Summer 8-13-2010

Socioecology, Acoustic Communication and Demography of Asian Elephants in Sri Lanka

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Recommended Citation

de Silva, Shermin, "Socioecology, Acoustic Communication and Demography of Asian Elephants in Sri Lanka" (2010). *Publicly Accessible Penn Dissertations*. 213.
http://repository.upenn.edu/edissertations/213

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Abstract

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Shermin de Silva (Author)

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The first chapter defines fourteen distinct acoustic signals based on their acoustic features, and describes the contexts in which they occur. Most vocalizations are employed in contexts of movement, and some vocalizations are used primarily during movement or non-aggressive social interactions. This suggests that elephants actively seek out association with particular individuals.

The second chapter tests the hypothesis that associations among adult female Asian elephants are governed by resourced availability, and describes the temporal structure and strength of bonds. This study population demonstrates fission-fusion social dynamics in which individuals change companions over short time scales, influenced by rainfall, but maintain stable relationships over long time scales.

In the third chapter I test the hypothesis that associations are purely the consequence of the spatial distribution of resources, rather than social preference, using a modeling approach based on the spatio-temporal coordinates of individuals. In all seasons, individuals appear to move in a coordinated manner, supporting the interpretation that observed associations reflect true social preference. At the same time, resource distributions do influence the size of social units, and their movements.

In the fourth chapter I review the most recent demographic studies of elephant populations in Asia as well as Africa, and highlight the lack of data for much of Asia. I outline methods based on individual identification that may be used to address this challenge to conservation and management. I apply these methods to offer demographic estimates for the study site, and examine what constitutes good practice, in the fifth chapter.

Degree Type
Dissertation

Degree Name
Doctor of Philosophy (PhD)

Graduate Group
Biology

First Advisor
Dorothy L. Cheney

Second Advisor
Robert M. Seyfarth

Keywords
Asian elephant, Elephas maximus, vocal communication, social organization, demography, movement

Subject Categories
Behavior and Ethology | Ecology and Evolutionary Biology | Life Sciences | Population Biology

SOCIOECOLOGY, ACOUSTIC COMMUNICATION AND DEMOGRAPHY OF ASIAN ELEPHANTS IN SRI LANKA

Shermin de Silva

A DISSERTATION

In

Biology

Presented to the Faculties of the University of Pennsylvania

In

Partial Fulfillment of the Requirements for the

Degree of Doctor of Philosophy

2010

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Socioecology, acoustic communication and demography of Asian elephants in Sri Lanka

2010

Shermin de Silva

To my parents, Ananda and Dane de Silva, whose decision to pursue a new life twenty years ago has made possible all opportunities for me, and who continue to lend me their unwavering support.

ACKNOWLEDGEMENTS

I thank Dorothy Cheney and Robert Seyfarth for enthusiastically taking on a student going in a direction of research distinct from their own, having faith that I could fulfill what I had set out to do despite striking out into uncharted territory, permitting me to follow my own interests freely, and encouraging me when necessary. I will be forever indebted to them for the many doors this has opened for me.

Devaka Weerakoon, Charles Santiapillai, and M.R. Mohammed helped to set up the field site, clearing numerous obstacles that arose along the way. I am extremely grateful to the Department of Wildlife Conservation, Sri Lanka, for enabling this research, particularly the Director General Brig. W.A.D.A. Wijesooriya, Mr. S.R.B. Dissanayake, and the Research Committee.

I thank David White, Peter Petraitis and Mark Liberman for their insights on analysis, and Marc Schmidt, and Arthur Dunham for their encouragement throughout the process. Christopher Cieri, Kevin Walker, Sarah Johnstone Drucker, and Ankit Jain provided valuable technical assistance. Colleen Gasiorowski and Laurel Sweeney shepherded me safely through these years; I was so reassured to know I was in good hands. Equally, Kelly McGinnis and Greg Milewski made sure I dotted my i's and crossed my t's when navigating the tricky waters of grants. Finally, undergraduates Anne Sharpe and Ariel Stein dedicated much effort to cataloguing and counting elephants.

This work would not have been possible without the dedication of Ashoka Ranjeewa, for whom the decision to join me has been a life-altering gamble. My success is equally his, our joint investment in the future founded on an unshakable trust. In

addition we relied heavily on his brother Kapila, our dear cook Anula Jorthipala, friend and assistant Sameera Weeratunga, constant and reliable tracker Saman, the back-up vehicles willingly provided by Grizzly Safari, and the good will of the other Uda Walawe National Park personnel and wardens.

The past six years were enlivened by the people whom I will forever associate with this stage of life - Anna Nesterova for blazing trails ahead, then showing me the way; Peter Descioli, Maria Rakhovskaya, Kinjal Doshi, Grace Freed-Brown, and Ewa Szymanska for sharing many adventures and making Philadelphia feel like home; Nivedita Srinivas who has remained a true friend, our distance apart notwithstanding.

I cannot express how much I owe to my dearest aunt Nisha Suhood, who has variously sacrificed time and money to help me during the times I needed her most. She is the rock that has firmly anchored our work.

It has been my great fortune to meet and work with Sergey Kryazhimskiy. May this be the beginning of a long and beautiful collaboration. He has steered me gently in times of doubt, with encouragement that never fails to lift my spirits and aspirations.

This work was carried out in compliance with requirements of the Institutional Animal Care and Use Committee of the University of Pennsylvania. It was partially supported by an Integrative Graduate Education and Research Traineeship grant from National Science Foundation (NSF-IGERT 0504487), a grant from the U.S. Fish and Wildlife Asian Elephant Conservation Fund (grant no. 98210-7-G167), a grant from the University of Pennsylvania Department of Biology Binns-Williams Fund, and a student research grant from the Animal Behavior Society.

Lastly I thank the unnamable and unseen, which shapes all that is or will be.

ABSTRACT

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structure and strength of bonds. This study population demonstrates fission-fusion social dynamics in which individuals change companions over short time scales, influenced by rainfall, but maintain stable relationships over long time scales.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I.

Acoustic communication in the Asian elephant, *Elephas maximus maximus*

SUMMARY

Existing knowledge of acoustic communication in elephants is based primarily on African species (*Loxodonta africana* and *Loxodonta cyclotis*). There has been comparatively less study of communication in Asian elephants (*Elephas maximus*). In order to provide a basis for understanding the evolution and function of acoustic communication in proboscideans, I present a quantitative description of vocal communication in wild Asian elephants. I classify calls by acoustic features into eight 'single' calls, five 'combination' calls and one possibly unique male call for a total of at least fourteen distinct call types. Some of these vocalizations have never before been described. Certain low-frequency calls are individually distinct. Acoustic signals occur in a wide range of social contexts, with some differences in call production among age and sex classes.

INTRODUCTION

Similarities in the communication systems of distantly related taxa may be due to similarities in socioecology. Development of general frameworks to explain convergence and divergence in the evolution of communication systems first requires the ability to quantitatively compare across the signaling systems of disparate taxa. Acoustic signals are used in searching and competing for mates (e.g. crickets [Mhatre & Balakrishnan 2006]; frogs [Ryan & Rand 2003]; birds [Mountjoy & Lemon 1996]). Distinct vocalizations are used by both bats (Bohn et al. 2007; Brown et al. 1983) and penguins (Aubin et al. 2000) to locate specific individuals in crowded colonies. In these contexts, acoustic signals aid navigation and spacing of individuals.

Acoustic signals also serve social functions. Social species typically have some mutual interest in being together (e.g. for defense, hunting, holding territory, or rearing offspring) and interact repeatedly. Hence, social input shapes communication among primates (McComb & Semple 2005), cetaceans (Connor et al. 1998) and birds (Nordby et al. 2000). Vocalizations help maintain social bonds and indicate rank in baboons (Cheney et al. 1995; Kitchen et al. 2003) as well as spotted hyenas (Holekamp et al. 1999; Holekamp et al. 2007), both of which have societies with linear dominance hierarchies.

Asian elephants (*Elephas maximus*) belong to the Proboscidean clade, whose only other extant members are the African savannah elephant (*Loxodonta africana*) and the African forest elephant (*Loxodonta cyclotis* or *Loxodonta africana cyclotis*) (Shoshani & Tassy 1996). Although the species status of African forest elephants is much debated

(Debruyne 2005; Eggert et al. 2002; Johnson et al. 2007; Roca et al. 1999; Roca et al. 2007), the Asian and African elephant species are separated by at least six million years, (Rohland et al. 2007; Shoshani & Tassy 1996) and social organization may differ among them. Savannah elephant family units led by the eldest adult females (matriarchs) form bonds with other families throughout their home ranges. Wet season aggregations break up during the dry season migrations, giving rise to a fission-fusion society with hierarchical 'tiers' (Wittemyer et al., 2005; Moss & Poole, 1983; Douglas-Hamilton, 1972). This suggests that companionship is preferred by African savannah elephants, as long as resources permit it. Moreover, matriarchs serve an important function by leading their groups to scarce resources by memory (McComb et al., 2001). There is no evidence of such migration by Asian elephants (Fernando et al., 2008). Past studies of Asian elephants also indicate low rates of association among relatives (Fernando & Lande, 2000; Vidya & Sukumar, 2005). It has been suggested Asian elephants do not appear to associate beyond the family level (McKay, 1973; Fernando & Lande, 2000; Vidya & Sukumar, 2005). If Asian elephants do not have a high affinity for conspecifics, one might expect fewer or less diverse acoustic signals serving social functions.

African savannah elephants use acoustic signals for mate-search (Poole et al. 1988), male-male competition (Poole 1999), and maintenance of social bonds (Poole et al. 1988). They detect low-frequency calls over a range of several kilometers (Garstang 2004; Langbauer 2000; Langbauer et al. 1991). Such calls also mediate inter- and intra-group social encounters (Berg, 1983; Leighty et al. 2008; Leong et al. 2003a,b; McComb et al. 2000; McComb et al. 2003; O'Connell-Rodwell et al. 2006; Poole et al. 1988; Soltis et al. 2005a,b; Wood et al. 2005). Less is known about the function of vocalizations in

African forest elephants, though calls are used to census remote populations (Payne et al. 2003). A partial vocal repertoire for Asian elephants has been verbally described (McKay 1973), and some acoustic (Nair et al., 2009; Payne et al. 1986) as well as seismic (O'Connel-Rodwell et al. 2000) features of vocalizations are documented. This study provides a quantitative description of acoustic signals produced by the Sri Lankan elephant (*E. maximus maximus*), including previously undescribed vocalizations.

METHODS

Study site and subjects

Uda Walawe National Park (UWNP), Sri Lanka, is located at latitude 6° 30' 14.0646", longitude 80° 54' 28.1268", and an average altitude of 118m above sea level. It occupies 308 km^2 and contains tall grassland, dense scrub, riparian forest, secondary forest, rivers, and seasonal streams. Over 300 adult females have been individually identified in UWNP using characteristics of the ears, tail, and other natural markings (Moss 1996).

Data collection

Data were collected from May 2006 to December 2007. Observations were performed by vehicle during park hours from 0600h to 1830h. We photographed or videotaped all adult females upon encounter. A 'group' was defined as animals within visual range of the observer (up to 500m) that were either moving or resting together. Identities of known individuals were noted in addition to the number of adult females

(>10 years and has been pregnant), sub-adults (8 - 12 years), juveniles (3 - 7 years), infants (6 months – 2 years), and newborns (<6 months). These size classes were based on height relative to that of an adult female. Corresponding ages were based on personal observations of wild calves of known age as well as animals of known age reared in captivity.

Recordings of vocalizations were made using an Earthworks QTC50 microphone shock-mounted inside a Rycote Zeppelin windshield, via a Fostex FR-2 field recorder (sampling rate 48 kHz) connected to a 12V lead acid battery. Recordings were initiated at the start of a call with a 10 sec. pre-record buffer so that the entire call was captured and loss of rare vocalizations minimized. This was made possible with the 'pre-record' feature of the Fostex, which records continuously, but only saves the file with a 10-second lead once the 'record' button is depressed. In order to minimize loss of low-frequency or potentially inaudible calls, recording was continued for at least three minutes following the end of vocalization events. During the first two months, hour-long recording sessions were also carried out opportunistically while in close proximity to a group. However, spectrograms showed that few vocalizations were captured thus, so this was discontinued. Extensive vocal activity and rare occurrences were also video recorded. When possible, distance from microphone to vocalizer was noted. Distances of 20m or less were visually estimated by the observer, greater distances were measured using a laser range finder, with accuracy of +/- 1m.

Behavioural data was collected with an HP iPaq 1945 hand-held pocket computer and custom software. *Ad libitum* observations during vocal events were whispered into a dictation microphone-mask, which fed into a second audio channel. This enabled precise time-synchronization between recordings and behavioural observations, as well as clearer tagging of vocalization to callers where caller ID was unambiguously observed. Keeping human speech on a separate channel from target recordings prevented interference with audio recordings. If there were multiple callers, callers were identified if they showed obvious behavioural cues such as an open mouth, lifted tail and head, or flapping ears. If there was ambiguity between callers, the probability of an individual calling was noted. For instance, if a call could have been produced by one of two individuals, the ID probability was listed as 1/2 and if it could have been produced by one of three, it was 1/3 etc. No overlapping calls were used in further acoustical analyses. Only calls where the ID certainty was 1 were used in analysis of individual variation.

Thirty-minute focal animal samples of known animals were initiated upon positive identification (Altmann 1974). Vocalizations produced by non-focal animals were audio-recorded and noted *ad libitum*. In sequentially sampling multiple individuals, it was possible to spend several hours with a single group and thus observe rare vocalizations, long call bouts, or periods of collective vocal activity. The ethogram consisted of feeding behaviours (grazing, browsing), orientation responses, listening, smelling (trunk held in an ‘S’ or ‘J’ position or toward some object), aggression (with or without body contact), movement (general movement, passing or approaching a specific individual, leaving, brisk walk, running), social interactions (touching the trunk to face or body parts), dominance or threat displays (trunk over another individual, tossing soil or vegetation over the back during a disturbance, charging, pushes, bites), mating (mounting), nursing, playing, urinating, defecating, and vocalizations. Start and stop times were recorded for resting, water and mud activity, and defensive huddling.

Contexts of vocalizations were broadly defined using eighteen months of behavioral data from September 2006 to December 2007. Situations in which one or more individuals showed directed movement toward or away from one another, orientation or listening responses, or non-aggressive bodily touches were subsumed under 'inter- or intra-group social interaction'. The context of 'searching' was characterized by the subject exhibiting orientation, listening and trunk lifting. 'Movement' was simply physical movement. 'Fear' was characterized by the subject showing widened eyes, brisk movements away from a source of disturbance or defensive huddling. 'Excitement' was characterized by any of the following: urination and defecation, ear flapping, widened eyes, temporal secretion, brisk movement with head, ears or tail held high, spinning, head tossing. 'Aggression' involved exhibition of aggression, threat, or dominance behaviours. 'Disturbed' encompassed all other situations in which vocalizations followed external disturbance (predators, startled animals, humans), or in which the subject appeared agitated. 'Other' comprised situations that rarely involved vocalizations, such as play, nursing, or mating. These contexts are not mutually exclusive. For instance, a call might be produced while moving with or without search behaviour.

Audio data annotation

Spectrograms of calls were first annotated manually on *Praat* v4.5.16 (Boersma & Weenink 2009) and later automatically extracted according to labelled segment boundaries.

Acoustic features

Periodic and a-periodic calls

Acoustic analyses were not performed on vocalizations from males as these were rare. Only calls of exemplary acoustic quality were used, as judged by the visibility of all measured components of the call on a spectrogram and the accuracy of automated measurements. This excludes overlapping calls or those with extrinsic noise.

'Harmonicity' quantifies the periodic nature of calls, expressed in dB (Boersma 1993; Boersma & Weenink 2009). A lower harmonicity indicates less periodicity or lower signal-to-noise ratio. Because this ratio changes over the course of a single call, average and standard deviation of harmonicity over an entire call were calculated from intervals of 0.05s for all calls except squeaks, for which I used intervals of 0.005s as they were otherwise too brief.

For all other measurements, vocalizations that showed clear fundamental frequencies (periodic) were analyzed separately from those that did not (a-periodic). Calls that did not have stable periodic structures were classified by duration alone. Vocalizations by juveniles were included as some calls types were primarily produced by calves.

For periodic calls, measurements were taken with *Praat*, using the program's built-in pitch tracker which identifies the fundamental (F_0) frequency. Calls from juveniles were excluded as pitch is likely to change with age. Settings for accurate pitch extraction were calibrated separately for each call category by visually inspecting the accuracy of the pitch line generated by *Praat* on spectrograms. Once pitch detection settings giving 100% accuracy were determined, eight measurements on the fundamental frequency contour for each call were automated: duration, minimum, time at minimum, maximum, time at maximum, mean, standard deviation and absolute slope (Boersma & Weenink 2009). From these measures, I further calculated percent at maximum (elapsed time at maximum/duration), percent at minimum (elapsed time at minimum/duration), and range (max. - min.).

Combination calls

Some vocalizations showed periodic and a-periodic regions as at least two distinct segments. These segments resembled calls that also occurred by themselves. I measured each segment separately and compared these to the calls that occurred singly to determine whether they could accurately be described as 'combinations' of calls. The first segment was almost always a-periodic, hence only duration and harmonicity were measured. The second segment was distinctly periodic, hence all features were measured.

Statistical analysis

Statistical analyses were performed on Matlab v.7.0. I used the Mann-Whitney U test to compare harmonicities and durations of single call types with the corresponding segments of combination calls. I also differentiated two classes of low-frequency calls by eye first on the presence or absence of harmonics above 500Hz, and then compared their standardized F_0 features with the Mann-Whitney U test. Two-tailed T-tests were used for comparing acoustic features of calls with sufficiently large and evenly matched sample sizes. Where there were multiple calls of a certain type from the same individual, only the mean value of an acoustic feature was used for that individual in order to avoid pseudoreplication. For the most common type of vocalization, I used MANOVA to test whether calls from certain identified individuals were distinctive based on the same F_0 measures. I further examined the acoustic similarity of low-frequency calls and call segments using principal components analysis.

RESULTS

In total 3,921 calls were recorded and annotated from the period of January – December 2007. They were classified into 14 categories, out of which growls were the most commonly recorded, comprising almost two thirds. Table I - 1 summarizes the distribution of vocalization types, abbreviations used throughout the paper, and general contexts. In all tables, N_{calls} is the number of measurable vocalizations whereas N_{ind} is the number of individual vocalizers responsible. Not all calls could be used for all measurements.

Harmonicity

The medians, ranges, and sample sizes of calls with measurable harmonicity are reported in Table I - 2. Growls were the most harmonic. Harmonicities of the first component of combination calls were not significantly different from those of corresponding single calls, nor did growls differ from rumbles (two-tailed Mann-Whitney U test, $P>0.05$). Squeaks (Figures I - 1a,b), squeals (Figures I - 1c,d), trumpets (Figure I - 2d), growls (Figures I - 3a,b & I - 4a,b) and rumbles (Figures I - 3c,d & I - 4c,d) all showed higher harmonicity (>10dB) than barks (Figure I - 2a) or roars (Figure I - 2c).

Longroars (Figure I - 2b), though very noisy vocalizations, did not differ significantly in harmonicity from growls (two-tailed Mann-Whitney U test, P=0.98). Also in contrast to expectation, trumpets showed low harmonicities overall. Harmonicity captures periodicity that is not solely a feature of the sound source (fundamental frequency) but also of the filter (resonances). Longroars thus may not have a clear fundamental frequency, but do show broad resonant regions, and calls of some individuals contain partial harmonic regions (Figure I - 2b).

A-periodic calls and segments

A-periodic calls were graded by duration (Figures I - 2 & I - 8), with ‘Barks’ being shortest and ‘Longroars’ being longest. The duration of the first component of combination calls (Figures I - 6—I - 8) were not significantly different from that of single calls for bark-rumbles (two-tailed T-test, $N_{BRM}=N_{BRK}=24$, p=0.275) or roar-rumbles ($N_{RRM}=N_{ROR}=28$, p=0.437), but was significant for longroar-rumbles ($N_{LRM}=N_{LRR}=30$, $p<0.05$). ‘Chirps’ and ‘Croaks’ were <1s long elements that were more tonal than barks and were always joined to a rumble or growl-like segment. The resulting compound calls were termed ‘Chirp-rumbles’ and ‘Croak-rumbles,’ (Figure I - 7). Chirps and croaks together are included for comparison with durations of all calls in Figure I - 8.

Periodic calls and segments

Table I - 3 summarizes all pitch contour measurements on calls and call segments that showed clear F_0 frequencies. ‘Growls’ were defined by eye as calls having little or no energy above 500 Hz, as opposed to ‘rumbles,’ which contain energy up to 1kHz.

This was not due to the attenuation of higher frequencies at greater recording distances, as both types have been recorded at close range from identified individuals (Figures I - 3 & I - 4). Moreover, rumbles could be distinguished from growls based on some but not all F_0 measures (Figure I - 5). Growls were individually distinct (Figure I - 9).

The second segment of combination calls were also initially termed 'rumbles' because many showed frequencies above 500Hz and resembled rumbles to the human ear. However, principal components of fundamental frequency and duration measures distinguished these 'rumbles' of compound calls from either growls or rumbles which occurred independently (Figure I - 10, Table I - 4). The visibility (and audibility) of upper harmonics may be dependent on recording distance, however, samples with known identities and distances were too few to test this relationship.

Contexts

Rumbles and growls

Observations of calls by context are summarized in Table I - 1. Growls (after McKay 1973) were given in almost all social situations. They typically occurred in bouts or choruses by several individuals while oriented towards an object of attention. Visual cues of growls were depressed cheeks while the mouth remained almost closed while ears were usually outspread and still. Growls were not audible to us beyond 20m, especially under windy conditions. On at least four different occasions they were produced repeatedly by adult females who appeared to be grazing or moving alone. On another occasion an adult female uttered a growl as she began to walk away from a sub-adult female investigating our jeep. The adult paused with her back towards us as they briefly exchanged growls that were barely audible, after which the younger individual turned and followed. Only once was an exchange of growls observed among adult males.

Rumbles (using the term of Poole et. al 1988) occurred in contexts similar to growls. They most frequently occurred in choruses, with calls by two or more individuals creating a continuous sound. Single rumbles in such cases were difficult to isolate. Rumbles seemed louder than growls to human ears, and were accompanied by more obvious visual cues such as slightly lifted head, rapidly flapping ears, and open mouth. They were audible at distances of at least 500m even with wind. No calls resembling rumbles or growls were recorded from infants under 2 years of age. Adult female vocalizers were typically approached by others. In one instance, an adult female gave a series of rumbles and was approached by a second adult female from 100m away. This female gave a trunk-bounce, touched her several times, and then left again, but was not followed by the initial caller. Rumbles or growls by juveniles or sub-adults did not elicit approach from adults, though they did sometimes elicit approach and exploratory behaviour from young. On two occasions growls and rumbles were observed to maintain distance between un-affiliated social groups. Individuals also sometimes moved towards growls and rumbles whose source was obscured by vegetation.

Barks, roars and longroars

Barks were short, a-periodic calls that did not repeat. They were seemingly spontaneous vocalizations that accompanied group movement preceded by loud rumbling, or aggression accompanied by a swift lunge with physical contact such as pushing or biting. They were usually directed at other elephants, especially calves. Calves could target other animals such as birds, apparently in play.

Roars were given primarily during movement, but also during disturbance and distress. Longroars are longer vocalizations that occurred largely during separation, movement, searching and distress. Infrequently (6 - 7% of occurrences), this included calves who either sought out their mothers in order to nurse, or were interrupted while nursing. However, the caller was not necessarily isolated. On one occasion the caller (a sub-adult female) was surrounded by a herd of familiar individuals but persisted in calling until joined by an adult female who had been absent. Longroars accompanied behaviour indicating high arousal, such as lifted head, extended tail and brisk movement. Both roars and long roars could occur in bouts by a single individual, or as choruses by several individuals. Bouts of longroars by a single caller could at times last an hour or more. Calling could also occur from multiple locations separated by a kilometer or more, out of view of observers. Roars and longroars were audible to us from such distances even under windy conditions.

Combination calls

Croak-rumbles occurred only in bouts that contained rumbles, typically in choruses where at least two or more individuals called in rapid succession. Chirp-rumbles were observed only on three occasions, and occurred in bouts of 3 or more calls by adult females who were among companions. On two of these occasions the caller was then approached by a juvenile or infant calf but on the third occasion vegetation obscured our view of any small calves.

‘Bark-rumbles,’ ‘roar-rumbles’ and ‘longroar-rumbles’ primarily occurred during movement and searching. All three calls may be functionally similar graded vocalizations though a small number of bark-rumbles (2.3%) and roar-rumbles (6.3%) also were produced by calves wanting to nurse.

Squeaks, squeals, trumpets, trunk bounces, and blows

Over 90% of squeaks (termed ‘chirps’ by McKay et al. 1973 and Nair et al. 2009) occurred in bouts of three or more in rapid succession (<1s apart) in response to disturbance, and were usually accompanied by blows (loud, rapid exhalations), trunk-bounces, where the trunk is curled beneath the chin then rapidly extended so that the leading edge hits the ground loudly (Figure I - 7c, termed ‘boom’ by McKay 1973), accompanied by behavior indicating fear or excitement. One recording session contained single calls separated by 30s - 60s or more, however the caller and context were unidentified. Other vocal activity at such times included squeals. They were sometimes produced by groups of females and sub-adults when approached by a male in musth, but were more often directed at humans.

Trumpets always occurred in response to disturbance, and sometimes were accompanied by squeaks. They could be accompanied other threats (e.g. throwing objects, charging).

Courtship and musth chirp-rumble

In 2007, 2008, and 2009 calls were observed from three separate males in musth that appeared distinct from all other vocalizations (Figure I - 11). We have not observed such vocalizations from female Asian elephants, although it is possible they produce them. We have also not observed calls corresponding specifically to mating or estrous, while such calls have been documented in African elephants (Poole et al. 1988, Langbauer 2000). Moreover, even though musth males were observed several times per month, this vocalization was rarely observed. The first component was a brief (0.25s), softly audible segment at approximately 250Hz, followed by a longer low frequency segment (0.75s) at approximately 60Hz. In some cases the second segment was absent altogether. Calls separated by 11 - 25s occurred in bouts which could last several hours continuously. It is possible that the first segment is the consequence of inhalation rather than exhalation. On two out of the three occasions the calling male was engaged in a protracted contest with another male who was also in musth. On the third occasion the male was calling while courting and guarding a female in oestrus.

Successful matings rarely occurred within clear view of observers, and were not accompanied by many vocalizations. On occasions when such behaviour was accompanied by sound, the caller could not be confirmed but we suspected the female who was mounted. Only single vocalizations such as a trumpet or roar were heard.

DISCUSSION

The Asian elephant acoustic repertoire consists of at least fourteen different types of vocalizations in addition to one non-vocal acoustic signal (the trunk-bounce) which seem to serve predominantly social and spatial functions. Of these vocalizations, nine have been previously described by McKay 1973 and Nair et al. 2009. ‘Trumpets’ are characteristic proboscidean vocalizations that are similar for both Asian and African species, but are confusingly also described as ‘a long high-amplitude squeak’ by McKay 1973. ‘Growl’ is the same vocalization described by McKay 1973. It is possible that they are acoustically similar to some subset of the vocalizations produced by African elephants which are uniformly termed ‘rumbles’ (Berg 1983, Langbauer 2000, Soltis et. al 2005b). ‘Rumble’ is comparable to low-frequency vocalizations of African elephants (Berg 1983, Nair et al. 2009), possibly described by McKay 1973 as ‘motorcycle’. ‘Squeak’ was previously termed ‘chirp’ by the same authors, but McKay 1973 and Langbuer 2000 describe it also as ‘multiple short squeaks’. I prefer ‘squeak’ to refer to the single call, which is intuitive and simple. Multiple squeaks in succession merely constitute a bout, as with any other vocalization. ‘Squeals’ have do not appear to have been described. Both squeaks and squeals appear unique to Asian elephants (see also Nair et al. 2009). ‘Roars’ have previously been seen as a single category (McKay 1973). While I split them into two categories based on duration, they may differ little functionally. ‘Barks,’ which I define by their short duration, have never been described before, though McKay 1973 mentions the ambiguous ‘snort’. None of the ‘combination’ calls have been recognized as such previously, though ‘bark-rumble’ may be comparable to the ‘Rev-followed-by-rumble’ of *Loxodonta* reported from captive study (Leong et. al 2003b) and roar-rumbles and longroar-rumbles may be acoustically similar to calls produced by *Loxodonta* calves when nursing, which adults are not reported to produce (personal observation). It is not clear whether *Loxodonta* produce ‘longroars’. ‘Musth chirp-rumbles’ have neither been documented in the wild, nor, to my knowledge, have they been reported in captivity for *Elephas*. They appear acoustically different from the 'musth-rumble' of *L. Africana* (Poole et al. 1988), and may be similar to contest vocalizations given in species such as chacma baboons (Kitchen et al. 2003).

It is unclear whether harmonics in trumpets are caused by source or filter effects. Double-voicing, where two sets of closely-spaced harmonic bands appear within a single vocalization, is evident in trumpets (Figure I - 2d). Birds such as king penguins use this feature, which originates in the uniquely avian syrinx, to identify each other (Aubin et al. 2000; Lengagne et al. 2001). It is not clear what the physiological cause of this could be for elephants, aside from perhaps the dual nasal passages of the trunk, or whether it serves any function.

Growls are individually-distinct, and therefore may be used for locating one another or maintaining spacing among members of different social groups. It is likely that other calls are also individually-distinct, though I could not test this. As sample sizes for some individuals in this study were small, it may be worth repeating analyses with additional data and call types. Figure I - 10 seems to suggest that growls fall into two groups along the second principal component. This may be because the second principal component is determined by the location of the minima and maxima of calls, and those with little change in the fundamental frequency can by chance have minima at either the beginning or end and thus appear different along these measures. Rumbles of African elephants have been shown to vary contextually (Leighty et al. 2008, Wood et. al 2005). Growls as well as rumbles may in fact be differentiable further using other acoustic and behavioural measures, however large sample sizes are needed.

Rumbles and growls comprise the bulk of vocalizations observed. Although the use of low-frequency communication by African elephants to coordinate movement over long distances has been much discussed (Garstang 2004; Langbauer et. al 1991; McComb et al. 2003; Payne et al. 1986), the function of similar calls by Asian elephants has not been explored. Rumbles and growls may permit coordinated activities in dense vegetation, however combination calls and longroars also occur with search behaviours. The significance of call types that appear functionally redundant deserves exploration. It is possible that growls are simply softer, less powerful, calls which carry less than 100m whereas rumbles enable coordinated activity over greater distance and longroars or combination calls are used to make contact still further away, as first proposed by McKay 1973. This proposition was made prior to the discovery of infrasonic communication. It is also possible that these calls reflect different levels of excitement. These hypotheses remain to be tested. Though we did not assess the power level of these calls directly, future study of their transmission properties or playback experiments would provide a better understanding of the spatial extent of these calls, and their interplay with social dynamics.

Combination calls are composed of distinct segments. Segments appear acoustically similar to calls that occur singly. The leading segments of all combination calls grade by duration. Differences in durations of the first segment of ‘longroar-rumbles’ and ‘longroars’ likely arise because they reach a physiological limit, lung capacity, hence the first segment of longroar-rumbles are not the same length as longroars. The second segments of combination calls overlap in acoustic space with rumbles more than with growls. Principal component loadings suggest that acoustic differences between these segments are largely due to the fact that these segments show falling F_0 contours as a result of being connected to a segment with higher frequencies at onset, whereas rumbles and growls show level F_0 contours. I maintain the term 'rumble' to describe the second segment of combination calls for parsimony.

There are suggestions of age and sex differences in call production. Repertoires may reflect the divergent life histories of males and females (see also Nair et al. 2009). Younger individuals only appear to produce a subset of the calls produced by adults and adults rarely produce certain vocalizations. It is not clear whether this is due to developmental reasons, or because certain contexts are more relevant to certain age and sex classes. Aults may not panic when separated from companions, and thus rarely produce longroars. Sub-adults and juveniles, as they wean and become independent, may simply be more likely to get lost then produce these calls. Adult males may not produce calls functioning in social cohesion if they do not maintain such relationships.

Vocalizations produced by infants may sometimes be superficially different to those of adults (e.g. higher frequency) simply due to differences in vocal physiology rather due to later modification through learning. However, some species do show changes in their vocal repertoires with age (Elowson et al. 1998; Tchernichovski et al. 2001). In certain non-human primates, calls may be acoustically well-formed from infancy but the appropriate contexts for production have to be learned through experience (Seyfarth & Cheney 1986). While only passerines, cetaceans and humans are commonly acknowledged to be capable of vocal imitation in addition to contextual learning (Janik & Slater 1997; Pepperberg 2006; Watwood et al. 2004), African elephants in captivity may learn atypical vocalizations (Poole et al. 2005). It is an open question whether Asian elephants demonstrate vocal learning or convergence among individuals. Indeed, frequency matching seems common when individuals chorus (personal observation).

Out of the 258 measurable calls described by Nair et al. 2009, close to 30% are trumpets, 22% are roars, 26% are ‘chirps’ (squeaks), and 22% are rumbles. This call type distribution is quite different from those reported here, and it is not clear whether other call types were observed at all and whether this distribution is representative of all observed vocalizations or merely those suitable for acoustic analysis. Three out of four of these call types occur primarily during disturbance whereas the fourth can also occur during disturbance, which is reinforced by the contextual descriptions by Nair et al. If such differences are not due to our methods of study or call classification, it suggests the Uda Walawe elephants are less disturbed, possibly due to differences in levels of habituation of the two study populations. On the other hand, as Asian elephants have evolved into populations that have been isolated from one another by the sea as well as human activities, acoustic signals could have differentiated sufficiently enough to constitute dialects. Further study of different populations of Asian elephants is likely to broaden and inform the description set forth here for comparison with African elephants and other species.

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Table I - 1. Summary of calls and contexts. N_{tot} is the total number of recordings of each type whereas N_{ctx} is the number of calls assessed for context. Only one call type per age class was counted during any single event in determining contexts. However, contexts are not mutually exclusive hence percentages do not sum to 100. The most common contexts for particular call types are in bold face. ‘Str’ is the temporal structure of calls, where (S) means that over 90% of the time, call occurs singly, only once within 5sec; (R) means that over half the time calls are repetitious and may occur in a bout (where the interval between calls is shorter than the duration of a single call), and also that multiple bouts may occur successively (where the interval between bouts is greater than the interval between calls within a bout); (C) means that multiple individuals may call simultaneously, hence chorusing. Contexts: 1) Vocalizer exhibits aggression with physical contact. 2) Vocalizer exhibits aggression without contact (threats). 3) Vocalizer receives aggression with or without physical contact. 4) Fear. 5) Excitement. 6) Disturbance. 7) Non-aggressive social. 8) Movement. 9) Searching. 10) Being dominated or coerced by another. 11) Musth. 12) Other: Nursing, play, mating. 13) Unknown. Age and sex classes are adult female, adult male, sub-adult female, sub-adult male, sub-adult of undetermined sex, juvenile, and infant.

Call	Ab.	N_{tot}	% of Tot	Str	N_{ctx}	Context (% calls)													Age and sex class (% vocalizers)						
						1	2	3	4	5	6	7	8	9	10	11	12	13	AF	AM	SF	SM	SB	JV	IN
Growl	GRW	2580	65.8	S, R, C	187	-	11.8	-	5.9	7.5	26.7	**53.2**	**38.8**	8.6	-	-	1.3	-	79.1	1.1	8.0	2.1	3.7	5.3	<1
Squeak	SQK	343	8.75	R	67	1.5	20.9	-	14.9	**31.3**	**29.9**	17.9	10.4	3.0	-	-	6.0	1.5	32.8	-	19.4	19.4	7.5	17.9	3.0
Longroar -rumble	LRM	225	5.74	R, C	31	3.2	-	-	9.7	-	19.4	9.7	**54.8**	9.7	9.7	-	-	9.7	41.9	3.2	-	3.2	9.7	38.7	3.2
Longroar	LRR	158	4.03	S, R, C	45	-	-	2.2	-	11.1	35.6	-	**46.7**	**42.2**	2.2	-	6.7	6.7	11.1	-	20.0	-	-	68.9	-
Rumble	RUM	151	3.85	S, R, C	103	-	6.8	-	3.9	5.8	**34.0**	**40.8**	**35.9**	8.7	-	-	2.9	<1	72.8	1.9	11.7	-	2.9	9.7	<1
Bark-rumble	BRM	133	3.39	R, C	43	-	2.3	-	11.6	-	18.6	11.6	**74.4**	30.2	-	-	2.3	2.3	53.5	2.3	7.0	-	4.7	32.6	-
Trumpet	TMP	129	3.29	S	74	1.4	**48.6**	-	21.6	10.8	10.8	7.4	8.1	6.8	-	-	4.1	5.4	33.8	4.1	21.6	5.4	4.1	23.0	8.1
Roar-rumble	RRM	68	1.73	R, C	16	-	-	-	-	-	18.8	18.8	37.5	12.5	-	-	6.3	18.8	43.8	6.3	18.8	-	3.1	28.1	-
Roar	ROR	45	1.5	S	66	-	4.5	1.5	6.1	7.6	25.0	-	**40.9**	16.7	1.5	-	8.3	1.5	28.8	4.5	10.6	9.1	-	40.9	6.1
Bark	BRK	39	0.99	S	15	**33.3**	13.3	-	-	-	20.0	-	13.3	-	-	-	6.7	20.0	40.0	20.0	6.7	-	6.7	26.7	-
Squeal	SQL	33	0.84	S, R	6	-	-	-	66.7	33.3	-	-	-	-	-	-	-	-	66.7	-	33.3	-	-	-	-
Croak-rumble	CRM1	15	0.42	R, C	11	-	27.3	-	18.2	27.3	-	63.6	36.4	9.1	-	-	-	-	56.4	-	18.2	1.8	-	-	-
Chirp-rumble	CRM2	2	<0.4	R	3	-	-	-	-	-	-	66.7	-	-	-	-	-	33.3	100	-	-	-	-	-	-
Musth chirp-rumble	MCR	3	<0.4	R	4	-	-	-	-	-	-	-	-	-	-	100	-	-	-	100	-	-	-	-	-

Table I - 2. Harmonicities of calls and call segments. Compound calls such as BRM are broken into segments such as BRM1 and BRM2.

Call	N_{calls}	N_{ind}	Median of Avg	Interquartile range of Avg	Min_{avg}	Max_{avg}	Median of stDev	Interquartile range of stDev	Min_{stdv}	Max_{stDev}
SQK	108	15	13.67	13.06	4.33	30.55	13.06	5.46	4.33	30.55
SQL	20	7	12.18	6.67	7.33	17.76	5.30	6.14	2.61	16.73
TMP	26	13	8.92	5.46	5.52	19.14	7.57	5.46	1.98	19.14
RUM	22	11	11.40	5.15	9.26	16.13	5.15	5.46	3.66	16.01
GRW	33	11	11.89	6.03	8.61	24.30	6.03	5.46	3.10	24.30
BRM1	12	7	5.18	5.18	3.78	12.17	5.18	6.01	2.93	7.29
BRM2	8	5	8.49	8.49	5.16	24.24	8.49	2.50	4.33	24.24
BRK	5	5	8.93	8.93	2.91	11.60	8.93	3.86	2.91	11.60
LRM1	9	7	8.38	7.58	2.06	15.15	7.58	3.86	2.06	15.15
LRM2	8	6	6.18	3.67	1.78	12.57	3.67	3.02	2.42	12.57
LRR	33	22	11.85	7.62	1.95	29.04	7.62	3.02	1.95	29.04
ROR	14	13	12.48	12.48	-1.92	20.85	12.48	3.10	-1.92	20.85
RRM1	3	3	-0.38	-0.38	-0.80	10.21	4.15	3.26	-0.80	10.21
RRM2	3	3	9.29	9.29	8.68	16.43	9.29	3.26	8.68	16.43

Table I - 3. F_0 features of calls showing harmonic structure. All are expressed as estimated mean ± SE. 'stDev' is the standard deviation of frequency points along the F_0 contour within calls, not the standard deviation from the mean F_0 among multiple calls.

Call	N_{calls}	N_{ind}	Duration	Min	Max	Mean	stDev	Abs Slope	Percent Min	Percent Max	Range (Max-Min)
SQK	107	15	0.24 ±0.01	1079.39 ±40.85	1208.84 ±48.36	1133.42 ±43.04	41.17 ±5.51	742.51 ±76.26	44.66 ±2.99	54.97 ±3.91	129.45 ±17.48
SQL	15	7	1.08 ±0.09	646.85 ±56.03	1041.80 ±79.59	906.33 ±70.24	103.24 ±15.20	680.42 ±153.35	79.12 ±7.51	29.86 ±5.40	394.95 ±56.65
TMP	19	14	1.08 ±0.14	491.95 ±25.76	580.37 ±29.79	542.16 ±26.78	24.37 ±3.56	141.00 ±17.28	67.26 ±8.52	40.68 ±5.73	88.42 ±16.43
GRW	39	14	7.48 ±0.33	16.64 ±0.48	21.59 ±0.61	19.90 ±0.48	1.37 ±0.14	1.32 ±0.13	62.17 ±7.05	46.49 ±4.11	4.95 ±0.46
RUM	18	10	7.38 ±0.77	20.22 ±0.73	26.59 ±0.95	24.27 ±0.83	1.75 ±0.19	2.13 ±0.29	79.44 ±7.41	48.46 ±4.22	6.48 ±0.78
BRM2	8	5	4.59 ±0.72	25.25 ±4.01	43.63 ±7.87	35.00 ±5.62	5.63 ±1.59	6.83 ±3.64	93.47 ±4.87	13.03 ±12.44	18.38 ±4.39
RRM2	4	3	2.60 ±0.31	34.63 ±3.69	50.63 ±3.13	41.88 ±3.69	4.06 ±0.44	6.77 ±3.08	93.94 ±3.36	4.07 ±1.64	16.00 ±1.08
LRM2	10	7	2.74 ±0.29	27.48 ±2.60	44.97 ±3.53	36.59 ±2.51	4.89 ±0.84	7.75 ±1.48	95.00 ±1.41	0.91 ±0.58	17.49 ±3.37

Table I - 4. Loadings for first two principal components for Growls, Rumbles, and the second segment of Bark-rumbles, Roar-rumbles and Longroar-rumbles. Only the first two principal components had eigenvalues >1.

	PC 1	**PC 2**
Duration	-0.29577	-0.37372
Min	0.35849	0.18488
Max	0.43359	0.056302
Mean	0.427	0.088993
stDev	0.38734	-0.0394
Abs Slope	0.3892	0.10737
Percent Min	0.16356	-0.74984
Percent Max	-0.29227	0.48962
Eigenvalue	5.10	1.27
Percent of variation captured	63.72	15.87

Figure I - 1. High frequency calls. a. Bout of squeaks (SQK) from same individual shows varied contours; **b.** Squeak (iii) exemplifies the most typical u-shaped frequency contour; **c- d.** Two squeals (SQL) from one individual during the same recording session.

