RESEARCH

Quantifying forest elephant social structure in Central African bai environments

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Abstract

Relatively little is known of social dynamics in forest elephants (*Loxodonta africana cyclotis*), although the fission-fusion model of sociality known in savanna elephants (*Loxodonta africana africana*) is used as a template. Until fission-fusion sociality or an alternative model is demonstrated, our understanding of how elephants use their environment remains incomplete. To date, there have been no published studies of associations between individuals in forest elephants. Direct observations of forest elephants made at forest clearings (bais) are used here as an approach to studying these questions. Bais represent a special environment, providing mineral and food resources, as well as potential social opportunities. We show that forest elephants at Mbeli Bai in Nouabalé-Ndoki National Park have association patterns that are consistent over time, and that certain conspecifics are preferred as associates in the bai environment. Coupled with significant differences in the group size and composition across age-sex classes, and a high proportion of sightings of lone individuals, we argue that the fission-fusion model of elephant sociality appears to hold for the bai environment. The extent of this system and the importance of bais as social resources remain to be explored.

Additional keywords: *Loxodonta africana cyclotis*; fission-fusion sociality; Republic of Congo

Résumé

Relativement peu est connu de la dynamique sociale dans des éléphants de forêt (*Loxodonta africana cyclotis*), bien que nous employions le modèle de la société d'éléphant de la savane (*Loxodonta africana africana*) comme calibre. En attendant que le lien de sociabilité en termes de fission et fusion ou un modèle alternatif soit prouvé, notre compréhension de la façon dont les éléphants utilisent leur environnement reste limité. A ce jour, il n'y a eu aucune étude publiée sur les associations entre les individus dans des éléphants de forêt. Les observations directes des éléphants de forêt effectuées dans les clairières forestières (« bais ») sont utilisées comme une approche pour étudier les interactions sociales. Les bais constituent un environnement spécial, fournissant des ressources minérales et de la nourriture, ainsi que des opportunités d'interactions sociales potentielles. Nos analyses montrent que les éléphants de forêt à Mbeli Bai, au Parc National de Nouabalé-Ndoki ont les associations qui sont constantes dans le temps avec une préférence notoire dans l'association de certains individus. Avec des différences significatives dans la taille et la composition sur base des classes d'âge et sexe, et une grande proportion des observations des éléphants solitaires, nous soutenons que le model « fission-fusion » des éléphants de savanes est évident dans l'environnement du bai. L'ampleur de ce système et l'importance des bais en tant que ressources sociales restent à les explorer.

Introduction

Sociality reflects the dynamic outcome of interactions between an individual, its conspecifics and environment. Thus, social systems can be viewed as the product of interactions between competing and cooperating individuals, seeking to maximize reproductive success when the environment provides opportunities or imposes constraints on individual resource acquisition (Wrangham 1980; van Schaik and van Hooff 1983). Social structure and dynamics influence how and when individuals use habitats and social behaviour interacts with population demography and dynamics (Wrangham 1980; Tuyttens and Macdonald, 2000). Elephants face resource acquisition challenges due to their large body size and the correspondingly high absolute energy and nutrient demands, and yet are found in a variety of habitats, including particularly harsh desert areas. Despite this habitat variability, the fission-fusion sociality of savanna elephants (*Loxodonta africana africana*) seems to be a conserved trait across their range (Lee 1991). Fission-fusion systems are theoretically interesting to behavioural ecology, as they may provide a trade off between the costs and benefits of living in a group, but they have significant cognitive demands associated with the costs of a complex social landscape (McComb et al. 2001; Barrett et al. 2003).

African forest elephants (*Loxodonta africana cyclotis*) are recognised as morphologically and genetically distinct from savanna elephants, though genetic information does not currently suggest a clear species distinction (Roca et al. 2001; Eggert et al. 2002; Debruyne 2005). What is clear is that elephants of the Congo basin inhabit a very different ecological niche as frugivores in dense rainforest habitats (e.g. Short 1981; White et al. 1993; Powell 1997; Blake 2002), where they represent about 10% of the estimated total African elephant population (Blanc et al. 2007). These populations are under significant and increasing threats from ivory poachers (Blake et al. 2007), and for elephants, as with other long-lived highly social species, managing and mitigating threats to population persistence can be most effective when the linked social and demographic consequences of environmental or social disturbance are understood.

