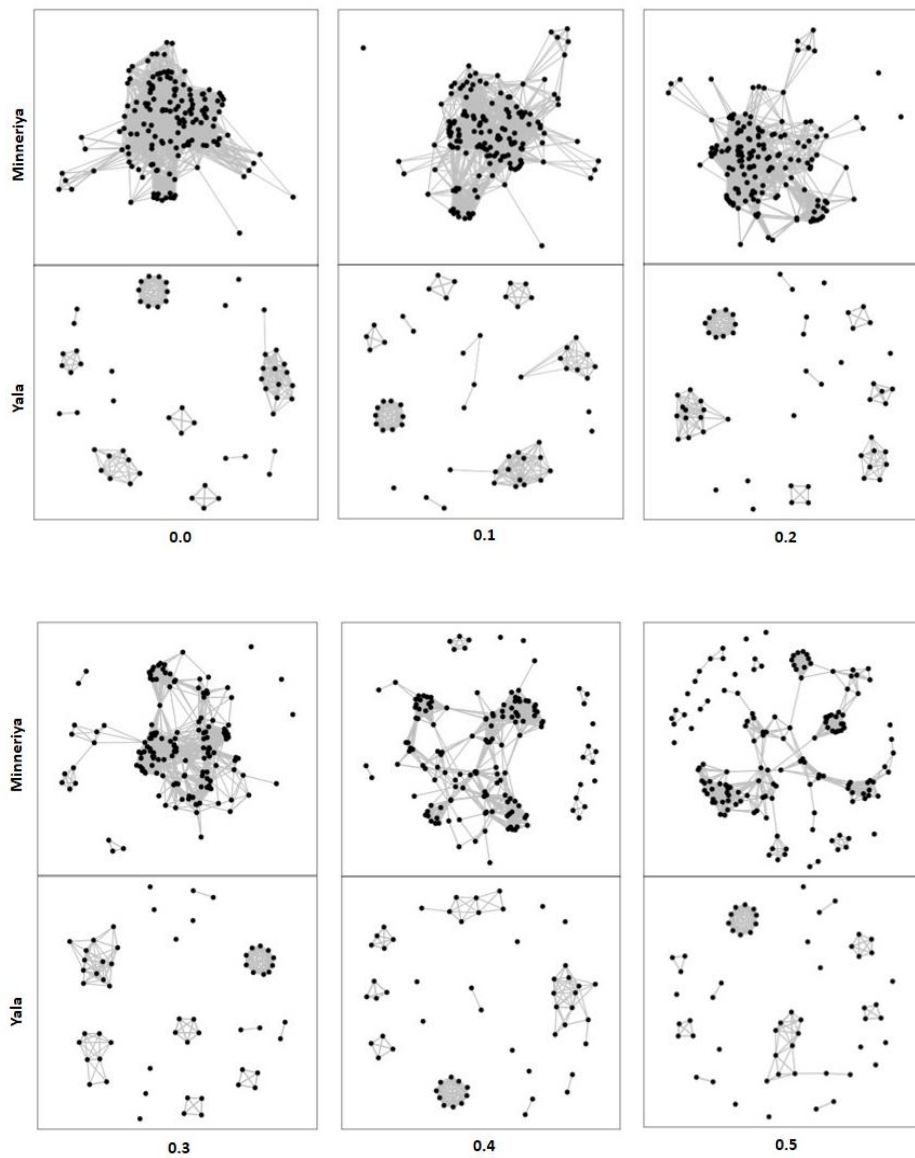


Figure 5. Network fragmentation with increased edge filtering for AI cut-off values ranging from 0.0 to 0.5. The first row of plots correspond to MNP and the second to YNP. Each point is an individual and lines indicate unweighted associations.

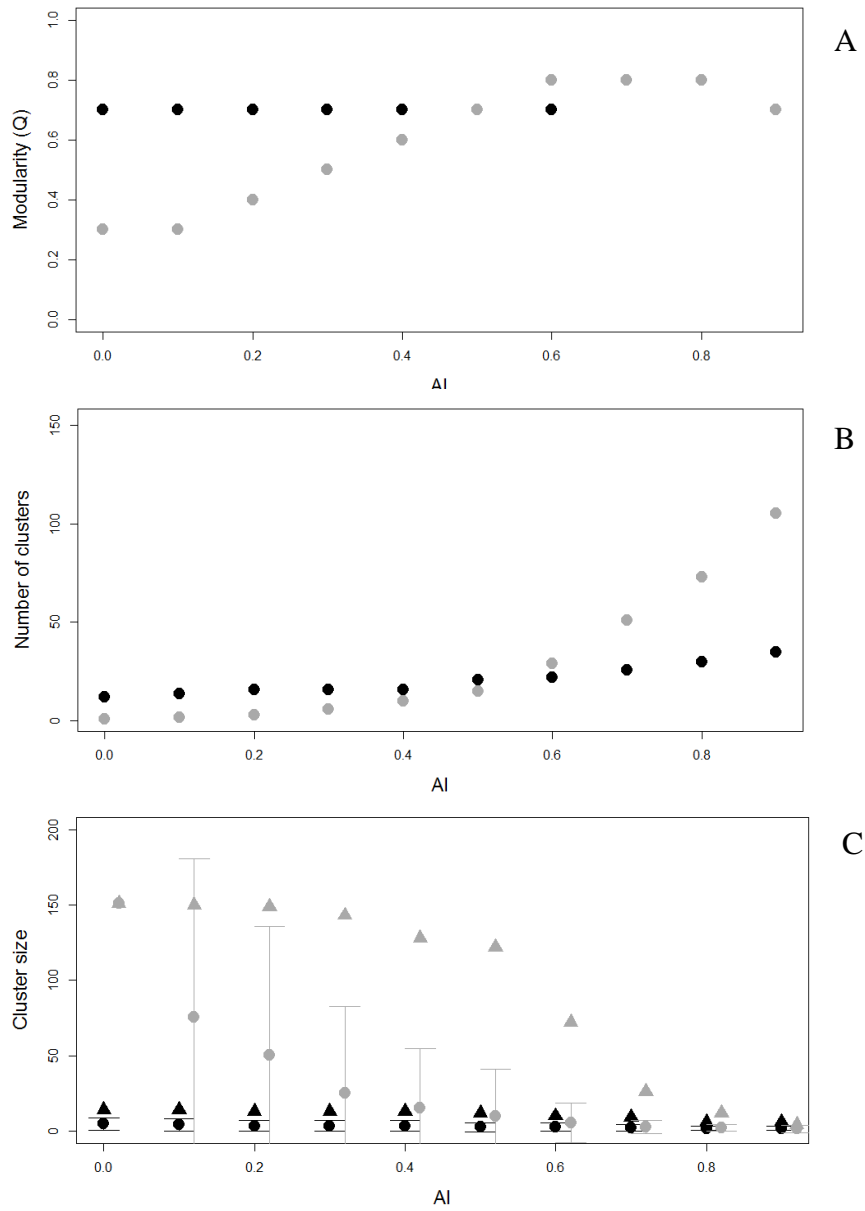


Figure 6. Community structure and network fragmentation for increasing AI cut-off values with 0.1 value increment. Color is indicative of site: YNP (black) and MNP (grey). In panel C, triangles correspond to the largest cluster size, and the points with error bars represent mean cluster size \pm SD.