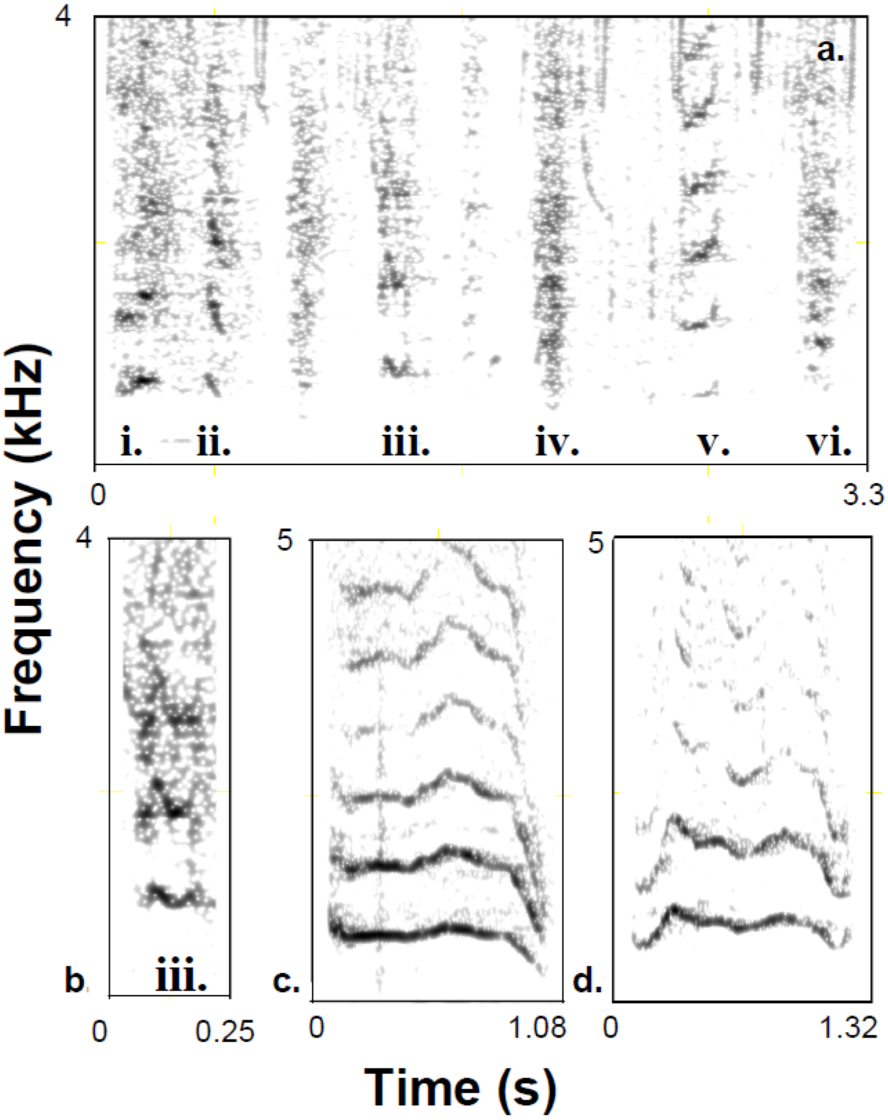


Figure I - 2. Calls with a-periodicities. **a.** Bark (BRK); **b.** Long roar (LRR) showing growl-like onset, chaotic region, and high-frequency harmonics; **c.** Roar (ROR); **d.** Trumpet with double-voicing.

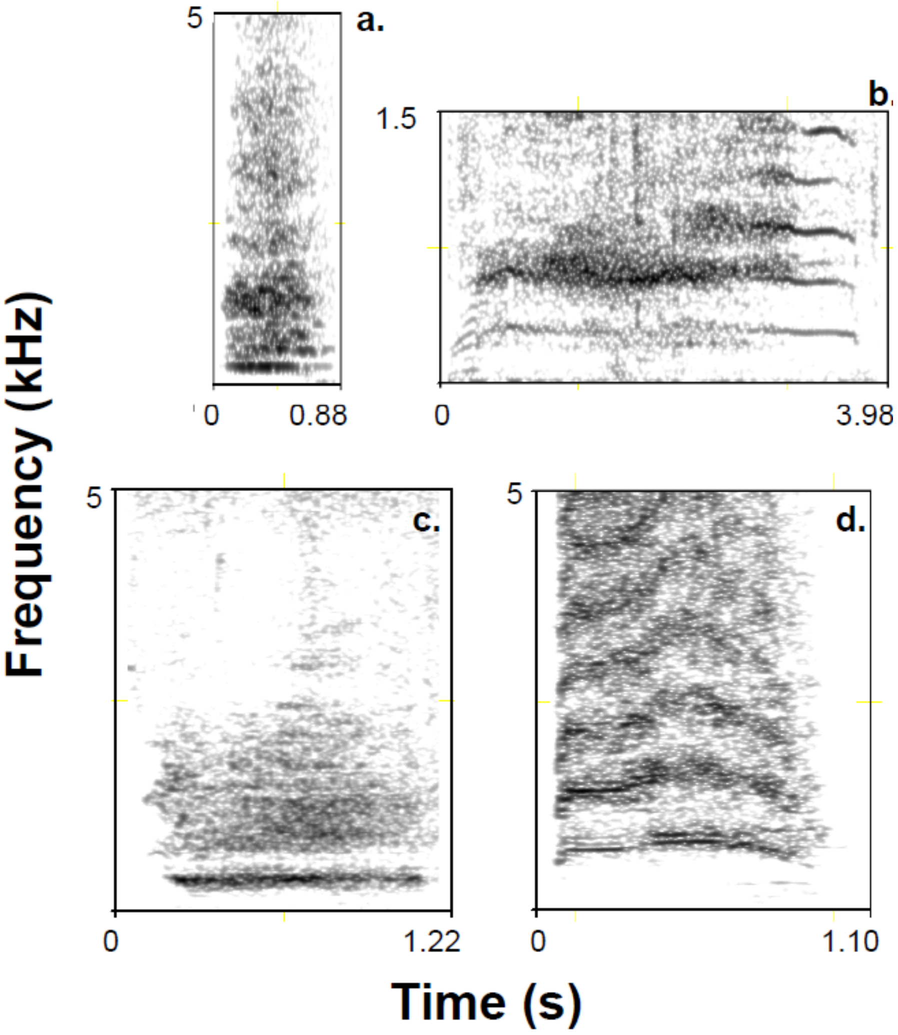


Figure I - 3. Growls vs. Rumbles by individual [440]. a-b. Single growl (GRW) by adult female [440] at 500 and 1000 Hz, recording at 3m; **c-d.** Rumble (RUM) by the same individual, same recording session, at 500 and 1000 Hz, recording at 10-15m.

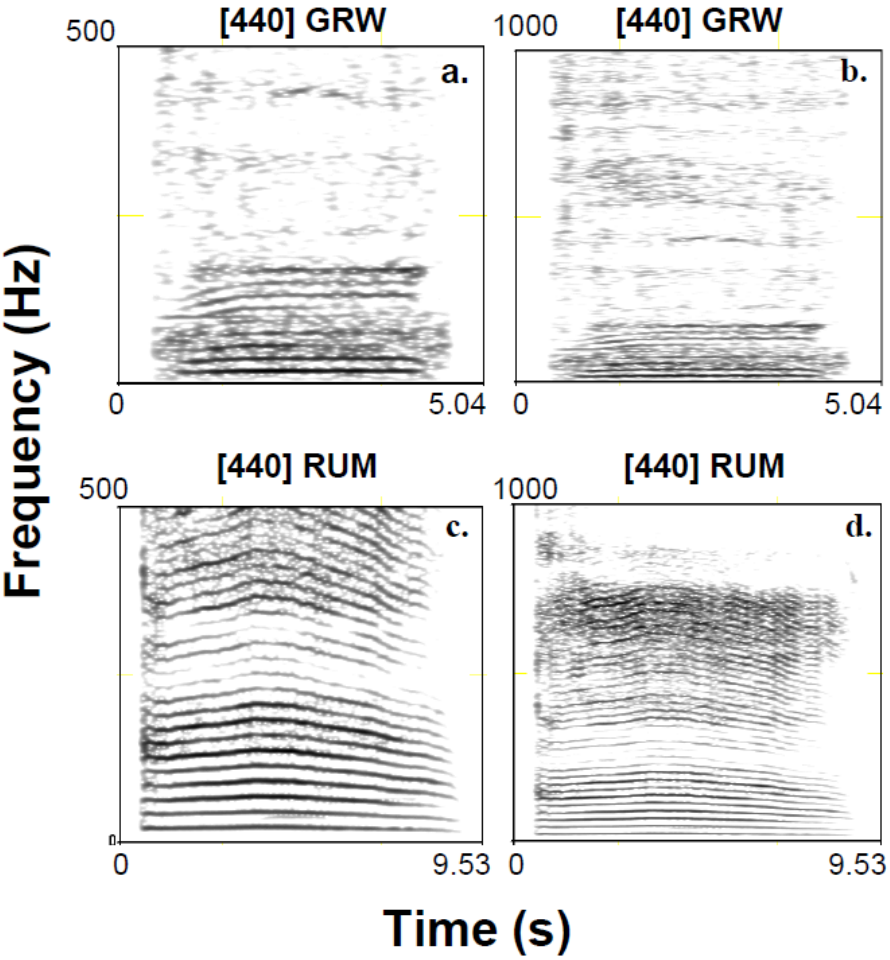


Figure I - 4. Growls vs. Rumbles by individual [208]. a-b. Single growl by adult female [208] at 500 and 1000 Hz, recorded at10m, slight overlapping call from another individual; **c-d.** Rumble by the same individual, same recording session, at 500 and 1000 Hz, recording at 10m.

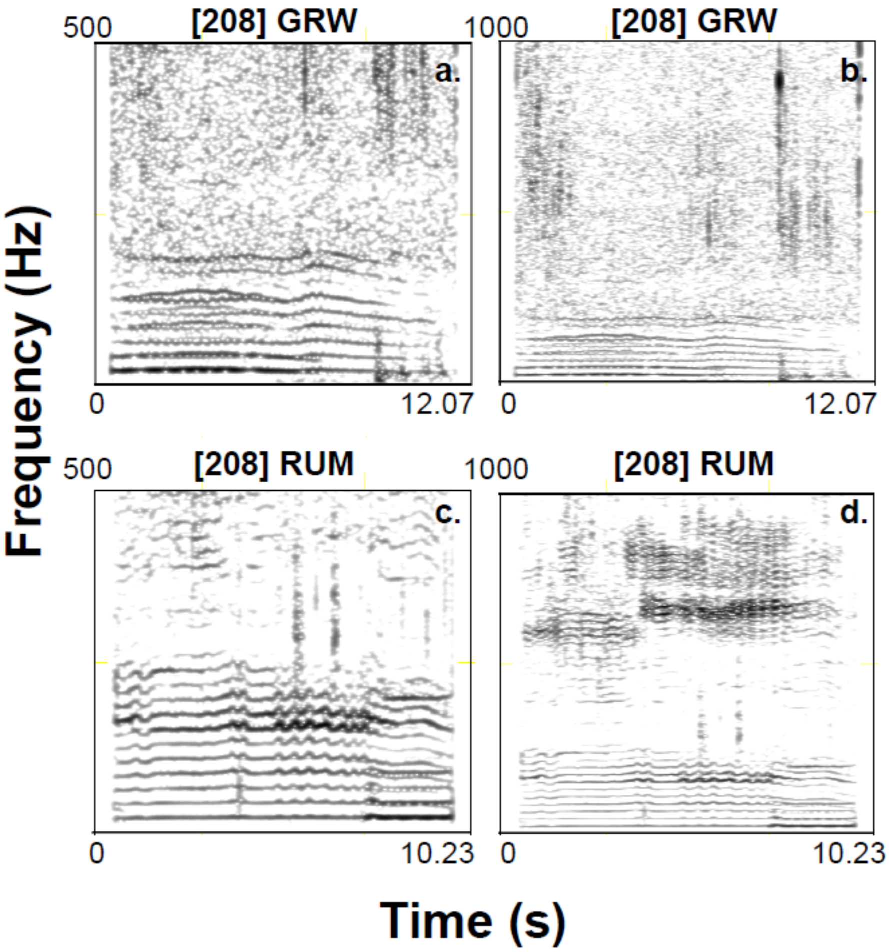


Figure I - 5. Growls and Rumbles are distinguishable by F_0 features. N_{RUM}=21 calls, 10 individuals, N_{GRW}=39 calls, 14 individuals. Plot shows standardized F_0 measure averages ± standard error for each. The two call types differed most in their minima, maxima, means and absolute slope (two-tailed Mann-Whitney: U_{Min}=25, P_{Min}=0.009, U_{Max}=37, P_{Max}=0.057, U_{Mean}=33.5, P_{Mean}=0.035, $U_{AbSlope}$=33.5, $P_{AbSlope}$=0.046). Growls are lower frequency vocalizations than rumbles, with a tendency towards longer duration. Rumbles show more absolute changes in frequency from start to finish (rise and fall).

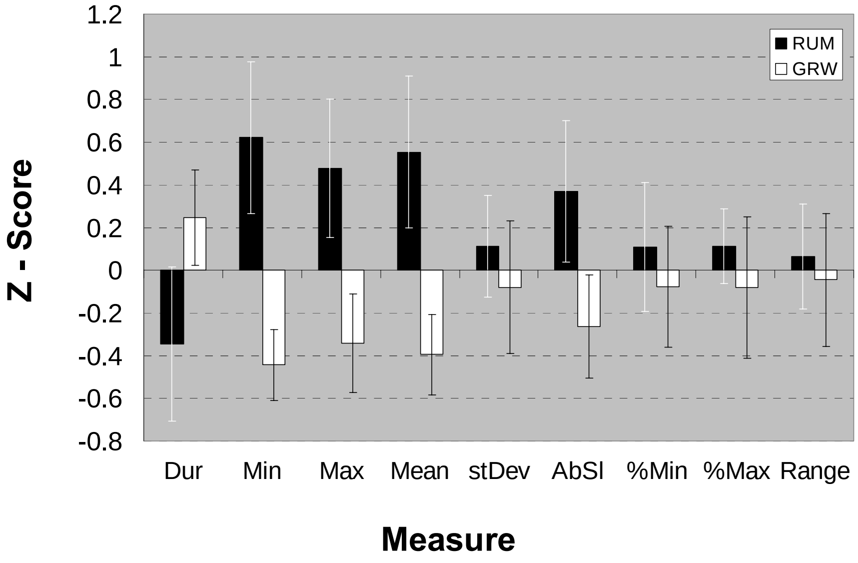


Figure I - 6. Combination calls with a-periodicities in leading segment. a. Bark-rumble (BRM); **b.** Roar-rumble (RRM); **c.** Long-roar rumble (LRM) in which first segment is shorter than the second; **d.** Long-roar rumble in which first segment is longer than the second.

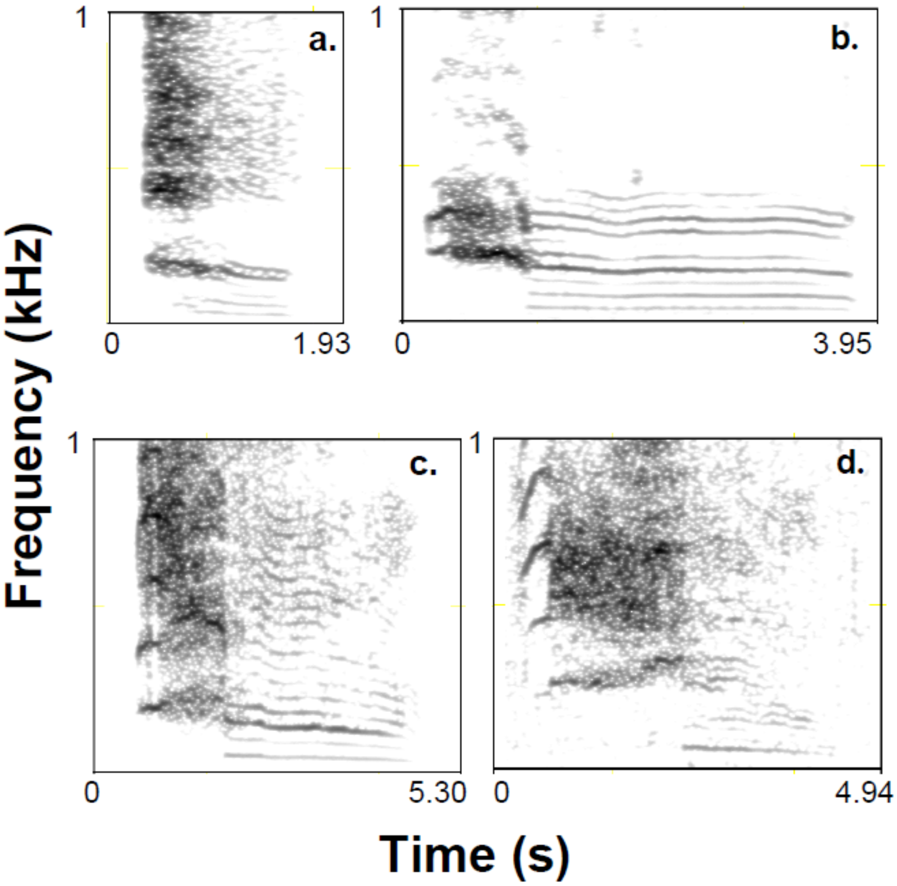


Figure I - 7. Combination calls with periodic leading segments and non-vocal acoustic signals. a. Croak-rumble; **b.** blow; **c.** trunk-bounce; **d.** chirp-rumble.

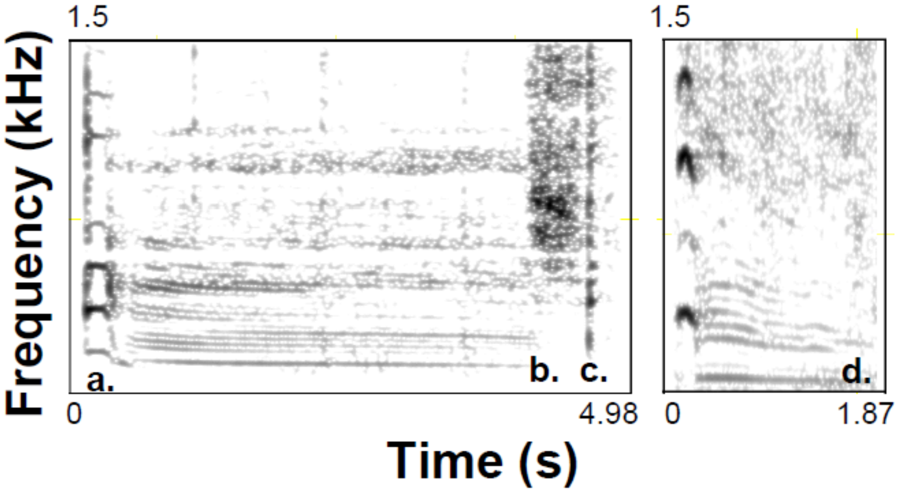


Figure I - 8. Durations of the first segment of combination calls and corresponding single calls. Durations of the leading segment of Chirp- and Croak-rumbles (CRM), Bark-rumbles (BRM), Roar-rumbles (RRM), Longroar-rumbles (LRM) compared to the duration of Barks (BRK), Roars (ROR), and Longroars (LRR). Asterisk indicates significant difference (see text).

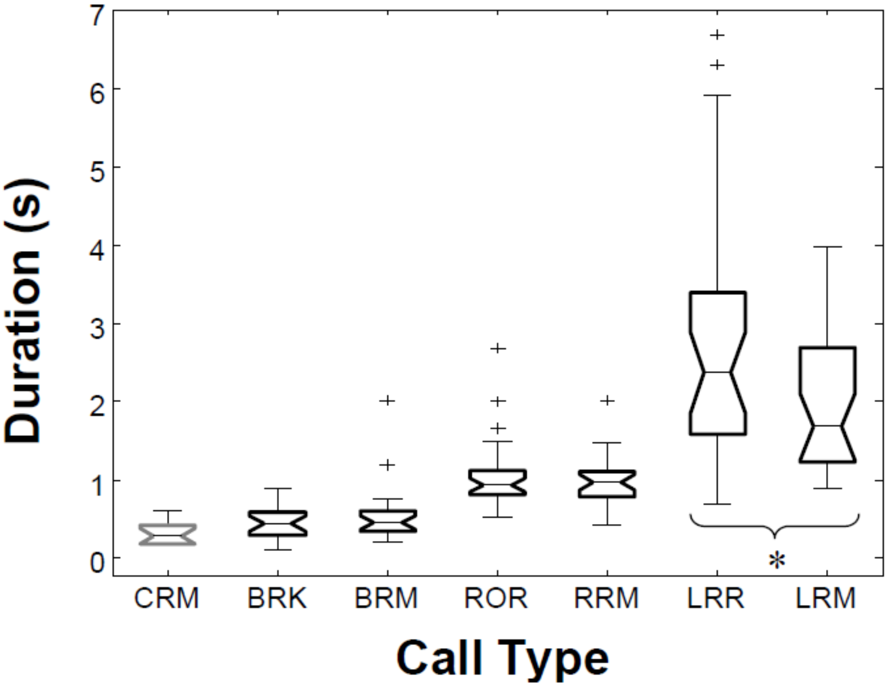


Figure I - 9. Growls by adult females are individually distinct. Individuals were maximally distinguishable based on the first two canonical dimensions (MANOVA, d.f.=28, $P_{canon1} << 0.0001$, $P_{canon2} = 0.0042$), which were linear combinations of the two harmonicity measures and all F_0 measures except ‘range’.

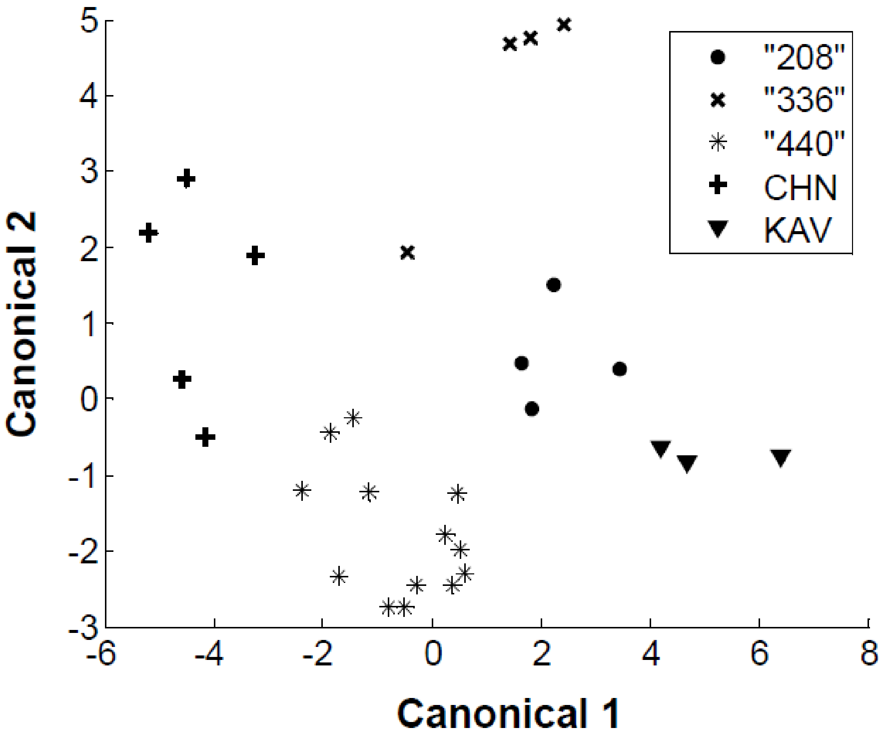


Figure I - 10. Principal components of growls, rumbles and second segment of combination calls based on F_0 contour. Principal component loadings are provided in Table I - 4. Higher values of PC 1 correlate with higher F_0 values. Values of PC 2 correlate positively with percent maximum (highest frequency occurs towards end of call) and negatively with percent minimum (lowest frequency occurs towards beginning of call). The reverse is true of PC1. Calls with falling F_0 therefore have negative values on PC 2 and positive values on PC1. The second segment of combination calls (circles) are distinguished from growls and rumbles primarily along PC 1 but are more similar to rumbles than growls. PC 2 distinguishes these segments from one another.

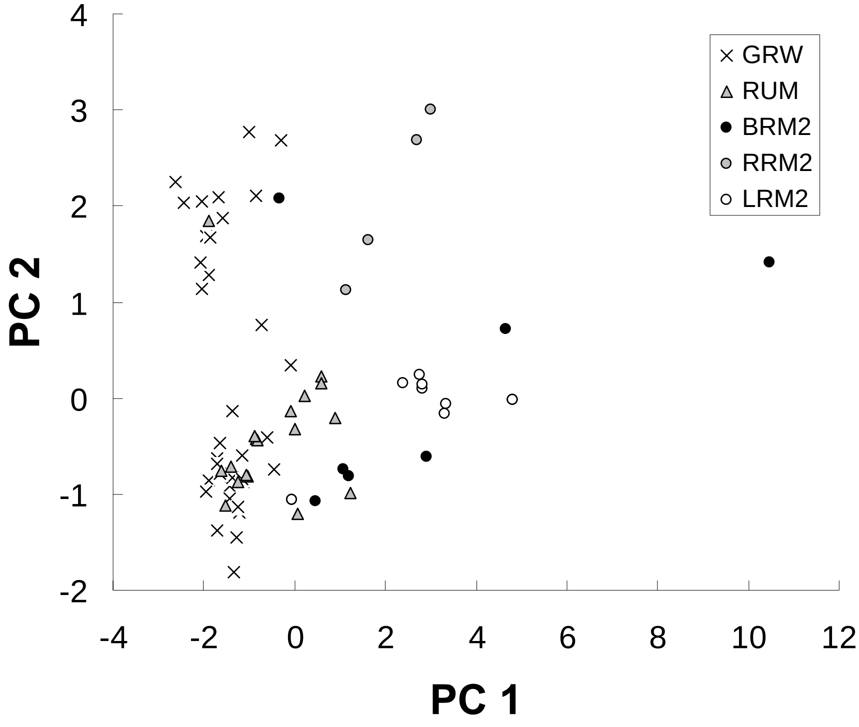
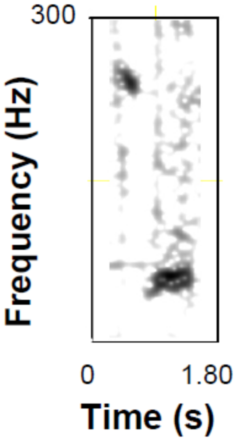


Figure I - 11. Musth chirp-rumble.



CHAPTER II.

From Individuals to Societies: Multi-level Social Organization of the Asian Elephant in Sri Lanka

SUMMARY

I present the first longitudinal study of associations among female Asian elephants (*Elephas maximus*), exposing the individual-level interactions that give rise to social structure. I examine whether social structure in a population of 286 individually-identified adult females at Uda Walawe National Park in Sri Lanka follows expectations based on resource availability. This population consists of seasonally variable social units, some of which combine into higher-order associations, or 'tiers'. Tier structures reorganize a-periodically. While most individuals do not maintain preferences for the same companions on short time scales, over longer time scales they appear to form relatively constant social units. Bonds vary greatly in both strength and stability, and most social units lack strong central leadership. The society of female Asian elephants is thus best characterized as fission-fusion. Nevertheless, while Asian elephants have lower rates of association than African savannah elephants, as predicted from differences in the resource abundance, lower association rates do not preclude the existence of complex extended networks of social affiliation.

INTRODUCTION

Understanding the factors shaping sociality is a basic concern of behavioral ecology. Among herbivores, groups typically form for defense against predation (Molvar and Bowyer 1994), or in response to resource distribution (Jarman 1974; Emlen & Oring 1977; Herrera & Macdonald 1989; Asensio et al. 2009). However, group formation can also decrease foraging efficiency (Molvar and Bowyer 1994; Boinski et al. 2000; Asensio et al. 2009). Group formation is expected to be favored when the costs of within-group feeding competition is outweighed by the benefits of defense against predators or other conspecifics (Wrangham 1980; Van Schaik 1983; Chapman et al. 1991; Boinski et al., 2000; Isbell & Young 2002; Silk 2007). In order to gain insight into the fundamental principles governing the diversity of social systems across species, it is necessary to have objective methods of defining the most basic components of societies – bonds among individuals, and the structure of their associations (Hinde 1977; Cairns and Schwager, 1987; Dunbar & Shultz2010). Here I examine how resource availability influences the strength and stability of female bonds in the Asian elephant (*Elephas maximus*), relative to those of African savannah elephants (*Loxodonta africana*) in quantitative terms.

The Asian elephant, African savannah elephant (*Loxodonta Africana*) and African forest elephant, (*Loxodonta africana cyclotis* or *Loxodonta cyclotis*) are the only living members of the proboscidean clade (Shoshani & Tassy 1996; Debruyne, 2005; Eggert et al., 2002; Roca et al., 2007; Rohland et al., 2007). The Asian and African species have diverged by at least five to six million years, being at least as distant from each other as they are from *Mammuthus* (woolly mammoths) (Fleischer et al., 2001; Shoshani & Tassy, 1996). Elephants are generalist herbivores, occupying diverse habitats ranging from dense forest to arid desert. Asian elephants are also found on islands with different ecologies from each other and the mainland. The social behavior of Asian elephants reflects evolution in environments separated in time and space from that of African elephants.

Much of what is known about the structure of elephant society is based on the African savannah elephant (henceforth referred to as 'savannah elephants'). Herds of savannah elephants are composed of females, sub-adults and calves whereas adult males are mostly solitary (Douglas-Hamilton, 1972; McKay, 1973; Moss & Poole, 1983). Thus savannah elephants are female-bonded and appear to discriminate among a large set of potential social affiliates (McComb et al 2000). The society of female savannah elephants has been described as 'multi-tiered,' based on association patterns among individuals as well as their apparent geographic ranges. The first tier simply consists of mother-calf units while the second consists of family units centered around older adult females, or matriarchs (Wittemyer et al., 2005; Moss & Poole, 1983; Douglas-Hamilton, 1972. They maintain bonds with other families, forming what have been termed 'kin-' (Douglas-Hamilton 1972) or 'bond-' (Moss & Poole 1983) groups which constitute the third tier (Wittemyer et al. 2005). The fourth tier (Moss & Poole 1983) consist of bond-groups that appear to coexist on overlapping ranges termed 'clans'. These 'clans,' are not necessarily genetic relatives (Charif et al., 2005) but it is unclear how they contribute to fourth-tier population structure (Wittemyer et al. 2005). Multiple clans form a local 'subpopulation,' and multiple subpopulations compose a regional 'population' (Moss & Poole 1983). These two last tiers have no precise geographic definition. Recent work on savannah elephants has quantitatively described the up to five tiers, based solely on seasonal patterns association (Wittemyer et al., 2005). Savannah elephants aggregate in sanctuaries during wet seasons when resources are plentiful, and break up during the dry season (Thouless 1996; Wittemyer et al. 2005). The aggregations are structured, such that higher-order social 'tiers,' extending beyond family associations, emerge when multiple wet season datasets are pooled. This includes the fifth-order tier, which appears to be a social phenomenon that does not correspond to the previous geographically or socially defined ones (Wittemyer et al. 2005).

In contrast to the savannah elephant, the nature of female associations is poorly understood in Asian elephants. Some authors have simply assumed that society is organized into stable, matriarch-based, social units identical to savannah elephants (Rasmussen, 1998; Katugaha et al. 1999), despite the geographic and phylogenetic separation between the two species. However, studies of Asian elephants in the wild based on behavioral observations, genetics, and movement tracking indicate low rates of association among even family members (McKay 1971; Fernando & Lande, 2000; Vidya & Sukumar, 2005). Female Asian elephants are described as having 'loose' associations (McKay 1971), lacking extensively large sets of social companions (Fernando & Lande, 2000; Vidya & Sukumar, 2005), unlike savannah elephants. However, there have not been large-scale longitudinal studies of associations among female Asian elephants comparable to those on savannah elephants on which to base this comparison. To date, it has remained unclear whether social bonds among Asian elephants are quantitatively or qualitatively different from those of savannah elephants.

One challenge to making quantitative comparisons of social structure is the tension between description of a state, and description of a process. Social organization emerges from bottom-up, individual interactions (Hinde 1977; Cross et al., 2005; Ramos-Fernández & Boyer, 2006; Sundaresan et al., 2007), as a dynamic process that responds to social and environmental variables. Studies of social association often give a single snapshot of group structure after some length of observation (Sundaresan et al., 2007; Wolf et al., 2007; Fernando & Lande, 2000; Vidya & Sukumar, 2005). However, studies that follow individuals longitudinally find that associations and group structure change with time (Baird & Whitehead 2000; Macdonald 2007; Parsons et al., 2009; Silk et al., 2006a; Silk et al., 2006b; Wittemyer et al., 2005). The degree to which associations change is an equally telling feature of a society as the static structure itself. I use the term 'social affinity' to describe the propensity of an individual to accompany a conspecific (cf. 'bondedness' Wrangham 1980; Dunbar & Schultz 2010). I examine this in terms of the strength and stability of bonds among individuals, as approximated by their tendency to associate with one another.

Ecological pressures

Elephantids, both extinct and extant, have historically faced predation by humans and large carnivores (Grayson and Meltzer, 2002). Very young calves of savannah elephants are vulnerable to predators without the protection of a group, but predation on older age classes has only been documented in Savuti (Loveridge et al., 2006; Power and Compion, 2009). Drought and humans have a greater impact on savannah elephant mortality in all age classes (Wittemyer 2001; Douglas-Hamilton 1987; Moss 2001;

Steinhart, 1989). Experienced matriarchs increase the efficiency with which their families respond to potential threats and find scarce resources (McComb et al., 2001). The death of a matriarch can precipitate the splitting of social units (Wittemyer 2005). In addition, sub-adults provide allomaternal care that relieves the burden on mothers (Lee 1987), a rare behavior among herbivores. While it is still unclear whether social units engage in resource defense or competitive exclusion, these finding suggest that companionship is beneficial to savannah elephants in coping with both predation and variability in resource distribution (Thouless 1996; Wittemyer et al. 2008).

Asian elephants have evolved with the Asiatic lion and tiger as potential predators on the Indian subcontinent, but there is little evidence tigers ever preyed on elephants, and lions are now confined to a single national park in India (Saberwal et al. 1995), though past distributions are not well known. However, the impact of human agriculture, trapping, and hunting on Asian elephant populations has been severe, responsible ultimately for their extinction in most of former western range by the 7th century BC (Olivier 1978). Capture and training records exist as early as 3000 B.C. (Olivier 1978), which continues today, as elephants were never domesticated. Predation pressures on Asian elephants and savannah elephants appear similar enough that I do not examine their possible effect on social organization in this paper.

Home range size has been suggested to influence social dynamics in savannah elephants (Thouless 1996). Changes in rainfall and primary productivity drive the fission and fusion of larger aggregations of savannah elephants (Wittemyer 2005). Resource abundance may similarly influence Asian elephant social organization. The tropical forest and grassland ecosystems occupied by Asian elephants typically have higher, more predictable rainfall and primary productivity than African savannah ecosystems (East 1984; McNaughton et al. 1989; Zubair 2008). Typical home range sizes for females in south Asia (59-266 km^2; Fernando et al., 2008 and references therein) are smaller than those typically reported for African elephants living on savannahs (102 to 5527 km^2; Thouless 1996), and South Africa (115 and 465 km^2 for females; De Villiers & Kok 1997), although some Asian elephant populations in India also have large ranges (623-800 km^2; Baskaran et al. 1993).

Hypotheses

Socioecological theory (Wrangham 1980; Isbell & Young 2002; Wittemyer 2005) predicts that the formation of groups should be favored when individuals benefit from defending shared resources. If resource defense drives group formation, Asian elephants in areas with higher annual rainfall and primary productivity should show lower affinity for conspecifics than those reported for savannah elephant populations in east Africa (Douglas-Hamilton 1972; Moss & Poole 1983; Wittemyer et al. 2005), because food is more abundant and predictable, competition among individuals is low, and collective resource defense is unnecessary. Nevertheless, localized resources such as water can deplete seasonally in the Asian tropics, and individuals may gain better access as part of a group. If water is a limiting resource, the cohesion of social units may be stronger during seasons when such it is scarce and localized, than during wet seasons when it is abundant. Associations among individuals may thus fluctuate with some regularity that corresponds to seasonal resource availability. I follow social relationships among Asian elephants over multiple ecological time scales: across seasons, and years. I examine whether these expectations are upheld with respect to three levels of organization: the study population as a whole, an individual's set of direct companions, and dyadic associations.

METHODS

Study site

Uda Walawe National Park (UWNP), has two highly predictable monsoons per year, in March-April and October-December (Zubair et al. 2008). There are only four permanent sources of water during the five month inter-monsoon period, whereas rain water collects in rock crevices, water holes, and man-made reservoirs during the rest of the year. The Sri Lankan subspecies of Asian lion (*Panthera leo sinhaleyus*) was extinct prior to the colonization of the island by humans (Manamendra-Arachchi et al., 2005). The leopard (*Panthera pardus cotiya*) is the current top land predator in Uda Walawe, but there is no evidence that it hunts elephants. The only other large predator is the freshwater crocodile (*Crocodylus palustris*), which may endanger unattended calves, but predation has not been documented. UWNP is encircled by electric fencing except for two gaps opening it to wildlife movement 'corridors,' and surrounded by human habitation.

Data collection

The data presented span 226 field days (twenty months) from 2007-2008, or three days per week on average except between January-April 2008, when UWNP was temporarily closed due to political unrest. We typically entered the park between 600-

700h (sunrise), remaining continuously inside until 1730-1830h (sunset). Driving routes were varied such that all accessible parts of the park were covered in a week. Locations where animals were closest to the road were marked on a hand-held GPS unit. Temperature, humidity and wind were recorded at least three times per day with a Kestrel™ pocket weather station. Rainfall (mm.) was recorded daily using a standard U.S. Weather Bureau rain gauge.

Individuals were identified photographically (Moss, 1996). All individuals were given numbers; some were also given names. We considered individuals within visual range of the observer (up to 500m) who moved, rested, shared resources together, or showed affiliative vocal or tactile behavior (de Silva, 2010), to be a ‘group’. The term ‘group’ here carries no implication of social history or permanence. The only resource excluded was water, because multiple groups could share water without interaction. Individuals from multiple groups which initially co-occurred in space or even passed through one another, were not counted as associated unless they showed concerted movement, and if they did, were reassigned as a single group. Thus two or more groups could clearly fuse, while fission events were behaviorally ambiguous. It was possible to spend several hours with a single group. We recorded identities of known individuals and counted the number of individuals in five size-based age classes (de Silva, 2010). Unidentified individuals were counted, but excluded from analyses.

Data Analysis

This paper examines only relationships among adult females, as most sub-adults and juveniles were not identified individually. Two individuals were considered to be ‘associated’ if they were grouped together at least once in a day, with each day considered to be one sampling interval. One individual’s ‘affinity’ for another over the course of several days (e.g. one season) was quantified in terms of their association index. I used the Simple Ratio Index or SRI (Cairns & Schwager, 1987; Gilby & Wrangham, 2008; Wittemyer et al., 2005), which describes the proportion of times any two individuals were seen together as $X_{ab}/X_t\text{-}X_n$ where X_{ab} is the number of times A and B were observed in a group together, X_t is the total number of observations, and X_n is the number of observations in which neither A nor B was seen.

Association data were partitioned according season. Months that had a total rainfall higher than the two year monthly average of 120cm were designated as ‘wet’ months and those that had less were designated as ‘dry’ (Figure II - 1), consistent with the monsoon cycle (Zubair et al., 2008). January-April, with two wet months and two dry months, was considered ‘Transitional’ rather than divided into dry and wet periods since two month periods were insufficient for analysis. May-September were considered the ‘Dry season’ and October-December was considered the ‘Wet season’. Henceforth, ‘T1’ refers to January-April 2007, D1 to May-September 2007, W1 to October-December 2007 and D2 and W2 to the corresponding seasons in 2008. Because this uneven partitioning results in an unequal number of samples in each season, data were also re-analyzed using four-month partitions (January-April, May-August, and September-December). Finally, to consider the effect of mixing wet and dry periods (the ‘Transitional’ time period), analyses were repeated separately for data from August-November in each year (labeled as ‘T2’ for 2007 and ‘T3’ for 2008), which also contain two dry months followed by two wet months.

Associations within seasons

The null hypothesis that associations within a season are random was tested by permuting seasonally partitioned datasets such that the number of sightings for each individual and the distribution of group sizes within the time periods were preserved. The 'fill' method was used to generate 1000 permutations per season, rather than swapping rows and columns (Sundaresan et al., 2009; Whitehead et al., 2005), with the average SRI value used as the test statistic. Dry seasons were partitioned into three-month periods (May-July and July-September) to speed up computations. Some of the random datasets generated were used in further analyses (below).

I examined whether observed associations could be attributable simply to spatial overlap, as opposed to social preferences. If space-use alone was responsible for which individuals were seen together, there should have been a positive correlation between the amount of area overlap and the SRI value among dyads. I used the Minimum Convex Polygon method to generate area polygons for each individual based on pooled position data from the entire study period. For each pair of individuals I calculated the percentage of their combined total area that consisted of overlapping regions. I then correlated SRI values for each dyad of adult females with this percentage of overlap in observed spatial range.

In order to compare Asian elephant social structure with that of African elephants, I first used hierarchical cluster analysis (Wittemyer et al., 2005; Whitehead et al., 2005). However this method was found to be inappropriate for this dataset (see Appendix). SRI matrices were next visualized as social networks (Krause et al., 2007; Wasserman & Faust, 1994; Wey et al., 2008). Nodes represented individuals, with ties among them having the corresponding SRI value. Individuals were assigned to clusters using the Girvan-Newman algorithm (Girvan & Newman, 2002). This process removes individuals with the highest 'between-ness centrality' and calculates the number of subdivisions yielding the highest 'modularity quotient'. 'Between-ness centrality,' measures the proportion of shortest geodesic paths between nodes that passes through any particular node such that those intercepting a greater proportion have higher 'between-ness' (Wasserman & Faust, 1994). 'Modularity quotient,' or 'Q' (Clauset et al., 2004; Lusseau et al., 2008; Wolf et al., 2007) values can range from 0-1, where 0 means the number of ties within a cluster is no more than expected by chance, and values above 0.3 indicate potentially meaningful subdivisions (Newman 2004). Each possible way of subdividing a network (i.e. assigning individuals to clusters) yields a modularity quotient value, of which the 'best' clustering would be that with the highest. I label this highest modularity value 'Q_{max}.' The term 'cluster' henceforth refers to individuals who are clustered this way during a season.

I looked for population substructure within seasons by removing ties below a certain threshold, eliminating individuals who then became isolated, and running the Girvan-Newman clustering procedure on the remaining individuals. I repeated this multiple times, incrementing the threshold at 0, 0.1, 0.11, 0.12…0.7 against which I plotted the number of clusters with the highest Q_{max}. If there was more than one possible clustering which yielded identically high Q_{max} values, all were included. As each season contained different numbers of elephants and not all individuals were present in all seasons, I repeated the procedure for some matched datasets, containing only those individuals who were present in the two or more seasons under comparison. This quantifies how relationships among the identical set of individuals may have re-organized.

Associations across seasons

If individuals maintained relationships with the same companions in different time periods, matrices for those time periods would be well-correlated. I tested the significance of correlations between matrices across pairs of seasons with the Mantel test, a standard test for the correlation between two similarity (or distance) matrices, in which entries are not independent of one another (Mantel 1967; Whitehead 2005). I conducted 10,000 permutations per test, using the Pearson product-moment correlation coefficient to compute the test statistic.

I then examined how relationships changed over time among those who were seen in every season. If individuals aggregate as a response to scarcity of resources and disperse when this constraint is removed, an individual should have more companions in dry periods than in wet periods. If a subject's companions are the same at times of year that correspond to similar levels of resource ability, their companions should be similar in dry periods across years and in wet periods across years, but different in adjacent periods within the same year. To quantify this, I made paired comparisons of specific 'ego network' measures for each individual in different time periods (see *implementation* below), where the subject was the 'ego' and only those who were directly connected to her constituted her local network. In order to avoid multiple testing, I matched two seasons at a time such that matrices contained only individuals seen in both. Thus different pairs of seasons contain slightly different sets of individuals, reported as N. I then compared biologically intuitive measures for each season, defined in Table II - 1.

In addition, I plotted the SRI values for each dyad through time and used K-means clustering of the correlation distance between pairs of curves to assess whether there were characteristic temporal association patterns – i.e. increase or decrease in associations through time, regardless of their absolute magnitude. If associations were stable, this would result in smooth, flat curves. If associations were temporary, curves would peak at particular time intervals. If associations were cyclic, there would be more than one peak, at corresponding seasons across years. In order to minimize noise in the data due to rarely observed individuals, this analysis was limited to individuals seen at least L times (specified in results). The appropriate number of K-means clusters was determined using the Bayesian Information Criterion (BIC) over 100 runs (Pelleg and Moore 2000) and actual clusters were determined with 1000 repetitions of the K-means clustering procedure. In order to avoid confusion with the Girvan-Newman procedure, K-means clusters will henceforth be referred to as 'curves.'