Among savanna elephants, females are known to have levels of association that extend beyond their immediate kin group (Moss 1988; Wittemyer et al. 2005; McComb et al. 2001; Archie et al. 2006a), and males also have consistent associates with whom they spend more time than expected from their availability – “preferred associates” (Poole et al. in press; Evans 2006). Although it is assumed that forest elephants follow a similar fission-fusion social structure, we have no direct evidence that this is the case. Forest elephant groups are small with a mean group size between two and three (reviewed by Morgan and Lee 2007), and this is hypothesised to be a response to the patchy nature of fruit distribution, which forms an important part of forest elephant diet (Blake 2002; Powell 1997; White et al. 1993). Indirect signs and opportunistic observations have failed to reveal evidence of larger aggregations in the forest (e.g. Blake 2002), and the basic social unit is thus assumed to be a mother with dependent offspring (Morgan and Lee 2007; Turkalo and Fay 2001). If this is indeed the case, it suggests that both male and female offspring disperse, and that female grouping does not occur, despite suggested predation pressure from leopards on calves (Blake 2004). This in turn implies that the allomothering known to be vital for calf survival in savanna elephants (Lee 1987) may be less influential for forest elephants, and that any complex social bonds within matriarch-led multi-female groups are less apparent on a day-to-day basis.

Forest clearings, known locally as *bais* are prominent aggregation points for forest elephants, with exceptional sites accommodating up to 100 individuals simultaneously (Turkalo and Fay 1996; Vanleeuwe et al. 1997; Querouil et al. 1999). They provide important mineral and vegetable resources (Blake 2002; Klaus et al. 1998) and have been proposed to offer significant social opportunities (Turkalo and Fay 1996; 2001). However, the use of bais could be constrained by potential risks due to poachers with easy access and good visibility, or even by predators of calves. Given these costs, we suggest that bai use is associated with a significant number of social benefits for elephants. As a first assessment of the social opportunities available in a bai environment, this paper examines patterns of social tolerance as indicated by simultaneous use of pools at Mbeli Bai, Republic of Congo. It explores the patterns of association over time by a population of known individuals, and inherent differences in these patterns according to age-sex class.