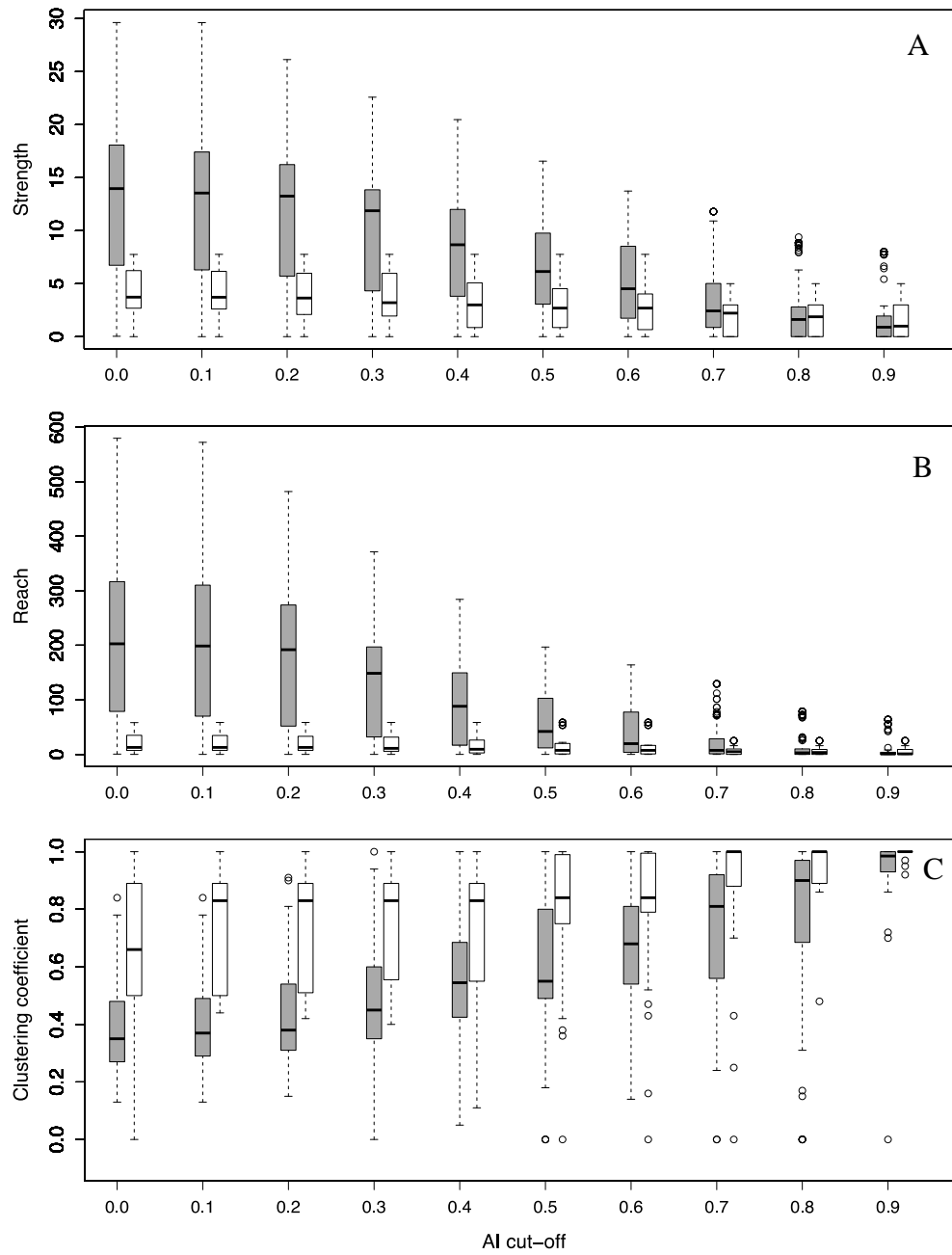


Figure 7. Strength (A), Reach (B), and Clustering coefficient (C) for increasing AI cut-off values. Color is indicative of site: MNP (grey) and YNP (white). In each box plot, the upper and lower bounds correspond to the upper and lower quartile and the black line to the median value.

Chapter 3: The effect of age and sex on associations in Asian elephants (*Elephas maximus*)

Abstract

For socially complex species with a long period of social development, such as Asian elephants, it is necessary to assess how different age and sex classes associate with one another in order to understand the social structure of populations. However, most studies of the social structure of wild Asian elephants focus only on a single class of individuals: adult females. Using 25 days of observations over a 3-month period, I investigated the effect of age and sex on group size, space use, and association patterns in a population of wild elephants at Minneriya National Park, Sri Lanka. I individually identified 1317 elephants and divided them into seven age and sex classes: juveniles, sub-adults, and adults of each sex, along with one class for calves of both sexes. Observations of solitary individuals were frequent for adult males but negligible for all other classes. Sub-adult males exhibited gregarious behavior intermediate between that of juvenile and adult males, revealing that the developmental transition from social to solitary habits in males is gradual and relatively prolonged. Females were social at all stages of development and pairwise associations involving at least one adult female represented more than 50% of all associations. Associations among adult females and between adult females and other age and sex classes formed the core of Asian elephant social structure. This study

indicates the importance of examining all age and sex classes for a meaningful understanding of animal social structure.

Introduction

Throughout their lives, individuals undergo both physical and behavioral changes essential to their integration into a community of conspecifics (Deputte 2000). In some species, from an early age males and females engage in different activities and show different patterns of social interaction that ultimately lead to segregation of the sexes (Bon and Campan 1996). In fission-fusion societies, associations among conspecifics vary over time (Dunbar 1992, Aureli et al. 2008, Couzin and Laidre 2009) adding to the complexity of social development that precedes sexual segregation. By explicitly focusing on behavioral differences between age-sex classes, we can determine the rate and timing of sex-specific developmental changes in association patterns.

In addition, contrasting patterns of aggregation and association as well as space use of adult males and females can provide important insight into a species' mating system. This knowledge is critical for effective conservation strategies because mating systems affect genetic diversity and because knowledge of the composition of a core social structure can help prevent detrimental management outcomes (Slotow et al. 2000, Slotow and Van Dyk 2001).

The endangered Asian elephant (*Elephas maximus*) (Choudhury et al. 2008) is a long-lived animal with a life span of 60 years in the wild (Sikes 1971, Lee 1987, Sukumar 1992, Lee and Moss 1999). In both African and Asian elephants, calves are born after a 20 to 22 month gestation period and remain in lactational dependence for

the first 3 to 4 years of its life (Sikes 1971, Sukumar 1992). Females become sexually mature after 8 or 9 years (Laws 1970, Laws et al. 1975, Sukumar 1992) and usually give birth to their first calf between 14 and 20 years (Sukumar 1992, Archie et al. 2008). Males typically reach sexual maturity at 17 years but do not successfully mate until 20 or 25 years, when they can outcompete other males for access to receptive females (Hollister-Smith et al., 2007; Lee et al., 2011). While no study has yet examined the social behaviors of individually identified male Asian elephants, field observations suggest differences in gregariousness between adults of both sexes. Adult males are often found alone (Eisenberg and Lockhart 1972, McKay 1973, Sukumar 1992) while females are mostly observed in groups (Eisenberg and Lockhart 1972, McKay 1973, Fernando and Lande 2000, de Silva et al. 2011). Because Asian elephants often occupy dense forest habitats, tracking of individual animals is difficult (Sukumar 1992, de Silva et al. 2011). Therefore, unlike the extensively studied savannah African elephants, which live in open habitats, little information is available on Asian elephant social behavior. Adult females are the easiest to identify and observe repeatedly and studies of Asian elephant' social structure based on individual identification have focused on this age-sex class (Fernando and Lande 2000, de Silva et al. 2011). Hence, these studies have proposed a simplified model for the social structure of Asian elephants and have not fully characterized how all age and sex classes associate with one another in a population.

In the present study, my aim was to answer the following questions: 1) How do individually identified adult males and females differ in gregariousness? 2) How does space used by adult males and females sighted at multiple locations compare? 3)

How does the size of groups that include each age-sex class vary? 4) How do males vary in social behavior over their development? 5) What age-sex classes make up the majority of both strong and weak dyadic associations? In order to answer these questions I quantified average group size, space use, and association patterns of different age and sex classes in a population of wild Asian elephants at Minneriya National Park in Sri Lanka.

