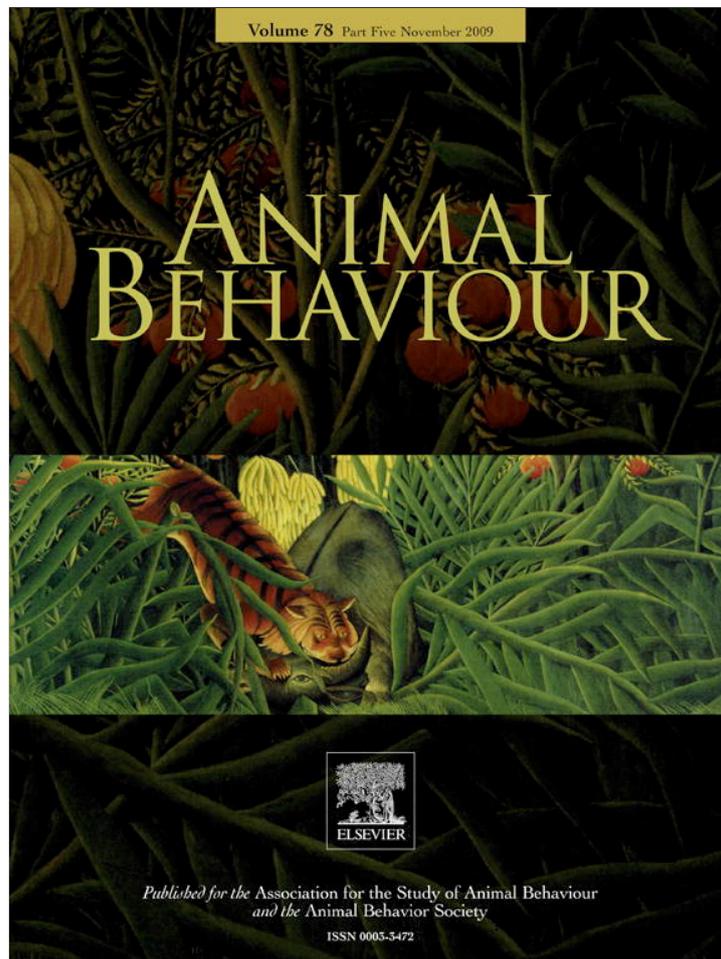


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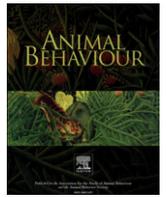
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Behavioural correlates of low relatedness in African elephant core groups of a poached population

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Poaching removed adult female elephants, *Loxodonta africana*, from a social system centred on kin support and female philopatry, creating a natural experiment in many matrifocal African elephant populations. We hypothesized that core groups lacking kin display less cohesion and cooperate and compete with elephants outside of their core group more frequently compared to more discriminating genetically intact core groups. We collected behavioural data on 77 known elephant core groups in Mikumi National Park, Tanzania, across three dry seasons (2003–2005) via focal group and scan sampling during transect and waterhole surveys. Pairwise relatedness was derived by genotyping females at 10 microsatellite loci. We categorized core groups as having low relatedness if their relatedness fell 1 SD below a simulation-generated threshold value; otherwise, they were considered to be highly related. We analysed indexes of cohesion, tolerance, affiliation and agonism to determine the influence of core group composition on the frequency of these behaviours. Cohesion, measured by a proximity index, was primarily driven by the actions of young adult females and was greater in core groups with an old matriarch. Between core groups, tolerance was the most frequent response. Core groups of low-related individuals displayed a higher frequency of affiliation and agonism with other unrelated core groups than did highly related core groups. Thus, less discriminating social behaviour may enable individuals that lack kin to avoid the risks of solitary foraging. However, this comes with the cost of increased agonism, potentially leading to negative consequences for these elephants.