The rank order of preferred companions could remain the same despite changes in the overall magnitude of association strength. 'Rank' refers to the position of an associate when ordered by their SRI value with respect to the subject, where the top ranked associate has the highest SRI value. For those individuals seen in all time periods, I counted the percentage of top ranked companions that were maintained across seasons. If associations were stable, the percentage of top ranked companions maintained was expected to be high, with SRI remaining high across time. For each individual, I ranked their companions and determined how many of the top 3, 5 and 10 spots were occupied by the same individuals. A companion need not have occupied the identical rank at different times. For instance, for individuals A and B, if B was in the 3rd, 2nd, 6th, 5th, and 9th positions with respect to A in seasons 1-5 respectively, then B was among the top 10 associates for all five seasons. If however B was ranked 11th or lower in any one season, she was in the top 10 for only four seasons, etc. Percentages were calculated as follows. An individual potentially has 10 x 5 or 50 total available 'top ten companion' positions for all five seasons. Of these positions, if one individual was consistently present among the top ten, she occupied 5 positions. An individual who was present in the top ten for 2 seasons occupied 2 positions. Thus an individual who had the same 7 companions consistently in the top ten for 5 seasons, 1 for 4 seasons, 2 for 3 seasons, 1 for 2 seasons, and 3 for only 1 season would accordingly have (7 x 5)/50 or 70% of the top ten positions held for all five seasons, (1 x 4)/50 or 8% held for 4 seasons and so forth. The same was calculated for the top 5 and top 3 positions.

Implementation

Data extraction, hierarchical clustering, and statistical tests were performed using SOCPROG v. 2.4 (Whitehead 2009), Matlab v. 7.0, and R v. 2.7 (R development core team, 2005). Because asymmetry of distributions, especially in large datasets, can inflate Type I error in Wilcoxon signed-ranks tests (Kasuya 2010), I made paired comparisons in Matlab using the command 'signtest' which performs a paired, two-sided sign test of the hypothesis that the difference between the matched samples in two vectors x and y comes from a distribution whose median is zero, where the differences x-y are assumed to come from an arbitrary continuous distribution with no assumption of symmetry. Permutations of associations, observed group sizes, and corresponding significance tests within and across time partitions were carried out using the 'CAML' programming language, using code which can be made available upon request. Social network analyses were carried out in UCINET (Borgatti et al., 2002) with network visualizations using the Netdraw package. All diagrams were visualized using a graph-theoretic layout with node repulsion and equal edge lengths (Borgatti et al. 2002). Spatial data were plotted and manipulated with ESRI ArcInfo^{TM}.

RESULTS

Group sizes and preferential association within season

We identified 305 adult females from September 2006 to December 2008. On average we identified 64% of all adult females encountered, and 84% of those in groups where at least one adult female was known. Identified individuals were seen 1-48 times, with a median of 9. Those seen only once were not included in further analyses. The median group size measured in terms of the number of adult females encountered in a group was between 2 and 3 across all seasons but ranged widely. Where N is the total number of adult females seen in that season, the range of group sizes were T1 (January-April 200): N=168, 1-15; D1 (May-September 2007): N=209, 1-14; W1 (October-December 2007): N=180, 1-12; D2 (May-September 2008): N=169, 1-20; and W2 (October-December 2008): N=165, 1-11. Dry seasons contained a greater number of larger groups than wet seasons within the same year. Groups with over 12 adult females did not occur in wet seasons.

The number of identified adult females seen per month in 2007 increased from 67 in January, to 152 in October, then fell to 120 by December (Figure II - 1). There was no data for January-April of 2008, but sightings for the rest of the year similarly rose to 113 in both September and October and fell to 103 in December. Sightings of adult females thus peaked at the end of the dry season, just prior to the onset of the long monsoon, and the rest of the year remained above 66 per month.

Within all seasons as well as transitional periods, SRI values among individuals were non-random (tested by permutation described in methods, $P<<0.001$), suggesting preferred association among individuals. SRI values were positively correlated with spatial overlap. In all 5 seasons, the slope of the regression line was significantly positive ($P < 0.001$). But the regression coefficients (R^2) for each season were low: 0.0214 (T1), 0.0248 (D1), 0.0305 (W1), 0.0480 (D2), and 0.0235 (W2). When data were limited to only those individuals who had been observed more than twenty times during the five seasons, results were qualitatively the same, with R^2 values that were even lower. Since groups are defined in terms of individuals jointly observed, it would be impossible to be socially associated without area overlap, accounting for the correlation. But the amount of shared space was not a good predictor of the strength of association between two individuals. Individuals could share parts of their range without necessarily meeting or interacting, accounting for the low R^2 values (Figure II - 3). Observed associations are thus unlikely to be solely the result of shared space or resources.

Population-level structure

The Girvan-Newman algorithm yielded 23 clusters in the 2007 January-April 'transitional' period, 22 clusters in the 2007 dry season, 18 clusters in the 2007 wet season, and 17 clusters for both the wet and dry seasons of 2008 (N same as above in each season). Each season had a dramatically different structure, when decomposed through the sequential removal of ties below particular thresholds (Figures II - 4 and II - 5). I also repeated this procedure for the randomized data obtained through permutation, which preserved the distribution of group sizes and sightings per individual, but not associations among individuals. The number of clusters in randomized data rapidly decreased with increasing SRI threshold, unlike observed data (Figure II - 4). Thus plateaus were not simply an artifact of the number of observations or group sizes. Plateaus represent within-cluster connections, and intervals between plateaus represent between-cluster connections. They occurred between approximately the same SRI intervals across seasons for real data. The number of plateaus changed from season to season. The plateaus prior to the peak (at SRI thresholds lower than 3.0) characterize relationships among social units, and the plateaus following the peak (at SRI thresholds higher than 6.0) are the strongest relationships within social units. But the latter sets of plateaus result from degenerate networks, which can even appear in random data (Figure II - 4), and must not be over-interpreted. I will henceforth call these plateaus 'tiers'. The highest modularity (Q_{max}) was at or above 0.8 for SRI thresholds above 0.1 in all seasons and was generally higher than for that of randomized data (Figure S3, Appendix).

Matrices matched to contain exactly the same individuals for two time periods revealed how the structure of relationships among the identical set of associates differed seasonally (Figure II - 6). T1 and D1 had N=142 adult females in common whereas T1 and W1 had N=123 in common. The tier structure of D1 more closely resembled T1 after matching (Figure II - 6a) and more closely resembled T1a than W1. It also had fewer clusters after matching. Tier 4 (Figure II - 4) coincided with the other seasons for D1 after matching (Figure II - 6a). Thus individuals who were not present in the T1 partition were responsible for ten additional clusters, forming the additional tier composed of low SRI values from 0.1-0.16. Tier 3 (Figure II - 4) was affected little except for a reduction in the number of clusters (Figure II - 6a). Tiers 1 and 2 of D1 merged before the matching whereas there was a distinct spike after matching. After matching (Figure II - 6a) plateaus in strong ties at 0.34-0.42 were nearly identical between T1a and D1 and were in fact identical for D1 and the T1b. Thus strong ties among the same individuals did not change much between T1 and D1. But the wet season showed less tier structure in both the complete dataset (Figure II - 4) and the matched dataset (Figure II - 6b). Moreover, there were fewer clusters beyond the SRI threshold of 0.36 compared to other seasons, reflecting that the number of individuals maintaining strong ties was lower in this wet season.

I examined whether tiers could arise in arbitrary partitions, or be the result of population-level changes between dry and wet seasons. For instance, if additional tiers emerged during temporary interactions among social units as they moved into or out of the observation area in the transition between seasons. T2 (N=206) and T3 (N=168) both contained two dry months followed by two wet months, but neither showed a clear tier structure (Figure S4, Appendix).

The SRI matrix and tier structure for pooled data were not simply averages of the two time intervals, though strong ties beyond 0.36 approach the average curve (Figure

S5, Appendix). Rather, apparent tiers emerge at lower SRI values which may not have been present in at least one of the original datasets and the absolute number of clusters increases. Thus one must be cautious of pooled datasets as they could misrepresent the substructure of ties.

Not all individuals had multi-tiered relationships. Many clusters were isolated from the outset in each season, though they were not necessarily the same individuals (Figures II - 2 and II - 5). Spatially, the two largest clusters may constitute separate clans because their observed ranges did not overlap for the most part. Tiers resulted solely from the fragmentation of these larger clusters – thus, they are differing degrees of association *within* clans. While some individuals in large clusters had multi-tiered relationships, those in smaller, isolated clusters did not. Moreover, clusters merged and split from one another such that the network was more fragmented in some seasons than in others (Figure II - 2). Thus relationships among the same individuals may comprise different tiers at different times. Even within this single population, the extent of social relationships varied from social unit to social unit. I next examine whether these changes arise from the re-organization of an individual's direct ties.

Structure of direct ties – ego networks

All ego network measures for matched datasets (containing the 105 individuals seen in all seasons) tended to have lower values in wet seasons than in dry seasons (Table II - 2), and did not change significantly except during wet seasons (Table II - 3). Dry seasons that were a year apart were not significantly different, but wet seasons were. The number of individuals directly connected to a subject (her network size) tended to be greater during dry seasons than during wet seasons, but this was not significant in 2007. The similarity of ego network measures across seasons could result from individuals associating with the identical companions, or simply a similar number of companions. However, visualization shows that subject's direct ties consisted primarily of individuals who were companions in previous seasons and the few relationships that were almost continuously maintained (Figure II - 7). In order see how bond strength itself changes across time, it was necessary to isolate dyadic patterns.

Structure at the dyadic level

Associations were significantly positively correlated across seasons, even when dyads that had SRI values of zero in all time periods were excluded. However, corresponding seasons across years were no better correlated than adjacent seasons within years. For Mantel tests with 10,000 permutations where N is the number of individuals seen in both time periods and R is the Pearson correlation coefficient, $P<<0.001$ for all comparisons: Tl vs. D1: N=108, R=0.4304; T1 vs. W1: N=101, R=0.4195; D1 vs. W1: N=173, R=0.4539; D1 vs. D2: N=152, R=0.4118. A dyad that was associated in one season was therefore very likely to be associated in other seasons, to a greater or lesser extent (discussed below). On the other hand, dyads that seldom or never associated in one season seldom or never associated at high levels in any other season.

Of those dyads that did associate, SRI values fluctuated with time. Data were first limited only to the adult females seen in all time periods. When further restricted to individuals seen at least $L \geq 30$ times, or more than once per month on average, it included 53. I considered only on those dyads that had at least one nonzero association – i.e. were seen together at least once in five seasons. That is, curves for individuals who never associated together in any time period were not generated. The number of K-means curves was either 5 or 6 according to the BIC, with 6 being slightly more likely (Figure S6, Appendix). Figure II - 8 and Table II - 4 show the resultant 'characteristic' association patterns with the number of dyads corresponding to each. There were no corresponding patterns across multiple wet seasons. 60-67% of all dyadic relationships (the top three most frequent patterns) corresponded to relationships that were strongest in either the 'Transitional' or 'Dry' periods. Pattern VI represents associations that were equally strong in dry seasons across years. The Girvan-Newman procedure suggests that ties above 0.3 indicate the strongest social affiliations, but only 7 dyads maintained ties consistently at or above 0.3 in all seasons. Thus relationships among the individuals most often seen were dominated by dyadic relationships that were temporary in the sense that most ties were either weak (SRI values below 0.3) or did not persist at the same strength for more than one season (fluctuating association curves). These results were qualitatively the same when I included individuals seen at least 20 times (N = 80), reported in the Appendix.

If an individual uniformly increases or decreases the strength of her associations with all others over time, the ranks of her preferred companions may remain unchanged despite fluctuations in SRI values. That is, her most preferred companions in one season, ranked by SRI, may still be her preferred companions in another, despite changes in the absolute strength of their associations. On the other hand, if she changes her preferences, their ranks should also change. Out of the set of 80 adult females seen over 20 times, individuals varied in how many of their top companions they consistently maintained from season to season (Figure II - 9). A few individuals maintained 60%-80% of their top companions throughout the entire study period, whereas most maintained fewer top companions over fewer seasons and none maintained 100%. A few individuals maintained up to 3 top associates in all five seasons. Thus an individual's closest companions tended to change, but individuals varied in how many of their close companions they kept consistently.

Adult female Asian elephants form a complex society with individual variation in the strength and stability of ties. Associations were non-random both within and across seasons. Associations tend to be weaker in wet seasons. Population-level networks are fragmented and change from season to season, with 'tiers' that were not strictly periodic according to a seasonal or annual cycle. When decomposed into sets of ego networks, most of an individual's companions appear to be those with whom she was previously seen, although she may not have associated with each of them in every season. An individual's direct ties tended to be greater and more similar in the transitional or dry periods than in wet periods. When further decomposed into dyadic relationships, only a small proportion of individuals maintained consistently high associations with one another from one season to the next, whereas most changed their closest companions. Some of these associations were cyclic.

DISCUSSION

Social affinity

This population shows fission-fusion dynamics in the sense that social clusters are comprised of individuals who do preferentially associate, but an individual may be with only a subset of her cluster-mates on any given day (thus 'group' and 'cluster' are not equivalent delineations). Group sizes are small except during dry seasons, when all members of a cluster may assemble together. Some individuals associate at high rates (SRI values exceeding 0.3) while others do not. This agrees with previous research that suggests close companions are likely to be relatives, but that even relatives do not associate very highly (Fernando & Lande 2000; Vidya & Sukumar 2005). The family-level SRI values of African savannah elephants on the other hand typically exceed 0.6 and family units do not fission due to seasonal ecological changes (Wittemyer 2005; Wittemyer, pers. comm.). Asian elephants appear to lack strong central leadership. Seven mature or post-reproductive adult females – putative matriarchs – were either solitary or became solitary over the course of this study. The availability of resources within a relatively small geographic area possibly removes the necessity for experienced, informed leaders, resulting in the scattered 'groups' we see. Asian elephants thus have lower affinity for conspecifics, and are thus more weakly bonded to one another, than African elephants, as expected under these ecological conditions.

This population also shows fission-fusion dynamics across seasons in the sense that many individuals change their closest companions from time to time, while maintaining ties with the same set associates overall. Ego networks and analyses of dyads are complementary in revealing these changes. Single season peaks in association curves do not signify that individuals never associated at other times, only that they associated at lower levels. This interpretation is consistent with the correlation of SRI matrices through time, ego network visualizations, and similarity in ego network measures for all but the wet seasons. The double-peaked association curve (curve VI, Figure II - 8), the absence of such a curve corresponding to wet seasons, and the lower frequency of peaks corresponding to single wet seasons, all suggest that similarities of ego network measures in dry seasons is due to the periodic splitting and reunion of some individuals in dry seasons. These results support the prediction that associations would be stronger in the dry seasons than in wet seasons, if motivated by resource defense. At the very fundamental level of association, those among individuals, this is the opposite pattern to that of savannah elephants (Thouless 1996; Wittemyer 2005). While overt aggression among females providing behavioral evidence of resource defense is rare, we have anecdotally observed physical confrontations when unfamiliar groups meet, dominance interactions around water and mud, as well as the vocal displacement of one social unit by another (de Silva 2010). Vocal and chemical signals may thus be used in maintaining social cohesion as well as avoidance despite the seeming fluidity of associations.

A result that deserves emphasis is that females differ greatly in their fidelity to companions. Kamala (KAM) and Kanthi (KAN) for instance were two mature individuals who were always seen together such that their ranges overlapped exactly, despite being the largest of all observed ranges (Figure II - 3). They were almost always observed with the same individuals, although they had additional companions, and occasionally joined with over 12 other adult females. The adult female “471” on the other hand appeared with many different individuals, who formed a large cluster (Figure II - 5) that spatially overlapped with the Ks (Figure II - 3), but which was seldom observed in its entirety at the same time. Such differences may represent individuals under different pressures. For instance social bonds among ‘residents’ of the protected area might differ from those among ‘transients’ who face must face threats outside the park or cover a greater area to meet their nutritional requirements (e.g. killer whales: Baird & Whitehead 2000). Alternately, these social units may differ in their genetic structure, demographic make-up, or simply the personalities of certain individuals. All of these hypotheses provide intriguing directions for future research on the causes and fitness consequences of different social strategies within species.

Multi-tiered structures

Despite low rates of association, and contrary to the expectations of previous authors (Fernando & Lande 2001; Vidya & Sukumar 2005), some Asian elephants do have multi-tiered associations. A *multi-tiered* social structure can emerge even if associations are not *hierarchically* structured. This is because two or more individuals forming one cluster may be indirectly connected to two or more individuals forming another via just two bridging individuals. Together these two clusters constitute a larger cluster, in which not all individuals are connected. Thus indirect ties may be weak, but structurally important. When networks contain valued as opposed to binary ties, thresholding and re-clustering at different values provides a way to plot internal structure more informatively. The number of clusters then seems to peak at some association threshold that maximally separates social units and declines when no further subdivision is possible. This easily replicable method can be used to quantitatively compare the social network structure (Sih et al. 2009) not only of elephants, but other animal societies.

How do tier structures compare to the social and geographic tiers of African savannah elephants? Tiers are numbered relative to how many are present at any given time rather by absolute SRI intervals, and those that arise from the splitting of clans could be termed bond-groups (Moss & Poole 1983). While a clan consists of individuals that share space, all individuals that share space do not constitute a single social tier that can be termed a 'clan'. Figure II - 3 shows putative 'clans' (Moss & Poole 1983) with overlapping ranges, colored according to their Girvan-Newman cluster designation in T1. These clusters are discrete even at SRI thresholds between 0-0.1 (Figure II - 5) – they never associated despite the spatial overlap. Thus none of the tiers in T1 represent clan-level differences *per se* since not all individuals that share range appear together as a group. Weak ties between SRI values 0-0.1, if they could be termed a 'tier,' would constitute another level – that of the entire 'sub-population' within the observation area, consisting of several clans or a mixture of residents and transients who appear only during either the wet or dry seasons. The dry season of 2007 would then contain six levels, not including mother-calf units. These tiers are based on social associations, as among African savannah elephants described in Wittemyer et al. 2005. 'Clans' are not always evident even in African savannah elephant populations, despite the mixing of individuals within the same area (Thouless 1996; Wittemyer et al. 2005). Thus tier designations based on space do not directly translate into those based on social affiliation. But unlike the analysis of Wittemyer et al. 2005, the higher-order tiers described here consist of associations among all adult females, not only matriarchs.

Fluctuation and variation in associations at the dyadic level makes it surprising that tiers appear at consistent intervals at all across seasons, when present. They may therefore correspond to biologically real structural levels, such as genetic relatedness. They were not artifacts of the data structure (e.g. number of observations of particular individuals, group sizes) as randomized or re-partitioned data with the same features did not show such patterns.

What is the biological relevance of indirect ties among elephants? Second-degree and higher-order ties, in addition to enlarging the pool of potential associates, may be predictive of her future ties. If an individual associates with two companions, and loses one, she may then associate more closely not only with the remaining companion but with the associates of that companion. Baboons seek to expand social ties upon loss of a close companion (Engh et al., 2006). Indirect connections may thus buffer an individual against isolation. Preliminary observations support this for Asian elephants. Such indirect connections may have important fitness consequences, which are rarely quantified and studied (Sih et al. 2009).

Perhaps because of the importance of indirect connections, tiers cannot simply be inferred from ego networks or lower order phenomena. Tier structures (dependent on direct and extended ties) differ between D1 and W1, as well as D1 and D2, but ego network measures (dependent on only direct ties) do not change significantly. One might also expect that 2-step reach, the only network measure that could potentially be affected by changes to tier structure, should change, but it does not. Changes in tier structures are thus likely to result from fission and fusion among sets of ego networks, which form entire social units, rather than from re-organization of an individual's direct companions. The two analyses are complimentary, but address different levels of organization.

A large population size may be a necessary, if not sufficient, condition for the emergence of multiple tiers. In this study, datasets that were reduced to 105 individuals (those present in all time periods) did not have tiers, even if the original datasets did. However, tiers are not simply a consequence of density– D1 contained the largest number of individuals, and the highest number of tiers; but W2 contained the second largest number of individuals, and no clear tiers. On the other hand, no procedure of data partitioning or reduction produced tiers if none appeared in the original data. In other words, it was possible to fail to detect social tiers that were originally present, but it was unlikely they could arise as methodological artifacts if originally absent.

Ecology alone does not explain grouping patterns. Tier structures and ego networks are not predictable from one year to the next only based on rainfall. The observed tiers in 2008 differed from corresponding seasons in 2007. Ego network measures were not significantly different between D1 and W1 but were different between D2 and W2. The tier structure gradually disappears over the course of 2007 but re-establishes itself by the end of 2008. There may thus be some cyclicity to tier formation, yet it does not strictly correspond to the seasons; the underlying processes remain to be discovered. Our ability to detect and understand such phenomena is drastically lessened by the steady global decline of some species, like the Asian elephant, that were historically more numerous.

Social and demographic events may be responsible for some of these changes. We have observed individuals change companions after giving birth. Those with newborns may not keep up with some of their former associates and instead move with others who have calves of similar age for some period of time before rejoining former companions. Females also leave their juvenile calves with other associates while foraging out of view, even though these associates were not their constant companions. Such groups were previously described as ‘nursing’ units (McKay 1973). But anecdotal observations also suggest that calves, rather than adults, may initiate contact between social units, which may also be true of some cetaceans (Lusseau et al. 2007). The role of calves in motivating or maintaining social contact deserves further investigation.

Socioecological theory largely frames the tradeoffs of group living in terms of within- vs. between- group competition, predation, and life history (Hatchwell & Komdeur 2000; Isbell 2002; Silk 2007). These address the bottom-most levels of social organization, in which individuals form groups or coalitions with one another. Multi-level social phenomena have been previously described in species other than elephants (Geladas: Kawai et al., 1982; sperm whales: Whitehead et al. 1991; sea lions: Wolf et al., 2007). All societies composed of more than mother-offspring units consist of at least three-tiered associations. It is unclear whether fourth tier and higher-order associations displayed by taxa such as elephants are anything more than simple aggregations resulting from foraging decisions, how levels of organization in one species compare to those in another, how they can be explained by existing theoretical frameworks, and which other species might be expected to show comparable higher-order structures if similarly characterized. This is further confused by ambiguities in terminology. As this study shows, the conditions under which higher-order tiers emerge, the number that occur, and their function are not straightforward to predict, and may in fact contrast with others (Wittemyer 2005). This is due to the fact that not all individuals have multi-tiered relationships, even within the same population, and those that do not behave predictably from one season to the next. Higher-order tiers may simply result from the same processes driving the lower levels – such as defense. Among the Gobi Khulan, *Equus hemionus*, which form herds of hundreds, stallions from multiple family groups cooperatively drive off predators (Feh et al. 2001). On the other hand, Wittemyer (2005) proposed that fifth-order social tiers may be a consequence of 'runaway sociality.' Perhaps all tiers that extend beyond immediate relatives are merely the vestiges of earlier fission events, maintained by chance short-term encounters among individuals that once belonged to the same social unit. A more interesting proposition, however, is that the tradeoffs between resource defense and defense from predation vary within populations across temporal and spatial scales (Wittemyer 2005) but do not affect all levels of organization similarly. To explore this possibility, socioecological models should be more widely tested on diverse species, using quantitative metrics and categories.

It would be of interest to compare this population to Asian elephants in India, where there is greater variation in habitat quality and home range sizes of females (34 – 3396 km^2; Fernando et al. 2008). In drier regions of Sri Lanka itself, elephants are reported to aggregate in wet seasons rather than dry seasons (Katugaha et al. 1999), suggesting a similarity to African savannah elephants that may be ecologically based. But this has not been systematically studied. More data is also needed on African 'savannah' elephants in various habitats including desert environments, with very large home ranges (1763 to 2944 km^2 ; Viljoen 1989), and African forest elephants, which occupy habitats that may be quite similar to those of some Asian populations. It is possible that elephant societies are far more flexible than previously thought. Additional research on these diverse elephant populations, and comparisons with other taxa, would go far towards disentangling the phylogenetic from the socioecological conditions that structure societies.

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Table II - 1. Ego network measures used.

Measure	Definition	Biological meaning
Size	Number of individuals directly connected to the subject (ego)	Individuals seen in a group with the subject at least once
Ties	Number of existing ties among individuals within that network	Connections between subject's direct companions, who were also seen with each other
Pairs	Number of ordered pairs present in the network (hence, the number of potential dyadic ties that could exist)	Number of ties if all of subject’s direct companions were also seen with each other
Density	Ties divided by Pairs	The proportion of actual ties to potential ties, hence how well-connected companions are to each other
2-step reach	Number of individuals within two links (degrees) of the subject	Friends of friends; indirect connections
Broker	Number of pairs that are not directly connected	Number of subject’s direct companions who were not seen with each other

Table II - 2. Ego network measures for individuals present in all time periods (N=105).

Season	**Network Measure (Avg ± SE)**												
	Size		**Ties**		**Pairs**		**Density**		**N_{dens}**	**2 Step Reach**		**Broker**	
Trans1	8.25	±0.58	56.63	±5.79	94.27	±11.69	75.31	±2.54	101.00	22.98	±1.53	18.82	±3.25
Dry1	10.91	±0.77	96.17	±10.06	169.45	20.72	69.57	±2.38	100.00	34.49	±2.12	36.64	±5.65
Wet1	9.89	±0.67	77.66	±8.91	134.34	±18.21	67.21	±2.41	100.00	28.22	±1.72	28.34	±4.93
Dry2	11.75	±0.92	143.94	±19.06	214.17	±28.79	70.25	±2.41	102.00	32.86	±2.00	35.11	±5.70
Wet2	6.17	±0.36	25.43	±2.03	45.24	±4.80	70.46	±2.79	102.00	16.94	±1.09	9.90	±1.54

Table II - 3. Two-tailed paired signed-rank comparisons of ego networks across seasons using matched datasets with only those subjects seen in all time periods. N is the number of individuals included in the comparison. A significance of '***' indicates two-tailed $P < 0.001$, '**' indicates $P < 0.01$ and '*' indicates $P<0.05$.

Measure	T1 vs. D1	N	D1 vs. W1	N	T1 vs. W1	N	D1 vs. D2	N	D2 vs. W2	N	W1 vs. W2	N
Size	0.86	132	0.93	155	0.06	125	1.00	148	***	133	***	130
Ties	1.00	132	0.74	155	*	125	0.62	148	***	133	***	130
Pairs	0.78	132	0.87	155	*	125	0.93	148	***	133	***	130
Density	0.11	121	0.60	140	**	110	0.66	139	0.92	125	0.55	119
Broker	0.20	132	0.93	155	**	125	0.86	148	***	133	***	130
2 Step Reach	0.72	132	0.87	155	**	125	0.28	148	***	133	***	130

Table II - 4. Association patterns across seasons for individuals who were seen in all seasons. 'Curve type' is the K-means curve that best describes the trajectory of the association between two individuals, shown in Figure II - 8. Curves I - V represent single peaks in each season, whereas curve VI shows dry season peaks. L is the minimum number of times an individual had to be seen in order to be included in the analysis and N is the sample size after this reduction. Nonzero dyads is the number of dyads that had a nonzero SRI value in at least one time period (i.e. were seen together at least once in the five seasons) whereas the number of possible dyads is the number of possible pairs of associations. Therefore % nonzero dyads is analogous to network density under these restrictions.

All dyads. L ≥ 30, N = 53			
Curve type	**No. dyads**	**No. indiv**	**% dyads**
Curve I	122	42	21.59
Curve II	110	48	19.47
Curve III	107	43	18.94
Curve IV	91	48	16.11
Curve V	80	47	14.16
Curve VI	55	34	9.73
No. nonzero dyads	565		
No. poss dyads	1378		
% nonzero	41		

Figure II - 1. Season designation based on rainfall. The number of elephant sightings increases over the course of a year but mirrors change rainfall on a monthly basis. T1 represents an alternation of seasons whereas the T2 and T3 are the intersections of two seasons.

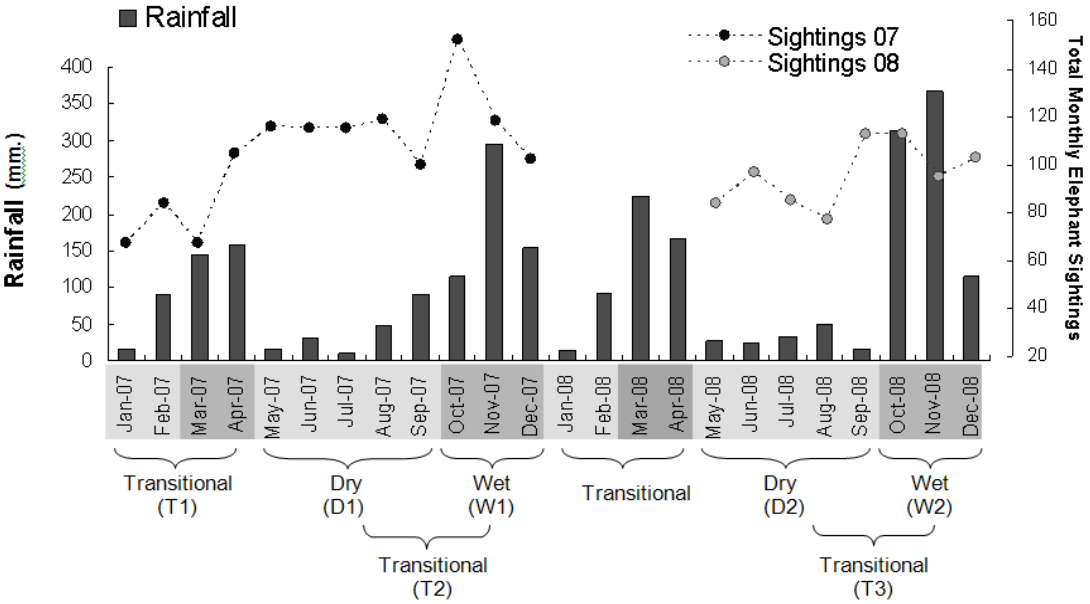


Figure II - 2. Complete social networks in each season. Nodes represent adult females and edges (ties) are dyadic SRI values. ‘Random’ is a dataset generated by permutation described in methods. Observed networks have distinct sub-networks, whereas randomized datasets do not. The second wet season is fragmented into larger sub-networks than any other season. N=168, 209, 180, 169, and 165 for T1, D1, W1, D2 and W2 respectively.

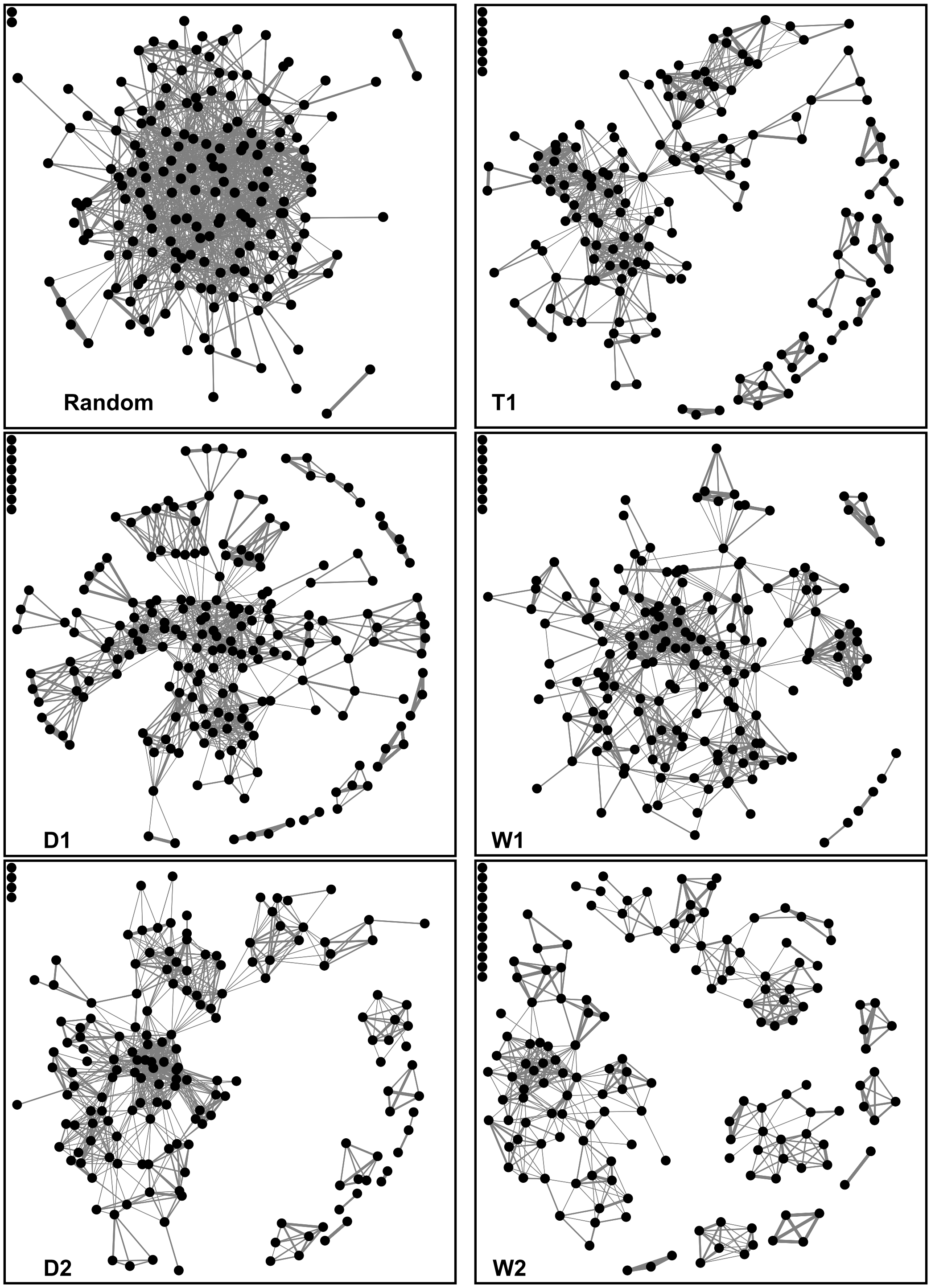

Random
T1
D1
W1
D2
W2

Figure II - 3. Overlap in total observed ranges among three social units. Individuals belonging to the same Girvan-Newman cluster in T1 are indicated by color. Individuals that cluster together have the best overlap, but a high overlap does not imply individuals are affiliated. Individuals with high overlap (brown, green) may cluster separately and never interact (see Figure II - 5).

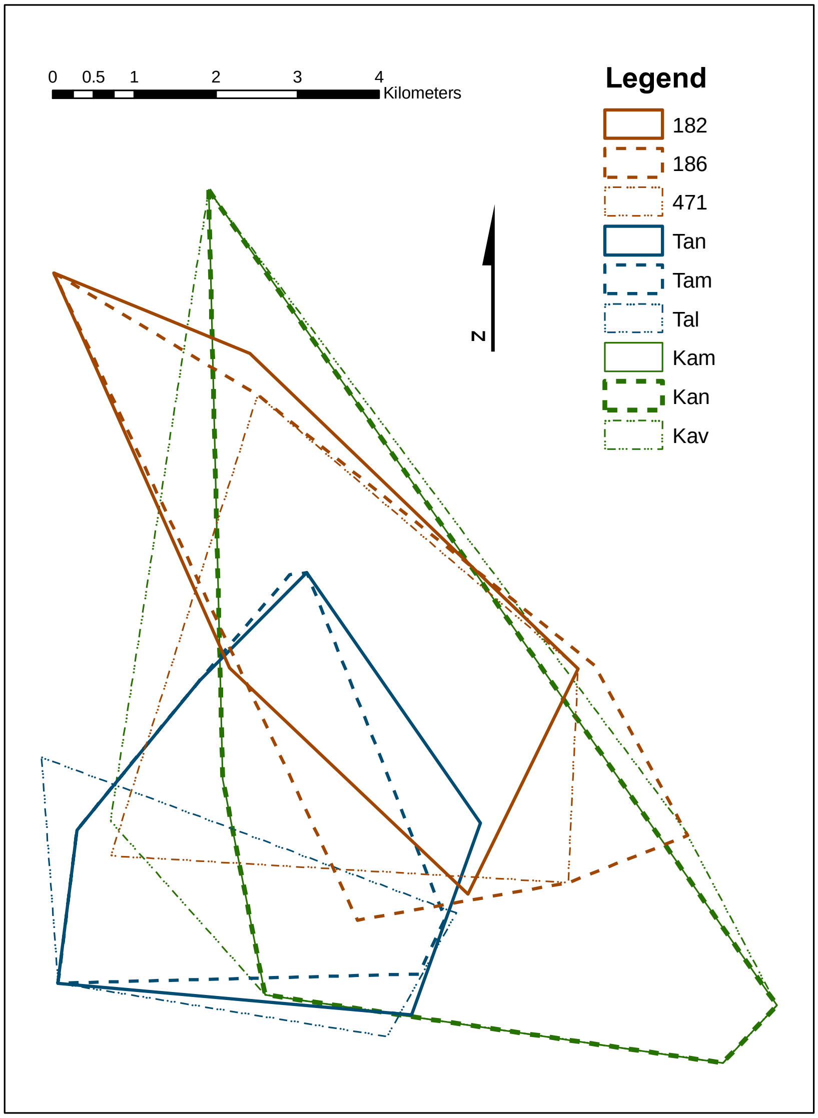


Figure II - 4. Seasonal tier structures. Plateaus or ‘tiers’ occur for T1 between SRI thresholds 0.17-0.24 (IV: 23 clusters), 0.25-0.28 (III: 28 clusters), and 0.35-0.56 (II: 36-38 clusters); for D1 at 0.11-0.16 (V: 25 clusters), 0.20-0.24 (IV: 34-36 clusters), 0.26-0.30 (III: 40 clusters) and 0.38-0.49 (II: 44-45 clusters); D2 at 0.13-0.16 (III: 20 clusters) and 0.25-0.49 (II: 29-32 clusters) W2 plateaus at 0.21-0.24 (IV: 24 clusters), 0.25-0.32 (III: 29-30 clusters) and 0.33-0.54 (II: 33-35 clusters). W1 peaks at 0.36 (35 clusters). Tier I mother-calf units are not considered. These are the total number of clusters into which the network can be divided, not the particular set of clusters that belong to that interval. It is the difference in the number of clusters between one tier and the next that are unique. E.g. plateau II in D1 represents 4-5 clusters which merge together forming plateau III, and this is composed of 4-6 clusters which merge to form plateau IV etc. Networks can be clustered more than one way at certain SRI intervals, notably 0.18-0.19 in D1 and 0.2-0.21in D2 and W2. Ties within these intervals position certain individuals in more than one possible cluster.

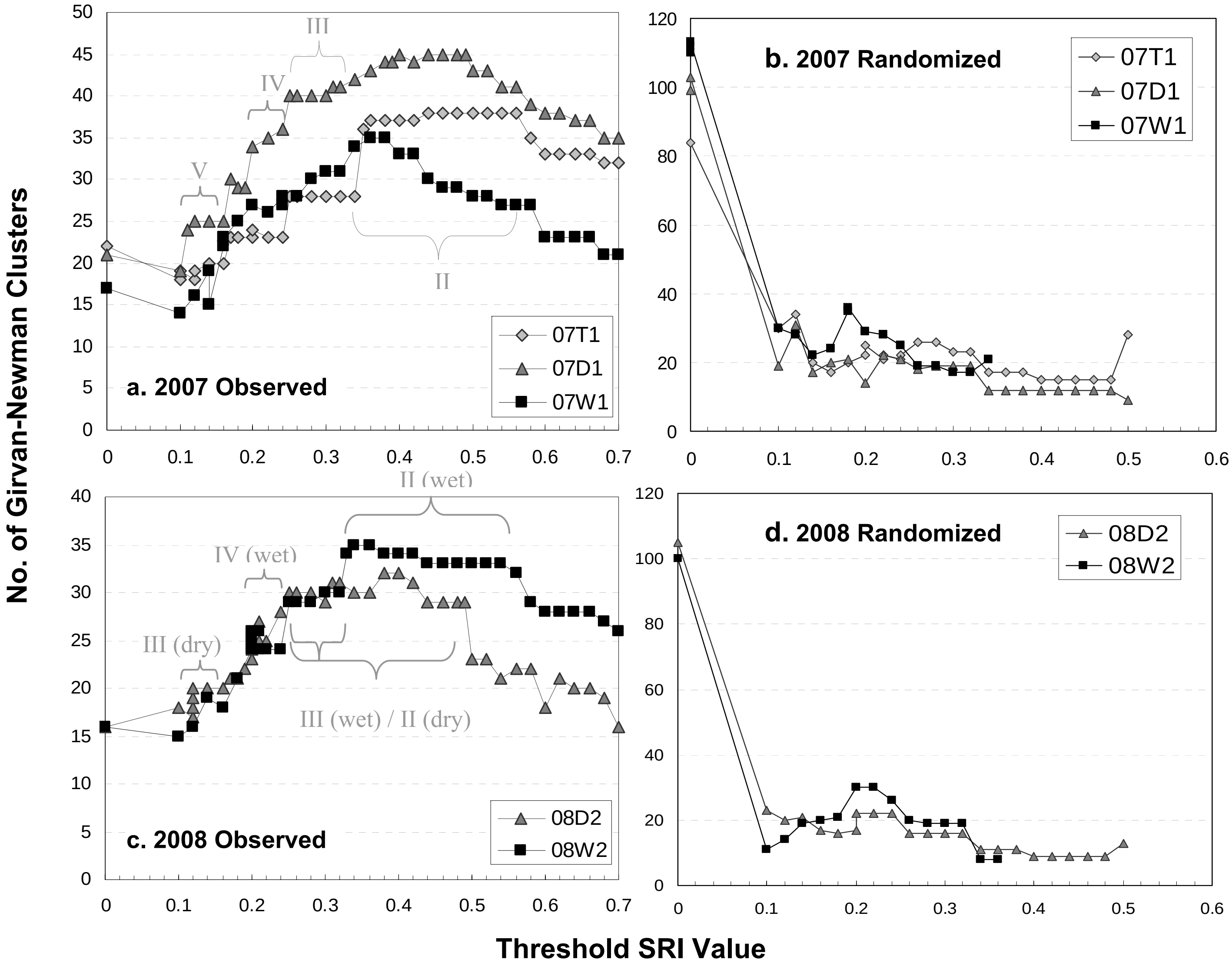

No. of Girvan-Newman Clusters
Threshold SRI Value
a. 2007 Observed
07T1
07D1
07W1
V
IV
III
II
b. 2007 Randomized
07T1
07D1
07W1
c. 2008 Observed
08D2
08W2
III (dry)
IV (wet)
II (wet)
III (wet) / II (dry)
d. 2008 Randomized
08D2
08W2
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0
5
10
15
20
25
30
35
40
45
50
20
40
60
80
100
120

Figure II - 5. Networks showing Girvan-Newman clusters for T1. Social networks for adult females in January-April 2007 colored according to the clustering with the highest Q value at the indicated threshold, T. The width of a tie indicates tie strength. Individuals who do not have ties at or above the threshold value are removed. Some individuals lack strong ties entirely. Arrows in (d) indicate groups enlarged in (e)-(g). Maximum separation of groups occurs at tie strengths (SRI values) above 0.4 (d) or 0.3 in other seasons. Beyond 0.6 however, these clusters also degenerate and beyond 0.7 too few individuals remain to continue (e)-(g).