Adult females move in search for food and water and have been observed in groups that change in size and composition over time (McKay 1973, Fernando and Lande 2000, de Silva et al. 2011). In addition, they are only receptive for a few days in their extended 16-week estrous cycle and have a 4-5 year inter-birth period (Brown 2000). Because receptive females constitute an unpredictable and limited resource, male competition for access to females is likely to be high. Thus, it would not be advantageous for a male to defend a territory nor to permanently join a group of females. Hence, I expected adult males to associate weakly with adult females. In addition, I expected that adult males would be more often observed alone compared to adult females, and that all-male groups would be rare. Because males are the dispersing sex, I expected that the average group size in which males would be found would decrease as they matured and left their natal group. Finally, given the age of sexual maturity, I anticipated that immature individuals would exhibit strong bonds with adult females.

Methods

Study sites

The study was conducted at Minneriya National Park (MNP) spanning 88 km² and located in the north central province of Sri Lanka (7°58'N 80°50'E). MNP is dominated by grasslands (Nekaris and Jayewardene 2004) surrounded by dry-mixed evergreen and scrub forests (Green 1990). Annual rainfall varies between 1,500 and 2,000 mm (Chandimala and Zubair 2007) with a dry season from May to September and a wet season from October to January (Perera et al. 2012). The main source of water is a reservoir which shrinks in the dry season, allowing for short grass to grow around the remaining water.

Data collection

Observation periods. Data were collected during 25 days from June to September 2010. Due to frequent visits by tourists, elephants were habituated to human presence, which facilitated behavioral observations.

Survey routes. Data were collected from a vehicle while following a circumscribed census route from 1200-1830. I covered all accessible parts of the park on average once a week.

Elephant identification. When elephants were spotted, I recorded the date, time, and GPS location. Solitary elephants were observed until they moved out of sight or up to 101 minutes, after which I continued along the census route. When several elephants were present, I defined a group as a temporary aggregation of individuals at a specific location and time with no individual at a distance from its

nearest neighbor farther than the group diameter at its widest point (Archie et al. 2006). I recorded when individuals moved in or out of gathering places and defined a new group for every change in aggregation composition. I observed groups until all individuals moved out of sight. Duration of group observations varied between 1 and 184 min.

I individually identified all elephants encountered based on distinctive physical features derived from digital photographs (Fernando and Lande 2000). I created identification cards (see Appendix 1), using unique features, such as ear lobe shape, ear folds (primary and secondary), back shape, tail length and tuft pattern, depigmentation pattern, tears and cuts, as well as the animal's approximate height and sex. I used the cards to confirm identities in subsequent photographs. Based on the sex of individuals and their approximate height relative to that of an adult female, I differentiated seven age-sex classes: adult female (AF), sub-adult female (SF), juvenile female (JF), calf (CA), adult male (AM), sub-adult male (SM), and juvenile male (JM) (see Appendix 1 and 3).

Data analysis

Group Size. I tested for effects due to age-sex class on the size of groups in which individuals were observed using linear models (LMs). For individuals observed in more than one group, I summarized group size values using median values to account for non-independence. I used a likelihood ratio test (LRT) to compare a model with and without age-sex class as a predictor for group size. Following the LRT, I examined contrasts (Wald t-tests) to determine the significance of pairwise differences between age-sex classes.

To compare the distributions of group size values for individuals of different age-sex classes, I first defined group size categories based on the four quartiles of the median group size values. I then used a X^2 test of independence.

I examined the effects of female presence on the size of groups in which males were observed using generalized linear models (GLMs) with a quasi-Poisson error distribution. I performed a likelihood ratio test (LRT) to compare a model with and without female presence as a predictor for group size. Due to the non-independence of multiple observations taken from a group with shifting composition at one location, I subdivided the original dataset and kept only the last recorded composition at each location.

Using the previously subset dataset, I compared the relative abundance of solitary versus social individuals for the adult male and adult female age-sex class using a X^2 test of independence.

Aggregation within age-sex class. I investigated whether some age-sex classes were aggregated more than expected by chance. Due to the non-independence of multiple observations taken from a group with shifting composition at one location, I used a subset of the original dataset and kept only the last recorded composition at each location. For each age-sex class, I calculated an index of clustering, J , which quantifies how observed counts of individuals differ from what would be expected if individuals were independently distributed according to a Poisson distribution (Ives 1991).

$$J = (\text{variance (counts)} / \text{mean (counts)}^2) - (1 / \text{mean (counts)})$$

Larger values of J correspond to higher levels of aggregation. I performed 10,000 permutations in which I randomized the age-sex class of each individual and calculated J for each class (keeping the number of individuals in each group constant and the number of groups each individual was observed in constant). P values for each age-sex class correspond to the proportion of 10,000 randomized J values for which observed J was greater. I used the Benjamini-Hochberg procedure with a false discovery rate of 0.1 to assess which P values were significant (Benjamini and Hochberg 1995).

Associations within and among age-sex classes. I considered 28 possible types of age-sex class associations and investigated whether some age-sex classes were more or less associated than expected by chance. I defined associations for pairs of individuals based on the gambit of the group: individuals found in the same group were considered associated (Whitehead and Dufault 1999). When two individuals were seen at least once in the same group, they were considered associated, and I used group composition to derive a measure of association strength between pairs of individuals. I used the half weight association index (HWI) to estimate the proportion of time that a pair of individuals (dyad) was observed together (Cairns and Schwager 1987). This index is most appropriate when not all associates of an individual are identified and when groups are weighted by the duration of observation (Whitehead 2008). I calculated HWI as $X / (X + Y_{AB} + \frac{1}{2} (Y_A + Y_B))$ where X is the number of minutes for which individuals A and B were associated, Y_{AB} is the number of minutes in sampling periods in which A and B were identified but not associated, Y_A is the number of minutes in sampling periods for which only individual A was identified

and Y_B is the number of minutes in sampling periods in which only individual B was identified. I used SOCPROG version 2.3 (Whitehead 2009), Gephi (Bastian et al. 2009), sna (Butts 2014), and network (Butts 2008, 2015) to calculate association indices (AI). To avoid bias due to individuals associating only once over the course of the entire study period, analyses were based on 151 individuals that were seen ≥ 2 times at different locations (Croft et al. 2008).

I calculated the relative abundance of each type of dyad in four datasets that either included all associations, those greater than $AI=0.5$, those greater than $AI=0.7$, or those greater than $AI=0.9$. I also calculated for each type of dyad, the relative abundance of non-zero dyadic associations for $AI<0.5$, $AI\geq 0.5$ and <0.75 , and for $AI\geq 0.75$. I examined different strengths of association because previous work has shown that the patterns of social structure can change as AI changes (Chapter 2).

Spatial distribution. To examine if there was an effect of sex on how adult individuals distributed themselves in space, I performed a Welch t-test and compare the average home range size of adult females (AF, $n=28$) and adult males (AM, $n=4$) observed at five or more different locations. In addition, I assessed whether females and males exhibited territoriality by examining the extent of home range overlap for individuals of the same class and by averaging the maximum overlap for each individual. I also calculated the extent of overlap for the home ranges of females and males.

All statistical analyses were performed in R version 3.2.2 (R Core Team 2015).

Results

Group size

There was a significant difference in the size of the groups in which different age-sex classes were observed (LRT: $X^2 = 7823.3$, $df = 6$, $P = 0.004$). The average size of groups in which adult males were observed was significantly smaller than for any other age-sex class ($P < 0.05$) except for sub-adult males. The average group size in which adult females were observed was significantly smaller than that of sub-adult females ($P = 0.011$) (Figure 8).