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In many gregarious animals, both within- and between-group competition shapes individual social and spatial behaviour (Sterck et al. 1997; Silk et al. 2006a, b). In matrifocal systems, kin selection and philopatry (remaining with one's natal core group) may act to preserve preferential, if not exclusive, bonds among female relatives. Tighter bonding and cooperation among close relatives is evident among many matrifocal mammals, including black-tailed prairie dogs, *Cynomys ludovicianus* (Hoogland 1983), spotted hyaenas, *Crocuta crocuta* (Holekamp et al. 1997), white-nosed coati, *Nasua narica* (Gompper et al. 1997), and African elephants, *Loxodonta africana* (Archie et al. 2006b), to name a few. Related members of stable social units may accrue inclusive fitness benefits proportional to the number of alleles they share, the strength of their bonds and time they spend together (Hamilton 1964). This unique advantage of remaining with close kin may offset the costs of living in a group, especially at times when resources are scarce,

competition is heightened and dispersal is an otherwise attractive option (Griffin & West 2003).

African elephants are a matrifocal species that typically maintain core groups of related adult females (Douglas-Hamilton 1972; Moss 2001; Archie et al. 2006b). The core group is the association of one or more adult female elephants and her immature offspring moving and behaving in a coordinated manner with no single individual at a distance greater than the width of the main body of the group (Moss 2001). Within core groups, a female dominance hierarchy based on age and size minimizes costs of competition for diffuse resources that vary by season (i.e. forage and water; Archie et al. 2006a). Large core groups of related females fission when the costs of within-group competition grow too large as a result of ecological pressures, although fissioning events are rare and lone adult females are uncommon in long-term studies (Moss 2001). Female elephants are not territorial. However, they engage in between-group contests and a dominance hierarchy forms among core groups based on matriarch age and size (Wittemyer et al. 2007). Agonistic displays between core groups are often observed at 'clumped' resources, such as waterholes (Western & Lindsay 1984; Owen-Smith 1988). Between-group competition may, in fact, contribute to the rarity of transfers of females between core groups

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and to the maintenance of matrilineal elephant populations (Moss 2001). At the same time, female philopatry may have evolved as a response to the high ecological and social costs of remaining alone in this competitive environment (Sterck et al. 1997). Solitary female elephants may incur costs such as increased vulnerability of their young to predation, reduced access to resources and unfamiliarity with resource distribution in new areas, as observed in some primate species (Alberts & Altmann 1995; Isbell & van Vuren 1996; Sterck et al. 1997).

Poaching created a natural experiment in many elephant populations by removing adult females from a social system centred on kin support and female philopatry. Poaching was intense in the Mikumi-Selous ecosystem, Tanzania, reducing the Mikumi National Park population by up to 75% in the decade prior to the institution of the international ban on the sale of ivory in 1989 (Balozi 1989; Poole 1989; Idhe 1991). Presently, Mikumi core groups are small compared to other savanna populations; 30% of them contain only one adult female (average core group size is 2.2 ± 0.1 adult females; Gobush et al. 2009). Historical records are few; however, the large group sizes observed in Mikumi in the 1950s are absent from the records of the 1980s (D. Western, personal communication). We assume the structure of the current population results from past poaching, as evidenced by the large number of poached adult skulls found in the park prior to the ban (Idhe 1991) and a relative absence of skulls and extreme environmental and human-related pressures (i.e. drought, disease, increased elephant density or tourism) during the subsequent 15 years (Wasser & Norton 1993; Ereckson 2001). The consistency of core group composition across days, seasons and years observed in a related study (Gobush et al. 2008) also indicates that small-scale ecological fluctuations are not a driving-force in uniting or dividing adult female kin in Mikumi.

Small core group size alone does not demonstrate that kin are missing as a result of poaching; for example, a subset may split from a larger natal core group on rare occasions. Such fissioning typically preserves group relatedness because subsets usually consist of several close relatives, such as a mother–daughter pair (Moss 1988). However, the low relatedness of many of Mikumi's core groups and the large number of lone females suggest that poaching rather than fissioning shaped the population (Gobush et al. 2009).

Forty-five per cent of the multiple adult female core groups we examined at Mikumi had low degrees of relatedness for their group size, indicating that adult female kin were likely to be absent (Gobush et al. 2009). Lack of close relatives, lack of an old matriarch (>30 years old) and lack of strong social bonds were all significantly correlated in this population (Gobush et al. 2008). Females in core groups missing these elements also had significantly higher stress hormones (faecal glucocorticoids) and lower reproductive output than those in core groups with intact genetic pedigrees (Gobush et al. 2008).