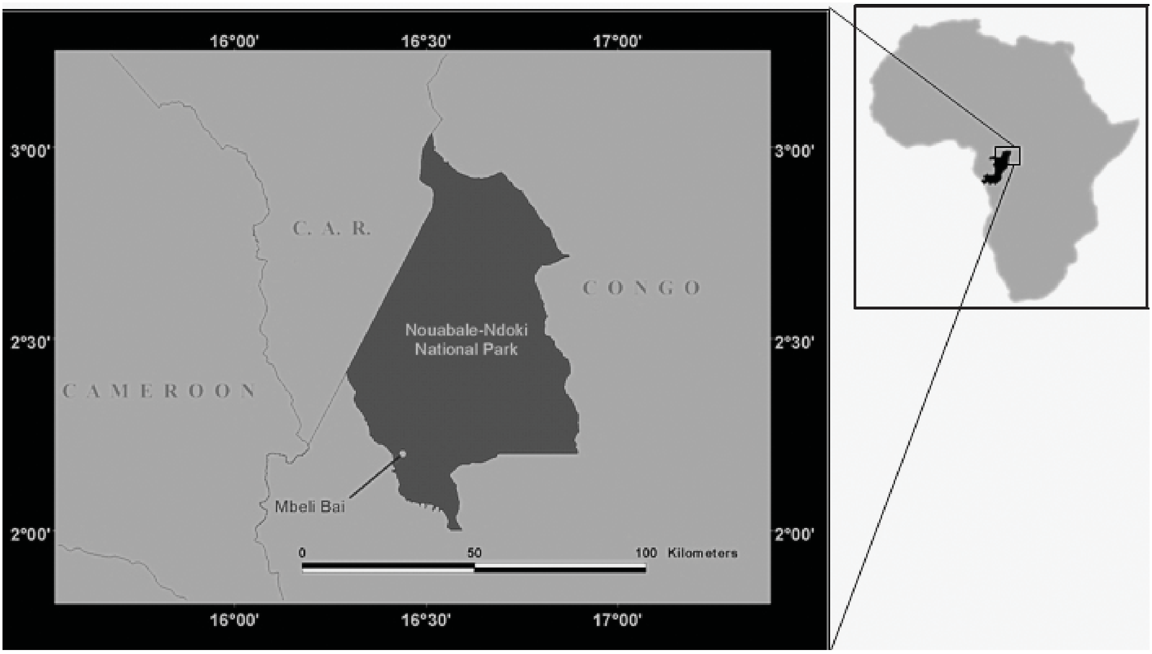


Figure 1. Location of the Mbeli study site within the region

Methods

Study Area

Mbeli Bai is a large (12.9 ha) swampy clearing in the southwest of Nouabalé-Ndoki National Park, Republic of Congo (02^{o}15.5’N; 16^{o}24.7’E; fig. 1). The forest surrounding Mbeli Bai can be described as semi-deciduous lowland forest with bimodal rainfall and mean annual rainfall is 1727mm (1998-2005; Mbeli Bai Study long term data). The clearing is permanently flooded and contains a floating mass of aquatic vegetation in the Cyperaceae and Poaceae/ Gramineae families, interposed by streams and elephant pools. Mbeli Bai is currently free from poaching, and has been for a number of years.

Data collection

Observations were made from a 9m-high platform overlooking the clearing, using 15-45 x 60mm telescopes. Elephants were habituated to the presence of observers, and identifications were made using the system developed for savanna elephants (Moss 1996) documenting tusk, ear and body morphology and age-sex class. Over the last 10 years more than 230 individual animals have been identified and assigned ID cards (Mbeli Bai Study, long term data).

Data were collected on a daily basis from January 2004 to the end of July 2005, with observers present at the bai from 0700h to 1700h. Most elephants visit the bai to extract soil/minerals from one of four permanent pools. Each pool contains multiple resource access points and has the physical space for at least eight adult animals. Elephants using pools simultaneously were considered to be a group, as animals can and do exclude conspecifics from pools, or avoid using pools when other elephants are present. When new individuals entered a pool and joined others, a new group was created. Each resource visit was considered as a separate event (i.e. choice) by the individual concerned, and therefore individuals may be represented more than once on each day, but in an independently constituted group. A total of 5279 sightings were made on 3828 groups, and 107 individuals were identified.

Data analysis

Data were manipulated and analysed using Excel and SPSS version 14. All data were tested for normality and log transformed if normality assumptions were not met (using the ratio of skew: SE of skew <3; Rohlf and Sokal 1994). For all analyses, elephants over eight years of age were considered. Due to a lack of information on precise ageing categories for forest elephants, especially for adults, individuals were assigned to approximate age-sex classes as defined in table 1. Variables were analysed using ANOVA models, with the number of sightings as a covariate, in order to examine differences between age-sex classes whilst taking into account the fact that some individuals were sighted considerably more often than others. Bonferroni corrections were applied to all pairwise comparisons. Analyses of association indices used data from the most frequently sighted individuals; we selected only the 25% of the population seen most often to ensure an even probability of individuals theoretically being able to associate with any other. When analysing group type, the proportion of time subadults spent in groups with immature conspecifics was disregarded, as these were mostly sibling pairs (subadult females n = 406, 20.9% of sightings; subadult males n = 327, 13.5% of sightings). Analyses also excluded groups of unknown composition (n = 72), which were usually due to the presence of only one individual of unknown age and sex, and which were less than 0.001% of sightings. We also excluded sightings (n = 3) of an independent young male using a pool with his mother and her most recent calf.