There was a significant difference in the distribution of group size values for individuals of different age-sex classes ($X^2 = 37.185$, $df = 18$, $P = 0.005$, Table 7). Groups that included at least one adult male were significantly greater in size when adult females were present than in the absence of adult females (LRT: $X^2 = 18.668$, $df = 61$, $P < 0.001$) (Figure 9). In 14.8% of the groups without an adult female, adult males were observed in the presence of other males. In addition, I found that the relative abundance of solitary versus social individuals was significantly different for adult males than for adult females ($X^2 = 112.97$, $df = 1$, $P < 0.001$). Solitary males represented 70.9% of the total number of solitary individuals versus 22.6% for adult females. However, solitary individuals represented 6.4% of sightings with an adult female, 3.3% of sightings with a sub-adult male, and 34.9% of sightings with an adult male.

Within age-sex class aggregation

The index of clustering, J , was significantly higher than expected by chance for juvenile females ($P=0.027$), sub-adult females ($P=0.008$), juvenile males ($P<0.001$), and sub-adult males ($P=0.016$) (Table 8). P values less than 0.05 were also significant according the Benjamini-Hochberg procedure with a false discovery rate of 0.1.

Associations within and among age-sex classes

When examining associations between all classes of individuals I found that for AI thresholds of 0.0, 0.5, 0.7, and 0.9, associations involving adult females represented 69.7%, 69.2%, 74.1%, and 69% respectively of all associations. At each AI threshold, associations between adult females and calves and between pairs of adult females were the most abundant (Table 9). Ten types of dyads were never observed associated at an AI threshold of 0.9, most of which involved an adult or sub-adult male.

For all types of dyads, most associations were weak ($AI<0.5$) although some strong associations ($AI>0.75$) were observed among adult females and between adult females and other age-sex classes. In contrast, only seven out of 45 possible pairs of adult males and one out of six possible pairs of sub-adult males were found associated, and in all cases associations were weak ($AI<0.5$) (Table 10). Isolated dyads represented 41.7% of clusters composed of strongly associating individuals ($AI\geq 0.75$). For 81.8% of the isolated dyads there was at least one adult female. For clusters with at least 3 members ($n=13$, $mean=6.3$, $SD=3.7$), 84.6% contained at least

two adult females. Calves were observed in 84.6%, juvenile individuals in 69%, and sub-adult females in 30% of the clusters composed of at least 3 elephants (Figure 10).

Spatial distribution

Adult male and female elephants differed in their use of space. Average home range size of adult females ($n=28$, $m=2.14 \text{ km}^2$) was significantly larger than that of adult males ($n=4$, $m=0.87 \text{ km}^2$) ($t=2.82$, $df=26.158$, $P=0.009$) (Figure 11). There was less home range overlap for males (49.7%) than for females (95%). The average maximal overlap of male within female home range was 91.2% and of female within male home range was 46.0% (Figure 12).

Discussion

While most studies of Asian elephant social structure have focused on adult females, I compared group size, association patterns, and space use of different age and sex classes in a population of wild Asian elephants at MNP, Sri Lanka. My findings confirm results from previous studies conducted on Asian (Eisenberg and Lockhart 1972, McKay 1973, Sukumar 1992) and African elephants (Moss and Poole 1983, Evans and Harris 2008, Lee et al. 2011) in that adult males and adult females differ in their gregariousness and space use. In addition, I report differences in gregariousness of males of different age classes consistent with a gradual change from social to solitary living with age. Females, on the other hand, were consistently social at all ages. Associations between adult females and calves and between pairs of adult females represented the most frequent types of associations. For any strength of association, more than 50% of the dyads involved an adult female: associations

between an adult female and a calf as well as associations among adult females represented the greatest proportions of all dyads. A smaller number of strong associations between other classes of individuals were also recorded, but those involving adult males and sub-adult males with classes other than adult females corresponded to fewer than 4% of all associations. These results indicate that while associations among adult females are important, those between adult females and other age and sex classes form the core of the Asian elephant social system.

Associations between adult males and adult females – difference in gregariousness

On average, adult males were observed in smaller groups than adult females. In 65.1% of sightings, adult males were in the presence of other individuals. When not with adult females, adult males were alone in most instances, as it was found by McKay (1973). In addition, the majority of solitary individuals observed were adult males. In African elephants, adult males are also observed with females in the majority of sightings but observations of all-male groups are more frequent (30.5%) (Lee et al. 2011) than what I observed (14.8%) or McKay (1973) reported (19.1%) for Asian elephants.

In African elephants, sexually inactive adult males move to “bull areas” where they associate with other males in a relaxed manner. Sexually active males, on the other hand, leave bull areas, are observed alone or in the presence of females, and more frequently engage in aggressive encounters with other sexually active males (Poole, 1982). In contrast to Eisenberg et al. (1971), I did not record any aggressive interactions among males, even for those in musth. The non-territorial nature of Asian

elephant males (McKay 1973, Fernando et al. 2008) was also confirmed by the overlap of adult male home ranges.

Wild Asian elephant males in musth have been observed mating females (Eisenberg et al. 1971). In African elephants, musth bulls are preferred by females in estrous and sire most offspring (Poole 1989, Hollister-Smith et al. 2007). The nature of associations between adult males and adult females at MNP is unclear: males in and out of musth were observed with females. While I recorded only three mating attempts (all performed by sexually immature males) I could have missed matings by musth males. In a 12 to 18 week estrous cycle, females are receptive only during a 4 day period (Brown 2000, Brown et al. 2004) and males remain in close proximity to females in estrous, presumably to ensure that females are inseminated at the optimal time for fertilization (Brown et al. 2004). Fewer than 3% of associations between adult males and females were strong ($AI > 0.5$) which indicates that adult males are not consistently associated with adult females. Loose associations between adult males and adult females could be the result of males moving between groups searching for females in estrous or female herds moving in and out of areas where males are found.

The home range of each male overlapped partially or totally with the home range of several females. For individuals sighted at multiple locations, the area used by adult males was significantly smaller than the area used by adult females. However, only four of the 58 individually identified males were sighted at five or more locations and so included in the analysis of home range size. Thus, the estimates of male space use based on these multiple resightings may reflect resident individuals

with relatively sedentary movement patterns. Males that were not repeatedly relocated (which represent a large majority of individually identified males) are likely to range more widely and may move beyond park boundaries. Fernando et al. (2008) examined home range sizes based on VHF tracking of elephants near YNP and found that male home ranges were about twice that of females, while McKay (1973)'s observations at YNP were similar to ours. McKay (1973) examined the home range of males known to reside in a specific area and found that these males were sedentary, remaining in an area less than 1 km² for several days before moving to a different locality where they repeated the same pattern. In conjunction with our results, this suggests that males may exhibit alternative mating strategies. Some males may adopt a resource defense strategy and defend a mating territory much smaller than a typical female home range, but frequently visited by females and including clumped resources. Others may actively roam in search of females in estrous (Emlen and Oring 1977, Clutton-Brock 1989). Future studies will require GPS data to obtain more precise home range estimates than possible with direct observation or VHF tracking (Leuthold 1977, Fernando and Lande 2000, Fernando et al. 2008) in combination with behavioral observations to determine whether these different ranging patterns reflect alternative mating strategies.