Given the appreciable impacts that a disrupted core group structure has on elephant condition and reproduction, we examined the influence of core group composition on cohesive behaviour as well as responses to other core groups. We hypothesized that low relatedness within core groups of females results in weak internal social cohesion compared to females in highly related core groups with old matriarchs. Thus, we expected that females lacking close kin maintain greater physical distances and frequently disperse from their low-related core groups, and at an extreme, they opt to remain alone with just their offspring. Opportunities for inclusive fitness benefits are likely to be diminished for these females (Hamilton 1964) and the costs of their foraging together may not be adequately offset, especially during times of scarcity.

We further hypothesized that females in low-related core groups without old matriarchs display a wider network of associations because opportunities to preferentially bond with kin are less available or unavailable. We assumed that the overwhelming benefits of sociality among female elephants cause them to attempt to forge new bonds when previous bonds are lost. Lacking a close-knit group of kin or strong leader, females may be prone to seek bonds elsewhere, leading to more direct interactions with other unrelated core groups. Such interactions may increase chances for both affiliative and agonistic exchanges as alliances are sought and tested. Such females are predicted to exchange mutual benefits with a range of females and focus on those individuals that benefit them the most at the time. For example, as an elephant ages or as her reproductive state changes, she may choose to associate with those elephants that best facilitate her acquisition of resources or increase her social position. At the extreme, we expect female immigration and emigration between core groups, a rare occurrence in protected African elephant populations (Douglas-Hamilton 1972; Moss 1988).

In contrast, highly related core groups are predicted to affiliate with other unrelated core groups less frequently, choosing instead to affiliate with their own members and share benefits primarily with kin. An exception to this rule would be affiliation among distant relatives in the 'bond group'. Bond groups represent a second-tier social tie between two or more related but distinct core groups thought to have fissioned in the past (see Methods; Douglas-Hamilton 1972; Moss 1988; Foley 2002; Archie et al. 2006b; Wittemyer & Getz 2007). Furthermore, we predicted that the stability and composition of these highly related core groups should also lead to fewer contests with other unrelated core groups overall and a higher likelihood of dominating other unrelated core groups when contests do occur. Consequently, tolerance, rather than direct affiliative or agonistic interactions, is likely to be the more frequent response of highly related core groups to other unrelated core groups.

METHODS

Identifying and Ageing Elephants

Mikumi National Park (6.9–7.7°S, 36.9–37.4°E; 3230 km²) has 1140–3100 free-roaming elephants (TWCM 1998; Blanc et al. 2002); the park habitats are described by Norton et al. (1987). We identified elephants in this population based on unique physical characteristics and a photo-identification file, built over repeated sightings of 109 unique core groups. We refer to social groupings at two distinct levels as defined by Moss (2001) and Archie et al. (2006b): the core group and the 'bond group'. The core group is the association of one or more adult female elephants and her immature offspring moving and behaving in a coordinated manner with no single individual at a distance greater than the width of the main body of the group. Each elephant was assigned membership to the core group that she associated with for the majority (>50%) of her sightings across days, seasons and years. For example, if a female was alone for one sighting and with two other females for five sightings, the core was defined as consisting of all three females. Based on these definitions, Mikumi core group size averaged 2.2 ± 0.1 adult females (range 1–6, $N = 109$ groups). A bond group (Douglas-Hamilton 1972; Moss 1988; Foley 2002; Archie et al. 2006b; Wittemyer & Getz 2007) consists of females from two or more established core groups that repeatedly affiliate in nearly a mutually exclusive manner (>2 times, but less than 50% of their sightings, indicating they are two distinguishable core groups). We detected six bond groups in Mikumi; four of which had closely related matriarchs between their constituent core groups.

We considered female elephants to be mature if they were at least 10 years old (Poole 1989). Researchers have suggested that Mikumi elephants are small in stature (although this could simply be from an overall lack of old females). We, accordingly, used a constellation of physical characteristics to age females into conservative 10-year age classes, rather than in 5-year increments typical for other studies on adult savanna elephants. Adult females were categorized as young (10–19 years old), middle-aged (20–29 years old), and old (≥ 30 years) based on shoulder height, back length, circumference of tusks (if present), ear position, shoulder protrusion, breast development and abdomen depth with known-age elephants (Laws et al. 1975; Kangwana 1996; Foley 2002), following in-the-field training by C. Foley. A core group was defined as having an old matriarch if the eldest female in the core group was at least 30 years old. We classified young as infants (≤ 2 years old) on the basis of small size, unerupted tusks and frequent nursing.