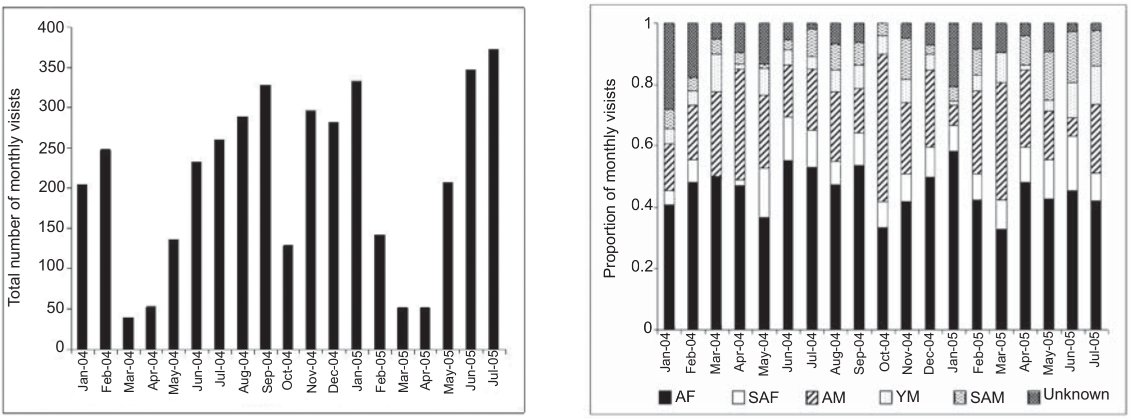
Table 1. Age-sex class definitions for the visiting population. (*including one adult-sized female with no breast development)

Age-sex class	Definition
Adult female	with breast development and/or calves*.
Subadult female	smaller than adult female, probably aged 8-15. No breast development, not yet attained adult body size.
Prime male	sexually active adult male.
Young male	approaching adult body size, without the head shape development and body mass seen in fully adult males.
Subadult male	smaller than young males, estimated ages 8-15. Not yet attained adult body size.

Simple association indices were calculated as:

$N_{AB} / (N_A + N_B + N_{AB})$

Where N_A is the number of sightings of individual A, N_B is the number of sightings of individual B and N_{AB} is the number of sightings of A with B (Ginsberg and Young 1992).



A)

B)

Figure 2. A) Monthly distribution of the number of visits by elephants from all age-sex classes combined; and B) Proportion of each month's total visits accounted for by individuals of each age-sex class.

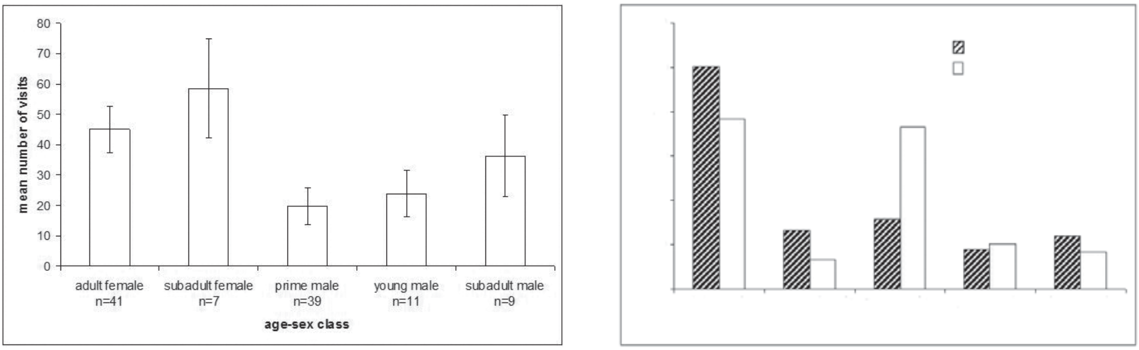
Results

Seasonal variation in total visitation rates was marked (ANOVA: $F_{11,114} = 14.73$, $p < 0.001$; fig. 2A) with monthly variation in age-sex class representation ($F_{5,114} = 33.7$, $p < 0.001$), but there was no interaction between age-sex class and monthly visitation numbers (fig. 2B; all analyses on log transformed data). In subsequent analyses of associates, we have therefore combined data across months and years.

Over the study period, 5279 pool use events were observed, and of these 3621 involved positive identification of 107 known elephants above eight years of age. For known individuals, the average number of visits was 34.1 (SD±43.1; median = 15, range 1-221) (figure 3A). The sex ratio of known individuals was 1.2M : 1F (fig. 3B). Younger animals tended to visit in proportion to their presence in the identified population, while adult males were disproportionately identified compared to their visitation rates and adult females tended to visit more than expected from their proportions in the identified population (overall $X^2 = 2379$, df = 4, $p<0.001$).