Males of different age classes

Juvenile males were observed in larger groups than adult males, but sub-adult males were found in groups that did not differ in size from the groups in which adult males were observed. My results corroborate observations in African elephants by Evans and Harris (2008) that male mean group size decreases with age. At MNP, both

juvenile and sub-adults males aggregated with individuals of the same age class more than expected by chance. While in most instances males of all ages were seen in the presence of other males or females, the percentage of solitary individuals increased from juvenile (0%) to sub-adult (3.2%) to adult males (70.9%). In a majority of polygynous mammals, males are the dispersing sex (Greenwood 1980) and during the period between puberty and actual reproduction behavioral and physical changes become apparent (Pereira and Altmann 1985, Pusey 1990). My results indicate that at MNP males make the transition from social to solitary living during the sub-adult age class.

The number of sub-adult males identified at MNP was similar to that of adult males and about 3 times less than the number of juvenile males (Appendix 3). This pattern, along with the small percentage of solitary sub-adult males, may indicate that sub-adult males move away from female herds or suffer higher mortality once they leave their natal group (Eisenberg and Lockhart 1972, McKay 1973, Vidya and Sukumar 2005, Lee et al. 2011). GPS tracking of sub-adult male Asian elephants will be necessary to tease apart these two hypotheses and evaluate the existence of bull areas in Asian elephants.

The social nature of sub-adult males observed at MNP could be the result of a long transition to independence. Early studies on African elephants inferred that males are forced out of their natal family as they become sexually mature (Sikes 1971, Douglas-Hamilton 1972). However, more recent studies indicate that male independence is a gradual process that can take up to 8 years and is not enforced by residents (Lee and Moss 1999). At Amboseli, male independence was not correlated

with the abundance or rarity of food. However, the number of peers available for social interactions influenced the timing of independence. Males from a small family with no peers quickly completed the transition to independence (Lee et al. 2011).

At MNP, a male's transition to independence may take longer than at other places in Asia where most sub-adult males are observed alone (Eisenberg and Lockhart 1972, McKay 1973). Indeed, MNP has a high density of sub-adult males (0.5 individual per km²) compared to other places in Asia (Eisenberg and Lockhart 1972, McKay 1973). In addition, the large gatherings that take place at this site may represent additional opportunities for sub-adult males to meet members of different social units, evaluate each other's physical strength, and develop social bonds. During these gatherings, I observed that juvenile and sub-adult males frequently engaged in play-fights with one another (personal observation). Vidya and Sukumar (2005) found that males within a location were related and suggested that related males disperse together. However, I did not find any evidence of strong associations between pairs of sub-adult males.

Associations among different age and sex classes

For any strength of association above 0.1, most dyads involved an adult female. In addition, associations between adult females and calves and between pairs of adult females were the most abundant of all associations observed. This result emphasizes the importance of adult females in Asian elephant social structure and support previous work on Asian elephant social structure that focus on associations among adult females (Fernando and Lande 2000, de Silva et al. 2011).

When examining the age and sex classes of individuals observed together at least 75% of their time, I found that more than half of the clusters had a minimum of 3 members. Most of these clusters were composed of at least two or more adult females with direct link rather than a connection through another individual. These clusters may represent families of related individuals as described in African elephants (Wittemyer et al. 2005, Moss and Lee 2011) where adult females of the same family unit spend between 70 to 100% of their time together. Genetic data that are coupled with behavioral observations would be necessary to test this hypothesis in Asian elephants. The measure of association used by Fernando and Lande (2000) was based on the number of encounters for which all members of the “family” were present. De Silva et al. (2011) examined dyadic association measures among adult females and found that despite low average associations, some individuals had strong ties ($AI > 0.3$), which is consistent with my results. Because elephants formed large aggregations at MNP, most individuals appear to be connected to each other when all associations were considered regardless of their strength (Chapter 2). Hence, filtering associations by AI strength revealed a core social structure of interconnected individuals that form a cluster.

Most clusters were composed of several closely associated dyads that included one or more calves and at least two females, which were either juveniles, sub-adults, or adults. In 11 out of 13 of these clusters there were more females than calves, which suggests that some of these females may provide cooperative offspring care. In African elephants the majority of care provided to a calf by an allomother involved either a juvenile, adolescent, or nulliparous adult female (Lee 1987). I

observed that in Asian elephants allomothers protected and cared for calves in a similar way as it has been described for African elephants, i.e. staying near calves that frequently laid down, herding them towards the mother, and protecting them from rough play fights by juvenile and sub-adult males. In African elephants, allomothers are essential to calf survival but also derive direct benefits from taking care of infants (Lee 1987). Allomothers gain experience that could increase their competence later as a mothers (Lee 1987). The lack of such experience may explain cases of infanticide by primiparous females reported in a zoo environment (Clubb et al. 2008).

Conclusion

My study indicates that associations among adult females and between adult females and other age and sex classes formed the core of Asian elephant social structure.

Most clusters of tightly associating dyads included in addition to a calf at least two or more females that may provide cooperative offspring care. Adult males were either found alone or with females while sub-adult males exhibited a gregarious behavior intermediate between that of juvenile and adult males. Studies that examine associations among and within different age and sex classes can give insight into the effect of anthropogenic changes on social and mating systems especially in long-lived species found in a variety of ecological conditions.

Table 7. Median group size distribution of different age-sex classes. In each cell, the first value is the observed count and the second is the contribution of the cell to the overall X^2 value. Group size categories are based on the four quartiles of the medial group size values. Age-sex class abbreviations: calf (CA), juvenile female (JF), sub-adult female (SF), adult female (AF), juvenile male (JM), sub-adult male (SM), and adult male (AM).

	Group size category			
Class	0-15.50	15.50-26.50	26.50-41	41-79
CA	85 0.340	71 0.395	82 0.107	72 0.092
JF	25 1.306	28 0.147	42 3.799	27 0.191
SF	38 0.373	39 0.037	38 0.309	48 1.959
AF	122 0.000	139 4.149	107 1.604	106 0.574
JM	30 1.529	25 3.376	47 2.553	44 2.233
SM	14 0.631	13 0.423	7 1.591	10 0.083
AM	25 6.793	10 1.300	13 0.218	10 1.124

Table 8. Intra age-sex class coefficient of aggregation (J). Null Js correspond to the average values of J obtained after 10,000 randomizations of age-sex classes. Positive J indicates more aggregation than expected by chance and negative J indicates less aggregation than expected by chance. Age-sex class abbreviations: calf (CA), juvenile female (JF), sub-adult female (SF), adult female (AF), juvenile male (JM), sub-adult male (SM), and adult male (AM).

	JF	SF	AF	CA	JM	SM	AM
Observed J	2.185	2.160	1.252	1.373	3.088	3.084	0.871
Null J	1.366	1.372	1.396	1.389	1.378	1.316	1.337
P value	0.027	0.008	0.204	0.954	0.000	0.016	0.300

Note: P values in bold are those greater or equal to 0.05 and significant according to the Benjamini-Hochberg procedure with a false discovery rate of 0.1.

Table 9. Relative abundance of dyads with AI values above varying AI thresholds.

Dyad types are ranked according to the percentage they represent at each of the AI thresholds. In grey are percentages higher or equal to 5%. Age-sex class abbreviations: calf (CA), juvenile female (JF), sub-adult female (SF), adult female (AF), juvenile male (JM), sub-adult male (SM), and adult male (AM).