Elephants use the entire range of habitats from grassland to woodland in Mikumi (Erickson 2001). Six distinct locations of elephant use, each centred around one to two waterholes, became apparent as sampling progressed (identified as: Kikaboga (K), Chamgore (C), Mwanamboga (MW), Dam (D), Visada (V), M'goda (MG)). African elephants maintain core home ranges faithfully, although they may expand their range seasonally beyond the main core areas (Western & Lindsay 1984). Most core groups in Mikumi remained in one of the six defined locations throughout the entire study, which we assumed to comprise part of their home range. Only a few groups very infrequently ventured into one of the other six locations.

Behavioural Observations

We systematically surveyed the northern one-third of Mikumi (1000 km² of a total area of 3230 km²) by vehicle during daylight hours each month, focusing on areas most frequented by elephants. We conducted repeat vehicle surveys of six tourist track transects (totalling 110 km) during dry seasons in 2003–2005. We drove transects at least two times per month on a rotating basis, with additional sampling of areas of high use by elephants, based on tracks and dung. New off-road transects and waterholes were continually sought. When we sighted a core group, we performed an initial scan from a maximum distance of 100 m and recorded the number of individuals, their sex and age class, and the number of visibly pregnant and lactating females (Laws et al. 1975; Kangwana 1996). After a 10 min habituation period, we attempted to drive closer for better viewing (minimum distance 35 m). We remained with the core group for as long as possible (10 min–2 h) and followed them off-road if necessary; observation sessions terminated when the group left our field of view or at dusk. We also conducted observation sessions at nine waterholes 10–15 times each month and collected data on all core groups present during each session. Initiation time of sessions alternated between morning (0600–1200 hours) and afternoon (1400–1900 hours), lasting up to 8 h.

Within-group behaviour sampling occurred on lone core groups consisting of at least two adults. After the initial scan and habituation period, we began instantaneous scans of the group at 4 min intervals; each scan recorded every female's activity state (feeding, resting, travelling, socializing, drinking, grooming) and distance from the nearest adult female in the group (measured in elephant body lengths, approximately 2 m; Altmann 1974; Garai 1992). Females changed distance (stepping forward or backward) from other group members an average \pm SE of 3.6 ± 0.9 times per interval, based on movement rates of seven females from three core groups for 65 min.

Between-group behaviour sampling occurred when the area occupied by two recognizably unique core groups overlapped. This

co-occurrence was most frequent at waterholes. We performed an initial scan to identify all core groups present and chose one core group as the focal. We chose each session's focal group in a manner that best enabled us to collect dung (for genetic analysis) and behaviour from as many core groups as possible for the duration of this study. We recorded affiliative and agonistic behaviours between adult females of the focal core group and those of other core groups continuously with an established ethogram (Foley 2002). Affiliative behaviours included any gentle body contact, parallel walking, back-walking towards and greeting rumbles directed at another elephant; aggressive behaviours included standing tall, quick turn towards, head shake, mock charge, strike, fast approach, chase, or scream directed at another elephant. A female won an aggressive bout if she displaced another female from her position; the loser typically showed a moderate to fast exit from the area or a quick turn away from the aggressor. If a series of agonistic displays continued between two elephants, we assigned dominance to the female that eventually displaced the other. We observed no reversals in dominance across multiple agonistic encounters between-group pairs in this study. However, we could not determine a transitive dominance hierarchy because not all core groups were observed to interact during the course of this study, similar to the experience of Lee (1987) in her 18-month study of the Amboseli elephants.

Cohesion Metrics

The frequency that an individual spends with another in close proximity is commonly interpreted as an indication of their level of bonding (Hinde 1976; Garai 1992; Kleindorfer & Wasser 2004). We used the program SOCPROG (version 1.2, Whitehead 1997) to derive an association index (AI) for each pair of females, calculated as the number cosightings of two elephants behaving as a core group divided by the total number of sightings of each individual (see previous definition for core group). A sampling period of 1 day was used to ensure that sightings were independent; thus, if an elephant was observed twice in 1 day (a rare occurrence), only her core group composition during the first sighting of the day was analysed. Individuals were sighted an average of six times across days, seasons and years (range 2–22 sightings). Previously, we discovered that core group composition was highly consistent and AI was not correlated with the number of sightings (linear regression: $R^2 = 0.01$, $F_{1,195} = 1.2$, $P = 0.28$; Gobush et al. 2008).