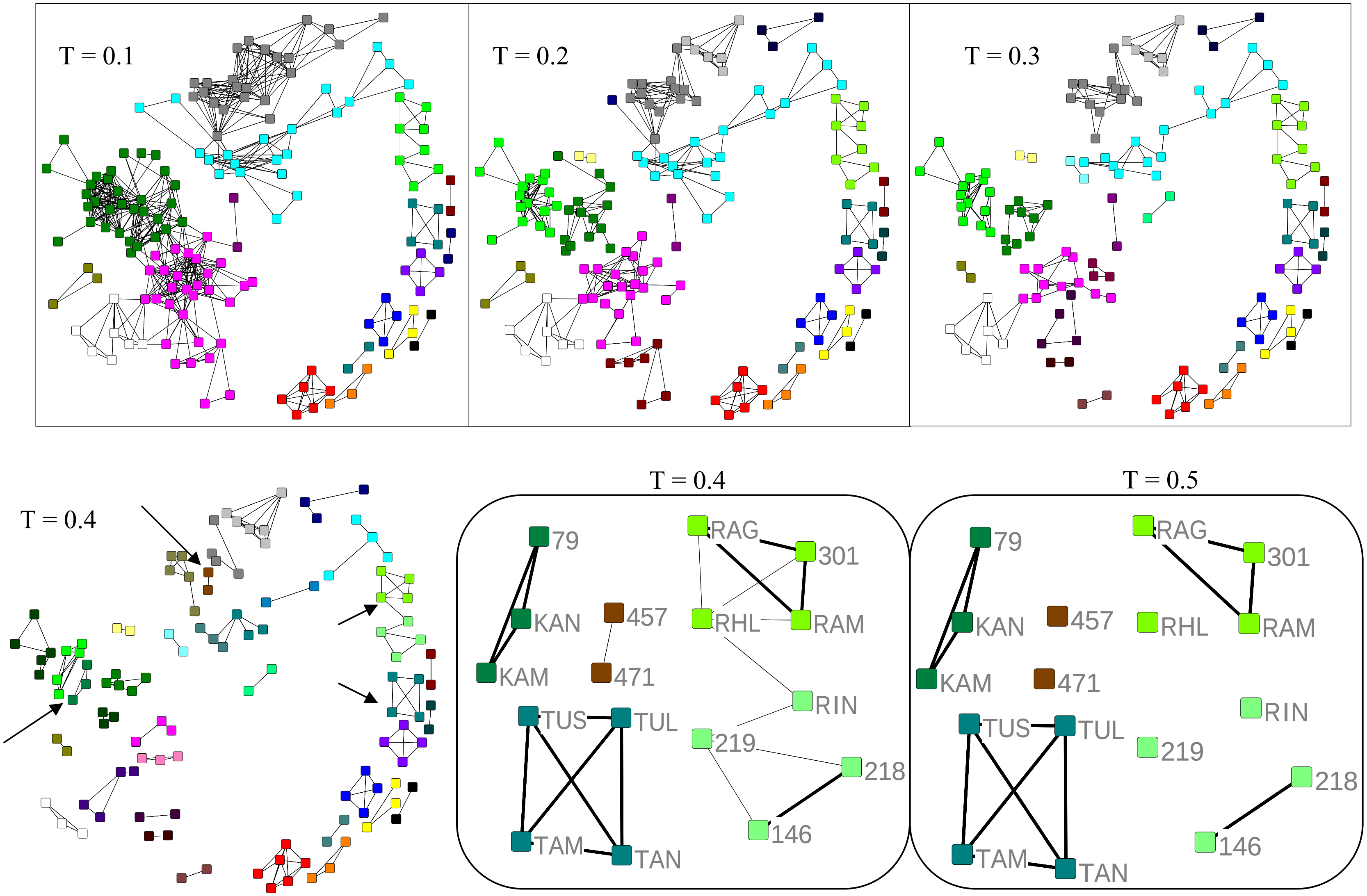

T = 0.1
T = 0.2
T = 0.3
T = 0.4
T = 0.4
T = 0.5
79
KAN
KAM
457
471
RAG
301
RHL
RAM
RIN
219
218
146
TUS
TUL
TAM
TAN
79
KAN
KAM
457
471
RAG
301
RHL
RAM
RIN
219
218
146
TUS
TUL
TAM
TAN

Figure II - 6. Tier structure for matched datasets. T1a is the T1 dataset matched to D1 (N=142 individuals) whereas T1b is the T1 dataset matched to W1 (N=123 individuals). Both D1 and W1 are matched to T1. Thus each panel shows how relationships among the same individuals have become re-organized. **a)** D1 remains similar to T1 and is more similar to T1a than to W1. **b)** T1b is similar to W1, but the number of clusters (SRI < 0.32) in W1 is lower and the number of strong ties within clusters (SRI > 0.34) is much lower.

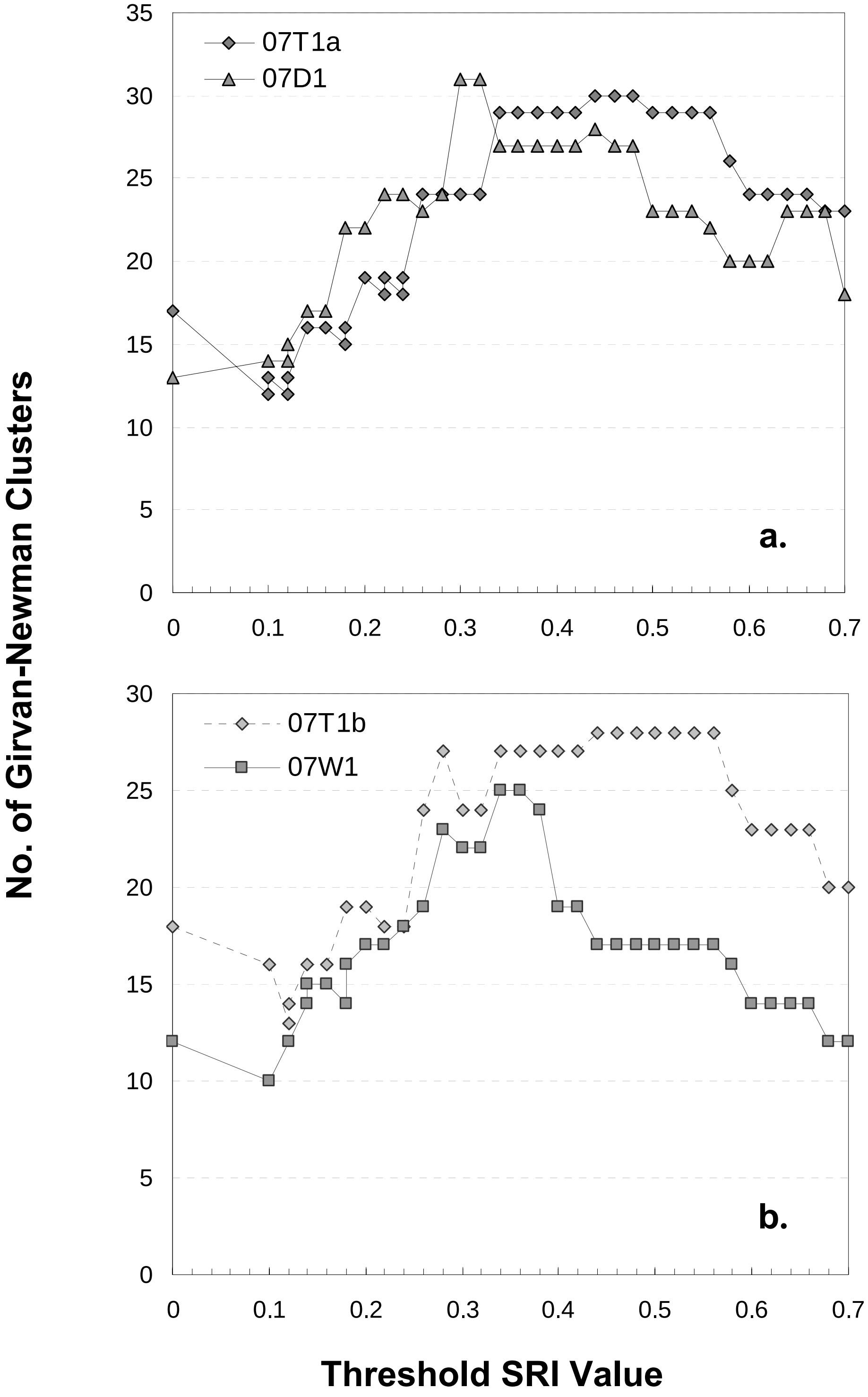

No. of Girvan-Newman Clusters
07T1a
07D1
a.
35
30
25
20
15
10
5
0
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
07T1b
07W1
b.
30
25
20
15
10
5
0
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Threshold SRI Value

Figure II - 7. Ego-networks of selected individuals. Egos are larger circles embedded in squares. T1 is colored according to the Girvan-Newman cluster assignment (Figure II - 5). In all subsequent periods, individuals in gray are those who were not associated with the ego in any previous time interval. Ego networks consist almost entirely of individuals who previously associated with the subject, even if not all associates were present in all seasons, but this is not apparent until the fifth season of observation.

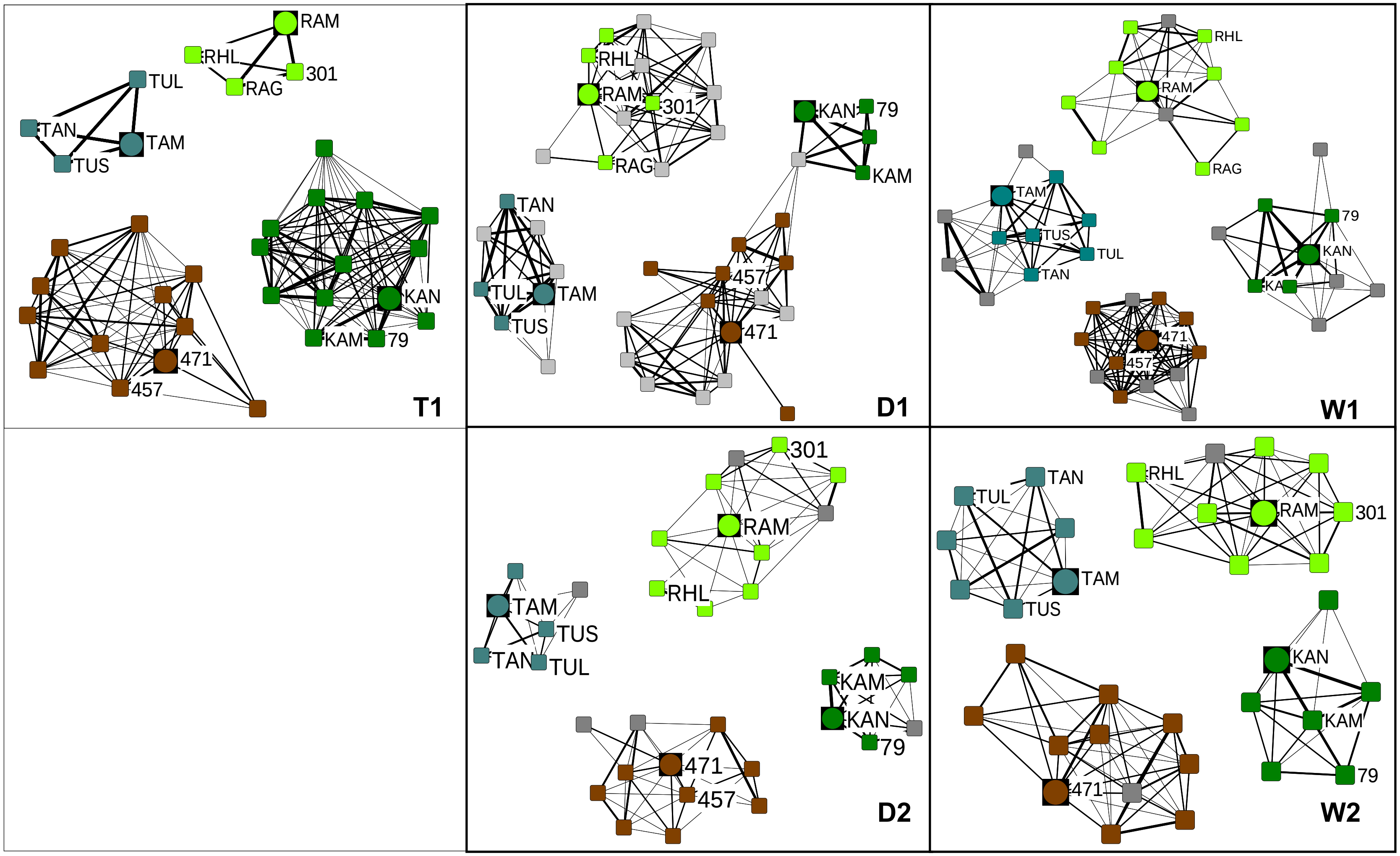
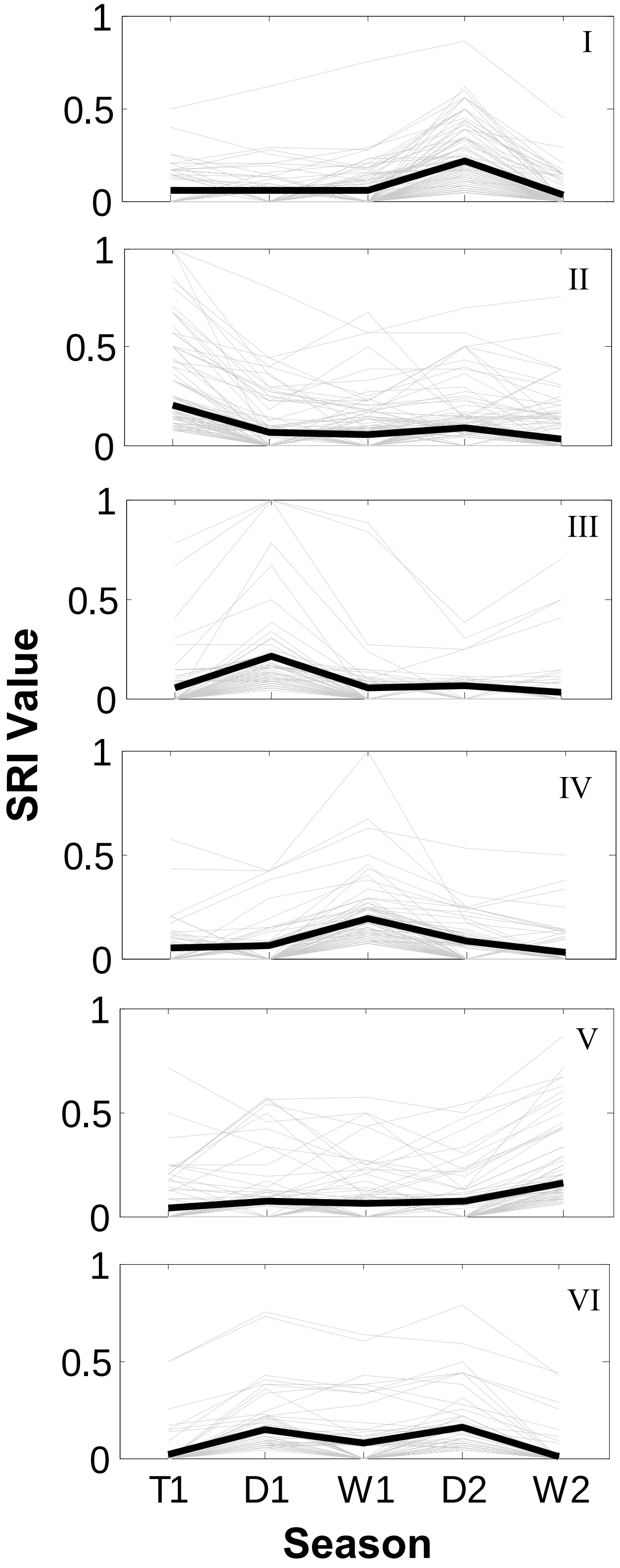
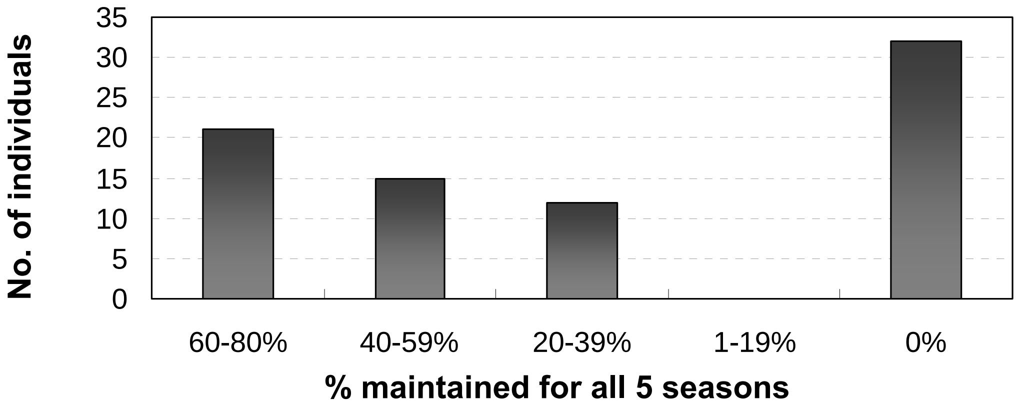

RAM
RHL
301
RAG
TUL
TAN
TAM
TUS
471
457
KAN
KAM
79
T1
RHL
RAM
301
RAG
KAN
79
KAM
TAN
TUL
TAM
TUS
457
471
D1
RHL
RAM
RAG
TAM
TUS
TUL
TAN
79
KAN
KA
471
457
W1
301
RAM
RHL
TAM
TUS
TAN
TUL
KAM
KAN
79
471
457
D2
TAN
TUL
TAM
TUS
RHL
RAM
301
KAN
KAM
79
471
W2

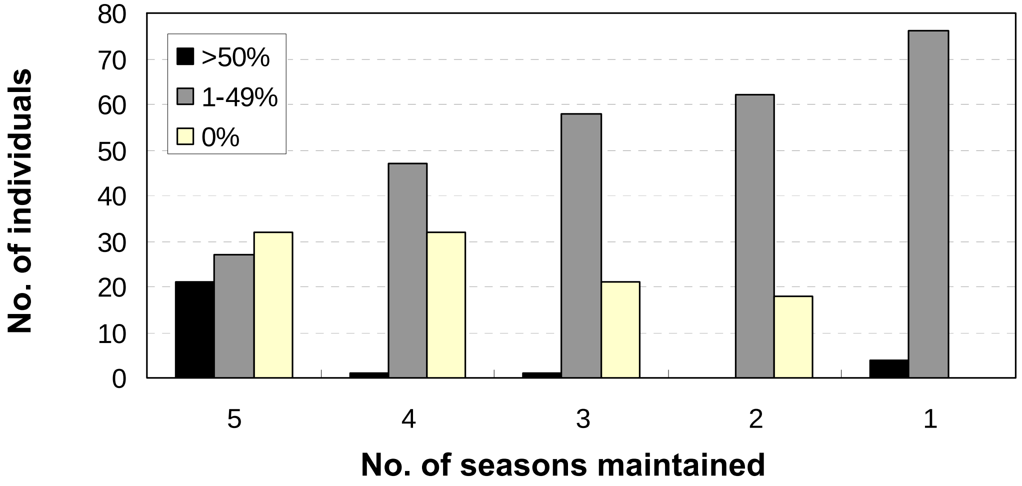
Figure II - 8. Characteristic association patterns based on K-means clustering for individuals seen in all time periods. Patterns are dominated by weak associations. Curves I - V represent associations that are strong for a single season, though many persist at lower levels in other seasons. Curve VI represents associations that were cyclic from one dry season to the next. The number of individuals and dyads that fall under each type of curve is given in table 4. Only 7 dyads maintained ties above 0.3 in all five seasons.



SRI Value
1
0.5
0
I
II
III
IV
V
VI
T1
D1
W1
D2
W2
Season

Figure II - 9. The length of time for which close associates are maintained. 'Close' means the top five companions for 80 individuals who were seen in all time periods and at least 20 times. All 'top companions' are those who cluster with the subject in most, if not all, time periods – hence, they are not individuals from different social units entirely. Rather, they are preferred companions from within an individual's own social unit. The top panel shows the percentage of companions maintained in all five seasons; none maintain over 80% in all five seasons. At least four individuals keep their top three preferred companions for all five seasons, but few consistently maintain the same top companions. The lower panel merges these percentages into three categories instead of five (0%, 1-49%, 50-100%), and shows the number of seasons for which they were maintained, regardless of chronological order. Hence a companion who was ranked in the top five in only season 1 and season 4 would have held the position for two seasons.


No. of individuals
35
30
25
20
15
10
5
0
60-80%
40-59%
20-39%
1-19%
0%
% maintained for all 5 seasons


No. of individuals
80
70
60
50
40
30
20
10
0
■ >50%
■ 1-49%
□ 0%
5
4
3
2
1
No. of seasons maintained

CHAPTER III.

Social Associations Among Female Asian Elephants And Resource Distribution

SUMMARY

Resource utilization is a basic determinant of animal movement and, by extension, social systems. Yet few studies actually incorporate resource distribution in determining whether or not individuals show preferential association, particularly in species that do not hold exclusive territories. We propose that a true social unit differs from a simple aggregation of individuals such that in the former (a) associations among individuals are likely to persist much longer, and thus (b) movement of individuals will be more coordinated. We fit spatially-explicit mechanistic models of movement to field observations of 310 female Asian elephants over two years. We assess which of three possible explanations best explain sightings: random movement (Model 1), random movement in the presence of changing resources (Model 2) or coordinated movement among multiple individuals in the presence of changing resources (Model 3). We show that Asian elephants engage in coordinated movement with select companions, demonstrating social preferences even after accounting for seasonal changes in resource distribution and shared use of space.

INTRODUCTION

The distribution of resources has a direct influence on how individuals in a population encounter and interact with conspecifics. This simple observation has important implications for the study of grouping behavior and social organization. An animal's need for resources is a fundamental determinant of its use of space, which in turn determines basic aspects of a species' biology, such as its mating system (Emlen & Oring, 1977), offspring sex ratios and dispersal (Silk & Brown 2008; Komdeur & Edelaar 2001), and social organization (Wrangham, 1980; Van Schaik, 1983; Pen & Weissing, 2000; Ingram, 2002; Johnstone, 2008). Together with the risk of predation, resource competition governs the degree to which individuals hunt (Smith et al., 2008), breed (Emlen, 1982; Emlen, 1984; Faulkes et al., 1997; Burgmuller et al. 2005; Beck et al., 2008), or forage (Heinrich, 1988; Chapman et al., 1995; Baird & Dill 1996; Asensio et al. 2009) collectively. Collective behavior need not be cooperative, as exemplified by the 'forced march' of Mormon crickets (Simpson et al. 2006). Resource distribution indirectly also governs higher levels of organization, the extent to which multiple groups of the same or different species occupying similar ecological niches, coexist in space (Rolando & Giachello, 1992).

Studies of social organization typically begin with computing the fraction of time an individual is observed together with some other individual, termed an association index (Hinde, 1977; Ginsberg & Young, 1992; Cairns & Schwager, 1987; Whitehead & Dufault, 1999; Whitehead et al., 2005). If a pair of individuals is seen together more frequently than expected by chance it is taken as evidence that these individuals "prefer" the companionship of one another, and conversely, those seen together less frequently than expected by chance are said to “avoid” one another (Whitehead at al. 1999; Whitehead et al., 2005). For species that hold exclusive territories, nests, or dens, defining social units is straightforward, as they are spatially distinct. Thus such indices can be used to quantify the strength of ties and apparent preferences within already defined social units.

However, deciding what constitutes a social unit is itself problematic for nomadic species that travel along with changing resources, or those who do not defend territories. Such individuals may come into contact without necessarily having any social affiliation. This is typified by many species whose social organization is termed ‘fission-fusion’ (spider monkeys: Boyer et al., 2006; African buffalo: Cross et al. 2005), though some still maintain territories despite this (chimpanzees: Goodall et al 1979; Chapman et al. 1995; hyenas: Smith et al., 2008). The challenge in the case of species with overlapping home ranges is to distinguish those individuals that indeed prefer one another from those that merely happen to be at the same place at the same time by chance. In practice, this poses two major problems. The first is in defining what constitutes "being together". The second is in quantifying the expression "more often than expected by chance". Only then may one infer which particular sets of individuals in fact constitute social units, if at all.

Whether one individual is ‘with’ another individual is usually determined by the observer, based on spatial proximity and behavior. The degree to which an individual ‘prefers’ the companionship of another – i.e. whether an association is stronger than expected by chance alone – is typically obtained by permuting matrices of association under the null hypothesis that any individual is as likely to be seen with any other individual, without explicit reference to location (Bejder et al. 1998; Whitehead 1999; Whitehead & Dufault 1999; Whitehead et al. 2005; Sundaresan et al. 2009). Both steps in this procedure raise non-trivial issues.

Observer-dependent definitions of association are advantageous on one hand because observers can take into account behavioral cues about who is actively seeking companionship with whom, such as coordinated activity, affiliative interactions, or vocal communication (Whitehead & Dufault 1999). But they can also introduce spatial biases. Some species may segregate into spatially disctinct subgroups within aggregates (Kawai et al. 1983; Wolf et al. 2007; Carter et al. 2009), and thus observers may group them by distance using procedures like the 'chain rule' (Whitehead et al. 1999; Carter et al. 2009). Others may segregate and fuse too rapidly to permit this (Cross et al. 2005). Even when there is apparent spatial structure, it doesn't necessarily mean it is biologically relevant to the animals themselves unless they actively maintain this structure (White & Smith 2007). What a human observer perceives as a 'group' may not be what the animals themselves perceive, for instance if their range of communication exceeds the perceptual range of the observer (Langbauer et al. 1991; Croll et al. 2002; Garstang 2004; but see McComb et al. 2003), which can depend on habitat or other arbitrary constraints. In such cases, the observer may perceive only part of the true social unit. To address these issues, individuals from 'groups' observed in the field must be re-clustered using alternate means into true social units (e.g. hierarchical cluster analysis: Wittemyer et al. 2005; simulated annealing: Wolf et al. 2007; Girvan-Newman algorithm: de Silva, Ch.II). Thus observing and quantitatively defining social units is far from standardized, making it unclear how to compare across taxa.

Permutation tests for preference and avoidance suffer from several major drawbacks. First, they may give spuriously significant results if the time intervals between observations are short relative to the time it takes for individuals to change associations (Sundaresan et al. 2009). In other words, individuals would appear to associate preferentially, even if they do not, if observation intervals are not sufficiently long enough to detect changes in companionship. A second problem is that individuals who are attracted to the same resources, which are themselves changing with time, may by chance appear to associate and thus show “fission-fusion” dynamics (Ramos-Fernández & Boyer, 2006). A third problem is that the permutation tests effectively assume that individuals are equally likely to be found at any location of the study site at any point in time. This assumption is unjustified if the observer travels further than a subject is likely to during the same interval. If two individuals are seen physically further apart than they would travel during some interval, it is misleading to treat them as though they could co-occur in that interval. In short, standard permutation tests ignore space and time.

The problem of spurious significance can be solved relatively easily if the data are partitioned by sampling occasions of appropriate length (Sundaresan et al. 2009). The problem of chance co-occurrence may be addressed if observers are in fact perceive social interactions that confirm a grouping of individuals constitute true associates. However, it is highly unlikely that an observer would ever see social interactions among all possible pairs of individuals at a high enough frequency to make any statistical statements. Finally, the problem of distance requires explicit treatment of resource distribution and movement. A more stringent null hypothesis should take into account that not every individual could be seen with every other individual simply based on their physical locations, and that even among those who share range, associations among individuals may not reflect social preference, but resource availability. We propose that a true social unit differs from a simple aggregation of individuals such that in the former (a) associations among individuals are likely to persist much longer, and (b) movement of individuals will be more coordinated. This potentially addresses these several issues simultaneously. Determining social units, if they exist, can be carried out through an automated process that does not rely on observer-based 'groups'. Moreover, coordinated movement is a universal metric by which to define social units that is applicable to a wide range of taxa, irrespective of spatial scale or observer constraints.

We quantify social affiliations among adult female Asian elephants using only the spatial and temporal coordinates of identified individuals. Bonds among female Asian elephants are very dynamic, constituting a fission-fusion social system in which individuals regularly change companions (Chapter II.), previous studies show that even relatives appear to have low rates of association (Fernando et al. 2001; Vidya and Sukumar 2005). We therefore ask whether associations among individuals could arise solely as a by-product of resource distribution – i.e. without social preferences among individuals. We define the following terms:

Group – A set of individuals that distinctly appear to field observers as interacting and moving together. But this phenomenon may or may not be permanent. At this field site, the visibility can range from 10m to >1km, and most observations are from areas with a visibility of 500m or more. We do not distinguish 'subgroup' from 'group' since observers have no way of distinguishing them initially without some analytical procedure and without making the assumption of permanence.

Aggregation – Multiple groups that appear to field observers as occurring in close proximity, for instance, at a resource. This also implies no permanence.

Cluster – A set of individuals that associate together with each other more than they associate with others over a time period. This differs from 'group' and 'aggregation' in being observer-independent units resulting from a quantitative procedure (Wittemyer et al. 2005; Chapter II) as opposed to qualitative definitions. However, it signifies nothing about the reasons for which individuals may associate together.

Social unit – A cluster of individuals that associate together more highly than expected based on environmental influences alone, and thus are likely to reflect preferential association over a defined time period.

We assess the probability of individuals co-occurring as functions of their movement. In this paper we ignore observer-defined phenomena such as groups and aggregations. We reason that social preferences would be distinguished from resource utilization if individuals actively moved together with only some conspecifics and not others despite shared space. True social associates should co-occur at a higher degree than expected from the shared space alone, regardless of whether an observer saw them simultaneously. We develop a set of spatially-explicit mechanistic models with parameters that could be chosen to suit three hypotheses about the process underlying data, where data are the observed spatio-temporal coordinates of individuals (Table III - 1). This allows us to detect coordinated movement among individuals regardless of the spatial scale on which it occurs, and regardless of whether multiple un-affiliated individuals in fact use the same space.

We test three possible models of association:

Model 1 (H0, M1): This basic null model assumes that each individual randomly moves around the center of its habitat. We assume that movement can be described as Brownian motion with a spring. Failure to reject this model would mean that observations of individuals were explainable simply by their movement.

Model 1 (H1, M2): The spatial heterogeneity model. Failure to reject this model would mean that observations were explainable by elephants' attraction to resources alone. We concentrate specifically on the availability of water, which constitute resources that changes seasonally in location and availability, unlike food (grass and browse) which is distributed similarly throughout the year. Placement of water influences the movement of African savannah elephants (Loarie et al. 2009).

Model 3 (H2, M3): Social affiliations despite resource heterogeneity. Individuals cluster into units that move in a coordinated manner. We make two simplifying assumptions that a) all individuals in the same cluster always move together and b) that clusters are independent. Under this framework, clusters are social units by definition.

Permutation tests for preferred associations among individuals (Bejder et al. 1998; Whitehead 1999; Whitehead & Dufault 1999; Whitehead et al. 2005; Sundaresan et al. 2009) are analogous to testing H2 against H0, without considering H1 or movement. In addition to providing a means to evaluate the probability of H1 itself, mechanistic models allow us to examine the effect of changes in the spatial distribution of water on elephant movement, and as a consequence, cluster formation.

METHODS

Data collection

We consider only observations within a national park, where human activity is least likely to affect movement. Uda Walawe National Park (UWNP), Sri Lanka, encompasses 308 km^2 at latitude 6° 30' 14.0646", longitude 80° 54' 28.1268", and average altitude of 118m. Habitat includes tall grassland, dense scrub, riparian forest, secondary forest, a permanent river, and seasonal streams. The park also contains several water holes and two man-made reservoirs with seasonal floodplains (DWC, 1997) constituting seasonal as well as permanent water sources. Rainfall measured using a standard U.S. Weather Bureau rain gauge ranged from 1293-1726mm annually. Dry months (January-February and May-September) received 45.5mm and wet months (March-April and October-December) received on average of 230.4mm, corresponding to two annual monsoons (Zubair et al. 2008). For our models, water distribution was simplified into rectangular areas based on the locations of actual water sources (Figure III - 1).

This study was begun in May 2006. The data presented span 175 field days (sixteen months) from 2007-2008, or three days per week on average. This constitutes four seasons, two wet and two dry. We typically entered the park between 600-700h (sunrise), remaining continuously inside until 1730-1830h (sunset). Driving routes were varied such that all accessible parts of the park were covered in a week. Locations where animals were closest to the road were marked on a hand-held Garmin GPS unit. The study included 310 females (286 adults and 24 subadults). All were individually-identified using photographs of natural markings (Moss 1983). Sighting dates and times were recorded using an HP ipaq hand-held PDA.

Model construction

In this section we describe a hierarchy of mechanistic models of the data presented in Table III - 1. As mentioned, the data consists of the coordinates and times of all observations for each individual in the population in a given season. The models depend on a number of parameters that have straightforward physical interpretations. If some parameters are set to certain values, the resulting model corresponds to a mathematical formulation of one of the hypotheses described previously. Our goal, therefore, is to fit each of the models to data and to decide which of the models most adequately describes the data.

For the sake of clarity, we will present the construction of the models in several steps, starting with the simplest one. We will first show how we model the movement of a single individual in homogeneous space (Model 1). We will then see how the model changes when resources are defined (Model 2). Finally, we extend the model to include the possibility that sets of individuals move together (Model 3).

Model 1. Independent individuals, homogeneous space

We model the movement of each individual by the "noisy spring model" which is borrowed from physics (Gardiner 2009) and is similar to the "localizing tendency model" used by Moorcroft and Lewis (2006). The noisy spring model has 4 parameters: the 'diffusion constant' *D*, where $D > 0$, the 'spring constant' κ, where $\kappa > 0$ and the 'range center' $(\bar{x}, \bar{y})$ which is a point in the center of an individual's observed spatial range. We assume that *D* and κ are the same for all individuals, while range centers may, naturally, differ between individuals. The fact that all individuals have the same diffusion and spring constants is equivalent to assuming that all individuals experience the same degree of randomness in their movement and occupy a space of the same size. Although clearly unrealistic, these two assumptions represent a starting point. The 'range center' is a point to which the individual is attracted. Although the movement of an individual is fundamentally stochastic, it is biased towards the range center. This ensures that, in accordance with biological reality (Fernando et al. 2008), an individual never moves away too far from its preferred area. Mathematically, this translates to the existence of a stationary distribution in this model.

The noisy spring model gives the probability $B(x_i, y_i, t_i \mid x_{i-1}, y_{i-1}, t_{i-1})$. In other words, the probability of finding an individual at location (x_i, y_i) at time t_i, given that it was at location (x_{i-1}, y_{i-1}) at some previous time t_{i-1}.

$$B(x_i,y_i,t_i \mid x_{i-1},y_{i-1},t_{i-1}) = \frac{1}{2\pi\sigma_i^2}\exp\left\{-\frac{(x_i-\mu_i)^2+(y_i-\nu_i)^2}{2\sigma_i^2}\right\}, \qquad [1]$$

where

$$\begin{aligned} \mu_i &= \bar{x}+(x_{i-1}-\bar{x})e^{-\kappa(t_i-t_{i-1})}, \\ \nu_i &= \bar{y}+(y_{i-1}-\bar{y})e^{-\kappa(t_i-t_{i-1})}, \\ \sigma_i^2 &= \frac{D}{2\kappa}\left(1-e^{-2\kappa(t_i-t_{i-1})}\right). \end{aligned} \qquad [2]$$

This is a multivariate Gaussian distribution with mean vector $(\mu_i,\nu_i)^T$ and covariance matrix $\begin{pmatrix}\sigma_i^2 & 0\\ 0 & \sigma_i^2\end{pmatrix}$. It can be seen from the set of equations [2] that this distribution is centered around the previous location, (x_{i-1},y_{i-1}), if the current observation is made soon after the previous observation, i.e., if $t_i - t_{i-1} << \kappa^{-1}$, and it is centered around the range center, $(\bar{x},\bar{y})$, if the current observation is made much later than the previous observation, i.e., if $t_i - t_{i-1} >> \kappa^{-1}$. Thus, after sufficient time has passed, the noisy spring model stops depending on the initial condition and distribution [1]–[2] converges to its stationary form $B_\infty(x,y)$.

$$B_\infty(x,y) = \frac{\kappa}{\pi D}\exp\left\{-\frac{\kappa}{D}\left((x-\bar{x})^2+(y-\bar{y})^2\right)\right\}. \qquad [3]$$

Parameters D and κ have intuitive physical interpretations that correspond to equations [1]–[3]. Diffusion constant D determines the degree of randomness in the movement of an individual: higher values of D imply more stochastic movement. Spring constant κ characterizes the strength with which individuals are attracted to their range centers: smaller values of κ imply that individuals can more easily diffuse away from the center of their range. From equations [2]–[3], the ratio $\rho = D/(2\kappa)$ equals the variance of the stationary probability distribution for the spatial location of an individual in this model.

Equations [1]–[3] are sufficient to compute the likelihood of the data such as those in Table III - 1 for each individual separately, assuming that the environment is homogeneous. If individual n is observed L_n times and if the observation coordinates and times for this individual are $(x_1^{(n)}, y_1^{(n)}, t_1^{(n)}), \ldots, (x_{L_n}^{(n)}, y_{L_n}^{(n)}, t_{L_n}^{(n)})$, then the likelihood of these observations is

$$L_{M1}(\text{data for individual } n; D, \kappa) = B_\infty(x_1^{(n)}, y_1^{(n)}) \prod_{i=2}^{L_n} B(x_i^{(n)}, y_i^{(n)}, t_i^{(n)} \mid x_{i-1}^{(n)}, y_{i-1}^{(n)}, t_{i-1}^{(n)}). \quad [4]$$

Here we omitted the range center $(\bar{x}^{(n)}, \bar{y}^{(n)})$ from the list of parameters for individual n. Although we can in principle estimate the range centers for all individuals, we would like to keep the number of free parameters to minimum. Instead we set the range center for an individual to be equal to the arithmetic mean of its observation coordinates (Moorcroft and Lewis, 2006), i.e., $\bar{x}^{(n)} = \frac{1}{L_n}\sum_{i=1}^{L_n} x_i^{(n)}$ and $\bar{y}^{(n)} = \frac{1}{L_n}\sum_{i=1}^{L_n} y_i^{(n)}$.

Finally, Model 1 states that individuals do not form any social units and, therefore, move independently from each other. Independence is meant in the probabilistic sense: knowing the position of one individual at any time, does not inform us about the position of any other individual at any other time. Mathematically, this means that the likelihood of data for all N individual together equals the product of likelihoods of data of each individual.

$$L_{M1}(\text{data}; D, \kappa) \;=\; \prod_{n=1}^{N} L_{M1}(\text{data for individual } n; D, \kappa) \quad [5]$$

Model 2. Independent individuals, heterogeneous space

One primary goal of this study is to understand how the movements of individuals are influenced by the presence of resources, which can be varied and complex in distribution. Here we focus on a single essential resource, water, and consider only the effect of attraction of individuals to water sources (cf. Moorcroft and Lewis, 2006). The locations of major water sources in UWNP are known: there are 10 water sources in the wet season and 3 water sources in the dry season (Figure III - 1). We ignore smaller ephemeral sources. We might expect that the probability of an elephant finding itself at or near a water source would be higher than elsewhere. We therefore designate areas A_j, where $j = 1, 2, 3, ..., R$, surrounding the known water sources and assume that the probability of an individual to be within any of these areas is increased by a factor of $1+\lambda$. Thus, λ ($\lambda \geq -1$) is a parameter of the model. Negative values of λ mean that areas A_j act as repellants.

For the sake of simplicity the areas A_j of increased probability are made rectangular, and some resources (e.g., the Uda Walawe Reservoir) are covered by several non-overlapping rectangles A_j (Figure III - 1). In order to write down the likelihood of data in the presence of water, we introduce the indicator function I_R such that, $I_R(x,y) = 1$ if the point (x,y) is located near a resource, i.e., if $(x,y) \in A_j$ for some j; and $I_R(x,y) = 0$ otherwise. Then the probability of finding an individual at location (x_i, y_i) at time t_i, given that it was at location (x_{i-1}, y_{i-1}) at some previous time $t_{i-1} \leq t_i$ is

$$P(x_i, y_i, t_i \mid x_{i-1}, y_{i-1}, t_{i-1}) = C_i B(x_i, y_i, t_i \mid x_{i-1}, y_{i-1}, t_{i-1}) \big(1 + \lambda I_R(x_i, y_i)\big). \qquad [6]$$

Here, $B(x_i, y_i, t_i \mid x_{i-1}, y_{i-1}, t_{i-1})$ is given by equation [1] and C_i is the normalization factor. Analogously to [3], the corresponding stationary distribution is

$$P_\infty(x,y) = C_\infty B_\infty(x,y)\big(1 + \lambda I_R(x,y)\big), \qquad [7]$$

where $B_\infty(x,y)$ is given by equation [3]. Finally, under Model 2, the likelihood of observations $(x_1^{(n)}, y_1^{(n)}, t_1^{(n)}), \ldots, (x_{L_n}^{(n)}, y_{L_n}^{(n)}, t_{L_n}^{(n)})$ of individual n is

$$L_{M2}(\text{data for individual } n; D, \kappa, \lambda) = P_\infty(x_1^{(n)}, y_1^{(n)}) \prod_{i=2}^{L_n} P(x_i^{(n)}, y_i^{(n)}, t_i^{(n)} \mid x_{i-1}^{(n)}, y_{i-1}^{(n)}, t_{i-1}^{(n)}). \; [8]$$

and the likelihood of the full data is

$$L_{M2}(\text{data}; D, \kappa, \lambda) \;=\; \prod_{n=1}^{N} L_{M2}(\text{data for individual } n; D, \kappa, \lambda) \qquad [9]$$

Note that $L_{M2}(\text{data}; D, \kappa, 0) \;=\; L_{M1}(\text{data}; D, \kappa)$, so that Model 2 with $\lambda = 0$ is equivalent to Model 1.

Model 3. Socially structured population, heterogeneous space

The other primary goal of this study is to understand how an individual's movement is affected by the movement of other individuals. Some individuals may prefer the company of some other individuals and thus move with them. In other words, the probability of an individual being at a given location may depend on the presence of other individuals at that location, such that individuals are in general not independent of each other in the probabilistic sense. Modeling a large collection of non-independent individuals in space is a difficult problem. In order to make it mathematically tractable, we make four crucial simplifying assumptions.

1. The set of all individuals observed in a given season is partitioned into subsets $C_1, C_2, \ldots, C_M$, which we call 'clusters', so that each individual belongs to one and only one cluster, and the union of all clusters consists of the set of all individuals. Let us call this partition *Z*. Critically, *Z* is assumed to be fixed through time, so that individuals cannot switch from one cluster to another. Biologically, this assumption implies that an individual's social preferences do not change within a season. *Z* is a parameter of the model.
2. Clusters are independent of each other in the probabilistic sense.
3. Each cluster behaves as a unit, which is to say that all members of the cluster share the same range and generally move together. The cluster range center is determined as the arithmetic mean of the range centers of its members.
4. There is a chance ε ($0 \le \varepsilon \le 1$) of failing to observe any particular member of the cluster, given that the cluster is present at the currently observed location. ε is another parameter of the model, and we call it 'the absence probability'.

These assumptions require perhaps some further clarification. Assumption 3 states that individuals share the range and generally move together as a unit, but does not necessarily imply that all members of a cluster are always *observed* together. Requiring the latter would be too strict, for the following reasons. First, there is a chance that the human observer fails to identify an individual that is present and observed. Second, there is a chance that, due to visual constraints, the human observer fails to notice an individual, even if the individual is currently nearby. Finally, there is a chance that an individual is absent from the currently observed location, even if most or all other cluster members are present at the location. Note that such situation does not violate assumption 1 as long as the individual is absent from its cluster temporarily and has not joined another cluster.