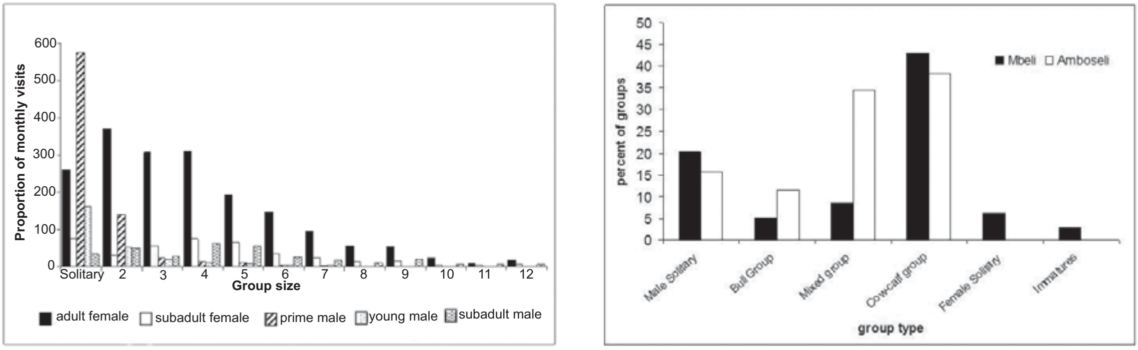
Solitariness

All age-sex classes were observed to make solitary visits and used pools without conspecifics present (fig. 4A). Although these analyses do not consider calves under eight, we did observe at least six animals of this age class coming into the bai and using pools alone; in the majority of such cases we could not assign a definite ID to young individuals. There



A) B)

Figure 3. A) Mean (+ SE) number of visits for known individuals of each age-sex class, n=107; and B) The proportion of total visits (n=3828) accounted for by individuals of each age-sex class, whether known or unknown individuals, compared with the proportions of age-sex classes represented by known individuals.



A) B)

Figure 4. A) Frequency distribution of group sizes (solitary to 12) for each age-sex class; and B) Distribution of group types for known individuals (n=3621 observations). Black bars represent this study. For comparison, data on known individual savanna elephants from Amboseli, Kenya are also presented (C. Moss, AERP long-term data; n=29,894 – Poole, Lee and Moss, in press).

were a number of solitary visits made by known adult females, a rare situation for savanna elephants (fig. 4B). In addition, we observed subadults in groups with no adult animals present.

Gregariousness and group size

Gregariousness was assessed as the mean proportion of visits that each age-sex class was seen with conspecifics in a pool. There was a highly significant difference in the overall tendency for different age-sex classes to be gregarious ($F_{4,107}$= 23.39, p<0.001; fig. 5A). Young and prime males were significantly less gregarious than other age-sex classes.

The maximum number of elephants in a pool at any one time was 12 (fig. 4A), but there were occasions when around 20 individuals were seen entering and exiting the bai area and in the forest edge, though not using pools simultaneously. Mean pool group size did not vary as a function of an individual's age-sex class, but age-sex class was a significant predictor of pool group size when solitary animals were excluded (log mean group size $F_{4,96}$= 2.85 p<0.01; fig. 5B); adult females were found in significantly larger pool groups than were prime males.

Group type

Groups were categorised by the age and sex of individuals present. Figure 6 shows the proportion of visits each age-sex class spent in these different group types. Subadult males spent more total time with females than did prime males, since these young males spend time in groups composed both of family females and with groups of mixed sex, non-family females. When immature males were with others, their associates tended to be female. In contrast, females of all ages were found in mixed groups for similar low proportions of visits. We examined the proportion of sightings that each individual from each age-sex class spent with same-sex conspecifics (excluding sightings of lone animals). There was a significant difference overall ($F_{4,78}$ = 65.56, p<0.001), with females being far more likely than males to be found with same-sex conspecifics (fig. 7).