We also calculated a proximity index (PI) for each adult female elephant as her average distance (measured in elephant body lengths) from her nearest neighbour given her activity. First, we averaged all scan distances recorded for each activity (resting, feeding or travelling) for each female during a sighting to yield her daily value for each activity. Averaging across scans minimized autocorrelation issues. Then, we averaged each female's daily values across all her sightings to yield her average resting PI, feeding PI and travelling PI. The PI naturally varies during different activities; therefore, we controlled for differences in time spent resting, feeding and travelling among individuals by combining these three separate PI averages into an overall PI average for each female. A PI was only derived for females in core groups with at least two adults, observed for at least 20 min in each of the three activities and sighted at least twice. Sample size for PI analysis was markedly reduced because of these criteria compared to the other indexes examined.

Responses to Other Core Groups

Core groups responded to others in a tolerant, affiliative, or agonistic manner at waterholes. A finite number of core groups

used each waterhole, and they appeared to time their drinking to interact with other groups or to avoid them; core groups often waited up to 3 h in the bush to coordinate their arrival to the water's edge with others. Hence, we assumed that a core group's timing reflected motivation to obtain water and to socialize. A tolerant response was recorded when two core groups were within each other's view (typically 100–300 m apart) but did not directly interact. An affiliative response was recorded when two core groups intermingled, exchanged greetings and/or engaged in physical contact and remained in close proximity. An agonistic response involved formal displays of dominance, submission and displacement between two core groups. We derived an index for each behaviour based on each core group's observed frequency, divided by the number of times the core group was sighted. A corresponding expected frequency was also derived from the total number of observations of the behaviour in the entire data set, divided by the number of times the core group was sighted. This index allowed us to delineate a core group's behavioural response as occurring more (positive values) or less (negative values) frequently than expected based on the populationwide incidence (zero value).

Core groups participating in bond groups had the highest affiliation indexes, as predicted. The majority of these bond groups had at least one highly related pair of females among their two core groups (Gobush et al. 2009). Therefore, affiliation indexes were examined with and without this subset to investigate factors beyond coancestry that influence the frequency of affiliation.

Genetic Relatedness

We attempted to collect faeces from all observed defecations by known adult females as soon as they departed the area. We successfully sampled all adult female elephants in 94 of 109 known core groups ($N = 203$ females). Samples were collected by pinching off portions from the outside of several clumped boli and placing the faeces in a 40 ml vial with 25 ml of 20% dimethyl sulfoxide in a tris EDTA NaCl buffer, initially stored at room temperature in Tanzania and subsequently stored at -20°C in the U.S. DNA was extracted, purified, amplified at 10 microsatellite loci and scored as detailed in Gobush et al. (2009). Tests for linkage and Hardy–Weinberg equilibrium were performed on Genepop version 3.1, applying the sequential Bonferroni test a posteriori (Rice 1989; Raymond & Rousset 1995). All loci were unlinked and met Hardy–Weinberg expectations.

We used genotypes to generate a pairwise coefficient of relatedness (r , ranging from -1 to 1) between all adult female pairs using KINSHIP (version 1.2), with an $r = 0$ representing the population average (Queller & Goodnight 1989). (The coefficient of relatedness differs from coefficient of kinship, range 0 – 0.5). Negative values occur that represent pairs sharing fewer alleles than the populationwide average. Thus, for example, $r = 0.125$ does not necessarily imply a first-cousin relationship. Relationship assignments for a given r value are calibrated by the r values of known relationships in the data set. The relatedness of seven known Mikumi mother–infant pairs averaged 0.41 ± 0.05 , determined by jackknifing across all loci. This approximated a theoretical r of 0.5 , as expected for first-order pairs, and is comparable to that reported in a similar elephant relatedness study (Archie et al. 2006b). We defined each core group's relatedness by deriving its average r and number of first-order relatives (assigned as zero for groups with only one adult female). For the present analyses, only core groups in which all females were genotyped were included. Minimum r for inclusion as a first-order relationship was 0.37 , consistent with our calibration (i.e. the average r for known first-order pairs in this data set, adjusted by its standard error). We substantiated this

designation by determining the most likely relationship of all within-group pairs of females (e.g. first-order, $r = 0.5$; second-order, $r = 0.25$; unrelated, $r = 0$) using maximum likelihood methods via ML-Relate version 1.0 (Kalinowski et al. 2006). In consideration of the resolution of our data set, we then definitively distinguished first-order relationships from unrelated females at the 0.05 significance level. Close relative assignment was in agreement for 95% (144/152) of within-group pairs tested using both methods.