In order to determine the likelihood of the data under this model (Model 3), first consider one cluster C that consists of K_C individuals, and let $(x_1^{(C)}, y_1^{(C)}, t_1^{(C)}),\ldots,(x_{L_n}^{(C)}, y_{L_n}^{(C)}, t_{L_n}^{(C)})$ be the coordinates and times of observations at which at least one cluster member was observed. Let $k_1^C, k_2^C, \ldots, k_{L_c}^C$ be the number of cluster members that were observed, so that all $k_i^C \geq 1$. Let $(\bar{x}^{(C)}, \bar{y}^{(C)})$ be the cluster range center. Since the cluster moves as a unit according to assumption 3, the probability that the cluster is present at location (x_i, y_i) at time t_i, given that it was at location (x_{i-1}, y_{i-1}) at some previous time $t_{i-1} \leq t_i$, is

$$P^{(C)}(x_i, y_i, t_i, k_i \mid x_{i-1}, y_{i-1}, t_{i-1}, k_{i-1}) = P_{obs}(k_i, K_C) P(x_i, y_i, t_i \mid x_{i-1}, y_{i-1}, t_{i-1}), \qquad [10]$$

where $P(x_i, y_i, t_i \mid x_{i-1}, y_{i-1}, t_{i-1})$ is given by equation [6] with the individual range center $(\bar{x}, \bar{y})$ replaced by the cluster range center $(\bar{x}^{(C)}, \bar{y}^{(C)})$, and

$$P_{obs}(k, K) = \binom{K}{k} \frac{(1-\varepsilon)^k \varepsilon^{K-k}}{1-\varepsilon^K}$$

is the probability of observing k out of K cluster members, given that at least one member was observed. Analogously to [3] and [7], the corresponding stationary distribution is

$$P_\infty^C(x, y, k) = P_{obs}(k, K_C) P_\infty(x, y), \qquad [11]$$

where $P_\infty(x, y)$ is given by equation [7]. Then likelihood of observations $(x_1^{(C)}, y_1^{(C)}, t_1^{(C)}),\ldots,(x_{L_n}^{(C)}, y_{L_n}^{(C)}, t_{L_n}^{(C)})$ of cluster C is

$$
\begin{aligned}
&L_{M3}(\text{data for cluster } C; D, \kappa, \lambda, \varepsilon) \\
&= P_{\infty}^{(C)}(x_1^{(C)}, y_1^{(C)}, k_1^{(C)}) \prod_{i=2}^{L_C} P(x_i^{(C)}, y_i^{(C)}, t_i^{(C)}, k_i^{(C)} \mid x_{i-1}^{(C)}, y_{i-1}^{(C)}, t_{i-1}^{(C)}, k_{i-1}^{(C)}) \cdot
\end{aligned}
\qquad [12]
$$

Note that expression [8] accounts for all observations of all member of cluster C and so, individuals within the cluster are clearly not independent. However, according to assumption 2, clusters are independent, and so the likelihood of the full data can be expressed as

$$L_{M3}(\text{data}; D, \kappa, \lambda, \varepsilon, Z) = \prod_{j=1}^{M} L_{M3}(\text{data for cluster } C_j; D, \kappa, \lambda, \varepsilon) \qquad [13]$$

Note that, if $Z_0 = \{\{1\}, \{2\}, \ldots, \{N\}\}$ is the set of singleton-clusters (so that each individual forms its own cluster), $L_{M3}(\text{data}; D, \kappa, \lambda, 0, Z_0) = L_{M2}(\text{data}; D, \kappa, \lambda)$, so that Model 3 with $Z = Z_0$ and $\varepsilon = 0$ is equivalent to Model 2.

To summarize, the likelihoods of data under different models can be obtained by fixing the values of certain parameters in equation [13] and leaving the others unspecified (free). Model 1 (H_0, M1) assumes that individuals are independent and space is homogeneous: $Z = Z_0$, $\varepsilon = 0$ and $\lambda = 0$. D and κ are free parameters. Model 2 (H_1, M2) assumes that individuals are independent, but space is heterogeneous: $Z = Z_0$, $\varepsilon = 0$ are fixed. D, κ, and λ are free parameters. Model 3 (H_2, M3) assumes that space is heterogeneous and individuals are not independent. D, κ, λ, ε as well as the partition of individuals into clusters, Z, are free parameters.

Model comparison and selection

Because number of possible parameter values is exceptionally large, notably for Z, it is impossible to use typical likelihood ratio tests among models, or AIC. Instead, we use the Bayesian framework (Gilks et al. 1992) to determine which of the models describes the data best. The parameters have the following prior probability distributions:

$$\begin{aligned} D &\sim \text{Gamma}(1,1), \\ \kappa &\sim \text{Gamma}(1,1), \\ \varepsilon &\sim U[0,1], \\ 1+\lambda &\sim \text{Gamma}(1,1). \end{aligned}$$

Here Gamma(α,β) denotes the Gamma distribution with the shape parameter α and the scale parameter β, and $U[a,b]$ denotes the uniform distribution on the interval $[a,b]$. In Model 3 we assume that all possible partitions of the individuals into clusters are equiprobable.

We then sampled the *posterior* probability distribution of the parameters under Models 1, 2 and 3 using the Markov Chain Monte Carlo (MCMC) algorithm (Gilks et al. 1992). That is, their probability distributions conditional on the actual data. Figure III - 2 is a flowchart of the algorithm. We initialized 5 independent runs of the MCMC. For Models 1 and 2 each run took 6×10^5 steps, with the first 10^5 steps discarded as burn-in. We recorded the parameter and statistic values (see "Cluster statistics" below) every 50 steps. The MCMC trajectories for parameter, statistic and likelihood values were visually examined for convergence. We found that Models 1 and 2 rapidly converged to their stationary distributions.

We found that the MCMC for Model 3 typically took longer to overcome local maxima. We decided to run the MCMC for Model 3 for 1.8×10^6 steps with the first 7×10^5 steps discarded. Even after this large number of steps some chains still displayed transitory behavior. We therefore chose one of the five replicate chains that found the partition with the best likelihood values and sampled the posterior probability distribution near that peak.

In order to compare Models 1, 2 and 3, we estimated the Bayes factors using the Candidate's estimator (Gilks et al. 1992). Briefly, the Bayes factor B_{ij} for comparing models *Mi* and *Mj* is $B_{ij} = \frac{P_{Mi}(\text{data})}{P_{Mj}(\text{data})}$. Here $P_{Mi}(\text{data})$ is the likelihood of data under model *Mi*, averaged over all parameter values, $P_{Mi}(\text{data}) = \int L_{Mi}(\text{data};\theta_{Mi}) P_{prior}(\theta_{Mi}) d\theta_{Mi}$, where θ_{Mi} denotes all free parameters in model *Mi*, $L_{Mi}(\text{data};\theta_{Mi})$ is the likelihood of data under model *Mi* with parameter values θ_{Mi}, and $P_{prior}(\theta_{Mi})$ is the prior probability of parameter values θ_{Mi}. Using the Bayes theorem, we obtain

$$P_{Mi}(\text{data}) = L_{Mi}(\text{data};\theta_{Mi}) \frac{P_{prior}(\theta_{Mi})}{P_{posterior}(\theta_{Mi} \mid \text{data})}, \qquad [14]$$

where $P_{posterior}(\theta_{Mi} \mid \text{data})$ is the posterior distribution of parameters, which we estimate using MCMC, as described above. Equation [14] is called the Candidate's estimator. This equation hold for all values of θ_{Mi}, but the most accurate estimation of $P_{Mi}(\text{data})$ is obtained if θ_{Mi} is close to the peak of the posterior distribution (Gilks et al, 1992). We apply this equation setting θ_{Mi} to be equal to the mode of the estimated posterior distribution.

Cluster statistics

In order to characterize the posterior distributions over partitions of individuals into clusters found in Model 3, we compute several summary statistics for these posterior clusters.

Number of clusters and mean cluster size. At each MCMC step when we recorded the parameter values, we also recorded the number of clusters and the mean cluster size in the current partition.

Consensus clusters. In order to find individuals that are most often put into the same cluster, we first computed the matrix of pair-wise posterior association probabilities (i.e., posterior probabilities that two individuals are in the same cluster) using the MCMC run with the highest Bayes factor. We then computed the 'consensus' clusters by applying the single linkage hierarchical clustering with the threshold of 0.95. In other words, these individuals were assigned to the same cluster in 95% of the remaining steps, after the initial 7×10^5 steps were discarded.

Cluster spatial overlap index. We computed the extent of the spatial overlap between consensus clusters as the expected probability density that two randomly chosen individuals from different clusters are found at the same location. Note that this is not simply a calculation of area overlap.

RESULTS

In all seasons, M3 was better supported by data than M2, and M2 was better supported than M1 (Table III - 2). Thus movements of some individuals were more coordinated than others (Figure III - 3), supporting the hypothesis that they in fact constituted preferred associations despite use of the same range. The ratio D/κ, which determines how far an individual ranges, increased in the dry season relative to the wet season by 42% in 2007 and by 41% in 2008 (Table III - 3). Individuals, and by extension, their clusters, tended to range further in dry seasons than in wet seasons (Figure III - 4).

Cluster ranges overlapped highly in wet seasons and did not encompass all sources of water (Figure III - 4). In contrast, cluster ranges overlapped less and were clearly distributed around all available sources of water in dry seasons. Despite higher range overlap in wet seasons, the mean cluster size was actually significantly smaller than in dry seasons within the same year (Table III - 3). This difference was 8.5% in 2007 and 38% in 2008. 'Consensus' clusters consisted of individuals who were assigned to the same cluster in 95% of partitions. These contained many more singletons in wet seasons (Figure III - 5). The probability of finding two individuals from different consensus clusters in the same area was extremely low (<3% in all seasons), but was nearly twice as high in wet seasons as in dry ones (Table III - 3). While water was therefore an important determinant of individual and cluster ranges, individuals nevertheless moved preferentially only with certain other individuals in either season.

DISCUSSION

Certain individuals have a propensity to appear repeatedly at the same place and time as certain other individuals. Out of three possible models of movement under which this might occur, the one best supported by actual observations was the one in which individuals move together, as a particular configuration of clusters. This supports the interpretation that these movements are based on social preference, rather than solely a response to the presence of particular resources.

Resource distribution nevertheless governs where and how far such clusters must range. Clusters range further and are more evenly distributed around available water in dry seasons than in wet seasons. However in wet seasons, despite many clusters sharing the same space, they appear to avoid each other temporally. This was the case even when we included only those individuals seen in all time periods; these changes are not simply a redistribution of ranges due to the appearance of other elephants that are not present at all times. One might expect that individuals should disperse themselves as widely as possible in order to avoid feeding competition. Therefore the unexpected result that not all water sources are equally utilized in wet seasons, suggests differences either in the quality of the water or forage in different areas and deserves empirical exploration. While water is the limiting resource in dry seasons, high-quality forage may be a more important determinant of movement, and social affiliation, in wet seasons.

Though sophisticated mechanistic approaches have been used extensively to model foraging and ranging (Moorcroft & Lewis 2006), they are rarely used to elucidate other facets of behavior. Yet even simplified models, as those presented here, can offer further insights. All studies of behavior using identified individuals in principle have access to observer-based positional data on their subjects (Whitehead 2001). A drawback of such data is that they can be biased towards those areas that are most accessible to people, with low spatio-temporal resolution. On the other hand, though automated tracking devices may provide higher quality data, it is typically not feasible to collar and track large numbers of individuals, especially of endangered species – as in this case – which limit the types of questions that can be explored. Spatially explicit mechanistic models incorporated into the Bayesian statistical framework offer a powerful way to negotiate the tradeoff between observer bias and reduced sample size. Here, they allow us to detect coordinated movement among individuals regardless of the spatial scale on which it occurs, and regardless of whether multiple un-affiliated individuals in fact use the same space. This then allows us to make probabilistic statements about the social relationships of more than simply pairs of individuals. Additionally, it allows us to infer coarse seasonal movement trends of many individuals as well as aspects of their collective behavior.

Elephants move in order to obtain resources in terms of nutrition (de Beer & van Aarde, 2008; Loarie et al., 2009), mates (Poole 1999; Whitehouse & Schoeman, 2003), or safety (Blake et al. 2008; Wittemyer et al. 2008) – as do all animals, whether or not they defend specific sites (Boinski & Garber 2000). The definitions and methods in this paper may be usefully applied towards understanding how this basic drive shapes other aspects of behavior, and in making useful comparisons across species with different observational constraints, acting on spatial scales that may not always be obvious to the observer herself.

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Table III - 1. Example data. Data consists solely of an individual's space-time coordinates. Models assess the probability of obtaining such data due to random movement (M1), presence of water (M2), or coordinated movement (M3). Under M2 individuals are more likely to be seen in some locations than others due to the presence of water; however, individuals are treated as though they move independently of one another. Under M3, individuals are in addition partitioned into clusters such that cluster-mates are treated as though they always travel together. Here it is evident (RAG) and Ramani (RAM) travel together, but not Jasmine (JAS), though sometimes seen in close proximity during the same day or week. Thus RAG and RAM would tend to be assigned to the same cluster during the Markov Chain process more often than JAS would be assigned to a cluster containing either of them. Consensus clusters are comprised of those who were assigned to the same cluster in 95% of the partitions.

ID	Date	Time	Latitude	Longitude
RAG	5/4/2007	8:35	6.4625216	80.9138006
RAG	5/4/2007	9:46	6.4611027	80.9124296
RAG	5/10/2007	14:16	6.4622701	80.8993161
RAG	5/11/2007	8:30	6.4641655	80.9151871
RAM	5/4/2007	8:35	6.4625216	80.9138006
RAM	5/4/2007	9:46	6.4611027	80.9124296
RAM	5/10/2007	14:16	6.4622701	80.8993161
RAM	5/11/2007	8:30	6.4641655	80.9151871
JAS	5/7/2007	15:50	6.4499079	80.8855460
JAS	5/11/2007	17:08	6.4542998	80.8880871
JAS	5/30/2007	17:40	6.4623175	80.9080018

Table III - 2. Log10 of the Bayes factor (see methods). Larger values indicate stronger support for the higher model number.

	2007 Dry	**2007 Wet**	**2008 Dry**	**2008 Wet**
M1 vs. M2	48.77	16.38	57.99	37.06
M2 vs. M3	243.92	96.63	340.88	85.66

Table III - 3. Parameter estimates with 95% CI under all models. D/K is consistently higher in dry seasons than in wet seasons, regardless of model. Model 3, in which individuals moved as groups, was best supported by data. Under this model, MCS is the mean cluster size. MCCS is the mean consensus cluster size where clusters are composed of individuals that were clustered together in at least 95% of the partitions. MO is the mean overlap among individuals from different consensus clusters (see methods). Differences in D/K, λ and mean cluster size between dry and wet seasons within year were significant (Wilcoxon signed-rank tests, $P<<0.001$, $N>10,000$ samples from the Markov Chain Monte Carlo process). Among consensus clusters, overlap in wet seasons is close to double that during dry seasons while mean cluster size is almost halved.

Parameter & Model	2007 Dry			2007 Wet			2008 Dry			2008 Wet		
M1:	**Est.**	**95% C.I.**		**Est.**	**95% C.I.**		**Est.**	**95% C.I.**		**Est.**	**95% C.I.**	
D	0.191	[0.168,	0.218]	0.474	[0.381,	0.594]	0.300	[0.254,	0.353]	0.247	[0.199,	0.309]
κ	0.034	[0.030,	0.040]	0.134	[0.106,	0.170]	0.055	[0.046,	0.066]	0.079	[0.063,	0.100]
D/κ	5.570	[5.230,	5.926]	3.537	[3.305,	3.785]	5.454	[5.123,	5.796]	3.122	[2.900,	3.361]
M2:												
D	0.197	[0.173,	0.226]	0.486	[0.392,	0.603]	0.293	[0.250,	0.346]	0.258	[0.209,	0.321]
κ	0.037	[0.032,	0.043]	0.139	[0.111,	0.175]	0.056	[0.047,	0.067]	0.083	[0.067,	0.104]
D/κ	5.323	[5.019,	5.65]	3.494	[3.27,	3.732]	5.223	[4.920,	5.543]	3.116	[2.898,	3.355]
λ	2.556	[2.227,	2.891]	1.122	[0.814,	1.466]	2.510	[2.117,	2.877]	2.372	[1.922,	2.948]
M3:												
D	0.596	[0.488,	0.701]	0.632	[0.527,	0.761]	1.727	[1.435,	2.074]	0.431	[0.337,	0.545]
κ	0.090	[0.073,	0.108]	0.163	[0.132,	0.201]	0.327	[0.264,	0.400]	0.139	[0.103,	0.184]
D/κ	6.665	[6.064,	7.325]	3.875	[3.505,	4.286]	5.290	[4.824,	5.797]	3.129	[2.738,	3.584]
λ	2.412	[1.489,	3.198]	1.081	[0.648,	1.441]	2.412	[1.739,	3.074]	1.984	[1.397,	2.868]
ε	0.883	[0.864,	0.891]	0.896	[0.883,	0.908]	0.907	[0.881,	0.918]	0.830	[0.808,	0.850]
Num. cluster	34	[34,	35]	34	[30,	37]	36	[36,	36]	33	[26,	41]
MCS	14.626	[13.018,	14.719]	13.020	[10.941,	14.353]	17.035	[13.215,	17.944]	11.205	[9.608,	12.402]
MCCS (95%)	12.658	-		7.353	-		13.205	-		7.361	-	
MO (95%)	0.012	-		0.027	-		0.016	-		0.029	-	

Figure III - 1. Uda Walawe National Park. Study site is enclosed by dotted line, which animals could freely move in and out of. Rectangles show water as represented in models.

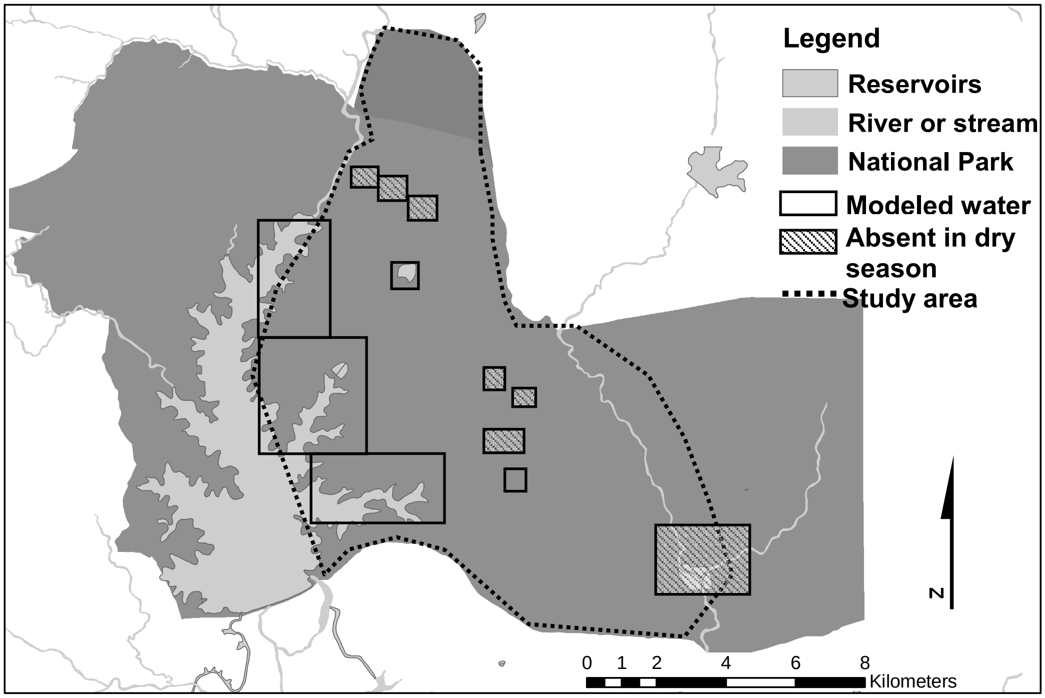


Figure III - 2. Schematic representation of modeling process. The accuracy of parameters under the Markov Chain Monte Carlo algorithm (MCMC) were tested with data from simulations with known parameter values before applying it to actual data. Chains ran for >10,000 steps per model per season.

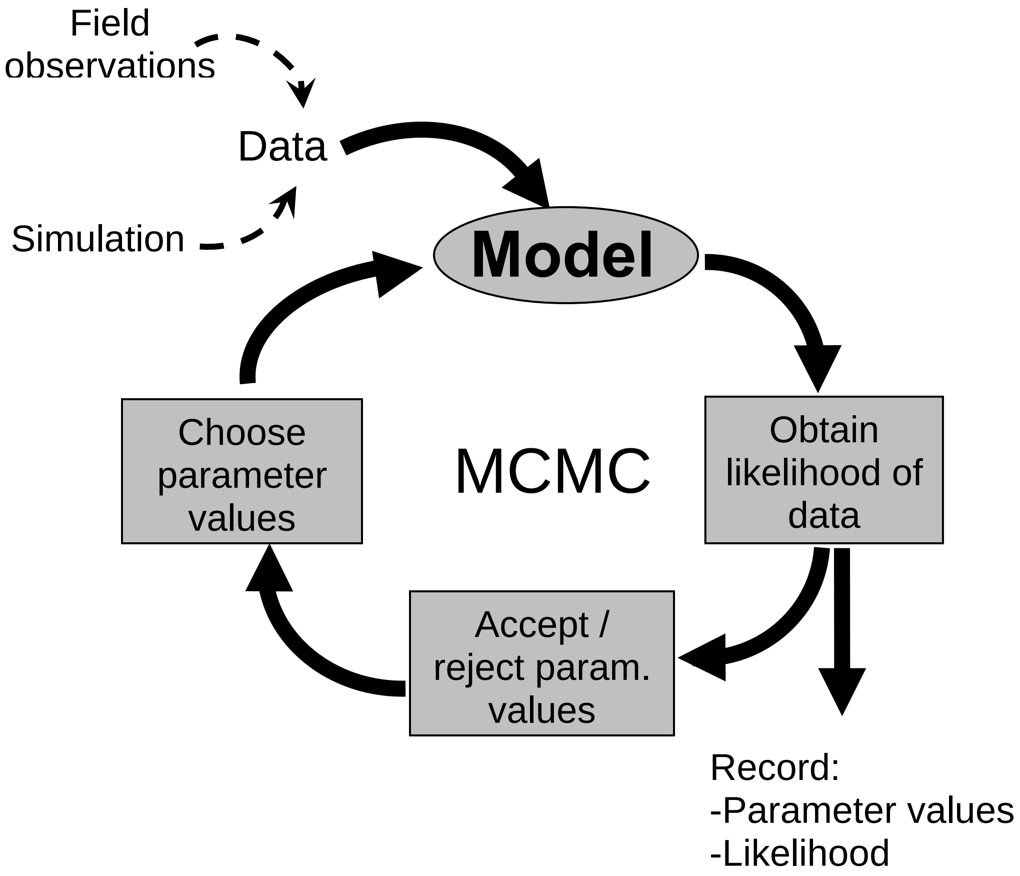


Figure III - 3. Coordinated movement. Movements of individuals in the same cluster are more coordinated than of those in different clusters. Color indicates cluster membership while each line is a different individual. Note that even though the two clusters use the same area, and on one occasion appear at the same water source, they do so at different times. Axes are centered on an arbitrary location, with water sources being the same as those in Figure III - 1.

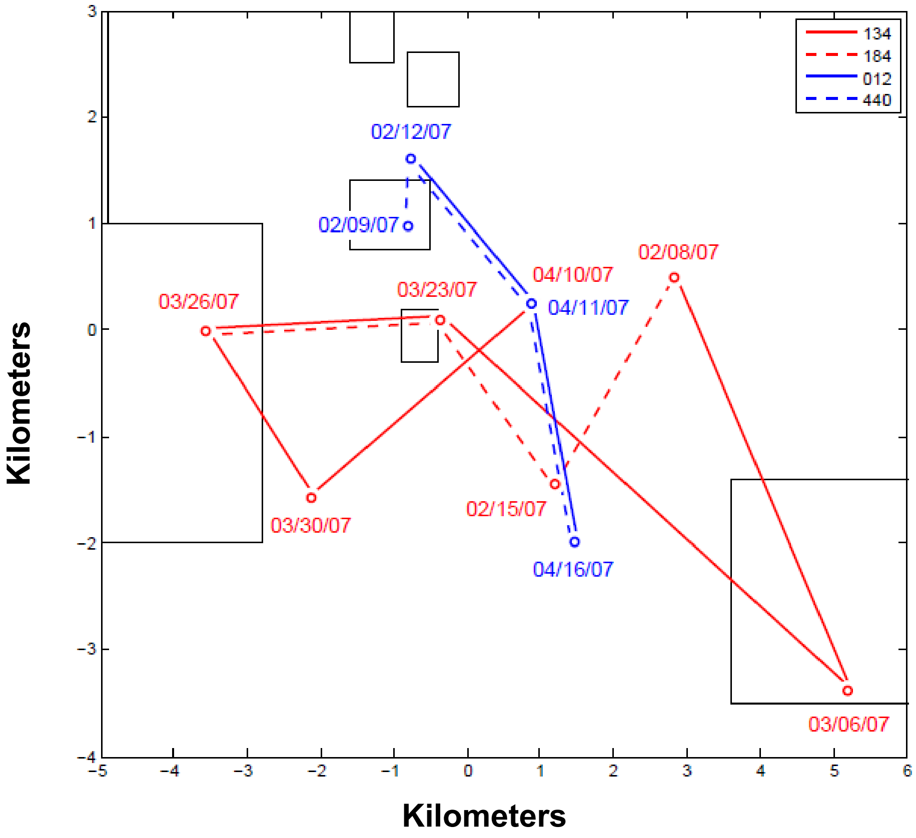


Figure III - 4. Observed space use of 95% consensus clusters. Individuals and their consensus clusters (those with whom they were likely to be grouped in 95% of partitions) travel further in dry seasons than in wet seasons, and cover a greater portion of the study area. This does not mean that individuals from the same cluster were physically further apart in dry seasons – there was no seasonal difference in the distance separating individuals from the same consensus cluster (see results) who were seen on the same day. Clusters are ranked by size (i.e. Cluster 1 is always the largest, see Figure III - 5). Numbers do not designate the same set of individuals in each season (see results and Figure III - 5).

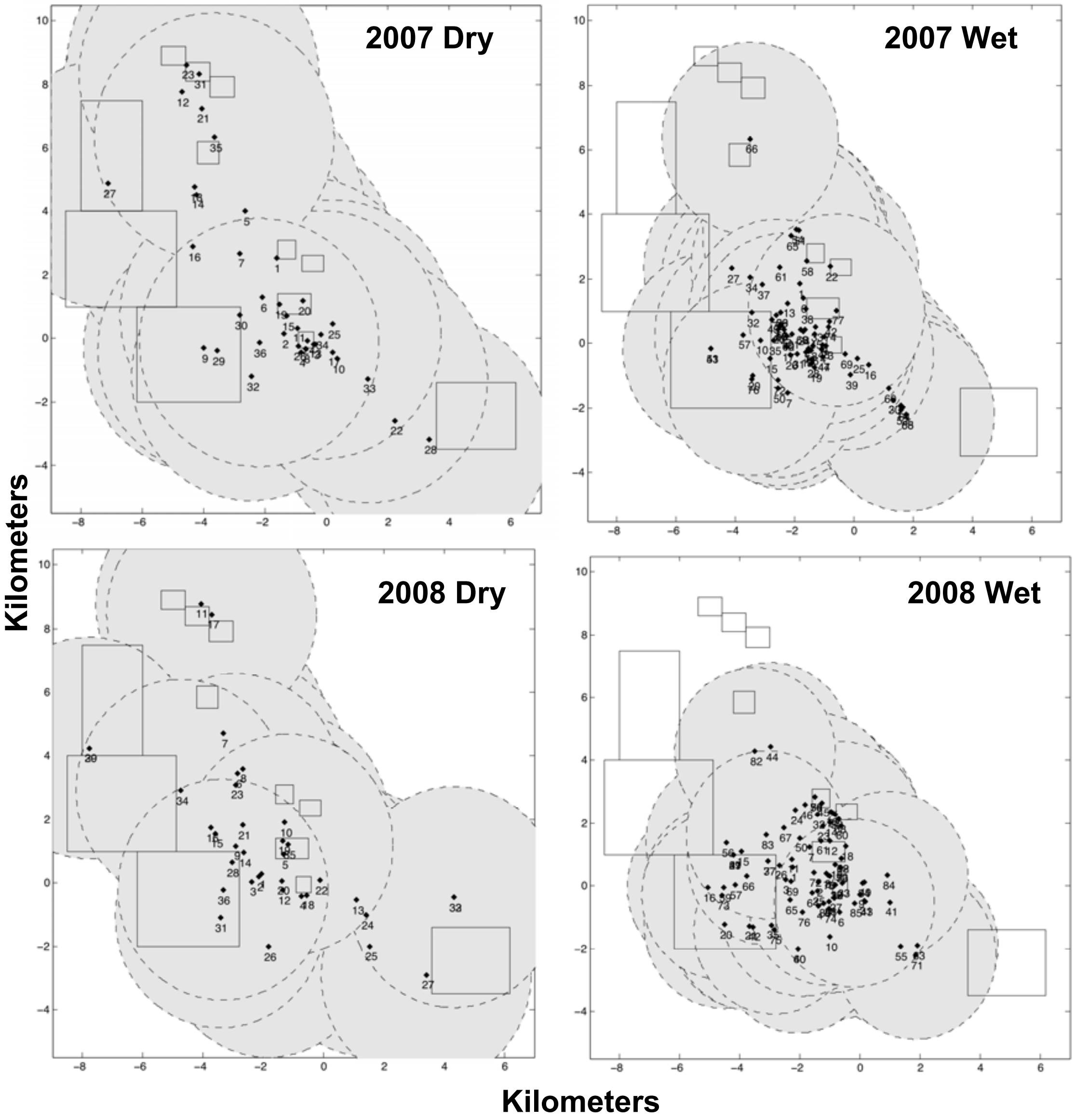
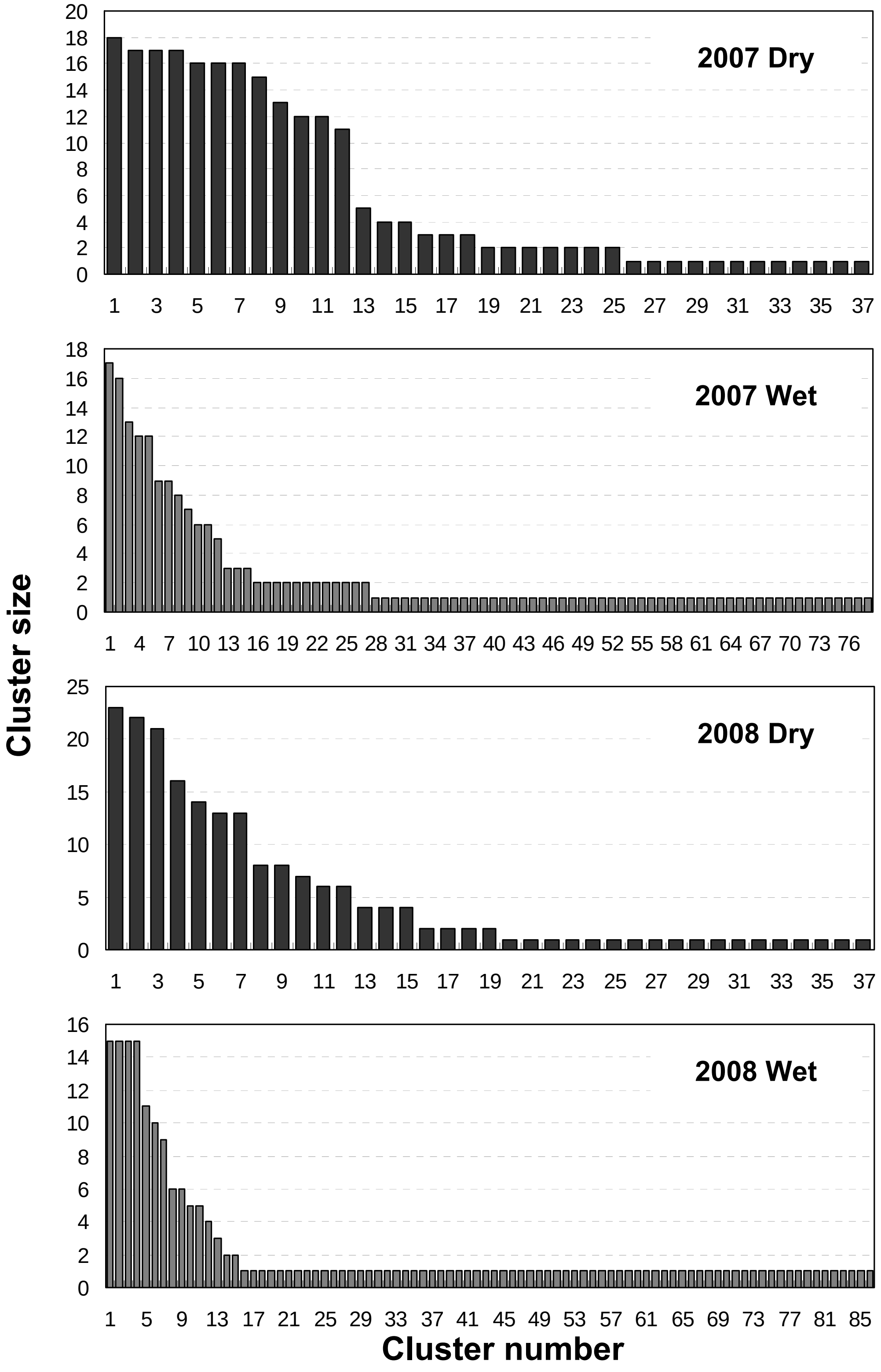

2007 Dry
2007 Wet
2008 Dry
2008 Wet
Kilometers
Kilometers
-8
-6
-4
-2
0
2
4
6
10
8
6
4
2
0
-2
-4

Figure III - 5. 95% Consensus cluster sizes by season. Cluster number gives the identity of the cluster and cluster size gives the number of individuals included in it. The number of clusters changes between seasons, and not all individuals are present in all seasons, therefore they are not meant to label constant entities. Dry seasons contain more large clusters and fewer singletons than wet seasons.


2007 Dry
0 2 4 6 8 10 12 14 16 18 20
1 3 5 7 9 11 13 15 17 19 21 23 25 27 29 31 33 35 37
2007 Wet
0 2 4 6 8 10 12 14 16 18
1 4 7 10 13 16 19 22 25 28 31 34 37 40 43 46 49 52 55 58 61 64 67 70 73 76
2008 Dry
0 5 10 15 20 25
1 3 5 7 9 11 13 15 17 19 21 23 25 27 29 31 33 35 37
2008 Wet
0 2 4 6 8 10 12 14 16
1 5 9 13 17 21 25 29 33 37 41 45 49 53 57 61 65 69 73 77 81 85
Cluster size
Cluster number

CHAPTER IV.

On Predicting Elephant Population Dynamics

SUMMARY

Studies of elephant population dynamics are motivated by the need to maintain elephant populations without straining the limited space and resources available to them. Analysis of this issue has focused on a population's capacity to reach a stable age distribution (SAD), which can be used to calculate its growth rate. I first evaluate this approach with some case studies on African elephant populations. It appears doubtful whether elephant populations ever could reach a SAD. I suggest some alternative approaches that may more accurately forecast elephant population trends. Unlike the data on African elephants, the data on Asian elephants are insufficient to perform similar analyses. I urge that more rigorous demographic studies be undertaken.

INTRODUCTION

Any science-based conservation project requires adequate data on the abundance and distribution of species. Study of demography is therefore an important prerequisite for effective conservation and management. Data on fecundity, age at first reproduction, inter-birth intervals, the number of individuals by age and sex class, age- and sex-specific survival, and age at senescence are essential for understanding population trends, and developing adequate management plans. Knowing these variables, one can model and predict population trends, discover populations that may be declining, and anticipate the needs of those that may be growing. Here I discuss some basic issues in conducting demographic studies of elephants, centering on the key predictive feature of populations: age distributions. I first discuss case studies of African elephant (*Loxodonta Africana*) populations, and what can be learned from them. I then discuss the prospects for conducting similar studies on Asian elephants (*Elephas maximus*).

A much-discussed concept in management planning is the 'stable age distribution.' A population has achieved a Stable Age Distribution (SAD) when the proportion of individuals in a particular age class does not change from one time interval to the next – e.g. typically, a year. A SAD implies a constant exponential growth rate (Birch 1948 and references therein), as well as constant population survival and fecundity. The SAD may thus be used to predict population growth (Fowler & Smith 1973). In elephant management schemes, it has two potential uses. First, it may serve as an aid in anticipating and planning for future growth. Second, it indicates a healthy, undisturbed population and thus may appear to be a desirable objective for any management scheme.

The SAD is not to be confused with 'stability at carrying capacity,' as implied by a logistic model with an 'S' shaped curve of population growth (Fowler & Smith 1973). The point at which such a curve levels off at a constant population size is its carrying capacity. A population with such a growth curve is *not growing* beyond the environmental carrying capacity. It ceases growing if, for instance, food scarcity curbs birth rates. Species such as elephants, however, can drastically change their habitats without stabilizing (van Aarde & Jackson, 2007). The alteration of habitats by elephants, primarily through damage to trees, can have severe consequences for animal and plant life in the limited conservation areas allotted for wildlife (Fowler & Smith 1973; Mackey et al. 2006). Hence, the 'carrying capacity' that elephant managers typically seek is the level at which an area can withstand the impact of elephants without significant deterioration in vegetation. For African elephants, this is 2 elephants per km^2 (Woodd 1999), though elephant populations could conceivably grow beyond this 'capacity' given the chance. For Asian elephants, potential densities may be higher since range lands in Asia receive more rainfall, have higher primary productivity, and can potentially support more large mammal biomass (McNaughton et al., 1989). It is a subject of much debate how elephant populations are regulated – be it naturally, or through human intervention (van Aarde & Jackson, 2007). Regardless, population limits that are artificially imposed by active management, such as culling, do not alter the age distribution since they target all age classes indiscriminately. Population limits imposed through other human activities such as poaching, typically do skew age distributions, in removing older individuals with larger tusks. Thus a population with a SAD may be growing or declining, but will not be 'stable' in terms of absolute numbers unless mortality affects all age and sex classes equally.

Could elephant populations ever reach SAD given the constraints of space and environmental variability? In the first section, I evaluate the utility of relying on this characterization of age structure in predicting and anticipating elephant population trends.

I. *Loxodonta* - case studies

I first discuss two studies which are based either on re-introduction records or tracking of known individuals, so cohorts are as closely monitored as possible. In contrast to census data, these methods provide reliable data on age distributions. The first study describes an age-structured model for the elephants at the Addo Elephant National Park (AENP), projected forward from 1976 (Woodd 1999). The study sought to anticipate the amount of time it would take the population at that time to reach the capacity of a proposed expansion of the park. Parameters included were: age of female sexual maturity and reproductive senescence, age-specific female fecundity, inter-calf interval, and age- and sex-specific mortalities (Table IV - 1). At the time of publication, it was only possible to compare the modeled population to the actual for the period 1976-1998 (Figure IV - 1) but the future population can be projected ahead 120 years (Figure IV - 2). The model fitted well with the actual population growth for the 21 year span. It projected the attainment of a stable age distribution (defined as no further fluctuations to the nearest 0.1% in all age/sex classes) by 2045 with an annual growth rate of 5.2%.

The AENP population is fairly unique for several reasons – it started from near-extinction with 11 individuals in 1931, grew steadily, undisturbed by poaching, and remained closed to migrants. At the time of the study, every individual in the park was known, and it had an almost perfectly unbiased 1:1 sex ratio. It was close to an ideal study population, which may be viewed as a null scenario in which the population could have reasonably been expected to attain a SAD if possible at all. And yet, the projected time to attaining SAD seems exceedingly high. If are environmental or human disturbances, it is unlikely to do so (discussed further below).

AENP is unique in another respect. Whitehouse & Hall-Martin (2000) conducted a massive reconstruction of individual histories for the period 1931-2000 using park records and photographs. The two studies (Woodd 1999 and Whitehouse & Hall-Martin 2000) together present the full span of growth that has been experienced by a single population along with a possible trajectory for its future. Woodd's model can be viewed with respect to the longer timescale. Does the model population follow the same trajectory as the actual? The real population showed a mean annual growth rate of 5.53 % for the period 1976-1998 (Figure IV - 3), which is exceptionally close to the 5.2 of Woodd's model. However no mention was made of the age distribution, nor could it be ascertained from the data presented (Whitehouse & Hall-Martin, 2000). The close match between the two growth rates could have been due to the overlap between the two studies from 1976-1998, the only period that contained solid data. Moreover, the 21 years of data Woodd's original model may be far too short with which to detect any divergence from reality, especially given that it takes multiple decades to settle into a SAD.

Woodd states that the proposed expansion of the park should have a pre-determined carrying capacity of 2700 elephants, reached by 2043. Thus the population would take at least 114 years to reach a SAD (2045-1931 = 114), and the resulting population size would be just over the park limit. Without expansion, the park could not accommodate close to this number of individuals. It is conceivable either way that this population would never in reality be allowed to reach a SAD even if it could, and if it did, it would not be free to continue growing due to space limitations. Why then address it at all? SAD cannot aid in anticipating and planning for future growth since it is reached beyond park capacity. Woodd's intent appears to be instead to argue that *because* the current population is far from reaching a SAD, an age-structured model is a better predictor of future growth than simple exponential growth projections.

Woodd cautions that his model relies on a few simplifications – 1) mortality rate is treated as constant because variation in age-specific mortality is minimal 2) fecundity of all breeding females is treated as equal since mortality rates are low in the adult age classes 3) environmental effects are not incorporated because they are unpredictable. These are made explicitly to simplify calculations. But is it possible that the SAD attained by the model is an artifact of these assumptions? I will later examine the effect of violating of each of these conditions.

The second model by Dominy & Ferguson (1998) is intended to determine when the population of elephants in Hluhluwe-Umfolozi park (HUP) would reach a predetermined limit of 320 animals. They note a number of similarities between HUP and AENP, notably the small founder population of 18 animals. However in HUP there were waves of juveniles as a result of new introductions (Table IV - 2). Similar but adjusted parameters were used in running a simulation for 30 years starting at 1990 (the birth of the first calf to a re-introduced female), which resulted in an annual growth rate of 6.6 percent and SAD within 20-25 years, or the year 2015. The population growth is therefore much faster than at AENP. But the AENP population, with its near-ideal conditions, has so far shown no signs of achieving a SAD. HUP, considering both its short history and waves of introductions, should seem even less likely to settle into a SAD as each wave of introductions artificially increases the number of juveniles. This then is a second example in which the SAD would not be a realistic expectation.

Most *Loxodonta* populations have not undergone severe bottlenecks as those in AENP and HUP. But there are still common features between those that have and those that have not. The reintroduction wave phenomenon at HUP could be treated as analogous to natural birth pulses, as occurred in Amboseli during recovery from drought or hunting (Moss 2001). The Amboseli dataset (1972-present) is valuable in having continuous long-term data for a population comprised of free-ranging known individuals, totaling 1778 in 2001. The population has shown no signs of settling into SAD as shown by a 6 year snapshot of age structure (Figure IV - 4). Compared to Amboseli, it may seem HUP's age distribution could settle down more quickly due to the relatively smaller number of individuals involved. However by the end of 1978 Amboseli contained only 480 animals, which was not much larger than HUP's 320 animal limit, thus these two populations had similar beginnings.

Now consider what happens when simplifying conditions are violated. Condition (1), constant mortality, does not seem justified by the mortality rates given in Table IV - 1. The inverse of this, survival, is therefore not constant and this would prevent the population from achieving a SAD. A sensitivity analysis by Dominy and Ferguson (1998) shows the population to be extremely sensitive to initial conditions (that is, the number and age structure of the starting population) as well as to changes in fecundity and survivability, particularly for the class of adults older than 5 years (Table IV - 3). For example, even a 10% decrease in survivability leads to extinction of the population. Loss of female adults also decreases breeding potential. The study concludes that:

> "…the model identified the adult breeding females as those animals that contribute the most to the dynamics of the total population. This group therefore needs to be closely monitored, managed and included in any population control measures."

Male mortality should be given equal attention. Life-history studies generally focus on females, since in practice the contribution of a female to a population is easily measurable by observing births whereas paternity is difficult if not impossible to establish. However we now have the tools to carry out paternity tests. Genotypic analyses of 270 calves born from 1979-2002 in Amboseli and their mothers as well as 117 adult male 'potential fathers' have established paternity for 138 calves (*adult* being individuals older than 17 yrs; Hollister-Smith et. al 2004). The long-term records available at this site permitted evaluation of paternity success by age, musth state at the time of conception, and family group. Elephants have a long delay in their reproductive success, peaking at 40-54 years which correlates with larger size and dominance as well as longer periods of musth (Hollister-Smith et. al 2004). Judged by their survival, these males may be bearers of the best genes in the population. Loss of such mature males may adversely affect the genetic structure of populations.