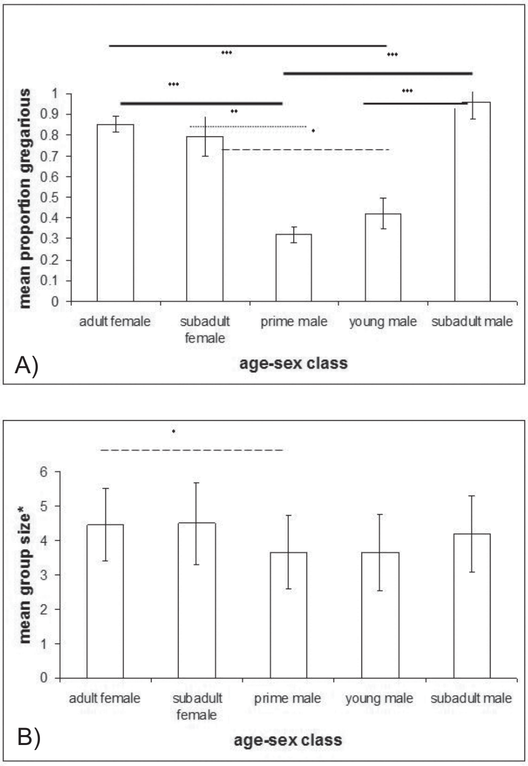


Figure 5. A) Proportion of visits by age-sex class where individuals used pools with conspecifics; and B) mean (+SE) group size in these visits, by age-sex class. Significant differences from pairwise comparisons indicated by lines above bars, with Bonferroni correction: ***p<0.001; **p<0.005; *p<0.05.

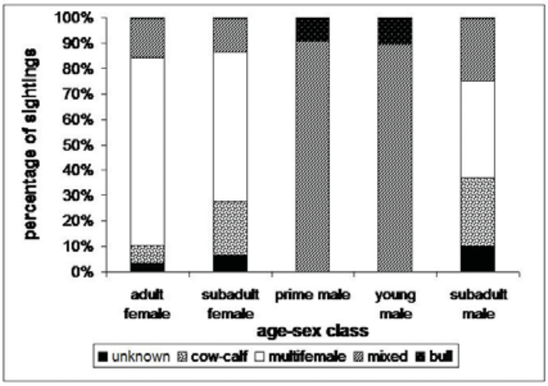


Figure 6. Overall proportion of visits classified by group type for individuals of each age-sex class. Group codes; unknown group compositions occurred where we could not identify age and sex of *all* animals present (n = 176/ 3828 observations); bull = males only; mixed = contains males and females over five years of age; multi-female = more than one adult female OR adult female plus offspring of another female; cow-calf = only mother-offspring present.

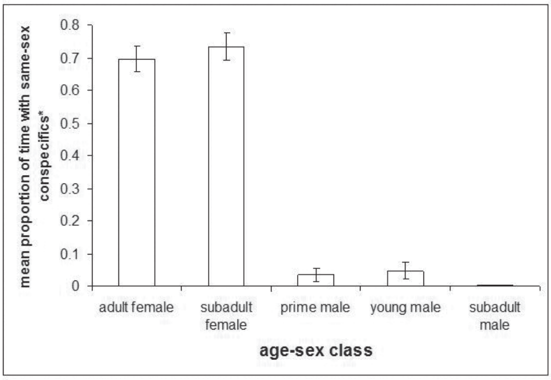


Figure 7. Mean (+ SE) proportion of time age-sex classes spent with same-sex conspecifics, excluding solitary visits. Significant pairwise comparisons with Bonferroni correction: adult females and subadult females were each significantly greater than all classes of male, all p<0.001.