Low versus High Relatedness

In a previous analysis, we categorized the relatedness of each Mikumi core group as low or high based on its deviation from an unpoached expectation in which related adult females exclusively form core groups (Gobush et al. 2009). Since comparable data from known unpoached groups of similar sizes to those found in Mikumi were unavailable, we derived the unpoached expectation through simulations (Gobush et al. 2009). The minimum simulated r value for a core group of two to three with a structure consistent with this unpoached expectation (i.e. a parsimonious pedigree with no missing female relatives) was 0.26 (0.18 SD) representing all half-sisters, a reasonable minimum relatedness given elephant mating behaviour and female philopatry. If a Mikumi core group's r fell below 1 SD of this minimum expectation, we classified it as having low relatedness; otherwise, it was classified as having high relatedness (core group's $r > 0.08$). Of 37 Mikumi core groups (sized 2–3) examined, 17 were classified as having low relatedness (r range -0.21 to 0.08 ; Gobush et al. 2009). We also classified single female core groups as having low relatedness.

To create the simulated genotypic data set and derive unpoached core group averages, we wrote a gene-drop analysis program in Microsoft Visual C++ Version 6.0 (detailed in Gobush et al. 2009). Briefly, gene-drop analysis is a Monte Carlo Markov chain simulation technique that successively drops alleles through a pedigree from founders to descendants. To accomplish this, the analysis randomly assigned genotypes to the pedigree's founders, the matriarch, and all fathers by allele frequencies derived from the Mikumi matriarchs (i.e. the eldest female per group born prior to peak poaching (1973) from 94 observed families, $N = 50$ old females). We assumed Mikumi founders were an unrelated, random sample of the population; any alleles they shared would represent the background relatedness of the population. Substantiating this assumption, relatedness among this subset averaged 0.01 ± 0.01 . Genotypes of descendants were then produced by simulating meiosis, recombination (genes were unlinked) and mating in chronological order. We constructed parsimonious pedigrees with no adult females absent for group sizes of two to three (86% of multiadult groups sighted in Mikumi were in this size range). For core groups of size two, three unique parsimonious pedigrees were possible; for core groups of size three, eight such pedigrees are possible. We independently repeated the gene-drop 1000 times for each pedigree to derive its average r . We then identified the minimum average core group r and SD among the pedigrees of each core group size.

Statistical Analyses

We conducted statistical analyses in SPSS (version 11.5, SPSS Inc., Chicago, IL, U.S.A.) and JMP (version 6.0, SAS, Cary, NC, U.S.A.). To examine the factors that influence within- and between-group behaviours, we analysed 375 h of data on 77 of 109 known groups across three dry seasons in 2003–2005. Wet season data were omitted because flooding prevented adequate surveying and sampling of many core groups. Constriction of the data set to the

dry season when forage quality and availability of water were decreased may overinflate PIs and the occurrence of agonism among core groups, while the occurrence of affiliation and tolerance may be deflated. However, significant relationships among dominance and spatial behaviour were detectable only in the dry season in a similar study (Wittemyer et al. 2007). Our analyses, although perhaps limited in scope, offer the best opportunity for examining variation in cohesiveness and competition across core group composition factors in Mikumi.

We used general linear mixed models (GLMM) to predict the occurrence of each behavioural index (i.e. PI, tolerance, affiliation and agonism) based on the independent variables described below. Data were log-transformed for normality, as needed. We used a backward stepwise process to create reduced models, removing all nonsignificant factors (two-tailed significance level was a probability of 0.05 or less). However, low sample size and lack of power in some models may have precipitated nonsignificance of some factors. We conducted a principal components analysis on factors known to be interrelated (e.g. AI, old matriarch and first-order relative presence), resulting in independent components, each with a single factor loading above 0.90, and lesser factors loading below 0.28. Factors tested in all models included the number of sightings, AI, location in the park, core group size, relatedness (low versus high), old matriarch presence and first-order relative presence, with the addition of age class, pregnancy status and infant presence in the PI model. We also included group ID as a random effect in the PI model to minimize autocorrelation issues. For each response index model, we included a core group's average AI and PI and other response indexes to test for cross-reactions.