Wittemyer (2001) found a pronounced female-biased sex ratio in Samburu and Buffalo Springs National Reserves, increasing exponentially down the age classes (Table IV - 4), as a consequence of conflict with humans. This particular population violates condition (1), and such violations are likely to be the rule rather than the exception. Even the Amboseli population, which is comparatively 'undisturbed' (i.e. has not been subjected to culling or extensive hunting) shows male survivorship decreasing more rapidly than female with only 39% of males surviving into their 30s, the age at which age they regularly enter musth (Figure IV - 5, Moss 2001). Human activity accounts for 67% of adult deaths in this relatively 'undisturbed' population. Since males in musth are the main inseminators (Hollister-Smith et al. 2004), they directly affect female breeding potential. The key demographic group in such a population would therefore be the musth males – since only one male may be reproducing over a large area, that male is worth several breeding females. Tracking female breeding potential would provide only an indirect measure of their impact. This impact may be lessened if females breed with non-musth males when musth males are absent, however I am aware of very little data on this, at least for African elephants. We have observed many male Asian elephants breeding out of musth, but this has not been studied systematically in the wild.

Condition (2), equal fecundity among females of all breeding age, also draws a connection between fecundity and mortality rates that may not be justified. Fecundity is not constant with age (Moss 2001), even if it is not greatly influenced by mortality in a particular population. Moreover, it is not simply reproductive individuals on whom African elephant societies depend. The reproductive success of an individual can depend on other individuals in her social group, and not all social groups may be equally successful (McComb et al. 2001). An older matriarch, who may not necessarily contribute to a herd reproductively, may nonetheless be crucial to their survival due to her accumulated experience. McComb et. al (2001) have found the age of the matriarch to be significantly correlated with the number of calves produced per female per reproductive year and conclude that whole populations may be affected by the removal of such “key individuals.” It is difficult to assess these indirect effects. One way would be to introduce a function relating the ages of the oldest individuals in a simulated population to calving rates and the survival probabilities of the other individuals. This would add another level of biological fidelity to modeled population dynamics.

Thus violating conditions (1) and (2) have consequences for whether the population persists at all, let alone whether it reaches a stable age distribution. This is unsurprising, as elephants are not highly fecund to begin with considering that the gestation period alone is 22 months on average (Sukumar 2003). African elephant populations may in addition be sensitive to loss of older males as well as non-reproductive females, to which calculations of SAD are blind. Age-specific sensitivity analyses that do incorporate this would be instructive.

Environmental conditions can lead to significant population fluctuations, violating condition (3). A major reason that simulated populations reach SAD may be that environmental factors are not included in the models due to their complexity and unpredictability (Dominy & Ferguson 1998, Woodd 1999). These effects, of course, have huge consequences in reality since not only does survivorship in general decrease during droughts, the younger age classes are more vulnerable (Moss 2001), thus directly changing the age distribution. Environment is perhaps the single most important external factor that makes the survival and fertility functions inconstant.

There are several reasons why environmental and anthropogenic effects may not typically be factored into simulations. They are difficult to quantify and can be confounded – for instance, where elephants compete with livestock and are shot (e.g. during a drought year: 1984 in Figures IV - 6a,b). Moreover, correlations between environmental conditions and birthrate may be chaotic, because the long gestation period results in a birthrate that lags far behind environmental changes. But rather than leaving out these two complications altogether, simulations could forecast a number of possible future scenarios for the population.

One such analysis has been done. A simulation by Armbruster and Lande (2001) assesses the ability of populations to survive drought in relation to the area of land available (Table IV - 5). A population model showing steady logistic growth becomes chaotic if environmental stochasticity is incorporated as a random variable with probability distributions corresponding to certain realistic scenarios, such as drought, along with age and sex-specific survivorship probabilities (Figures IV - 7a,b). Along with considerations of genetic viability and land yield they find that an area of 1000 miles^2 as minimum habitat size in semi-arid areas. This technique can be modified to fit the conditions of any particular area under consideration, such as rainfall schedules.

Although Woodd and Dominy et. al do not try to suggest their models extend to populations other than the ones they are based on, AENP and HUP are susceptible to the same disruptions experienced by elephants elsewhere in Africa. HUP can never get close to reaching a stable age distribution in reality as the park's 320 animal carrying capacity may have been reached by 2002-03 (Figure IV - 8). We do not know the present status. Age and gender-specific effects along with environmental variables, using procedures like sensitivity analysis, should be fed back into simulations. The projections which then emerge may be more instructive than models relying solely on calculation of maximum growth rate and horizon for reaching SAD. SAD is merely a marker of predictability in an otherwise unpredictable system. Indeed what truly counts as 'stable' is an open question for species like elephants which are today restricted not by some intrinsic growth rate or population density but by the swiftly changing boundaries they share with us. In the next section, I discuss Asian elephant management.

II. *Elephas* – similarities and dissimilarities

While the models just discussed may be improved, they are essential tools for anticipating the needs of animals in protected areas. If one moves away from characterizations based on SAD, and instead projects populations based on multiple environmental regimes as well as age- and sex- specific sensitivity analyses, they become powerful predictors of population trends. It would not be possible to build such models or evaluate their success without basic demographic information. There is a substantial body of literature assessing these variables for multiple populations of African savannah elephants, a few of which have been discussed thus far. Where comparable methods have been used, it is possible to compare population changes in multiple areas over time (Blanc et al. 2005), and to address the causes of these changes. Is there such a literature for Asian elephants?

Unfortunately, there is not. We are aware of only one long-term study of Asian elephant population dynamics (Katugaha et al. 1999), conducted opportunistically over a period of thirty one years in southern Sri Lanka. Continuous, systematic studies are necessary if we are to identify population trends unbiased by sampling effort. Blake and Hedges reviewed the state of forest elephants – both African and Asian – in 2004, and found large gaps in knowledge of the locations and sizes of extant populations. A recent IUCN review (Choudhury et al. 2008) finds little change in this state of knowledge where Asian elephants are concerned. The primary reason for this absence of information in both species is their relative inaccessibility compared to savannah elephants. Of the studies discussed so far, two populations (in Addo and HUP) were extremely small founder populations in restricted areas that could be monitored as they grew, and the other two (Amboseli and Samburu) represent dedicated effort to continuously monitor wild populations. Several other present-day population models represent deliberate introductions in to restricted areas (e.g. Mackey et al. 2006). All these savannah populations are more or less tractable to census by vehicle or air. While some researchers have tried to census African forest elephants using vocalizations (Payne et al. 2003), this method is not well validated nor tried elsewhere. Typically, censuses have relied on indirect methods such as dung transects, which can have sizeable errors associated with them, especially for small populations (Barnes 2002). In recent years there are only two published surveys of Asian elephant populations (Goswami et al. 2007; Hedges et al. 2004). This is clearly insufficient to inform management and conservation.

Other difficulties in obtaining demographic parameters in elephants generally are their longevity and extended developmental times. Estimates of most demographic variables are impossible with dung transects. Whereas the greater visibility of savannah elephants allows demographic parameters to be estimated for identified individuals, continuous studies of identified individuals are typically rare for forest species - both Asian, and African, as pointed out by Blake & Hedges (2004). Goswami et al. (2007) have attempted to identify male Asian elephants, recognizing the potential consequences of sex-biased mortality in for the reproductive potential of populations. In contrast to approaches in African elephant management, there has in fact been a lot of attention dedicated to males in Asian elephant management, who are perceived to contribute more to human-elephant conflict through crop raiding etc. While this is a start, adult females must also be identified and monitored if we are to predict population trends.

Some species can be individually-identified even when they are not readily visible, either through automated camera-traps, or observers positioned at key resources. Demographic estimates based on identified individuals have been performed on everything from marine mammals (humpback whales: Smith et al., 1999; Stevick et al. 2001) to tigers (Karanth, 1995; Karanth et al. 2006). Studies of social organization in Asian elephants have been based on identified individuals (Fernando & Lande 2000; Vidya & Sukumar 2005; Chapters II & III). Therefore there are at least some natural populations accessible enough for this method to be feasible. At Uda Walawe National Park in Sri Lanka we have had a unique opportunity to study Asian elephants. The Walawe river dam has transformed this 308 sq. km area from seasonal forest to a mix of grassland, scrub, and residual forests in the past 40 years. It now bears much resemblance to an African savannah. The addition of roads and fire gaps (areas of cleared vegetation to prevent the spread of fires) in approximately 1/3 of the park has made it reasonably accessible to vehicles. Many elephants have become habituated to vehicles, unthreatened by humans at least within the park boundaries. The extent of this park is similar to that of Amboseli. Also like Amboseli, UWNP also has water available year-round. Like HUP and Tsavo National Park, Uda Walawe has had cohorts of juveniles periodically translocated to it. As a national park surrounding a reservoir, it is comparable also to parks such as Nagarahole in India and Minneriya national park, also in Sri Lanka. Unlike Amboseli, the perimeter of Uda Walawe has been progressively fenced from 2006 onwards, leaving only two narrow exits. It is possible that UWNP may come to resemble smaller reserves in South Africa, that are similarly constrained. Unlike much of Asia, elephants are seen year-round at UWNP and have a noticeable effect on vegetation. Here we have had a chance to study a wild Asian elephant population as closely as some African populations have been. We used individual identification (Table IV - 6, Figure IV - 9) to estimate demographic variables for this population (Chapter V).

There are undoubtedly other locations where wild Asian elephants can be regularly monitored. Where it is not possible to follow them by vehicle, it should be possible to set up camera traps at commonly visited water sources. Where this is not feasible, it may at least be possible to conduct mark-recapture studies through non-invasive genetic sampling using dung (Arrendal et al. 2007; Frantz et al. 2003; Jacob et al.; Kohn et al. 1999; Prugh et al. 2005). Genetic sampling raises separate issues of accuracy that have to be carefully considered, but it may be a good way to assess even small populations (Miller et al. 2005). I renew the call by Blake and Hedges (2004) for better estimates of abundance on Asian elephants. There remain political and logistical challenges to observing Asian elephants. However, monitoring Asian elephants on an individual-by-individual basis is not only possible, it is crucial.

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Table IV - 1. Demographic parameters for the Addo elephant population, based on data for the period 1976-1998 (Woodd 1999).

Age of first conception:		11.2 years	
Intercalf interval:		3.8 years	
Age of reproductive senescence:		49.2 years	
Age and sex-specific mortalities:	Age class	Male	Female
	0	0.062	0.062
	1 – 9	0.009	0.001
	10 – 19	0.02	0.004
	20 – 29	0.031	0.003
	30 – 44	0.051	0.012
	45 – 59	1	0.016
	60+		1

Table IV - 2. Percentage of total population represented by each age class over a 50 year period (Dominy & Ferguson, 1998).

Year	Calves	Adults	Juveniles	Young Adults
1990	0	0	95	5
1993	11.5	14.5	62	12
2000	32	45	12	11
2005	33	45	12	11
2010	28	42	24	7
2015	29.5	43	19	8.5
2020	30	44	20	6
2025	29	44.5	20	6.5
2030	30	43	20	7
2035	29	43	21	7
2040	28	44	21	7

Table IV - 3. Percentage change in total population as a result of variable adjustments in the deterministic model. Normal variation within the total population of the model is +/- 3.0% over a 30 year simulation (Dominy & Ferguson, 1998).

Variable	% change in total population						Normal Variable Level	Carrying Capacity (years)
	% adjustment of variables							
	-30	-20	-10	30	20	10		
Survivability								
0 to1	**-17.2**	**-10.9**	**-4.7**	-	-	-	1	2004/2005/2005
1 to 2	**-19.4**	**-13.5**	**-4.6**	-	-	-	1	2004/2005/2006
2 to 5	**-48.1**	**-33.8**	**-19.2**	-	-	-	1	2005/2005/2010
5 to 49	*****	**-99.5**	**-91.8**	-	-	-	1	**?/?/2013**
Fecundity								
sub adult females	-0.8	0.8	-0.2	-	-	-	0.95	2004
adult females	**-11.5**	**-6.3**	**-3.3**	-	-	-	0.99	2004/2004/2005
Breeding								
10 to 11	1.5	1.3	-0.5	-0.2	-1.1	0	0.45	2004
11 to 12	-0.5	-0.7	0.9	1.7	-0.5	0.5	0.7	2004
12 to 13	0.7	-1.7	-0.7	-0.3	-	-	0.85	2004
13 to 14	-0.9	-0.4	-2	-	-	-	0.92	2004
14 to 15	0.5	0.9	-0.4	-	-	-	1	200
15 to 55	**-10.2**	**-7.7**	-2.3	-	-	-	1	2004/2004/2005
Sex								
mean	-1.2	-0.9	-0.7	0.6	1.2	1.6	0.2	2004

Bold print indicates values greater than the normal variation from within the model;
* = population reached 0;
2013 = the year the population died out;
? = carrying capacity not reached;

Table IV - 4. The age and sex structure of the Samburu and Buffalo Springs National Reserve's elephant population (Wittemyer, 2001).

Age groups (years)	Males	Females	Sex ratio of aggregated ages M:F	Group population (%)
0-4.9	129	121		34
5-9.9	77	89	258:279	22
10-14.9	25	37	(1:1.1)	8
15-19.9	27	32		8
20-34.9	47	80		17
35-49.9	14	59	62:145	10
50+	1	6	(1:2.3)	1
Total	320	424		

Table IV - 5. Sensitivity of extinction probabilities to the frequency of drought events (Armbruster et al., 1993).

	Extinction probabilities ± S.E.		
Area (mile^2)	10/25/125-Year droughts	10/50/250-Year droughts	10/100/500-Year droughts
20	1 ± 0	0.917 ± 0.009	0.573 ± 0.049
50	0.976 ± 0.005	0.485 ± 0.016	0.098 ± 0.009
100	0.888 ± 0.0.010	0.197 ± 0.013	0.020 ± 0.004
200	0.707 ± 0.014	0.061 ± 0.003	0.003 ± 0.0008
500	0.431 ± 0.007	0.012 ± 0.002	0.002 ± 0.0006
1000	0.272 ± 0.006	0.003 ± 0.0008	0 ± 0

Note: The 10-, 25-, 50-, 100-, 125-, 250-, and 500-year droughts occur with probabilities of 0.41, 0.2, 0.1, 0.05, 0.04, 0.02 and 0.01 respectively. Simulations incorporate three levels of drought severity.

Table IV - 6. Features used to identify adult Asian elephants (see Figure IV - 9).

Ears:	**Ear lobes:**	**Tail:**	**Backbone:**	**Other:**
Hole	Long	Long	Straight	Wounds
Tear	Square	Short	Raised	Growths
“Fingers”	Wedge	White hair	Sunk	
Notch	Curve	Crooked		
		Broken (at base, middle, tip)		
Top curl (forward, backward)				
Flap (forward, backward)				
	Face:			
Plain	Forehead profile			
Long	Depigmentation			
Veins				
Depigmentation				

Figure IV - 1. Actual population growth compared to model (Woodd, 1999: Figure A).

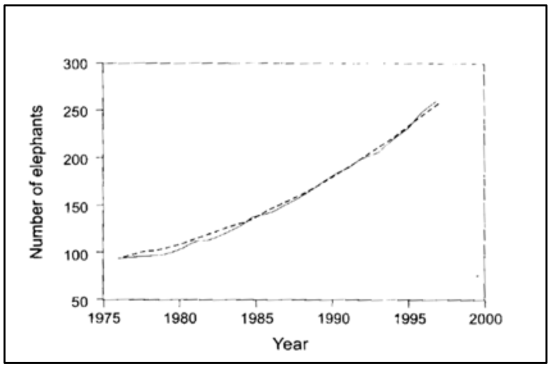


Figure IV - 2. Projected population growth (Woodd, 1999: Figure B).

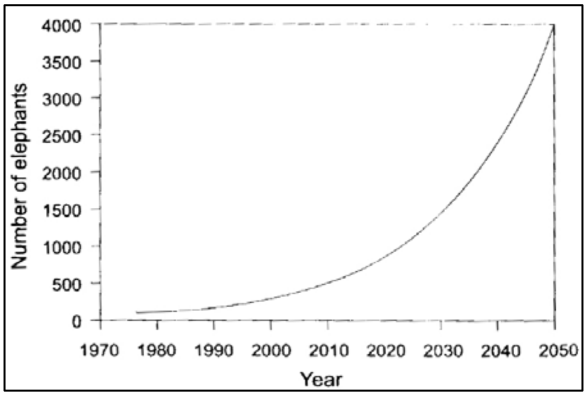


Figure IV - 3. Reconstruction of AENP population 1931-2000 (Whitehouse & Hall-Martin, 2000: Figure C).

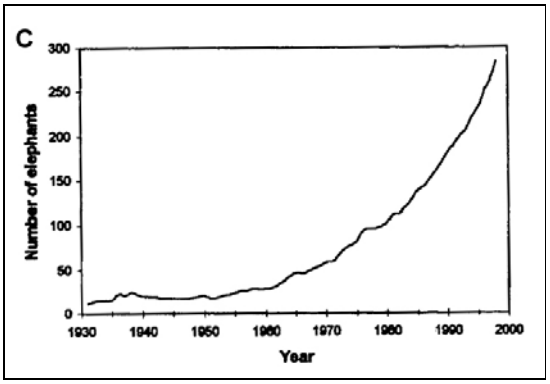


Figure IV - 4. Age and sex distribution of Amboseli population for 6 years illustrating changes over time - Males, solid bars; females open bars (Moss, 2001: Figure 3).

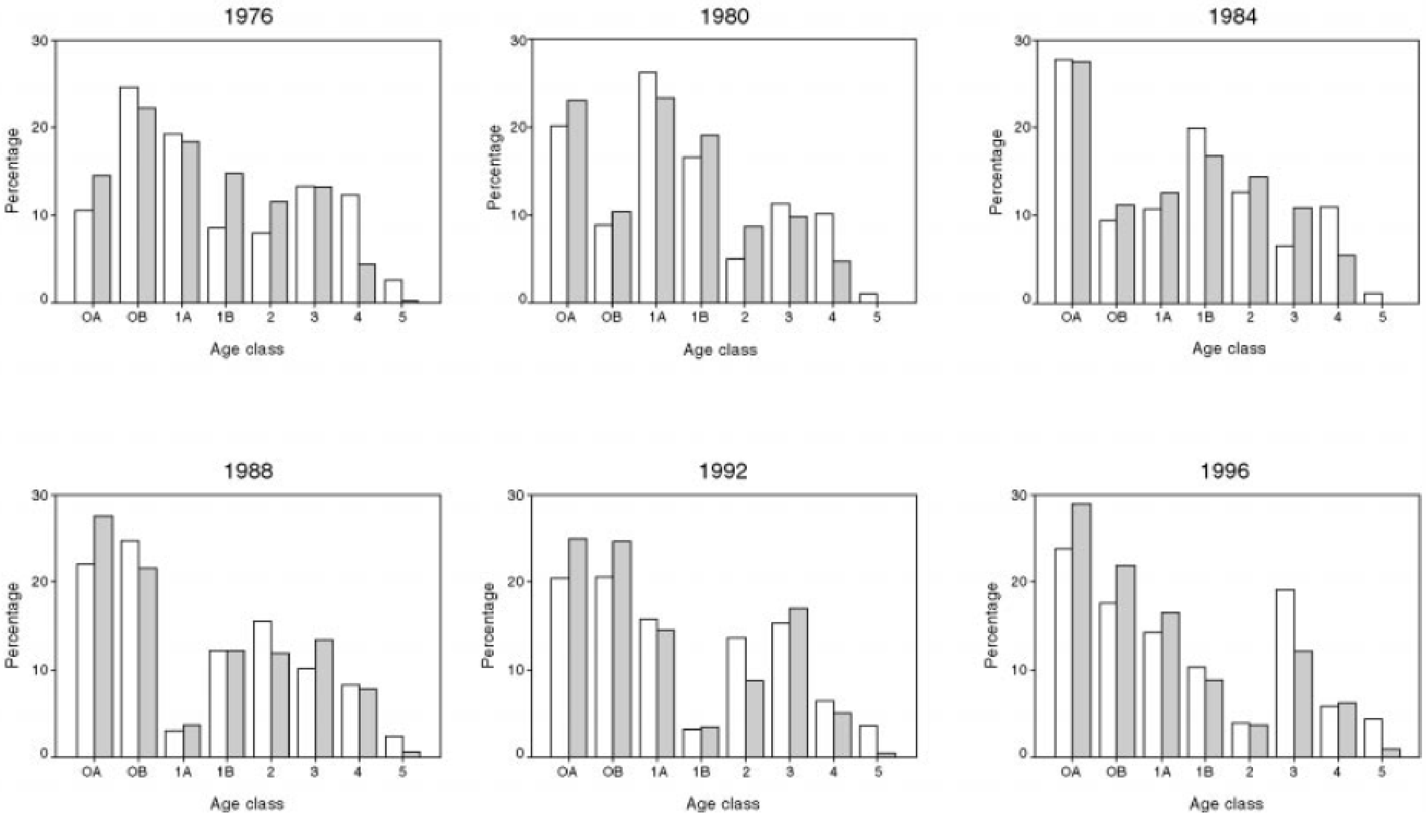


Figure IV - 5. Age-specific survivorship for male and female elephants (Moss, 2001: Figure 10).

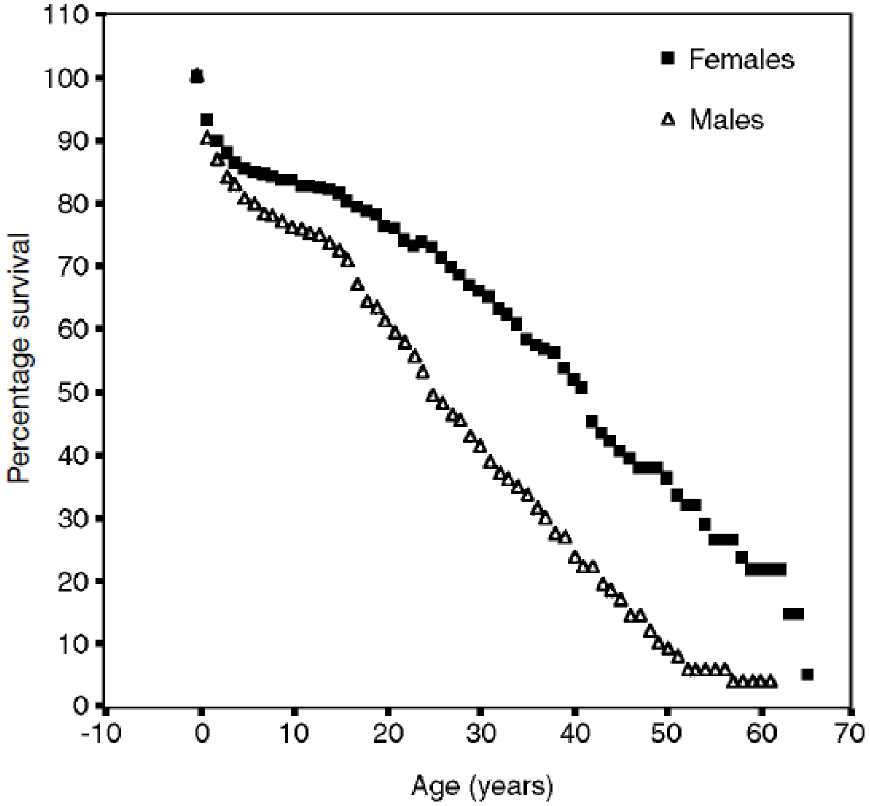


Figure IV - 6a. Rainfall (mm) in 'Amboseli years' from 1974-1999 (Moss 2001: Figure 1).

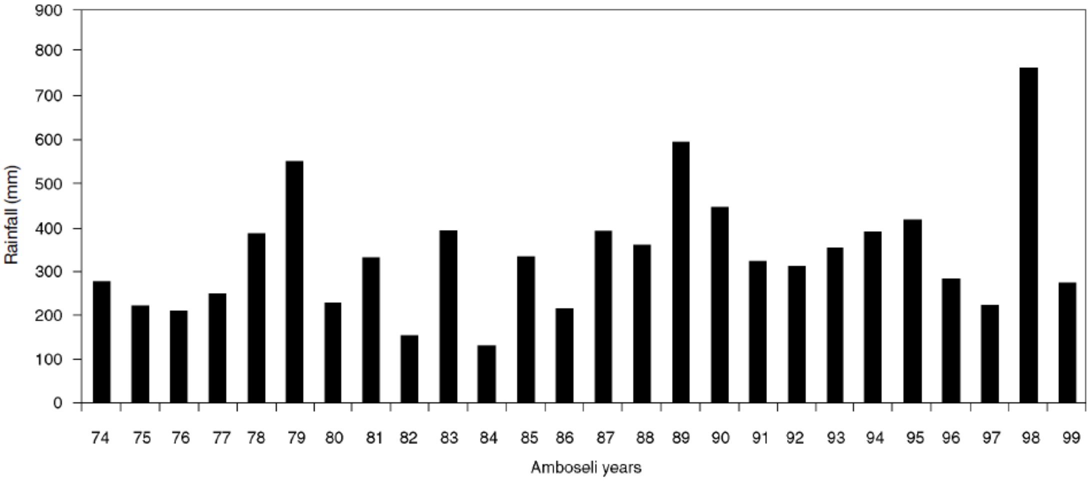


Figure IV - 6b. The sex-specific distribution of mortality by year (N=691) (Moss 2001: Figure 9).

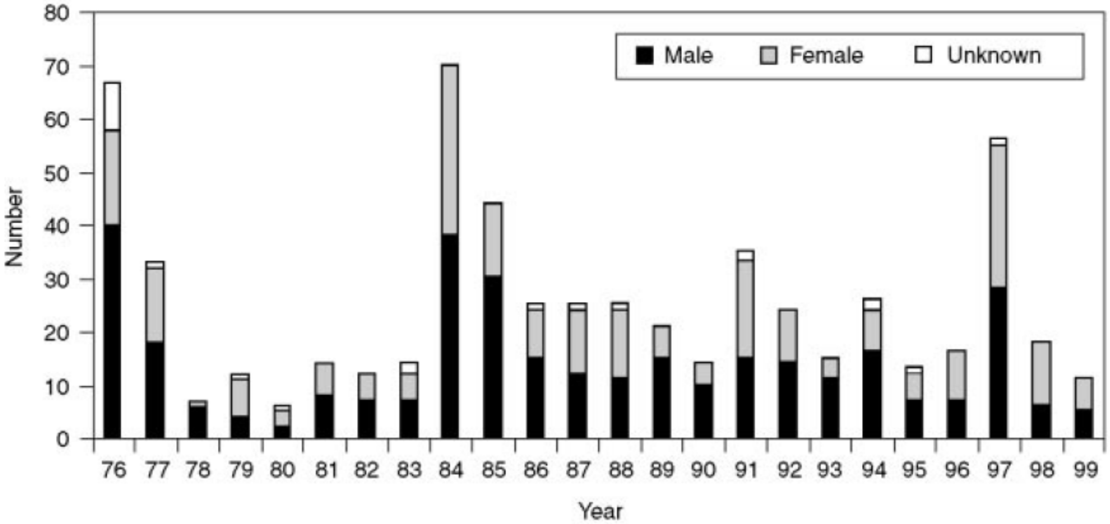


Figure IV - 7a. Growth from an initial population of 11 males and 11 females in an area of 4000 mile^2 for 625 years with no environmental stochasticity (Armbruster et al. 1993: Figure 1).

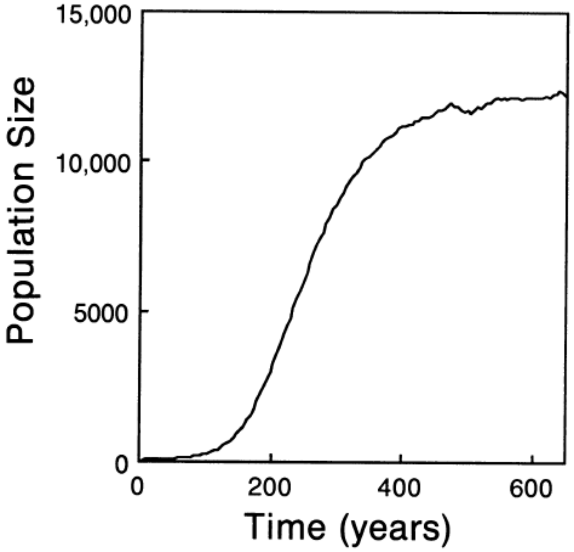


Figure IV - 7b. Simulation of total population size with 10-, 50-, and 250-year droughts over 5000 years (Armbruster et al. 1993: Figure 2).

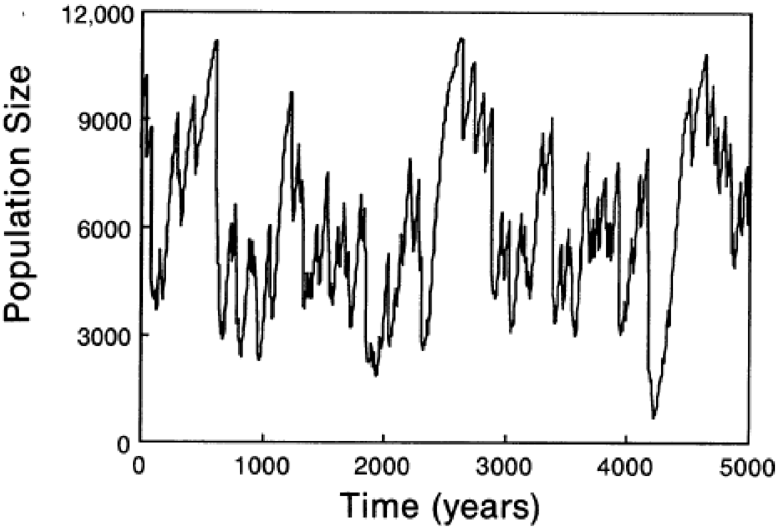


Figure IV - 8. Projected time until population reaches predetermined limit (Dominy et al. 1998).

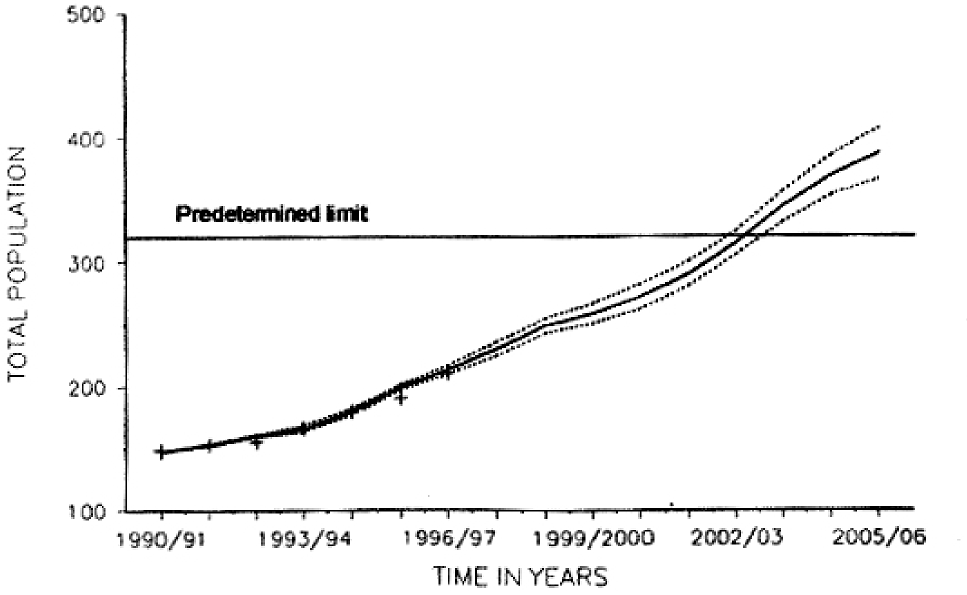


Figure D Total elephant population in the Hluhluwe-Umfolozi Complex. —— Mean total populaion, ... 95% confidence intervals, +++ real data.

Figure IV - 9. Examples of features in Table IV - 6.

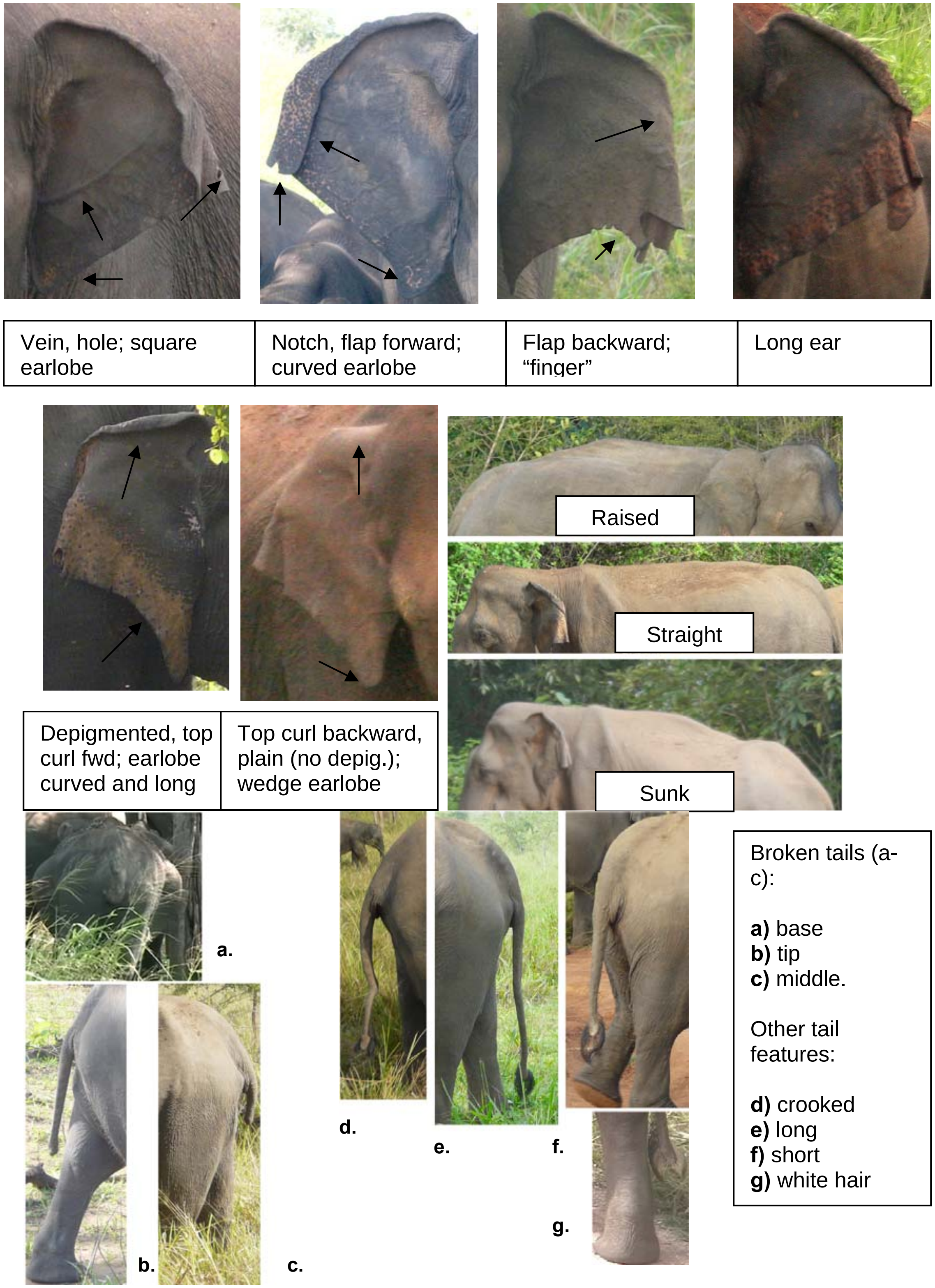
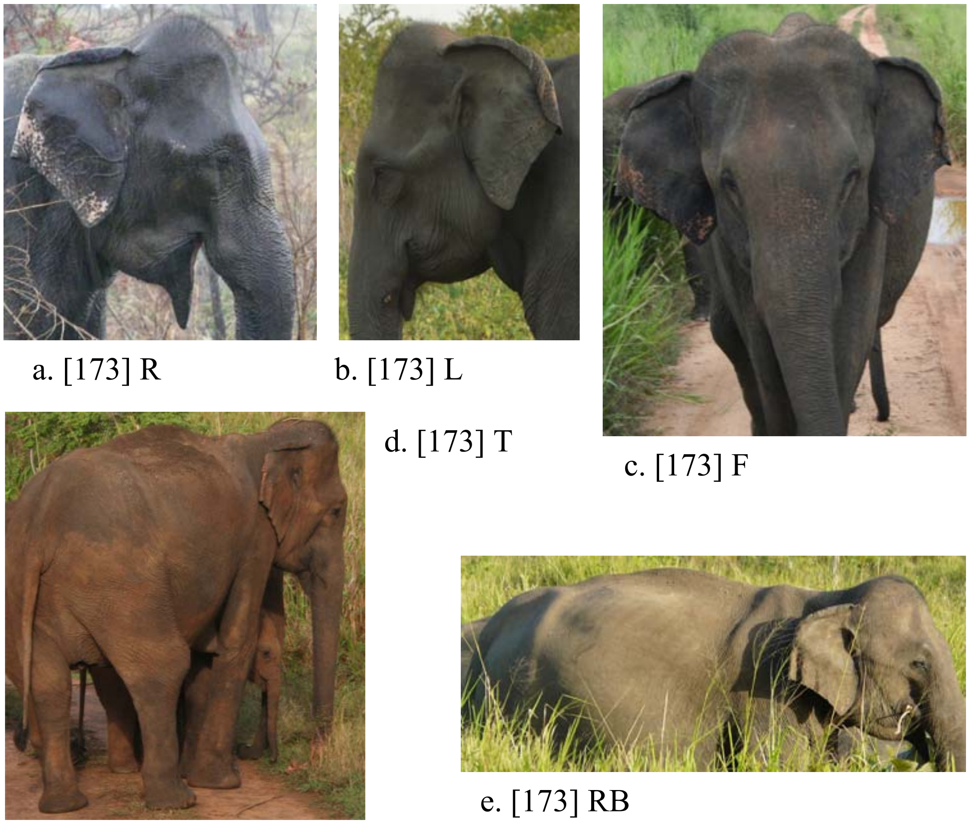


Figure IV - 10. Multiple views. Individuals with asymmetric ears can look different when seen from the left (a) than from the right (b) and be mistaken for two animals. Therefore a full frontal view (c) is essential before a new ID can be assigned. When wet, veins and/or depigmentation are more clearly visible (a). d) Tail length. e) Backbone and forehead profile.



a. [173] R

b. [173] L

c. [173] F

d. [173] T

e. [173] RB

Figure IV – 11. Some individuals may look similar. One has to be careful not just to look at ear features in isolation, but the entire shape of ears and head.

CHAPTER V.

Demography Of Asian Elephants At Uda Walawe National Park, Sri Lanka, Based On Identified Individuals

SUMMARY

I provide estimates of population size and demographic variables for individually-identified Asian elephants in Uda Walawe National Park (UWNP), Sri lanka based on twenty months of observation from 2007-2008. Population size estimates vary substantially depending on the family of models used, length of study, and capture sessions. Estimates using longer time intervals are preferable whenever possible. A robust design model, with seasons as primary intervals and months as secondary intervals, and seasonally varying immigration and emigration probabilities, is the most appropriate for this population. I also calculate number of individuals other age and size classes relative to the number of adult females. At least 286 adult females were identified, with the highest monthly total occurring at the end of the dry season, either in September or October. Thus peak density was at least 1.4 adult females per km^2. At least 183 adult males were identified, of which only four adults (2%) had tusks. By the end of 2008 there were at least 457 potential breeders, using the park seasonally. UWNP should thus be of global conservation priority. These methods and findings may guide population estimation for other elephant populations or cryptic species. I urge that other locations be systematically surveyed as well using photographic identification.

> “The frequently cited global estimate of 30,000–50,000 Asian elephants is often acknowledged as little more than an educated guess…However, conservationists and the media have repeated this estimate so often that it has come to be accepted as fact. Astonishingly, these estimates of the global population have been accepted without revision for a quarter of a century… despite major losses of Asian elephant habitat over this period.”
>
> - Blake and Hedges, *Conservation Biology* 2004

BACKGROUND

The Asian elephant, listed as endangered under the IUCN red list (Choudhury et al., 2006) is part of the unique Proboscidean clade, represented by only three extant members (Debruyne, 2005; Fleischer et al., 2001; Roca et al., 2007; Shoshani and Tassy, 1996). It performs vital long-range seed-dispersal (Campos-Arceiz et al., 2008) and is the only remaining mega-herbivore fulfilling this role in parts of Asia. But Asian elephants are globally threatened by rapid fragmentation and loss of habitat (Leimgruber et al., 2003), poaching for ivory that skews sex ratios, and heavy-handed management measures such as forced translocation of individuals as well as breeding cow-calf units, the impact of which is unknown (Kemf & Santiapillai 2000; Sukumar 2003). In confronting these issues, it should be of grave concern that the global population estimate of 35-50,000 is based on data that are inaccurate and out of date (Blake & Hedges 2004; Choudhury et al., 2006). If successful conservation depends on sound data, then Asian elephant conservation has a formidable challenge to overcome.

Estimating Asian elephant populations has been difficult primarily due to the dense habitats in which they are found. The indirect methods employed under such circumstances, such as dung counts along transects, is strongly influenced by population size itself and subject to wide error depending on dung decay rates (Barnes 2002). Even direct observation via aerial counts of closed populations, which should be unchanging in number, are subject to inaccuracy and can sometimes give worse estimates than dung counts (Barnes 2002; Morley & van Aarde 2007).

Mark-recapture could perform better than these indirect methods. Typical mark-recapture refers to a procedure of trapping, marking, and releasing subjects. But analogous procedures, photographic and genetic mark-recapture - or ‘capture-recapture’ - have long been used in the study of species that are either cryptic, or not easily ‘trapped’ (humpback whales: Smith et al., 1999; Stevick et al. 2001; felids: Karanth, 1995; Karanth et al. 2006). To be applicable, individuals should be identifiable either without direct contact (e.g. photographically) or with small genetic samples obtained through skin or feces. For photographic capture-recapture, a photo taken upon first encounter is taken to the initial ‘capture’ and subsequent re-sightings or photographs are the ‘recapture’. Photographs can be taken by automated camera-traps (Karanth et al. 1996) or human observers. As elephants are individually-identifiable through natural markings, photographic capture-recapture has recently been applied in estimating population sizes in both Asian and African species (Goswami et al., 2007; Morley & van Aarde 2007).

Currently, Sri Lanka is thought to have possibly the second or third largest Asian elephant population in the world, estimated at 3500-4000 (Choudhoury et al. 2008; Perera 2009; P. Leimgruber pers. comm.). If so, this would represent 10% of the wild Asian elephant population, but only 2% of the available global range (Perera 2009). However, few official estimates from within the country have so far been reported (Katugaha et al. 1999).

In this paper I estimate the size of one population of Asian elephants in Sri Lanka using standard models for capture-recapture data (Schwarz & Arnason 1996; Kendall and Nichols, 1995; Kendall et al., 1997; Kendall et al., 1995). I discuss the utility and constraints of certain capture-recapture models for estimating survivorship, immigration, emigration and abundance of Asian elephants. I also provide other demographic data for comparison with other populations and aid in anticipating population trends.

METHODS

Data collection

This paper considers only data collected from 2007-2008 as part of a continuous study of Uda Walawe National Park begun in May 2006 (Figure V - 1). Sampling effort was quantified in terms of the number of field days per month (Table V - 1). Driving routes were alternated such that all parts of the road network were covered at least once per week. Thus the entire motorable area of the park was covered each week, which constituted approximately 1/3 of the total 308 km^2 area of the national park.

I identified individuals using characteristics of the ears, tail, posture, and other natural features (Chapter IV; Moss 1996). Individuals thus assigned an identification number are henceforth referred to as 'catalogued'. Adult females were catalogued from May 2006 onwards and adult males were catalogued from September 2007 onwards. I photographed or videotaped adults upon encounter. Adult females are defined as individuals showing evidence of having been pregnant at least once (such as prominent breast development, belly swelling, or the presence of nursing offspring). I noted the identities of known individuals in addition to the number of unidentified individuals of each sex or age-size class: sub-adult, juvenile, infant, or newborn that was encountered. These size classes were based on height relative to that of an adult female, with corresponding ages based on our observations of wild calves of known age as well as animals of known age reared in captivity (Figure V - 2). Males pass through several size classes that females do not, which are not described in this paper.