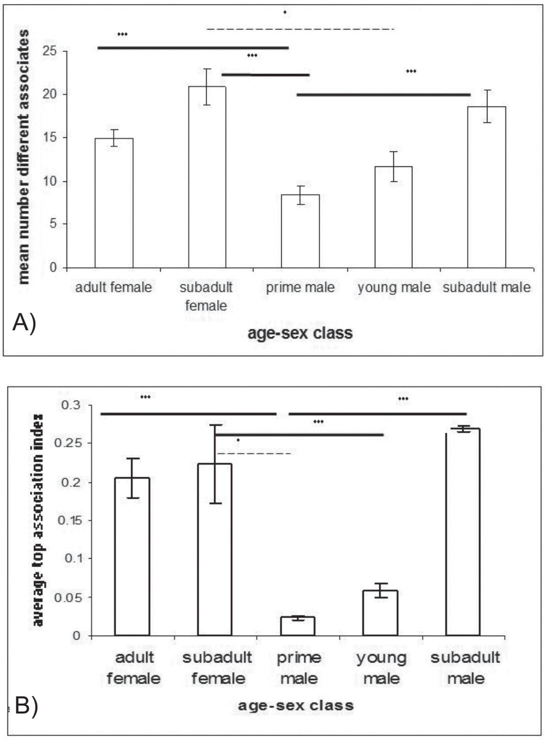


Figure 8. A) Mean (+ SE) number of associates as a function of age-sex class, and B) average association levels. Significant differences for specific pairwise comparisons with Bonferroni correction are indicated by lines above bars: ***p<0.001; *p<0.05.

Group type

The number of different associates observed in a pool differed significantly between age-sex classes ($F_{4,94}$ = 11.03, p<0.001; fig. 8A). Prime males had the lowest number of associates, but for both sexes there was a non-significant trend for younger animals to associate with more individuals. Prime males had fewer associates than females and subadult males, whilst young males had fewer associates than subadult females. Thirty elephants were sighted on over 40 occasions. Of these frequent visitors, the minimum number of associates was four, and we explored these observations in detail in order to capture the major associates in the population. There was a significant difference in the top association index score between age-sex classes (one-way ANOVA: $F_{4,29}$ = 5.79, p<0.01, fig. 8B); adult females associated with their most frequent partner significantly more than did prime males or young males. Top associates of both males and females were significantly more likely to be found together relative to the mean association partner for all dyads (fig. 9). We call these top individuals 'preferred associates'.

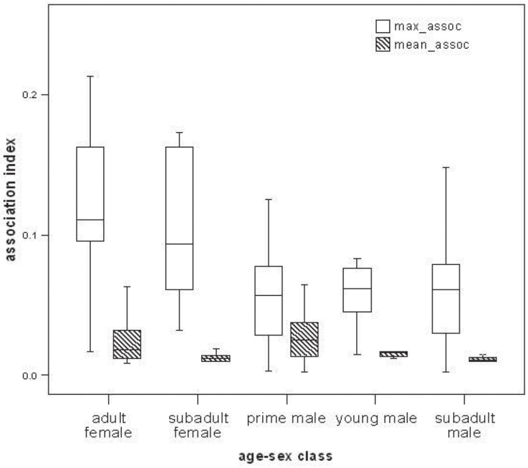


Figure 9. Maximum and average association indices for each age-sex class. Paired samples T-test t_{95}= 12.34, p<0.001.

Discussion

Monthly or seasonal frequencies of bai use by elephants are likely to be a function of resource availability within and outside the bai (Blake 2002; Vanleeuwe et al. 1997; White 1994) as well as levels of human disturbance or threat; however the associations between individuals that we report on here reflect choices about whom in the bai to associate with once an individual has chosen to enter.

The observed male-biased sex ratio is likely to be due to the relative ease of confidently identifying prime and young adult males. These individuals tended to have observable tusk development and differentiation and thus they were distinctive compared to females and subadult animals; they also tended to use a pool in the centre of the bai rather than those at the forest edge. The bias towards recognition of males by comparison to their rates of visiting may also be due to the way that males range; typically they range further than females and therefore a greater number of different individuals may be likely to use any single bai (Moss and Poole 1983; Leggett 2006). Males do not appear to be attracted to Mbeli Bai in search of oestrous females, as we observed relatively few mixed groups especially containing musth males. Mean pool group size in the bai context appears to be larger than groups within forests (Morgan and Lee 2007; Turkalo and Fay 2001), although the high proportion of time spent solitary is consistent with previous observations for forest elephants (White et al. 1993; Blake 2002).