AI threshold							
0.0 (n=2827)		0.5 (n=705)		0.7 (n=313)		0.9 (n=103)	
AF-AF	19.9	AF-CA	21.7	AF-CA	25.6	AF-CA	28.2
AF-CA	18.5	AF-AF	21.3	AF-AF	20.8	AF-AF	14.6
AF-SF	11.2	AF-SF	10.5	AF-JM	9.9	AF-JM	12.6
AF-JM	7.2	AF-JM	8.9	AF-SF	8.0	CA-CA	5.8
AF-JF	6.6	SF-CA	6.0	CA-CA	4.8	CA-JM	5.8
SF-CA	5.5	AF-JF	4.5	AF-JF	3.8	AF-SM	4.9
AF-AM	4.9	CA-CA	4.1	AF-SM	3.8	JF-CA	4.9
CA-CA	4.6	AF-AM	3.1	CA-JM	3.8	SF-CA	4.9
JF-CA	3.4	CA-JM	2.8	JF-CA	3.5	AF-JF	3.9
CA-JM	2.7	JF-CA	2.7	SF-CA	3.5	AF-SF	3.9
SF-JF	2.2	SF-JF	2.7	SF-JF	2.9	SF-JF	2.9
CA-AM	2.1	AF-SM	2.3	AF-AM	2.2	CA-SM	1.9
SF-JM	1.7	SF-JM	1.8	SF-SF	1.6	AF-AM	1.0
SF-SF	1.5	SF-SF	1.8	AM-JM	1.3	CA-AM	1.0
AF-SM	1.4	CA-AM	1.3	CA-AM	1.0	JF-JM	1.0
SF-AM	1.3	CA-SM	0.7	CA-SM	1.0	JM-JM	1.0
JF-JM	1.2	JF-JF	0.7	SF-JM	0.6	SF-JM	1.0
AM-JM	1.1	JF-JM	0.6	SM-JM	0.6	SM-JM	1.0
JF-AM	0.7	JM-JM	0.6	JF-AM	0.3		
JM-JM	0.6	AM-JM	0.4	JF-JM	0.3		
JF-JF	0.5	AM-SM	0.4	JF-SM	0.3		
CA-SM	0.3	JF-AM	0.3	JM-JM	0.3		
SM-JM	0.3	JF-SM	0.3				
AM-AM	0.3	SF-AM	0.1				
AM-SM	0.3	SF-SM	0.1				
SF-SM	0.2	SM-JM	0.1				
JF-SM	0.1						
SM-SM	0.04						

Table 10. Percentage of dyads in three ranges of AI values for different dyad types.

Age-sex class abbreviations: calf (CA), juvenile female (JF), sub-adult female (SF), adult female (AF), juvenile male (JM), sub-adult male (SM), and adult male (AM).

	AI range		
	>0 - 0.5	0.5-0.75	>0.75
AF-AF	73.31	18.86	7.83
AF-AM	85.51	12.32	2.17
AF-CA	70.75	17.59	11.66
AF-JF	82.89	10.7	6.42
AF-JM	68.97	19.21	11.82
AF-SF	76.58	17.72	5.7
AF-SM	60	20	20
AM-AM	100	0	0
AM-JM	90	3.33	6.67
AM-SM	85.71	14.29	0
CA-AM	84.21	14.04	1.75
CA-CA	77.69	13.08	9.23
CA-JM	71.43	18.18	10.39
CA-SM	37.5	37.5	25
JF-AM	89.47	5.26	5.26
JF-CA	80.21	10.42	9.38
JF-JF	73.33	26.67	0
JF-JM	88.57	8.57	2.86
JF-SM	50	50	0
JM-JM	70.59	23.53	5.88
SF-AM	91.89	8.11	0
SF-CA	72.9	19.35	7.74
SF-JF	68.85	18.03	13.11
SF-JM	72.92	22.92	4.17
SF-SF	69.77	20.93	9.3
SF-SM	80	20	0
SM-JM	75	0	25
SM-SM	100	0	0

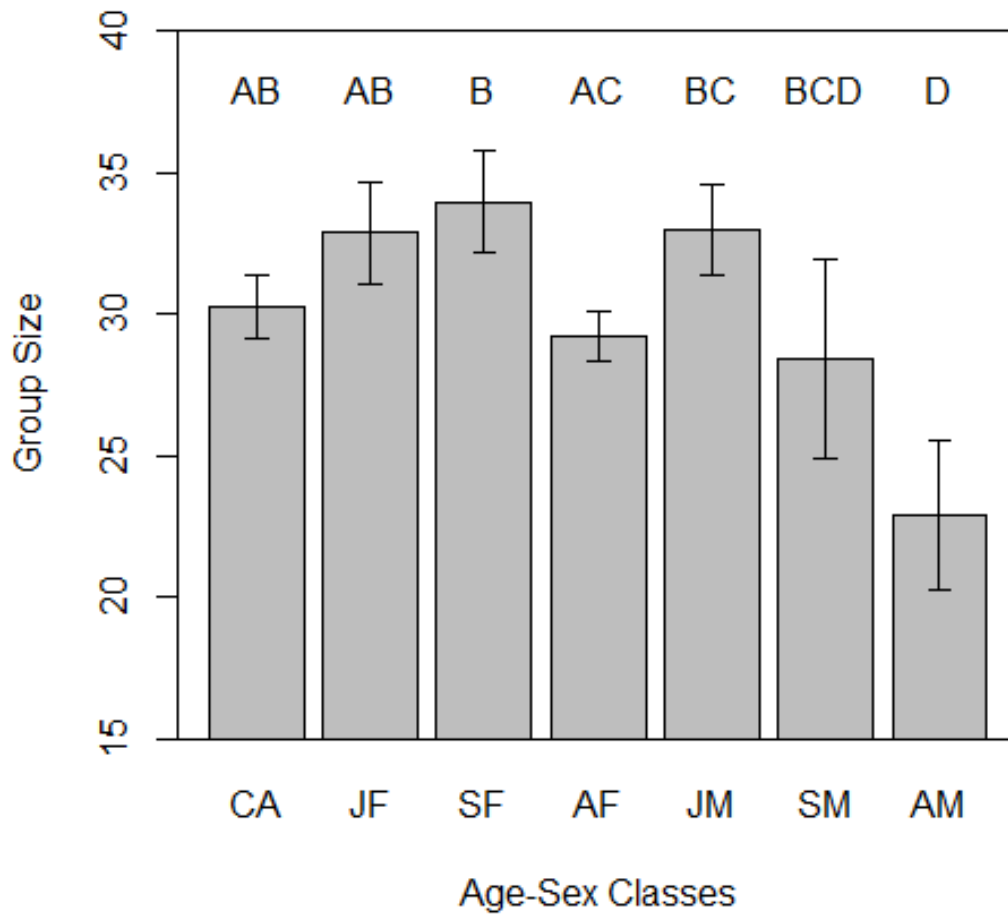


Figure 8. Average group size of different age-sex classes \pm SE. Age-sex class codes: calf (CA), juvenile female (JF), sub-adult female (SF), adult female (AF), juvenile male (JM), sub-adult male (SM), adult male (AM). Means that share the same letter are non-significantly different ($P < 0.05$) according to contrasts performed using a linear model assuming a Gaussian error distribution. Group size values for individuals observed more than once were summarized by medians to account for non-independence.