Data analysis

Adult females

I only modeled estimates of population variables for adult females. Sightings of identified individuals were processed in SOCPROG (v. 2.4 Whitehead 2009). The number of adult females was then estimated using three types of population models in program MARK (White & Burnham 1999). The initial identification of an individual was analogous to the 'marking' event, with subsequent sightings being 'recaptures'. Because the study area consists of only part of the available area, and the national park adjoins corridors, I considered the observed population to be an open population, where gains and losses of individuals are possible.

I first generated population estimates under the Jolly-Seber model with the Schwarz and Arnason parametrization (Schwarz & Arnason 1996) implemented in the POPAN module of MARK. This model provides estimates of the survival probability (ϕ), the probability of entering the population at each time interval (p_{ent}) and the 'superpopulation' size (here referred to as N*). The superpopulation is the hypothetical pool from which all observed individuals are drawn; in this case, the total number of adult females present during the study period. The model also provides derived estimates of population size at each time interval (N-hat). I considered only models with constant survival because it is unlikely that survival probability changes from month to month for this long-lived species at this study site.

I constructed capture histories based on monthly sampling sessions for the 20 month study period in 2007-2008. An individual was marked as 'present' in any given month if she was seen at least once during that month. I generated variations on the fully time variant model (in which each parameter is estimated for each time interval), which were ranked by MARK according to AICc. AICc is Akaike's Information Criterion corrected for small sample sizes (Burnham and Anderson 2004). Using the highest ranked model from this set, I next considered what would happen if a study was performed for a shorter lengths of time. For this I constructed capture histories based three, four, or five months of data drawn from consecutive months in 2007-2008, and generated estimates under the highest ranked model.

I was concerned whether two key assumptions of CJS models were met for this study population. These assumptions require that: a) all marked individuals have the same probability of being re-sighted; b) all individuals have the same probability of survival from one interval to the next (Schwarz & Arnason 1996). The first assumption would be violated if individuals left the study area temporarily (e.g. seasonal immigration or emigration) and thus were not seen during intermediate time intervals. The second assumption would be violated if individuals marked at different times somehow differed in their apparent survival, which may also be the case if individuals marked on later occasions failed to be re-sighted due to temporary emigration. Permanent immigration or emigration poses no such logical problem. I tested how well the general (fully time-dependent) Cormack-Jolly-Seber (CJS) model fit data using two standard χ^2 tests (commonly known as ‘Test 2’ and ‘Test 3’: Cooch, 2010) implemented with the program RELEASE, within MARK. A significant combined result for Test 2 and Test 3 would indicate violations of these assumptions.

I then considered ‘robust design’ types of models (Kendall and Nichols, 1995; Kendall et al., 1997; Kendall et al., 1995). This family of models explicitly addresses temporary absences using two levels of sampling. Immigration, emigration, birth and deaths can occur between primary sampling intervals that are widely spaced. Within these intervals are several secondary intervals which are spaced closely enough that gains and losses are unlikely, making the population effectively closed. I tried models using months as primary intervals with weeks as secondary intervals, or seasons as primary intervals with months as secondary intervals. Probabilities of first capture and recapture (‘p’ and ‘c’ respectively) were estimated between secondary intervals. Estimates from primary intervals included survival probability, population sizes, and also the probability that an individual was not in the study site in any particular interval depending on whether or not she was present in the previous one. γ” is the probability of emigration from the study area, 1-γ” is the probability of remaining, 1-γ’ is the probability of immigration, and γ’ is the probability an of an individual staying away from the study area. I used both the ‘closed captures’ and ‘Huggins’ versions (Huggins 1989, 1991). The ‘random emigration’ model was obtained by setting γ”=γ’ for all intervals, which means that an individual is as likely to enter the study area as she is to stay away from it (Kendall et al. 1997). The ‘no emigration’ model was obtained by setting all γ parameters to zero. All other models contained markovian emigration with gamma parameters varying by different times. Only constant survival was again considered.

In contrast to the Jolly-Seber model, no super population size is estimated under the robust design model. Nevertheless, determining population size is a primary concern of conservation and management. In order to obtain upper and lower bounds on the total abundance in a year, I make use of the number of adult females who were seen but not identified. Unidentified individuals may be individuals entering the site for the first time in the study, or previously catalogued individuals who we failed to identify. To obtain the lower bound on the population size of adult females, I assume that all unidentified individuals are previously catalogued, so that the total number of adult females equals to the total number of cataloged females. In order to obtain the upper bound, I assume that all unidentified individuals are un-cataloged and unique, so that the total number of adult females equals the number of cataloged females plus the number of unidentified individuals. This upper bound ignores those individual who may be in the population who are never seen. In order to estimate the number of un-cataloged individuals, I assume that both cataloged and un-cataloged individuals are re-sighted at the same rate, so that for a particular year:

$$N_u/S_u = N_i/S_i \qquad (1)$$

holds, where N_u is the number of un-cataloged adult females, S_u is the total count of sightings of un-cataloged individuals, N_i is the number of cataloged adult females, and S_i is the total count of sightings of cataloged individuals. For instance, in 2007, $S_i = 1611$, $N_i = 255$ (i.e. 255 cataloged adult females accounted for 1611 sightings), and $S_u = 738$. Equation (1) yields the number of uncataloged individuals to be 117. The total adult female population would thus be 255 + 117 = 372. In reality, unidentified individuals would be a mix of these two categories and the total population would be between the lower and upper bounds.

Other age and sex classes

To determine the number of individuals in age classes other than adult females, I summed the total number of individuals seen in each age class annually, and calculated the proportion of the total that belonged to each age class. If the same group was encountered more than once in a day, I counted individuals using only one encounter for that day. If the number of individuals in the group differed between encounters on that day, I used the encounter with the larger number of individuals. I determined the number of individuals in an age class in proportion to the number of identified adult females observed in that year in the same way as above, assuming that:

$$N_a/S_a = N_i/S_i \qquad (2)$$

where N_a is the number of individuals in a particular age class, and S_a is the total count of individuals in that age class. I performed this calculation for each year separately because individuals changing age classes between years would be double counted otherwise. In addition, younger age classes would not be re-sighted as often as older age classes over longer intervals (e.g. newborns, who by definition would only be present in one year) and would therefore be underrepresented.

For adult males, I provide only the count at the end of 2008, as capture histories have not yet been constructed.

RESULTS

I identified a total of 286 adult females over the study period. On average, I identified up to 80% of the adult females in groups where at least one individual was known. The highest number of identified adult females seen in the study area in a month was 152, in October 2007. This density exceeds 1.48 adult females per km^2, assuming all individuals were present throughout the month.

Jolly Seber models

Using the full dataset, the combined goodness of fit result for Test 2 and Test 3 was $\chi^2 = 395.12$, d.f.=102, $P<<0.001$. This highly significant result means that the population did not meet assumptions of the CJS models, because whether an individual was identified during a particular sampling interval affected whether she was seen in subsequent intervals. This set of models was therefore not appropriate for this dataset. Results are still presented here to draw attention to their divergence from data, as well as comparison with robust design models.

The top ranked model had a unique entry probability for each month (for a total of twenty entry probabilities, Figure V - 3). AICc ranks for models with entry probabilities varying by other time partitions were also considered, and are listed in the Appendix. Super population sizes estimated with fewer months of data under the same model were never close to the population size estimated with the full dataset, nor even the total number of adult females actually seen at the end of twenty months - the minimum number alive, assuming no deaths (Table V - 1). Instead, estimates closely tracked the number of individuals actually seen, though yielding a slightly higher number (Figure V - 4a). Monthly population size estimates diverged noticeably from those obtained using the full dataset (Figure V - 4b). Survival estimates under various partitions are provided in Table V - 2.

Robust design models

For closed-captures models, population size estimates were only possible when the probability of re-sighting was set equal to the probability of first sighting (i.e. the probability an individual being re-sighted within a sampling interval was set equivalent to the probability of being seen at all in that interval). This was not necessary for Huggins models. These two probabilities would not be equivalent if the initial encounter altered the probability of re-sighting an individual – for instance through habituation (becoming increasingly tolerant of approach by observers) or aversion (avoiding observers). Experience suggests that this is not the case for elephants in this population, as they are already habituated to tourists and researchers.

Designating seasons as primary intervals and months as secondary intervals yielded the most reliable results, judging by the spread of confidence intervals for estimated parameters. Shorter time intervals were subject to wide inaccuracies, as reported in the Appendix. I considered only closed-captures models, as they seemed most reasonable based on the results just described. All yielded nearly identical seasonal population estimates, which very closely matched the total number of identified individuals who were actually seen in a season, and the results using the Schwarz & Arnason set of models previously discussed (Table V - 3). Model 7 represented the situation where immigration and emigration vary during each primary interval (season) but an individual is sighted during the same time of year across years (month). It gave the most reliable estimates with the least number of parameters, as judged by sizes of the associated confidence intervals. It also represents the most biologically plausible scenario. This model was therefore chosen as the most appropriate for describing this data out of those that were run, despite its lower AICc rank with respect to several others. Estimated survival under this model was 0.95 (95% C.I. = [0.89, 0.97]). Other relevant estimates are graphed in Figure V - 5. Immigration and emigration from the study area are evident both from model results as well as visible seasonal patterns in the sightings of known individuals (Figure V - 6). Bounded estimates of population size by age class are provided in Table V - 4.

The earliest age a female was first observed in oestrus was nine years old, with successful pregnancies completed by age eleven. This was known in part due to juveniles of known age that were rehabilitated and released from the Uda Walawe Elephant Transit Home (ETH). Not all adult females identified had calves – some were post-reproductive. The inter-calving interval appears to be approximately four years; however the study does not have enough repeated observations at this time to determine an average. After accounting for senescence and deaths of known individuals, the population of potential breeders at Uda Walawe National Park at the end of 2008 was 275 adult females.

The total number of adult males identified was 183. Of these, only four mature adult males (2% of the adult male population) had tusks, as well as two sub-adults and three juveniles. As of 2009 one adult tusker was killed, and another seriously wounded, but in 2010 a new tusked male was trans-located into the park, and where it continued to be sighted during musth and thus may potentially have bred. One juvenile was an individual trans-located from the ETH. One of the juvenile tuskers has been in ill health following the death of his mother, who was part of this study.

DISCUSSION

The number of potential breeders is a more informative figure than population estimates themselves, and the most reliable figure is the number of potentially breeding individuals I have actually observed. At Uda Walawe, this number is at minimum 458. Not all adult males breed, so the effective population size and its genetic implications are as yet unknown. Yet if all of Sri Lanka is estimated to have a population of four thousand elephants or less (Choudhury et al. 2008; Perera 2009), the rotating presence of nearly one thousand adults and calves (taking the upper bound) in UWNP, means either that this area contains nearly a quarter of the total national population, or that the total estimate is questionable. While the former is possible, it is more likely that the total estimate is inaccurate and that other areas should be carefully studied as well. The spread between the lower and upper bounds for the estimate of this population alone is on the same order of magnitude as that for the national population estimate. Locations such as Minneriya and Wasgamuwa may have comparable populations (M. Gunawardana, pers. comm.). These data suggest Uda Walawe should be an area of top priority nationally, and Sri Lanka an area to target globally, for the conservation of this endangered species.

In terms of global estimates, these data draw further attention to the importance of reporting reliable estimates from elsewhere, as called for by Blake and Hedges (2004).

Model selection

The assumptions of Cormack-Jolly-Seber (CJS) model types were clearly violated at this study site. Shorter studies may fail to detect such violations. This may not be a severe failing if a large enough portion of the population is identified that estimates generally agree under multiple models. However, estimation of abundance is not the sole concern. Survivorship and migration are key requisites for predictive demographic models and conservation planning. The estimate of survivorship under the Schwarz and Arnason model using the full dataset was higher than that under the robust design model based on identical capture histories. On the other hand, the latter was higher than estimates obtained with most partial datasets, unsurprisingly. Short study periods under-estimate survival probability and population size if individuals temporarily leave the study area. While longer studies are preferable, if they are not feasible, estimates of survivorship may need correction.

A population may consist of individuals who remain at the study site for the duration of a study period if ecological conditions do not change. At least some of them may nevertheless be replaced by others during another period (e.g. season), which would not be detected if observers are absent. This may be less problematic if a study site does not actually have year-round occupancy. Those individuals who appear when it is occupied may could represent nearly the total population in an area if it is the only source for a scarce or vital resources such as food, water, nest sites etc. At the very least, it would be wise to repeat the study at the same time of year for multiple years and determine whether the number of new individuals entering the population appears to have stabilized to low levels. If it has not, then an estimated ‘superpopulation size’ is more likely to be an estimate of the population size in the study area at that particular time interval, rather than size of the total population that makes use of that area over the long term.

If there is in fact temporary immigration and emigration, it is *not* advisable to view derived population estimates as having any biological basis in the short-term. There would be more new identifications than re-sightings, and apparent fluctuations in population size would be a consequence of the time lag until observers detect a substantial fraction of the population, rather than a reflection of fluctuations in the actual number of individuals in the study area. One should therefore consider whether or not the study population is likely to be changing before model selection and interpretation of results, especially if it involves a species capable of ranging over a distance that is greater than the observation area.

The duration of a mark-recapture study determines how many individuals can be observed, which in turn influences estimates of abundance. But for many species, and indeed, for Asian elephants in most habitats, it is may not be feasible to observe individuals year-round. Capture-recapture can still be a very useful method to employ in such cases, but one should carefully consider how much can be inferred under such limited conditions. At the very least, automated tools such as camera traps should be used. Moreover, the ‘best’ model must be selected not solely on the basis of AICc or initial assumptions, but ultimately how ecologically realistic and true to data it is.

While the model parameterizations I considered were not exhaustive, the overall agreement among models, and the biological significance of the robust design model ultimately chosen, is fairly good. I consider here some potential failings. It is possible there is some leakage of individuals between months, and thus the population is not completely closed between secondary intervals; it is possible that not all individuals have arrived by the beginning of the primary interval, or are present at the end of it. This would be true if individuals arrive and leave the study site in a staggered manner. The shorter the primary interval, the less likely that this will be a problem. However, short primary intervals require even shorter secondary intervals, during which the ability to re-sight individuals may be severely limited. It is possible that long-term data would allow models with monthly primary intervals and weekly secondary intervals to stabilize and provide estimates with greater accuracy. On the other hand, it may simply not be possible to cover enough ground to obtain such accuracy without substantially increasing the amount of labor. In this case, it may be necessary to consider 'open robust design' models, in which secondary intervals are not closed (Kendall & Bjorkland 2001; Kendall & Nichols 2002; Schwarz & Stobo 1997). Nevertheless, I do not think it a problem for this study site, where transitions between monsoon and inter-monsoon are quite abrupt, with which the sightings of known cow and calf groups are timed fairly closely in our experience. The greater utility of these models and this growing dataset will be in evaluating longer time scales. This is not true of adult males, discussed further below.

Other assumptions

Calculating the number of 'unidentified' individuals makes a simple assumption: that the adult females that are identified and those that are unidentified are re-sighted the same number of times, on average. More precisely, I assume that even though some individuals may be seen more often than others, the distribution of sightings for one group is proportional to that of the other and that this proportionality holds constant over time (Equation 1). This may not be true if, for instance, individuals that are seen rarely (seasonal occupants) are a) more likely remain unidentified because observers are less likely to recognize them and b) account for a smaller fraction of sightings per individual than those that are regularly seen. On the other hand, some portion of 'unidentified' individuals are likely to be those who are in fact catalogued. In groups where at least one individual was known, it is likely that the other individuals were also previously catalogued, but not clearly visible. These individuals would be 'really' present more often than recorded. These two sources of 'unidentified' individuals place the upper and lower bounds on the population estimate. They are wider than the confidence intervals under any model, but in being based on logical extremes, they may be more realistic representations of possible error.

The same proportionality assumption is made in obtaining the number of individuals in different age classes. Here I justify the assumption on the basis that cows and calves travel together, therefore their sightings are correlated. The best correlation is likely to be between a mother and her juvenile calf, who is likely to be old enough and big enough to be seen whenever she is seen. The assumption may not be as good for sub-adults, males especially, who may occasionally roam and switch groups (personal observation); nevertheless over many observations such error should be minimized. The assumption may also be poor over long time intervals for infant and newborn age classes for two reasons. They may occasionally missed in the vegetation due to their size, and newborns by definition are not present the full year. The associated adult females (e.g. their mothers) would then have been seen more often, and the proportionality (Equation 2) would not hold. These estimates are therefore rather crude. For this population at least, better counts of the demographic classes and survival will be possible in future by monitoring a subset of the calves of known individuals and generalizing from this to the entire population.

The proportionality cannot hold between sightings of adult males and adult females. Adult males, especially when in musth, are well documented to range over greater areas than females (Fernando et al. 2008, Leggett 2006). There may be even more turnover among males than among females. Moreover, males use space differently – for instance, they are often observed on the Uda Walawe reservoir bed at times of year when herds are absent from it. It is not advisable to estimate the population size of males from sightings of adult females, or vice versa.

Implications for conservation

While I have shown that elephants range in and out of the study site, the extent to which they also range outside of the park entirely is not known. Certainly, some individuals that are seen less frequently must spend a part of their time in areas of the park that are inaccessible to us on a regular basis, as evidenced by dung and footprints. But it would be extremely surprising if known individuals who are seen on the edges of unfenced park boundaries did not also range outside it. Distinctive males, such as identified tuskers, have been documented in areas outside the park (Dr. B.A.D.S. Jayawardana, pers. comm.); I also observe these individuals within the park at very specific times of year. There are still elephant populations whose ranges are outside protected areas, but the amount of suitable habitat for herds is dwindling (Fernando et al. 2008; P. Fernando, pers. comm.)

The issue of cultivation and settlement alongside elephant corridors is contentious, and there are conflicts between people and elephants on these adjacent lands (personal observations). But I maintain that UWNP alone could not support this number of elephants if they did not also have range outside it. Therefore it is vital that routes between UWNP and other potential elephant habitats be maintained. Further restriction of movement would impose a more severe burden on the resources available within the national park. Habitat fragmentation elsewhere would have the same effect. Asian elephants have been predominantly forest-dwelling. However, in places like UWNP, there is a noticeable impact on vegetation that deserves further study. Loss of trees would have consequences for other native species, such as leopard, deer, and birds, not only elephants themselves. The issue would not be solved by simply increasing the local availability of resources, such as water, since it fails to address ecosystem effects.

If elephant populations are locally higher than expected – or, for that matter, appear to increase – it is critical to determine whether this is the result of healthy breeding or the concentration of more individuals into smaller remaining areas due to loss of other portions of their home ranges. It is an incontrovertible fact that habitat loss has deprived elephants of much of their historic range, particularly in tropical deciduous forests, which are in rapid decline due to agricultural conversion (Miles et al. 2006). It is likely in fact they have declined elsewhere (Hedges et al. 2005). An increase in one area may reflect a decrease in others. This can only be evaluated if there is a concerted effort to monitor multiple locations. In either case, the ecological effect of elephant densities should be considered before restricting them behind fences.

The biggest challenge in Asian elephant conservation is not getting them to breed in captivity, preserving domestic populations, or even preserving tusked individuals *per se*, even though they seem on the brink of disappearing from certain populations, like this one. Ivory poaching is not a major conservation problem for Sri Lanka's elephants since most male elephants are tusk-less. Despite being cultural icons, tusked males may not persist in Sri Lanka. Nevertheless, the primary problem for Asian elephant conservation and management remains in indentifying the location and size of extant breeding populations, valuable habitats, and facing head on the land-use challenges raised by trying to protect them.

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Table V - 1. Sampling periods. Sampling effort per month is quantified in terms of the number of days; the area covered was the same. 'Dry' months have a total rainfall less than the two year average of 108.6 cm and 'Wet' months have rainfall greater than this average.

Month-Yr	No. days	Rain (cm.)	Season
Jan-07	10	16.9	Dry
Feb-07	12	90.6	Dry
Mar-07	13	143.3	Wet
Apr-07	13	158.9	Wet
May-07	17	16.0	Dry
Jun-07	9	30.8	Dry
Jul-07	17	10.7	Dry
Aug-07	14	46.4	Dry
Sep-07	11	89.7	Dry
Oct-07	16	114.8	Wet
Nov-07	14	295.7	Wet
Dec-07	14	154.0	Wet
Jan-08	0	14.1	Dry
Feb-08	0	91.9	Dry
Mar-08	0	222.6	Wet
Apr-08	0	165.6	Wet
May-08	11	27.6	Dry
Jun-08	14	23.8	Dry
Jul-08	16	31.8	Dry
Aug-08	9	49.6	Dry
Sep-08	12	17.0	Dry
Oct-08	15	313.3	Wet
Nov-08	9	366.2	Wet
Dec-08	13	114.7	Wet

Table V - 2. Estimated survival under the Schwarz and Arnason JS model with full and partial datasets. Datasets with fewer months in general provide lower estimates of survival, where comparable partitions across different years do not necessarily provide similar estimates. The full dataset is likely to be the most reliable since it minimizes failure to re-sight individuals.

				95% C.I.	
Season (month)	**Partition**	**ϕ**	**SE**	**Lower**	**Upper**
12 dry, 8 wet	**Full**	0.970653	0.002895	0.964416	0.975825
7 dry, 5 wet	**2007 only**	0.948917	0.006368	0.934892	0.96005
5 dry, 2 wet	**2008 only**	0.953064	0.008888	0.93223	0.967715
2 dry, 2 wet	**Jan-Apr 07**	0.884212	0.036574	0.791298	0.938952
5 dry	**May-Sep 07**	0.957025	0.016751	0.909284	0.980188
3 wet	**Oct-Dec 07**	0.834799	0.037415	0.748059	0.895834
5 dry	**May-Sep 08**	0.932512	0.018998	0.884346	0.961492
3 wet	**Oct-Dec 08**	0.902814	0.05998	0.70869	0.972582

Table V - 3. Robust design models ranked by AICc. Following the notation in MARK, brackets denote intervals, '.' denotes a constant parameter, 't' denotes a parameter that changes between every interval (i.e. it is fully time-varying), and a number denotes a fixed value for that parameter. Gamma values of zero represent a model without immigration or emigration. Gamma values set equal to one another represent random immigration. The 'Num. Par.' column lists the number of parameters that were actually estimated under the model. Model 1 has 1 survival (ϕ) estimate, 5 (γ") estimates (one for each of six seasons except the first), 4 (γ') estimates (for all but the first two seasons), 20 capture/recapture (p) estimates (for each month), and six (N) estimates for a total of 36 parameters; out of these only 34 are estimable. While all models provided nearly identical population estimates and similar survival estimates, the estimability of gamma values and size of associated confidence intervals varied greatly. Models 1 and 7 provided the most reliable estimates. Model seven had the same number of gamma parameters as model 1, but only twelve capture/recapture parameters, corresponding to each calendar month. Model seven thus had only twenty eight parameters in total, and as it successfully estimated all but one, it was chosen as the most adequate model despite its lower AICc rank. It represents the condition under which immigration and emigration vary during each primary interval (season) but an individual is sighted during the same time of year across years. This also represents the most biologically plausible scenario. Further results for this and other models are provided in the Appendix.

Rank	Model	AICc	Δ AICc	Num. Par.	Deviance
1	ϕ(.) γ''(t) γ'(t) p=c(t) N(t)	-2554.18	0	34	2471.59
2	ϕ(1) γ''(t) γ'(t) p=c(t) N(t)	-2551.98	2.1921	33	2475.85
3	ϕ(.) γ''(season) γ'(season) p=c(t) N(t)	-2546.42	7.7586	31	2485.54
4	ϕ(.) γ''=γ'(t) p=c(t) N(t)	-2539.46	14.7196	30	2494.57
5	ϕ(.) γ''=γ'(season) p=c(t) N(t)	-2538.07	16.107	29	2498.01
6	ϕ(.) γ''(t) γ'(t) p=c(t) N(.)	-2530.26	23.9108	30	2503.76
7	ϕ(.) γ''(t) γ'(t) p=c(month) N(t)	-2523.65	30.5274	27	2516.55
8	ϕ(1) γ''(t) γ'(t) p=c(month) N(t)	-2523.05	31.1286	26	2519.20
9	ϕ(.) γ''(season) γ'(season) p=c(month) N(t)	-2521.74	32.4376	23	2526.66
10	ϕ(.) γ''=γ'(t) p=c(month) N(t)	-2513.48	40.6951	22	2536.96
11	ϕ(.) γ''(t) γ'(t) p=c(month) N(.)	-2507.49	46.6872	22	2542.96
12	ϕ(.) γ''=γ'(0) p=c(t) N(t)	-2474.59	79.586	27	2565.61
13	ϕ(1) γ''=γ'(t) p(t) c(t) N(t)	-2389.64	164.5387	33	2638.20

Table V - 4. Cow and calf population sizes.

	2007 (12 months)				2008 (9 months)			
Age/sex class	**Count**	**Lower bound**	**POPAN N***	**Upper bound**	**Count**	**Lower bound**	**POPAN N***	**Upper bound**
Identified AF	1611	255	-	255	1727	200	-	200
Unidentified AF	738	0	-	117	645	0	-	75
Tot AF	2349	**255**	264	**372**	2372	**200**	209	**275**
SF	323	35	36	51	531	45	47	61
SM	160	17	18	25	161	14	14	19
SB	499	54	56	79	341	29	30	39
Tot SB	982	107	110	155	1033	87	91	120
JV	1559	169	175	247	1754	148	155	203
IN	549	60	62	87	833	70	74	96
NB	150	16	17	24	280	24	25	32
Total	5855	**607**	**627**	**885**	6272	**529**	**553**	**726**

Figure V - 1. Uda Walawe National Park. Study area is indicated by diagonal hatches. Inset: location in Sri Lanka (http://schools.look4.net.nz/).

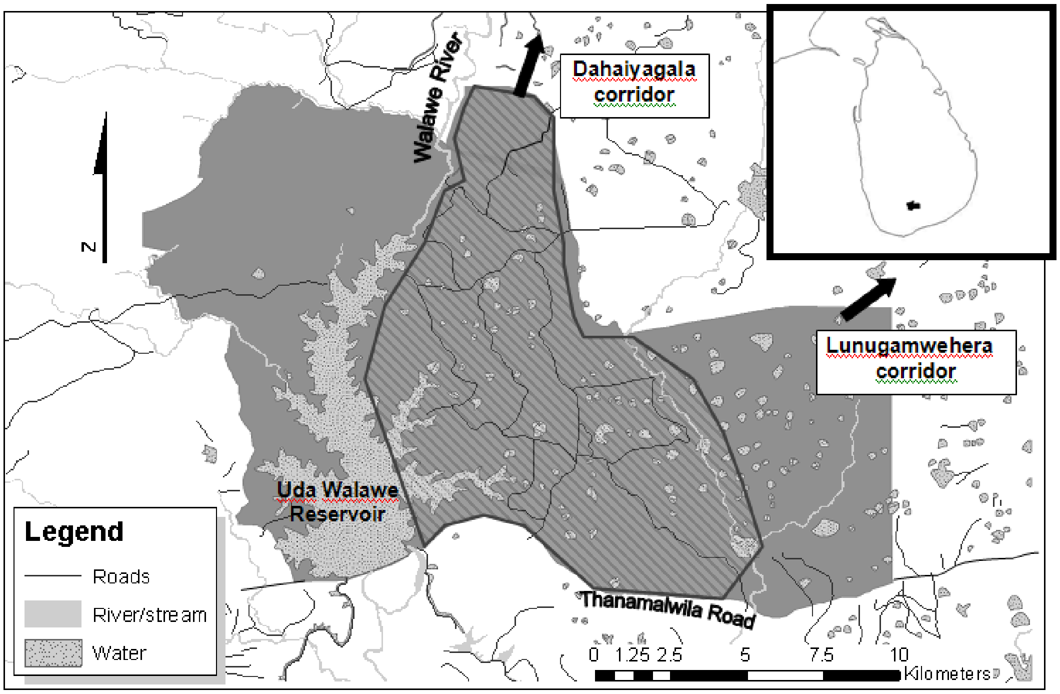
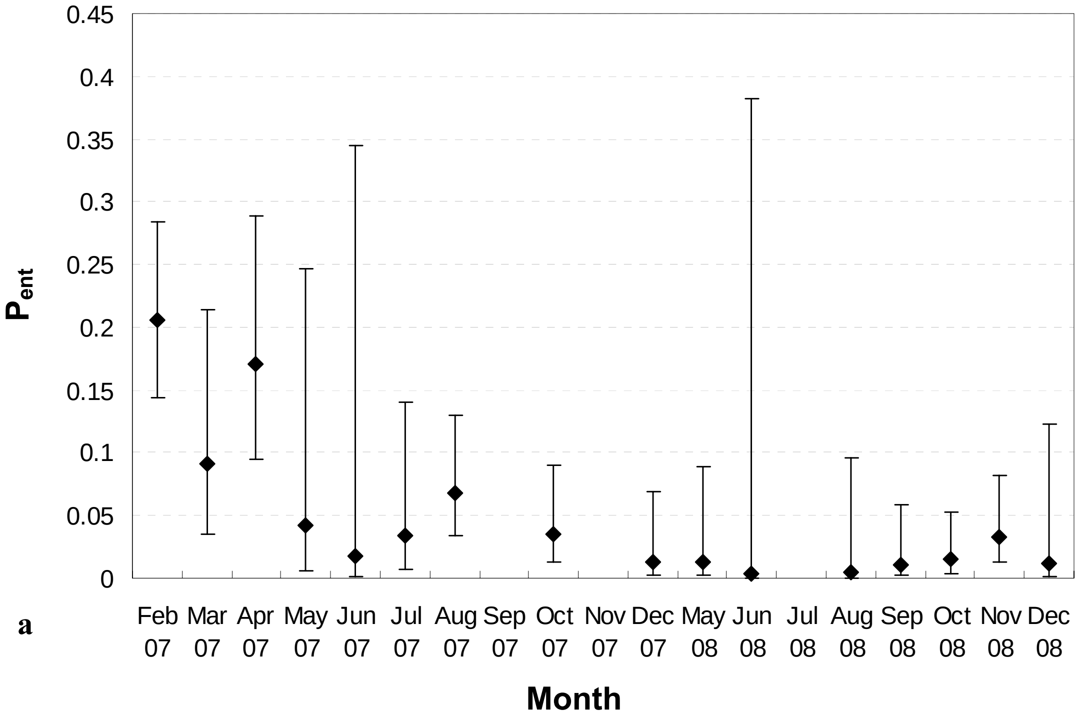
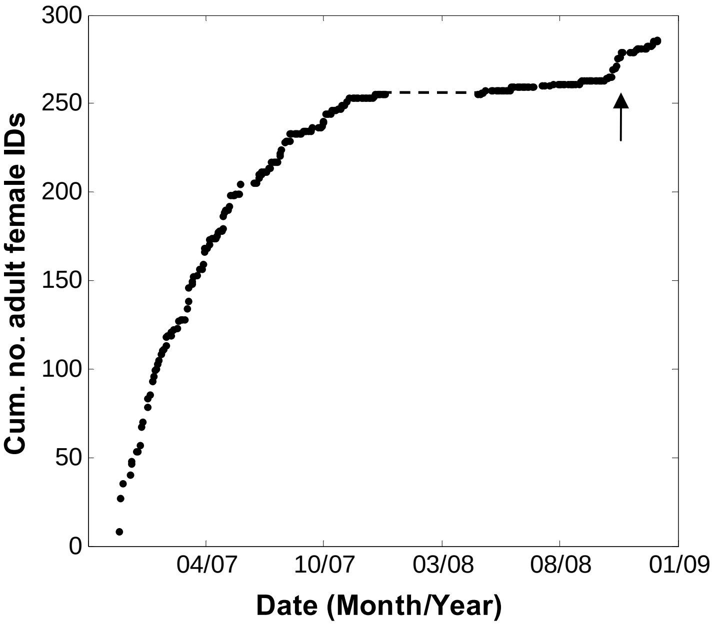


Figure V - 2. Age and size classes of calves relative to the height of an adult female. The size class 'newborn' designates calves that are less than six months old, who can pass beneath the forelegs of an adult female. The 'newborn' pictured here is close to the maximum size for this class, whereas true newborns aged a few days would pass beneath her belly without touching it. 'Infants' (7 months – 2 years) are calves that are too tall to pass easily beneath an adult female, but fit comfortably beneath her chin. 'Juveniles' (3-7 years) may reach half the height of an adult. 'Sub-adult' (8-12 years) females may be equivalent to the height of an adult female, without yet having enlarged breasts or entered oestrus. 'Sub-adult' males are of equivalent size to sub-adult females for the purposes of this paper. However, males continue to grow larger than adult females before fully maturing.

Figure V - 3. New identifications with time. a) The estimated probability of new individuals entering the population under the Schwarz and Arnason Jolly-Seber model, where error bars indicate 95% confidence intervals with a lower bound at 0. The probability of seeing new individuals remains below 5% for most months following April 2008, reflecting that most individuals in the population have been identified. In both years June has greater uncertainty in this estimate. **b)** Discovery curve, by sampling interval. The inflection in the discovery curve corresponds to April, as in (a), after which new individuals appear at a lower rate than previously. However, the arrow indicates an apparent small increase in new identifications in late 2008, which is not apparent in (a).

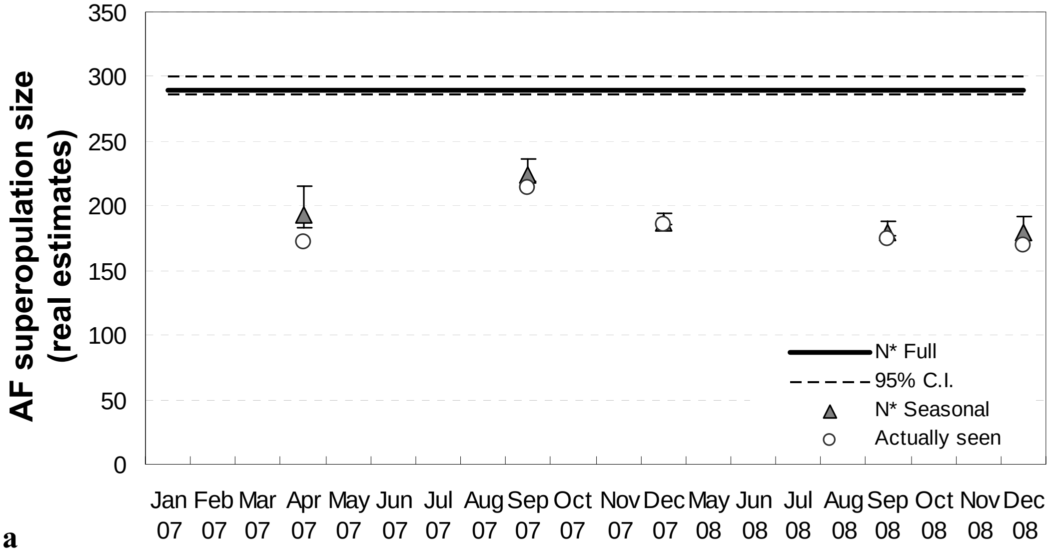

0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
P_{ent}
Feb 07
Mar 07
Apr 07
May 07
Jun 07
Jul 07
Aug 07
Sep 07
Oct 07
Nov 07
Dec 07
May 08
Jun 08
Jul 08
Aug 08
Sep 08
Oct 08
Nov 08
Dec 08
Month

a

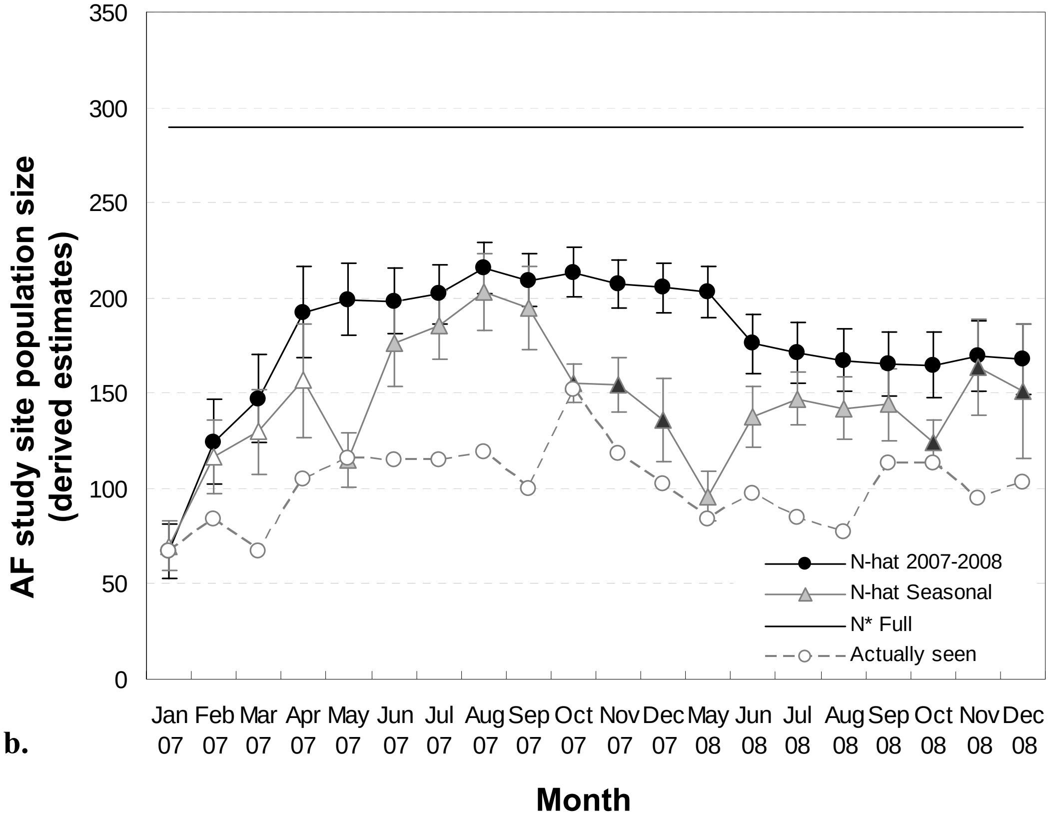

300
250
200
150
100
50
0
Cum. no. adult female IDs
04/07
10/07
03/08
08/08
01/09
Date (Month/Year)

b.

Figure V - 4. Schwarz and Arnason JS models. a) N* line is the estimated total population of adult females ever to appear in the study area (the superpopulation) as estimated from the full 20 month dataset under the Schwarz and Arnason model. This estimate is slightly higher than 286, the total number of adult females actually seen over this period. Triangles represent N* with 95% C.I. bars under the same model, estimated using only 3, 4 or 5 months of data partitioned according to one or more seasons. The first partition uses only data from January-April 2007, the second from May-September 2007, the third from October-December 2007, the fourth from May-September 2008 and the fifth from October-December 2008. All are clearly below the number estimated with the full dataset, but closely match actual sightings. Circles represent the number of unique adult females actually seen within those time periods (when each individual is counted only once for that season). b) Derived monthly estimates of population size for the same models and datasets as in (a). Estimates using the full dataset stabilize after four months, corresponding to the decrease in the probability of encountering new individuals, whereas estimates from smaller datasets do not.


AF superpopulation size
(real estimates)
350
300
250
200
150
100
50
0
N* Full
95% C.I.
N* Seasonal
Actually seen
Jan 07
Feb 07
Mar 07
Apr 07
May 07
Jun 07
Jul 07
Aug 07
Sep 07
Oct 07
Nov 07
Dec 07
May 08
Jun 08
Jul 08
Aug 08
Sep 08
Oct 08
Nov 08
Dec 08

a


AF study site population size
(derived estimates)
350
300
250
200
150
100
50
0
N-hat 2007-2008
N-hat Seasonal
N* Full
Actually seen
Jan 07
Feb 07
Mar 07
Apr 07
May 07
Jun 07
Jul 07
Aug 07
Sep 07
Oct 07
Nov 07
Dec 07
May 08
Jun 08
Jul 08
Aug 08
Sep 08
Oct 08
Nov 08
Dec 08
Month

b.

Figure V - 5. Closed-captures robust design model 7. Seasons are primary intervals and months are secondary intervals. The solid line in panel 1 is the total number of adult females seen after 2 years, which was 286. The seasonal number of sightings corresponds closely to the estimated size of the adult female population in the study area, which remains below the total at any given time. The highest number of adult females seen coincided with the highest estimated population size of 214, which occurred in June of 2007. The second and third panels are the probabilities of emigration (or death) and immigration respectively. Emigration probabilities show a slight positive trend, which may be partly due to the missing months of data from 2008. Immigration probabilities show a decreasing trend, corresponding to the fact that most individuals are identified by the end of this period, thus fewer new individuals are entering the population. Individuals who were seen previously also contribute to both sets of probabilities by temporarily leaving and re-entering the study site.