Even though solitary bai use was observed, there is every possibility that unseen individuals were present in the forest edge. For example, three known females occasionally came into the bai pools without their calves. Immatures using the bai alone may have done so more confidently knowing that their mothers were in the nearby forest edge. We observed six calves habitually entering the pools at the forest edge, joining their mothers briefly to suckle before returning to the forest. The bai is usually several degrees hotter than the forest interior (Mbeli Bai Study, long-term data) and smaller animals may be more sensitive to thermoregulatory costs in the open bai environment, as well as to any potential predator threats in the open. In addition, suckling calves acquire most of their nutrition requirements from their mother's milk, and therefore have no need to ingest them directly from the bai.

This visiting population, although small compared to other bais in the region (Turkalo and Fay 2001; Querouil et al. 1999), shows fidelity in individual associates and provides evidence that the fission-fusion model of sociality may apply to forest elephants in a bai environment. All age and sex classes were represented in the visiting population, and their association patterns were consistent with the expectations from a fission-fusion model: individuals did not always visit with the same conspecifics, or in constant group sizes, yet they had preferred associates that were statistically distinctive and which were consistent over time. Forest elephants at Mbeli Bai were much more solitary than savanna elephants, where females are almost never seen alone except when ill or in oestrus (Moss 1988). Although forest elephants appeared to be solitary for a relatively high proportion of their time spent in bais, vocal or olfactory communication may have maintained some level of grouping based on knowledge rather than propinquity. Research on acoustic communication in elephants suggests this may be particularly important in forest environments (Payne 2003).

From these comparisons, there are potentially interesting implications regarding dispersal mechanisms and the exchange of social information for forest elephants. With both sexes dispersing from the natal group, individuals cannot rely on the social knowledge and experience of matriarchs (McComb et al. 2001). Transmission of information may therefore occur in more discrete events for forest elephants rather than as cumulative experiences during daily life of a large family unit. There also may be trade-offs in relation to the exchange of social information; dominance interactions are expected where nepotistic females exploit fixed resource points (e.g. Archie et al. 2006b) and thus aggregations in pools could have both competitive costs and benefits. Bais may provide a specific arena where calves can begin the dispersal process and interact with individuals of a similar age and size (Evans 2006), with whom they can more effectively test and hone their competitive skills. Such contacts might be especially important given a low probability of contact or interaction within individual home ranges of potentially 1000-2000 km^2 (Blake 2002), and with densities of approximately 1/km^2 (Breuer, unpublished data).

If bais provide arenas which facilitate the social exchange of information, then not only do they supply important nutritional resources for forest elephants, but also are of crucial importance for the development and maintenance of relationships and for sexual access. The differences presented here in age-sex class use of bais may reflect varying requirements for physical or social resources; evaluating these needs requires detailed quantification of the behaviours and interactions seen in bais. Understanding the social systems of forest elephants remains crucial for understanding of the evolution of fission-fusion social systems, as well as to develop suitable landscape scale strategies for elephant management and conservation, if we wish to ensure the persistence of these populations in the long term. When poachers use bais to target elephant populations with devastating effects (Blake et al. 2007), they remove both generations of experience and opportunities for interaction and transmission of information with potentially negative consequences. The long-term future of elephants in Central Africa thus could be even more threatened than previously thought.

Acknowledgements

We thank the Ministère de l'Économie Forestière et de l'Environnement for permission to work in Nouabalé-Ndoki National Park and WCS Congo Program for crucial logistical and administrative support, particularly Mark Gately, Pierre Ngouembe and Emma J. Stokes. Mireille Ndoundou Hockemba and Ella Emeline Bamona helped with data collection. We thank Cynthia Moss and the Amboseli Trust for Elephants for use of press data on savanna elephant groupings. Christine Caldwell and Hannah Buchanan-Smith made valuable comments on earlier drafts, and three anonymous referees also made useful suggestions as well as corrections to the French abstract. Long-term financial support to the Mbeli Bai Study was provided by The Columbus Zoo and Aquarium, Cincinnati Zoo and Botanical Garden, Sea World & Busch Gardens Conservation Fund, Toronto Zoo, Wildlife Conservation Society and Woodland Park Zoo. TB is also supported by the Max Planck Society.

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