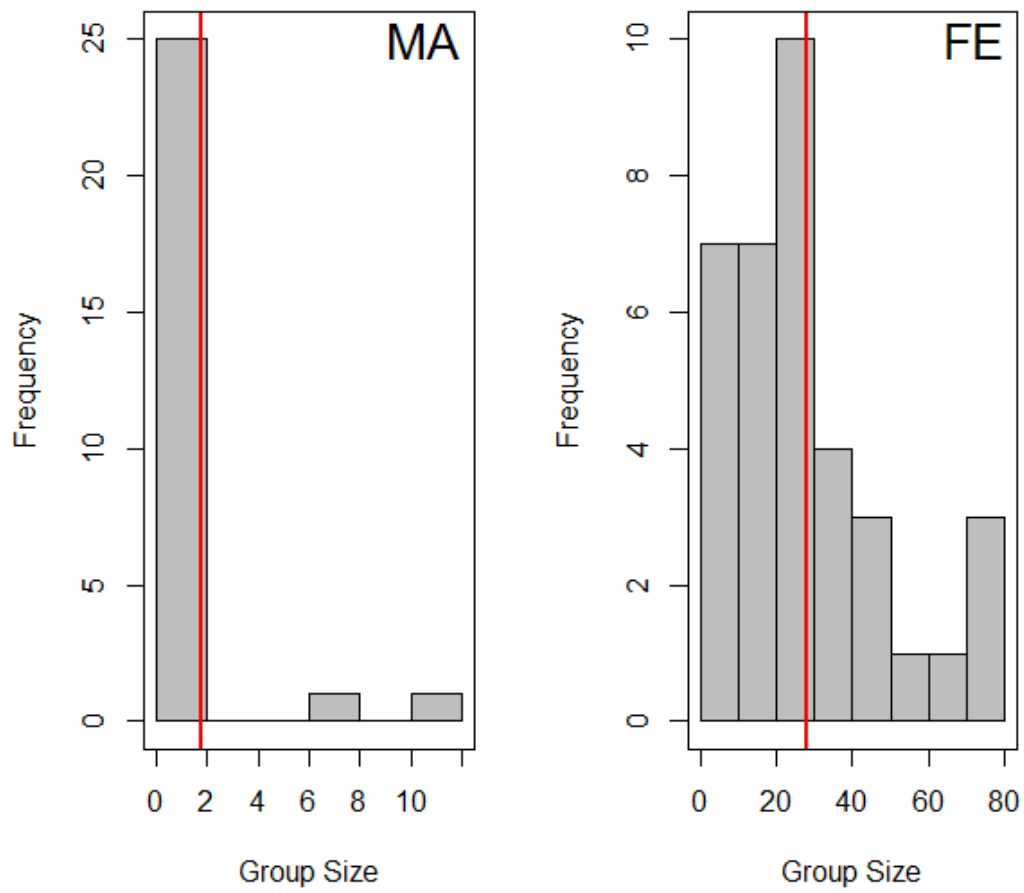


Figure 9. Distribution of group sizes for different group types. One group type (MA, $n=27$) contained adult males and no adult females and the other group type (FE, $n=26$) contained adult males and adult females. The red vertical line corresponds to the average group size observed for each of the group types.

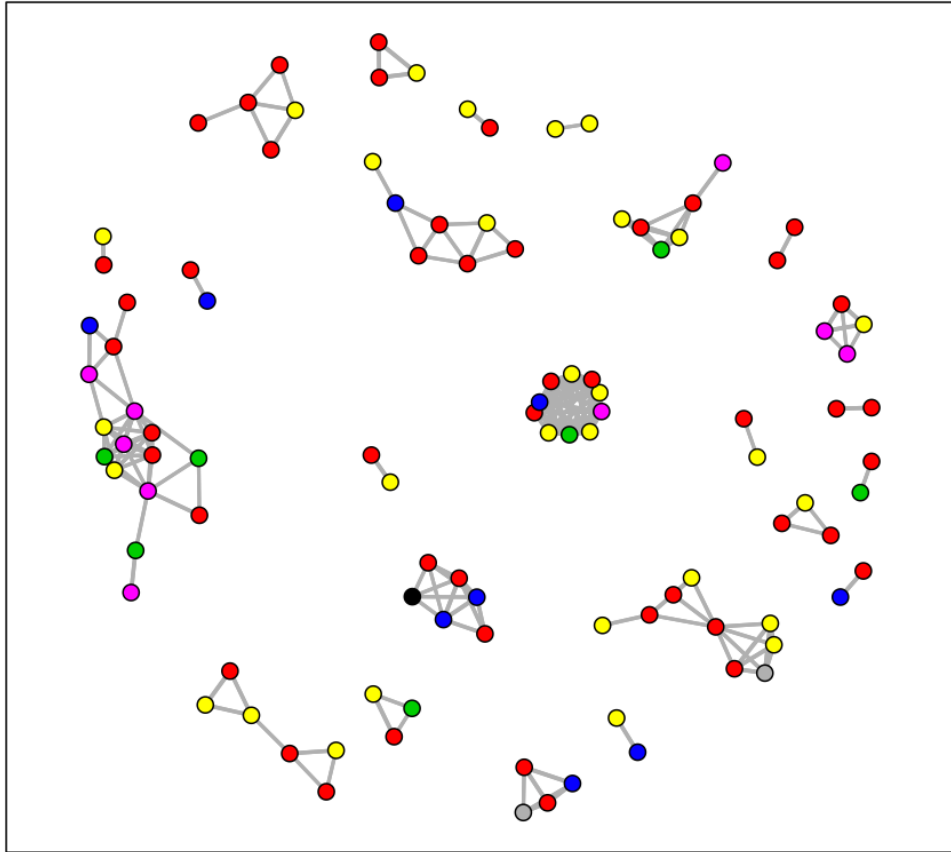


Figure 10. Network of associations for AI greater or equal to 0.75. Individuals are represented by nodes and a line between two nodes indicates an association. Node color is indicative of the age-sex class of an individual: Adult female (red), sub-adult female (pink), juvenile female (green), adult male (black), sub-adult male (grey), juvenile male (blue), and calf (yellow).

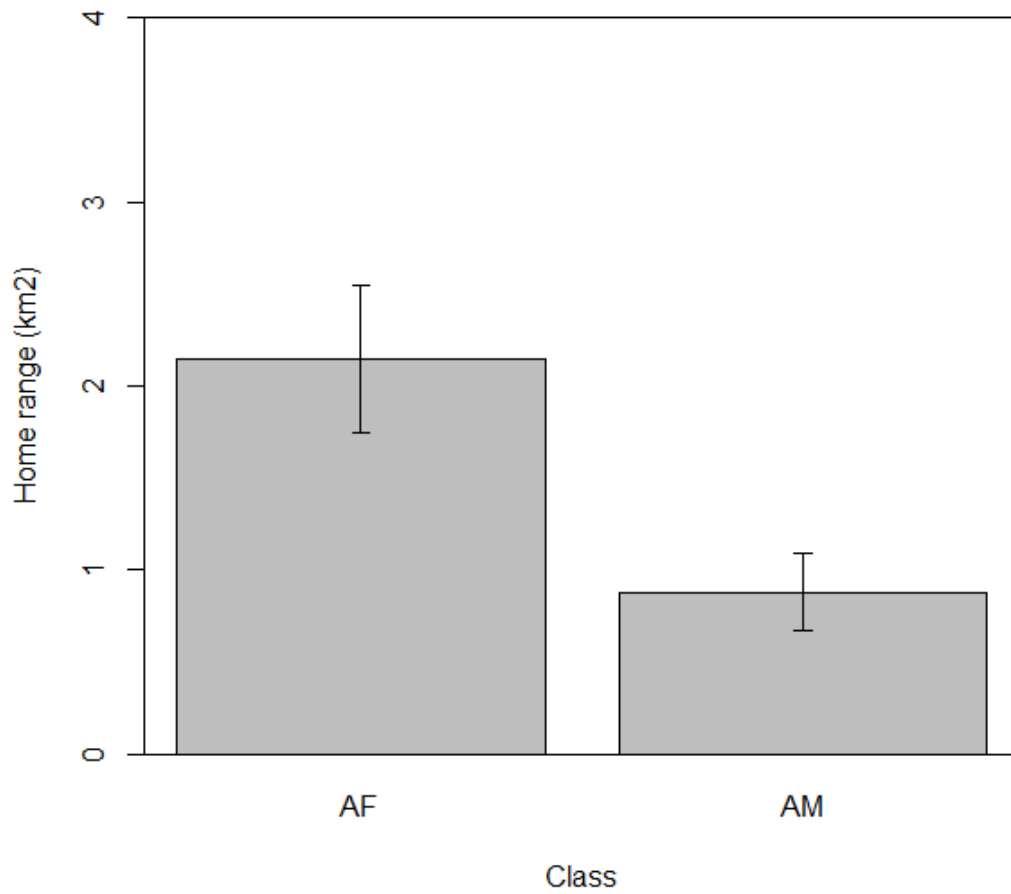


Figure 11. Average home range size of adult females (AF) and adult males (AM) +/- SE.