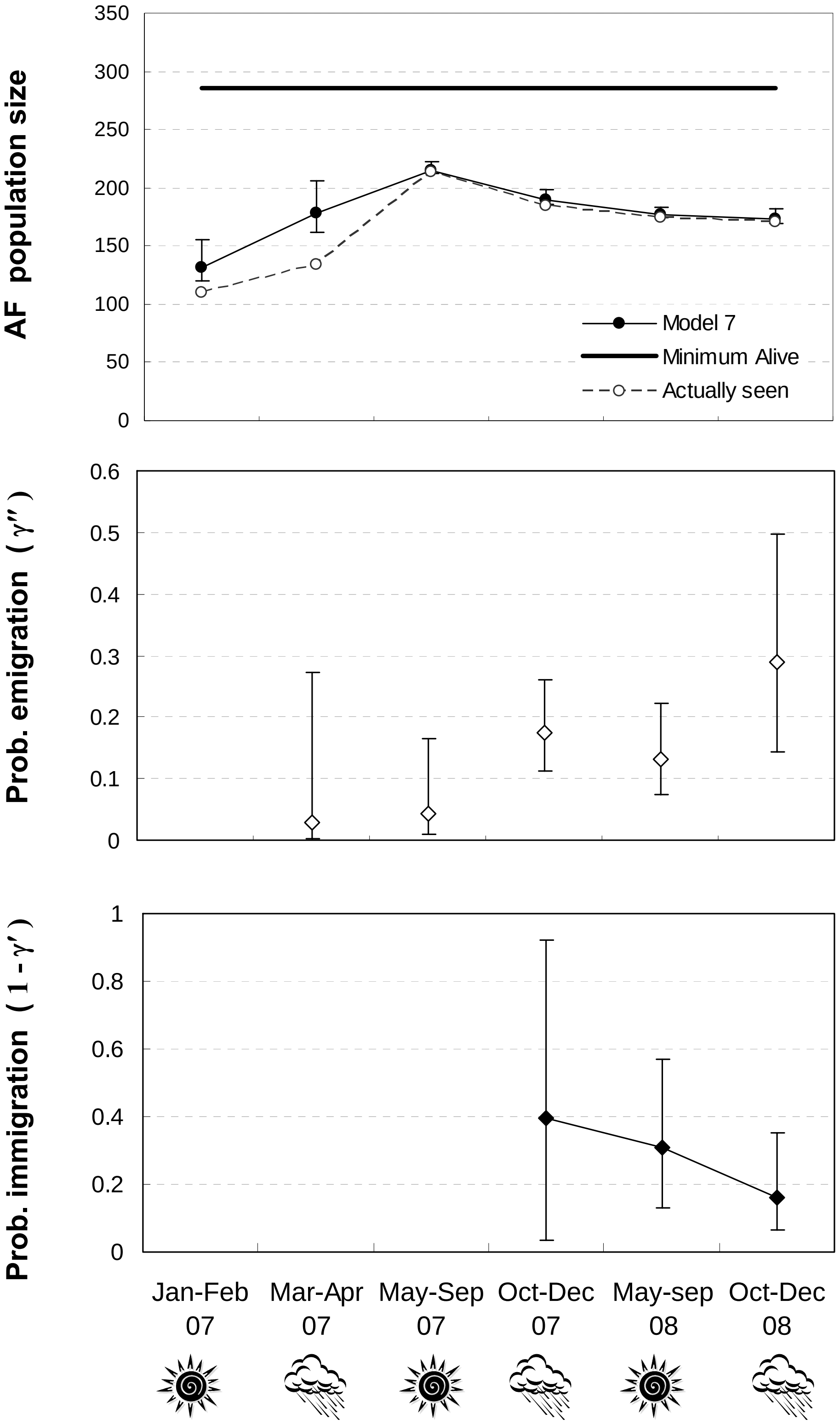
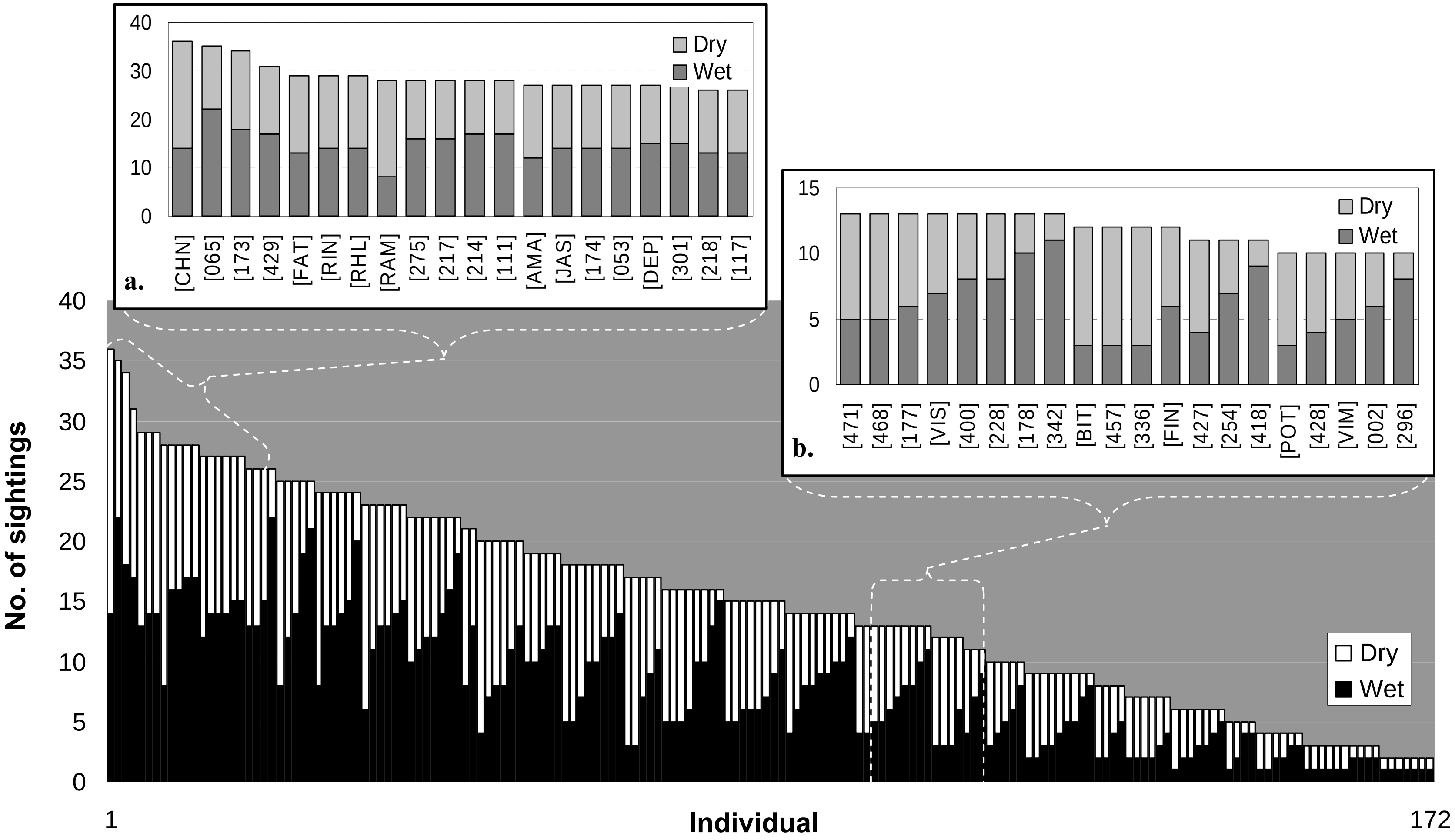

AF population size
350
300
250
200
150
100
50
0
Model 7
Minimum Alive
Actually seen
Prob. emigration (γ′′)
0.6
0.5
0.4
0.3
0.2
0.1
0
Prob. immigration (1 - γ′)
1
0.8
0.6
0.4
0.2
0
Jan-Feb 07
Mar-Apr 07
May-Sep 07
Oct-Dec 07
May-sep 08
Oct-Dec 08

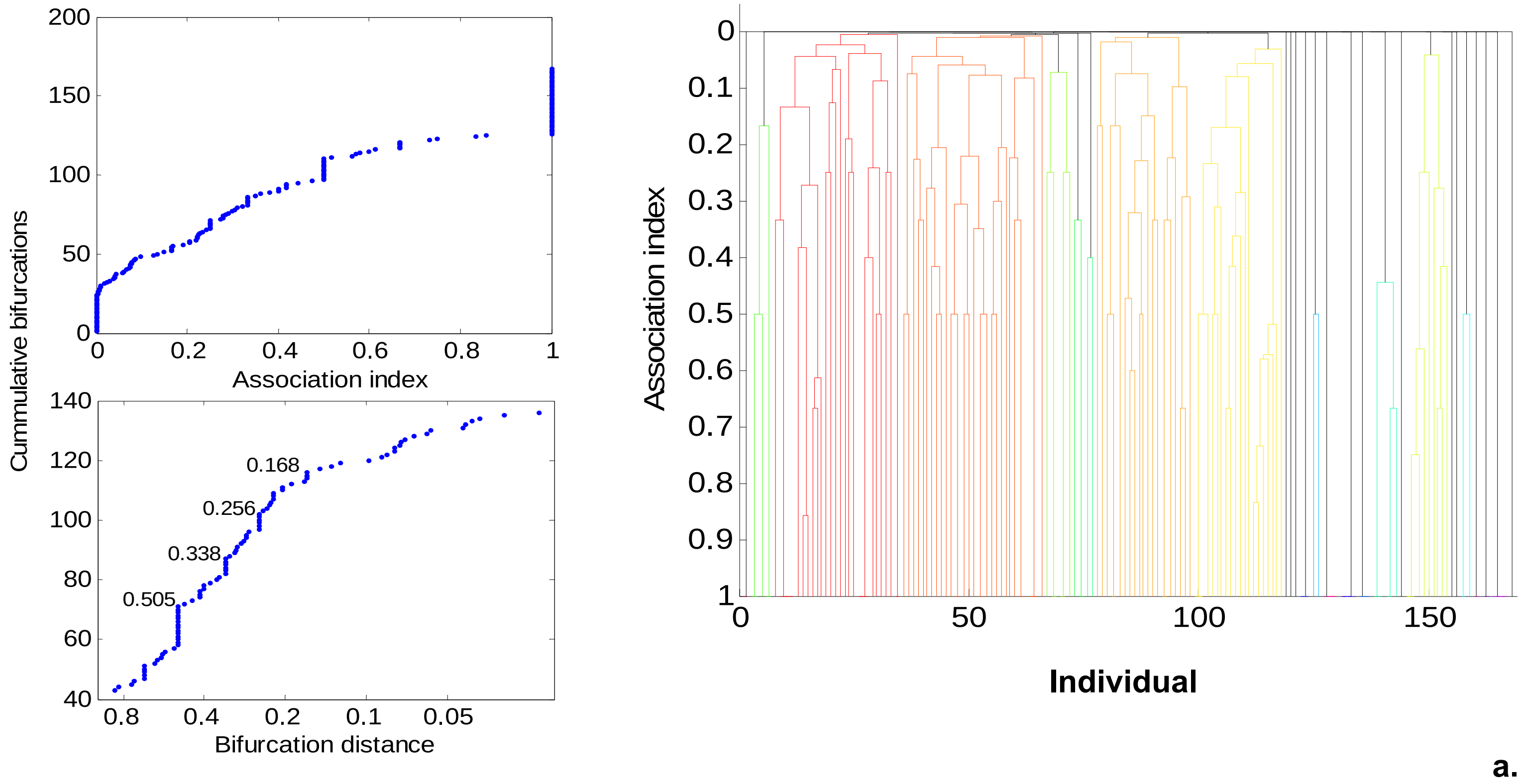
Figure V - 6. Seasonality in sightings. N = 172 adult females present in May-December 2007 and 2008. Individuals who are seen most frequently (>25 times in these 16 months) tend to be seen in equal proportions in wet and dry seasons (a). But most individuals tend to be seen seasonally (b). Wet:Dry sightings ratios were below 0.75 for 58 individuals, and above 1.25 for 64 individuals, with the remaining 50 falling between 0.75 and 1.25. These correspond roughly to individuals for whom the study site is primarily part of their dry season range, wet season range, or year-round range. This is a crude distinction - since ratios do not fall into three discrete categories - however, it suggests a sizeable population turnover between seasons.


40
30
20
10
0
Dry
Wet
[CHN]
[065]
[173]
[429]
[FAT]
[RIN]
[RHL]
[RAM]
[275]
[217]
[214]
[111]
[AMA]
[JAS]
[174]
[053]
[DEP]
[301]
[218]
[117]
a.
15
10
5
0
Dry
Wet
[471]
[468]
[177]
[VIS]
[400]
[228]
[178]
[342]
[BIT]
[457]
[336]
[FIN]
[427]
[254]
[418]
[POT]
[428]
[VIM]
[002]
[296]
b.
No. of sightings
40
35
30
25
20
15
10
5
0
Dry
Wet
1
Individual
172

APPENDIX

Figure S1a. Hierarchical cluster analysis and corresponding 'knot' diagrams for January – April 2007 (T1) period. Bifurcation distance on the x axis of the lower panel of knot diagrams is the negative log of the association index (SRI) on the upper panel, and can be considered an association distance (Whitehead 2009). That is, two individuals with a high association index would diverge at a low bifurcation distance. The lower figure is analogous to that of Wittemyer 2005, where changes in slope are taken to indicate structural changes in the dendogram that indicate social 'tiers.' Dendograms show clusters colored according to community division by modularity (Newman 2004; Whitehead 2009). Each season is colored independently of the other. The number of putative 'tiers' and individuals in each cluster differ among seasons. Sample size for each season is as indicated in the primary text.

Figure S1b. Dendograms and knot diagrams for each season.


Cummulative bifurcations
200
150
100
50
0
0
0.2
0.4
0.6
0.8
1
Association index
140
120
100
80
60
40
0.8
0.4
0.2
0.1
0.05
Bifurcation distance
0.168
0.256
0.338
0.505
Association index
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
0
50
100
150
Individual
a.

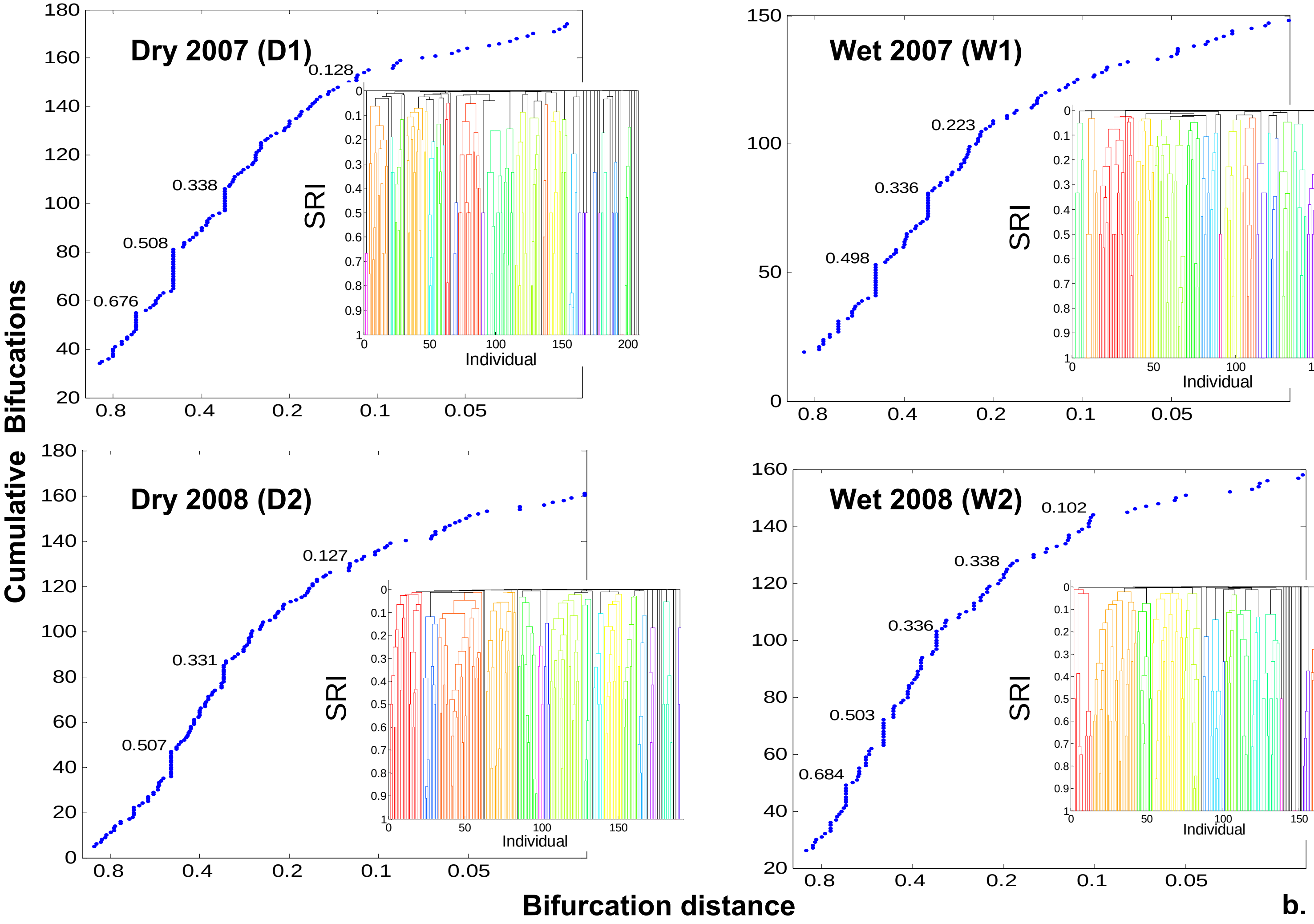

Dry 2007 (D1)
Wet 2007 (W1)
Dry 2008 (D2)
Wet 2008 (W2)
0.128
0.338
0.508
0.676
0.223
0.336
0.498
0.127
0.331
0.507
0.102
0.338
0.336
0.503
0.684
SRI
Individual
Cumulative Bifurcations
Bifurcation distance
0.8
0.4
0.2
0.1
0.05
b.

Figure S3 – Maximum modularity (Q) suggesting the number(s) of clusters when ties below SRI threshold are removed. It should be interpreted as a measure of the appropriateness of the clustering. Even random data can be clustered by modularity. Dark symbols are for actual data and light symbols are for randomized data. Randomized data degenerates completely when ties ≥ 0.5 are removed and generally has lower modularity than observed data.

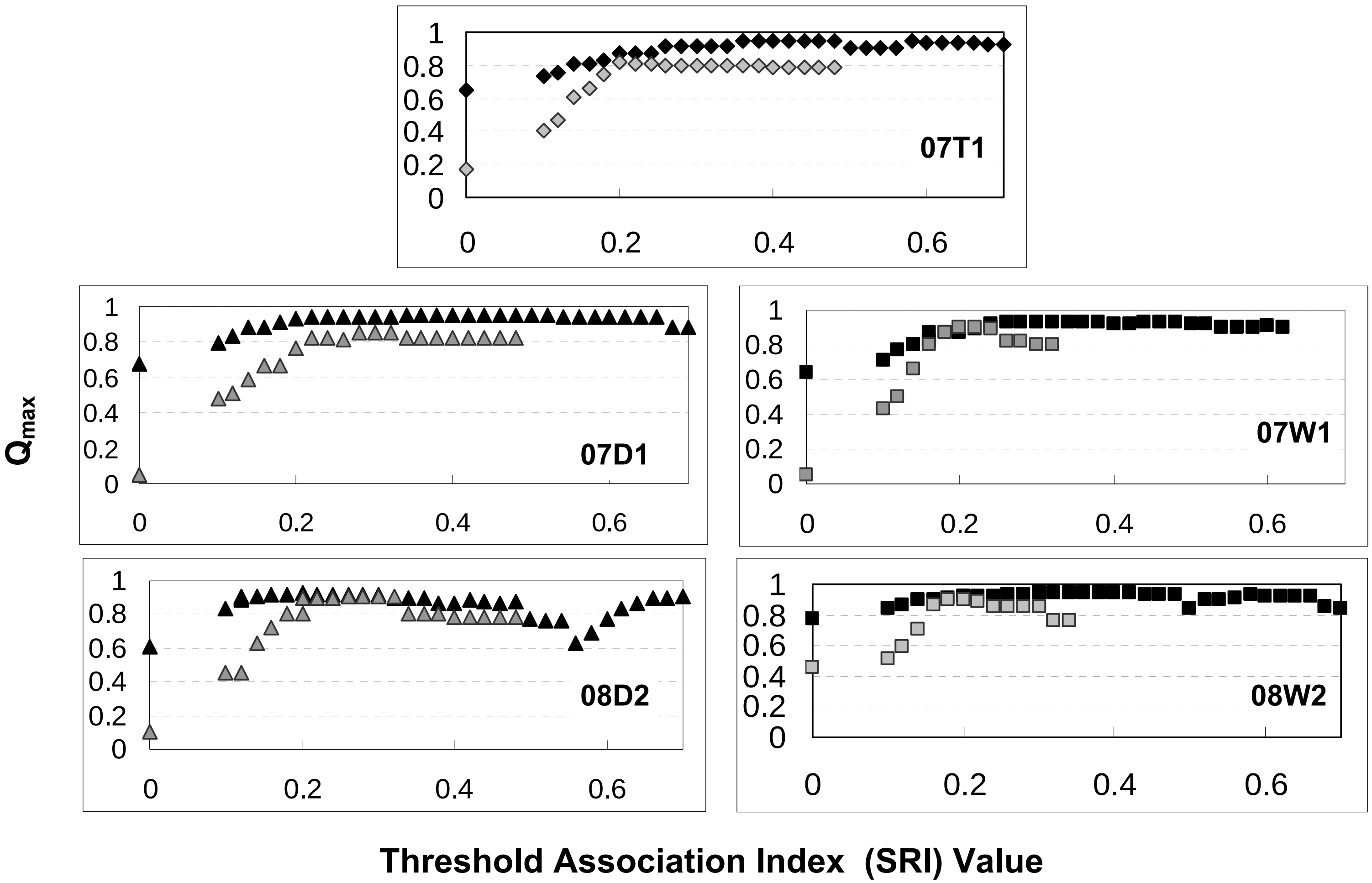

1
0.8
0.6
0.4
0.2
0
0
0.2
0.4
0.6
07T1
07D1
07W1
08D2
08W2
Qmax
Threshold Association Index (SRI) Value

Figure S4 – Transitional periods were not more likely to contain tiers than periods that clearly fell into a seasonal definition. T1 contained clear tiers whereas T2 and T3 did not. T1 may represent a more abrupt transition of the social network between wet and dry periods than the artificial partitions T2 and T3 (See figure S1).

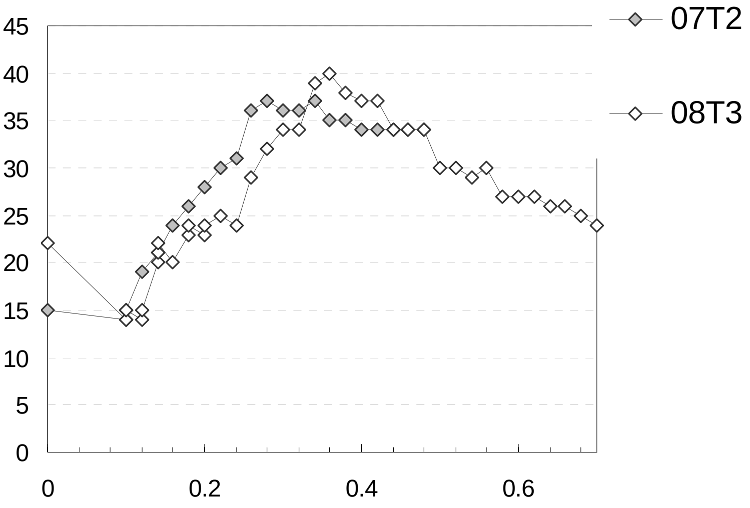


Figure S5 – Pooled data from dry seasons (N=229) shows structure that differs from either of the individual seasons.

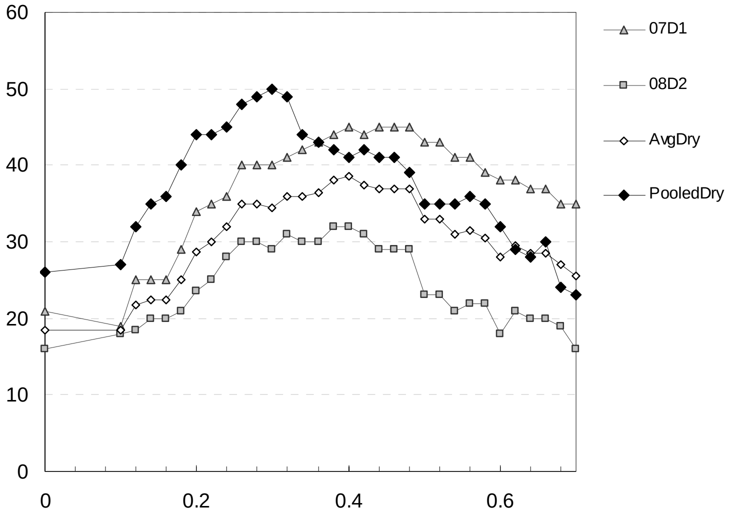


Figure S6 – Dyadic associations across 5 seasons among individuals seen in all seasons were clustered using K-means to determine whether there were characteristic patterns of association. The BIC was used to determine the appropriate number of such clusters. Thus temporal association patterns could be viewed as falling into 2, 5 or 6 k-means clusters. Resultant curves are plotted in Figure 8.

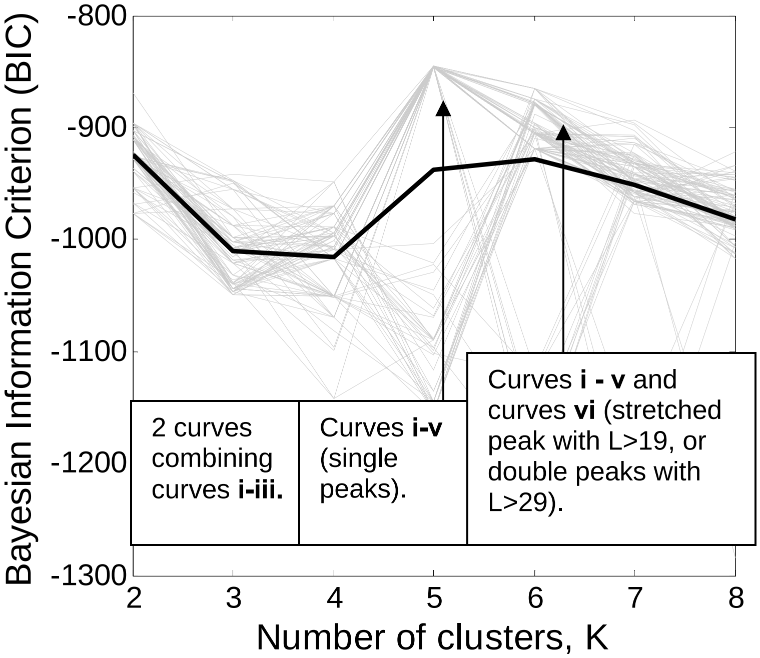
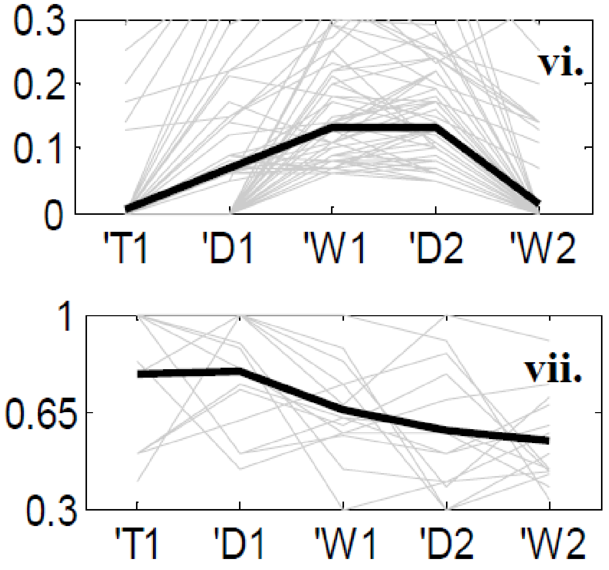


Figure S7 – Dyadic K-means curves of associations across 5 seasons among individuals seen in all seasons. Top curve replaces curve VI in Figure 8, when data are restricted to individuals seen at least 20 times. Though data for January-April 2008 were lacking, some individuals may have maintained associations throughout that period. Curve VII represents the dyads that maintained associations above 0.3 in all periods.



The association index values at which the highest community subdivision occurred was assessed according to modularity (Newman 2006). Data were analyzed by seasonal partitions, as well as pooled dry season or wet season data from both years. Dendograms were generated using 'average,' 'Ward's,' 'single,' and 'complete linkage'. The cophenetic correlation coefficient (Sokal & Rohlf, 1962) was used to determine how faithfully tree topography resulting from each method preserved distances among individuals. Higher values indicated better fit and values above 0.8 signified reasonable accuracy. Curves of cumulative bifurcations in the tree (Wittemyer et al., 2005; Whitehead, 2009) were examined for evidence of social 'tiers,' which were taken to indicate whether certain groups of individuals associated more closely than other groups of individuals.

Dendograms had a cophenetic correlation coefficient greater than 0.9 using average linkage, and less than 0.6 by other methods for all seasons and pooled data for wet or dry seasons. Resultant trees had the highest modularity, and hence the highest level of community subdivision, at extremely low association index values (<0.1 for all partitions). This suggests that the population is composed of individuals or social units that are well-differentiated and seldom interact with one another. Nevertheless, curves of cumulative bifurcation rates showed changes in slope indicating two or more tiers in each partition at higher SRI values.

Hierarchical cluster analysis may not be an appropriate way to describe the Asian elephant datasets, as associations are not nested (Whitehead 2009). It is only applicable if individuals from multiple social units are observed together as a group while in the field. The use of bifurcation rates in detecting 'tiers' is only justified if, as a consequence of the nested structure of relationships, several social groups physically associate with one another. This condition is not met for Asian elephants. Networks are not organized as a set of nested relationships in which all members of a particular set of social cluster are associated with all or most members of another set of social cluster. Instead, individuals from one cluster may be connected to those of another *through* particular individuals in their own cluster. Community subdivision and ‘tier’ delineation based on hierarchical cluster analysis is therefore not appropriate (Whitehead 2009). The graph-theoretic layout combined with the Girvan-Newman clustering procedure may be a more flexible tool since it does not pre-suppose a hierarchical data structure.

Table S1. POPAN models, ranked by AICc. Notation follows conventions in MARK (see main text). Model 1 has recapture and entry probabilities (‘p’ and ‘p_{ent}’ respectively) that vary monthly. It therefore has 1 survival probability, 20 recapture probabilities, 19 entry probabilities, and 1 population estimate for total of 41 parameters, of which only 38 are actually estimated. Model 2 has recapture probabilities that the same for a particular month across years. Model 3 has recapture probabilities that differ by seasons and differ for each season across years (5 recapture probabilities corresponding to the five seasons). Model 4 has recapture probabilities that are the same for each season across years (3 recapture probabilities). Models in which p= p_{ent} are those in which the probability of recapture was set equal to the probability of first entering the population. The likelihood function for model 11 failed to converge.

Rank	**Model features**	**AICc**	**Δ AICc**	**Num. Par.**	**Deviance**
1	ϕ(.) p(t) p_{ent}(t) N(.)	4970.63	0	38	1920.12
2	ϕ (.) p(month) p_{ent} (t) N(.)	4983.17	12.54	29	1951.27
3	ϕ(.) p(season*year) p_{ent} (t) N(.)	5005.29	34.66	22	1987.76
4	ϕ(.) p(season) p_{ent} (t) N(.)	5010.70	40.06	20	1997.24
5	ϕ(.) p(season) p_{ent} (season) N(.)	5013.98	43.35	10	2020.84
6	ϕ(.) p(.) p_{ent} (t) N(.)	5057.18	86.55	19	2045.77
7	ϕ(.) p= p_{ent} (month) N(.)	11527.33	6556.70	13	8528.11
8	ϕ(.) p(t)= p_{ent} (t) N(.)	11708.07	6737.44	20	8694.62
9	ϕ(.) p(season*year) p_{ent} (season*year) N(.)	96910.03	91939.40	11	93914.87
10	ϕ(.) p(month) p_{ent} (month) N(.)	96952.85	91982.22	19	93941.44
11	ϕ(.) p(season*year)= p_{ent} (season*year) N(.)	-	-	-	-

Table S2. Robust design models, ranked by AICc. Model 1 has 1 survival parameter, 19 (γ”) parameters, 18 (γ’) parameters and twenty of the other two parameters for a total of 78, from which 70 were actually estimable. This represents the case in which individuals appear unpredictably at different intervals. Model 2 has the same number of parameters for survival, capture, recapture, and population size, but 11 (γ”) parameters (for each calendar month except the first, with months being the same across years) and 10 (γ’) parameters, for a total of 62 parameters of which 57 were estimable. This represents the case in which individuals appear during the same month each year. Likewise, ‘Season*month’ denotes (γ) parameters that were the same for months that corresponded to the same season, such that they differed within a year but were the same across years (9 γ terms). This represents the case in which individuals appear during same season each year. ‘Season*year’ accounts for seasonality in sightings that differed across years (13 γ terms). This represents the case in which individuals appear in different seasons depending on the year. Changing the capture (p) and recapture (c) parameters in similar ways yielded population estimates that are were very similar (Figure S7) and sometimes better than models that were time-varied, though they ranked lower. All models estimated survival probability to be close to 0.97, but fixing survival at 0.97 or 1 did not greatly improve estimates of other parameters. Models with random emigration and no emigration ranked consistently lower than analogous models with Markovian emigration. Model 2 among the closed captures set of models is comparable to Model 9 of the Huggins set; estimates from both were very similar (Figure S9). Huggins models permitted (p) and (c) to differ, but these generally did not provide reliable estimates (Figure S9).

Rank	Closed Capture models	AICc	Δ AICc	Num. Par.	Deviance
1	φ(.) γ"(t) γ'(t) p=c(t) N(t)	44.44	266.76	70	11352.89
2	φ(.) γ"(month) γ'(month) p=c(t) N(t)	47.89	270.21	57	11383.48
3	φ(.) γ"(season*year) γ'(season*year) p=c(t) N(t)	55.53	277.85	50	11405.64
4	φ(0.97) γ"(season*month) γ'(season*month) p=c(t) N(t)	69.52	291.83	46	11427.89
5	φ(.) γ"(season*month) γ'(season*month) p=c(t) N(t)	71.67	293.98	47	11427.98
6	φ(0.97) γ"(t) γ'(t) p=c(t) N(t)	89.33	311.65	68	11401.97
7	φ(.)γ"(t) γ'(t) p=c(month) N(t)	96.42	318.74	64	11417.43
8	φ(0.97) γ"(month) γ'(month) p=c(month) N(t)	100.62	322.93	48	11454.86
9	φ(0.97) γ"(month) γ'(month) p=c(t) N(t)	101.65	323.97	56	11439.33
10	φ(.) γ"(month) γ'(month) p=c(month) N(t)	103.76	326.08	50	11453.88
11	φ(.) γ"(season*month) γ'(season*month) p=c(month) N(t)	129.04	351.35	39	11501.83
12	φ(0.97) γ"=γ'(t) p=c(t) N(t)	175.94	398.25	54	11517.76
13	φ(.) γ"=γ'(0) p=c(t) N(t)	255.42	477.74	41	11624.10
14	φ(1) γ"(t) γ'(t) p=c(t) N(t)	302.09	524.40	68	11614.72
	Huggins models				
1	φ(0.97) γ"(t) γ'(t) p(t) c(t)	14409.08	0.00	77	25702.80
2	φ(.) γ"(t) γ'(t) p(t) c(t)	14409.77	0.69	77	25703.50
3	φ(.) γ"(t) γ'(t) p(month) c(month)	14420.32	11.24	70	25728.76
4	φ(0.97) γ"(month) γ'(month) p(t) c(t)	14422.62	13.55	61	25749.89
5	φ(.) γ"(month) γ'(month) p(t) c(t)	14424.50	15.43	62	25749.68
6	φ(.) γ"(month) γ'(month) p(month) c(month)	14434.20	25.12	54	25776.03
7	φ(.) γ"(season*year) γ'(season*year) p(t) c(t)	14442.06	32.98	54	25783.88
8	φ(1) γ"(t) γ'(t) p(t) c(t)	14458.57	49.49	77	25752.30
9	φ(.) γ"(month) γ'(month) p=c(t)	14479.78	70.70	42	25846.40
10	φ(.) γ"(t) γ'(t) p=c(t)	14484.84	75.76	58	25818.35
11	φ(.) γ"(season*year) γ'(season*year) p=c(t)	14487.07	77.99	34	25870.11
12	φ(.) γ"(t)season γ'(t)season p=c(t)	14500.16	91.09	30	25891.38
13	φ(.) γ"=γ'(t) p(t) c(t)	14518.67	109.59	60	25848.02
14	φ(.) γ"=γ'(0) p(t) c(t)	14558.62	149.54	41	25927.30

Figure S8. Possible ways to model capture probabilities. This is an example in which seasons are primary intervals, indicated by arrows, and months are secondary intervals, indicated by subscripts. A) p(t): capture probability is unique for each interval. B) p(month): capture probabilities are the same in corresponding months across years. C) p(season*year): capture probabilities change with each season and each year. D) p(season*month): capture probabilities are the same for corresponding seasons across years. D) p(season): capture probabilities are the same for corresponding seasons, irrespective of time of year or calendar year. It is possible to vary all other variables similarly. Since gamma variables address changes *between* primary intervals, there can be at most k-1 γ” and k-2 γ’ parameters, where k is the number of primary intervals.

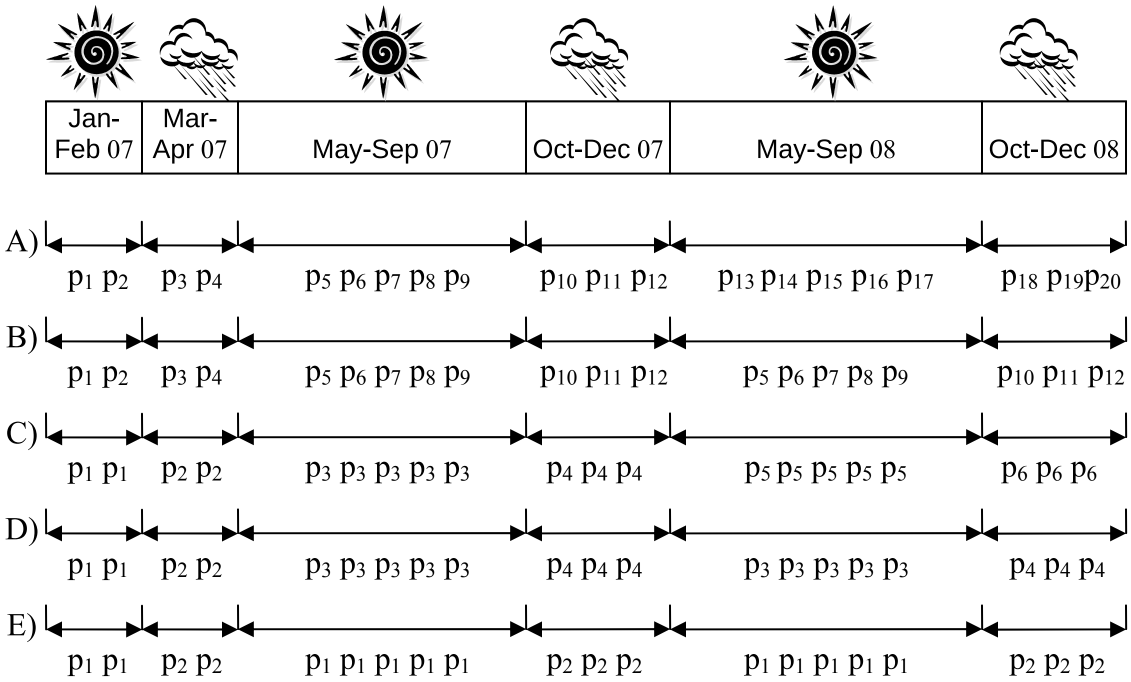
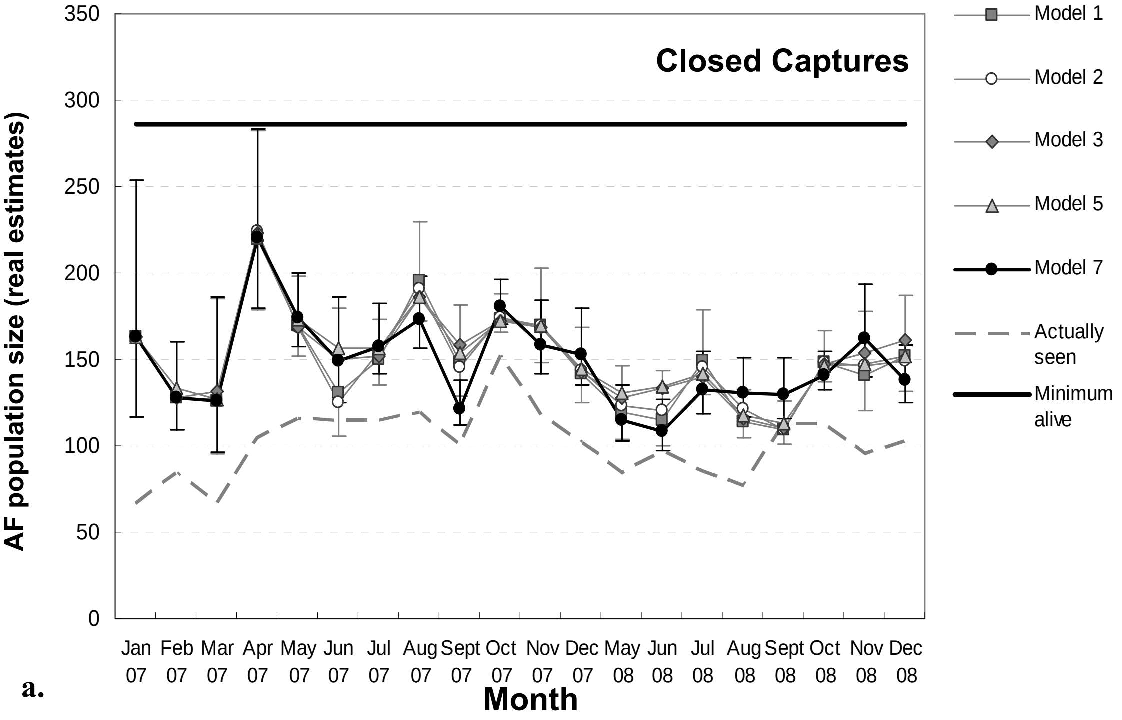
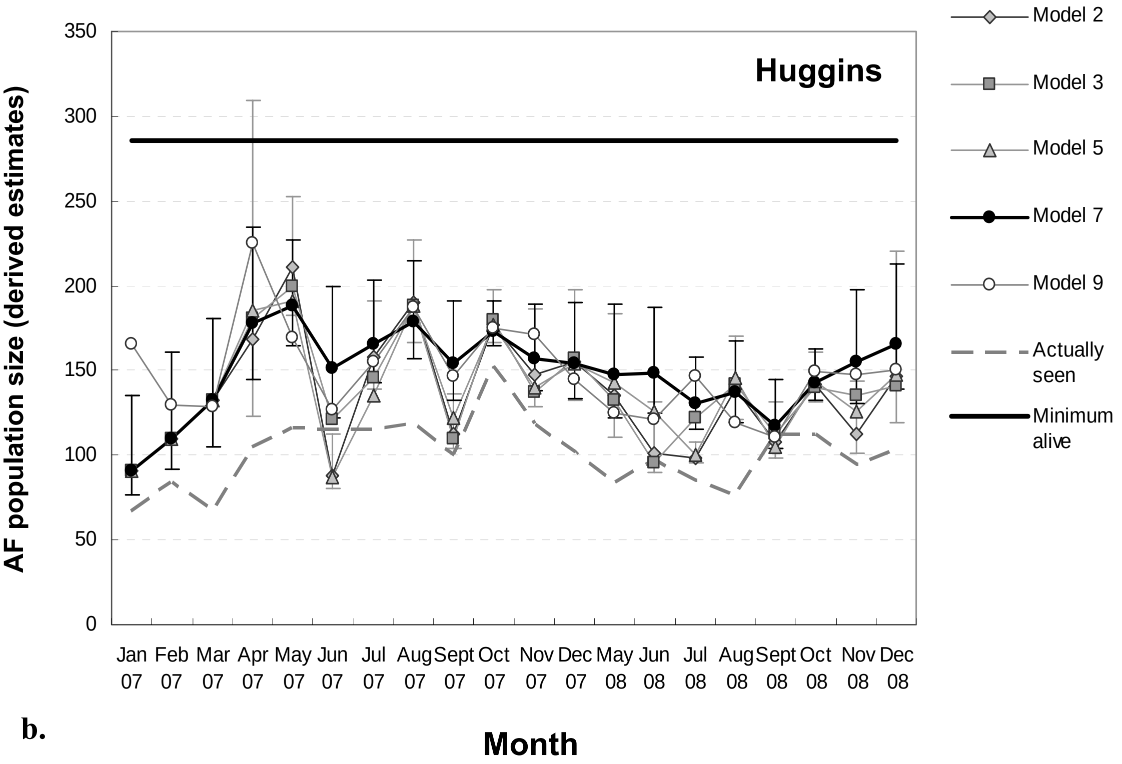


Figure S9. Robust design models with months as primary intervals and weeks as secondary intervals. Model numbers correspond to the ranks in Table S2. Note that model 2 of the closed captures is analogous to model 9 of the Huggins (open circles) and that both perform similarly. Several of the Huggins models give population estimates that are unreasonable in being lower than the number actually seen, whereas most closed captures models perform better. Estimates seem to improve when capture and recapture probabilities are set equal to each other (p=c). Model 7 is appears to give the most reliable estimates in each set sets, though not the top ranked model according to AICc. They differ from one another, however. In the closed captures set, it represents the case in which gamma values vary between each of the twenty months and capture/recapture probabilities vary by month, but are the same across years. In the Huggins set, it represents the case in which gamma probabilities vary between each season and capture and recapture probabilities again vary for each of the twenty months. But all of the models show populations peaking in April 2007, whereas actual sightings peak in October. Moreover, gamma estimates had extremely wide confidence intervals for most models. These discrepancies do not favor the use of such short primary and secondary intervals in estimating these parameters, as there may not be enough data for accurate estimates at least in the short term. Long term datasets may be better.


Closed Captures
AF population size (real estimates)
Month
0
50
100
150
200
250
300
350
Jan 07
Feb 07
Mar 07
Apr 07
May 07
Jun 07
Jul 07
Aug 07
Sept 07
Oct 07
Nov 07
Dec 07
May 08
Jun 08
Jul 08
Aug 08
Sept 08
Oct 08
Nov 08
Dec 08
Model 1
Model 2
Model 3
Model 5
Model 7
Actually seen
Minimum alive

a.


Huggins
AF population size (derived estimates)
Month
0
50
100
150
200
250
300
350
Jan 07
Feb 07
Mar 07
Apr 07
May 07
Jun 07
Jul 07
Aug 07
Sept 07
Oct 07
Nov 07
Dec 07
May 08
Jun 08
Jul 08
Aug 08
Sept 08
Oct 08
Nov 08
Dec 08
Model 2
Model 3
Model 5
Model 7
Model 9
Actually seen
Minimum alive

b.