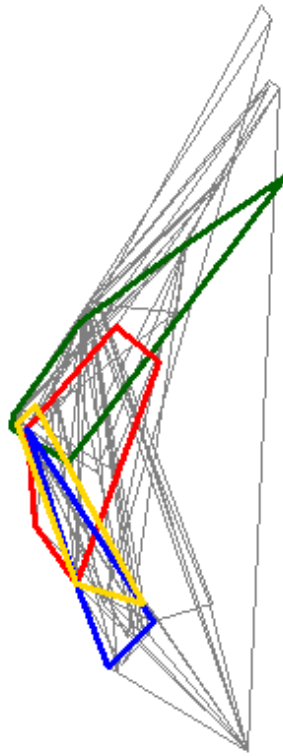


Figure 12. Minimum Convex Polygon (90%) for home range of adult females and adult males. Home range of adult females are in grey and home range of adult males are represented in ticker colored lines.

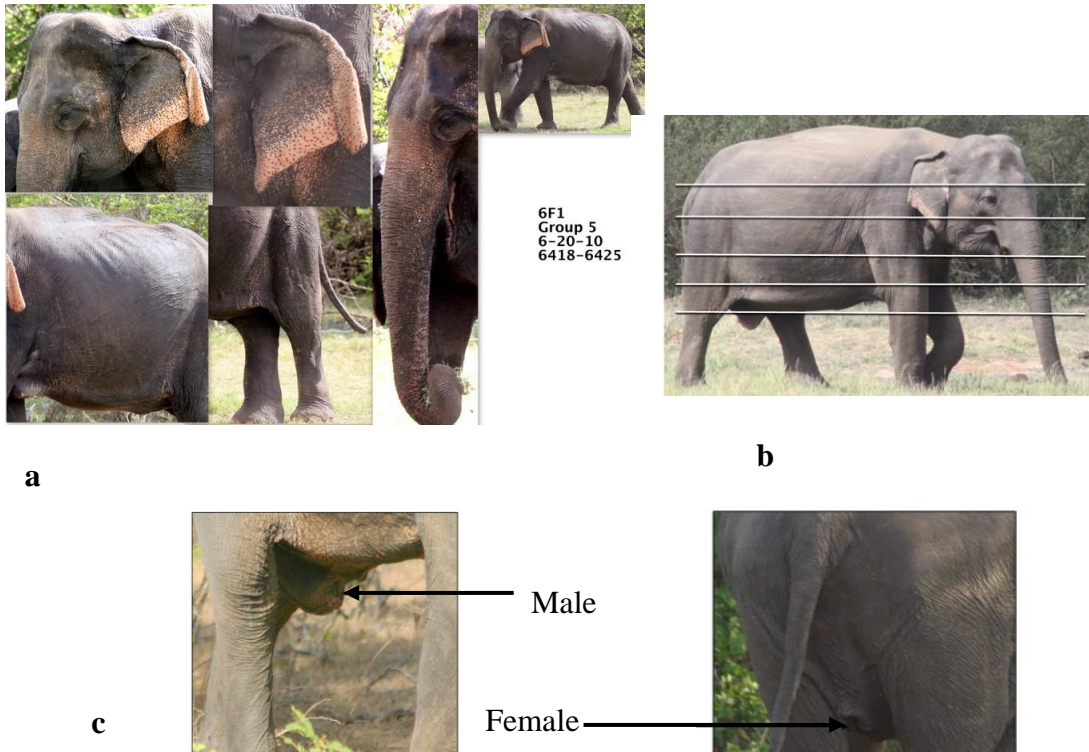
Conclusion

In order to better understand social behavior in wild Asian elephants, I conducted behavioral observations at three sites in Sri Lanka: Minneriya, Udawalawe, and Yala National Parks. I found that elephants were either solitary or in groups of up to 83 individuals. To examine how environmental variables affect grouping behavior, I quantified the effects of NDVI and distance to water on group sizes. These variables were chosen because they could be collected through remote sensing and could be used as proxies for forage and water availability. NDVI and distance to water were both significant predictors of group size and their effects varied depending on site. Because the groups I observed could have either represented transient aggregations or true social groups, I identified individuals to tease apart these hypotheses. At both sites, elephants exhibited non-random associations consistent with the presence of social groups. By examining associations between identified individuals at Yala and Minneriya National Parks and filtering out weak associations, I revealed that a core social structure was preserved across the two sites. At both Yala and Minneriya, individuals with strong ties formed small isolated social clusters of tightly associated members. At Minneriya where all age and sex classes were well represented, I showed that these strong associations were observed among adult females as well as between adult females and age-sex classes other than adult and sub-adult males. With a better understanding of the social structure of Asian elephants inhabiting different habitat conditions, we will be able to implement site-specific conservations strategies that take into account the behavioral needs of this endangered species.

Asian elephants, are social animals that are found in a diversity of environments. They offer an opportunity to examine effects of habitat conditions on the degree of fission-fusion exhibited by a species and can help us better understand the evolution of sociality and costs and benefits of group life. In addition, elephants which have a polygynous promiscuous mating system and exhibit sexual segregation provide an interesting comparison with other social species that differ in their mating systems. For instance, comparing Asian elephants to chimpanzees which also have a promiscuous mating system but no sexual segregation or to gorillas that have a harem system can help us better understand the effects of mating systems on the degrees of fission and fusion. Finally, fission–fusion has been described for many endangered species. Studies that aim at understanding how complex social systems are influenced by habitat characteristics may have crucial implications for the conservation of species in a broad range of environmental conditions.

Appendices

Appendix 1. Identification features and card.



Identification features and card. The identification card (a) was made for each elephant encountered at a unique location and gathered all characteristic features of an individual including its sex and size class.

The size class referred to the height of an individual (b) and was evaluated in reference to the size of an adult female in a group. I considered seven size classes, with 6 being an adult female and 7 and adult male. Size 1 was leveled with the ventral side of the adult female's abdomen, size 2 with the superior portion of her elbow, size

3 with the ventral side of her chin, size 4 with a line below her eye, size 5 with a line just above her eye, and size 7 corresponded to any elephant taller than size 6.

I evaluated the sex of an individual (c) by examining the orientation of the external genitalia's orifice. The preputial orifice opens frontward while the vaginal orifice opens downward. From the seven sizes and two sex classes I defined seven age-sex classes: adult female (female size class 6), sub-adult female (female size class 5), juvenile female (female size class 4), calf (male and female size class 3 or below), adult male (male size class 7), sub-adult male (male size class 6), and juvenile male (male size classes 4-5).

Appendix 2. Percentage of individuals observed at different numbers of locations at YNP and MNP.

	Number of locations where each elephant was seen								
	2	3	4	5	6	7	8	9	>10
YNP	36.8	21.0	14.0	7.0	5.3	3.5	3.5	1.7	6.9
MNP	29.1	19.9	12.6	7.9	8.6	6.6	5.9	3.3	5.9

Appendix 3. Number of observations and unique individuals in each age-sex class at MNP. Age-sex class abbreviations: calf (CA), juvenile female (JF), sub-adult female (SF), adult female (AF), juvenile male (JM), sub-adult male (SM), and adult male (AM).

	AF	SF	JF	CA	AM	SM	JM	Total
Nb of observations	1433	413	261	754	159	156	401	3577
Nb of unique individuals	474	163	122	310	58	44	146	1317

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