RESULTS

Cohesiveness within Core Groups

Mean \pm SE distance between core group members (PI) was 5.3 ± 1.9 elephant-lengths during feeding, travelling or resting for 91 Mikumi adult female elephants from 37 groups (size range 2–5 females). A GLMM of log PI showed that AI, old matriarch presence and age all significantly influenced this variable (GLMM: adjusted $R^2 = 0.76$; AI: $\chi^2_4 = 8.0$, $P = 0.01$, old matriarch: $\chi^2_4 = 4.1$, $P = 0.05$; age class: $\chi^2_4 = 5.1$, $P = 0.01$). AI significantly predicted proximity, indicating that elephants that spent more time together also maintained a closer distance to each other. Presence of an old matriarch predicted strong familial cohesiveness as expected (Fig. 1). Younger adult females stayed closer to their core groups than did the two older adult age classes, suggesting a stronger tendency among young adults to maintain group cohesiveness. No other factors were significant.

Responses to Other Core Groups

We sighted core groups 569 times: 223 sightings were of lone core groups and 346 sightings included two or more core groups together, each responding to others present in a tolerant, affiliative or agonistic manner. We recorded 503 between-group responses; this exceeds the number of multigroup sightings because, for example, when a trio of groups was observed in one sighting, three separate responses occurred. The most frequent interaction between core groups was tolerance (213 of 503 responses; Table 1). Sixty-three of the 77 core groups displayed tolerance, meaning they were within 300 m of another core group with no direct interaction (Table 1). Tolerance index was predicted by location and its interaction with first-order relative presence after controlling for the number of sightings (GLMM: adjusted $R^2 = 0.15$, $\chi^2_{12} = 25.0$, $P = 0.02$; sightings: $\chi^2_{12} = 11.1$, $P = 0.0009$; location: $\chi^2_{12} = 11.3$,

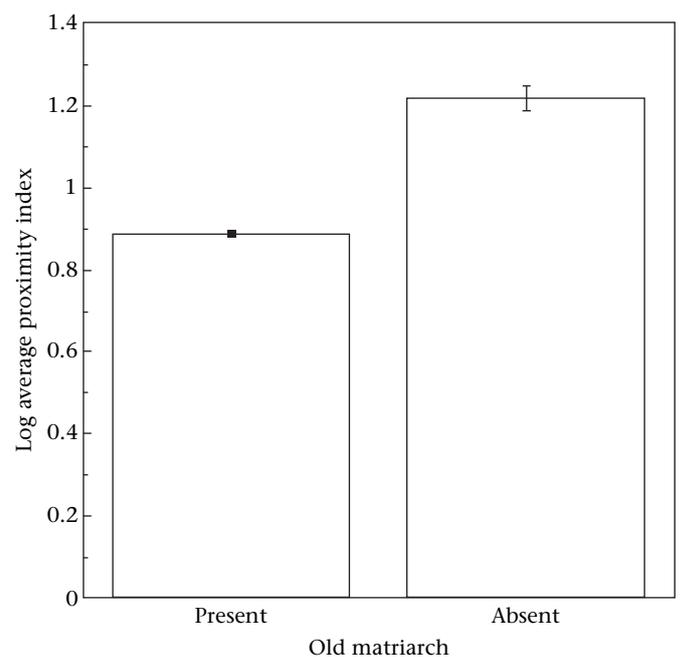


Figure 1. Log average \pm SE proximity index when an old matriarch was present or absent in elephant core groups ($N = 91$ adult females from 37 unique groups).

$P = 0.05$; first-order relatives: $\chi^2_{12} = 1.3$, $P = 0.26$; location*relatives: $\chi^2_{12} = 13.0$, $P = 0.02$). Core groups were significantly more frequently tolerant than expected in location K. Core groups with first-order relatives at location MG were most frequently alone, leading to a significantly reduced opportunity for and frequency of tolerance (Table 2). No other factors tested were significant.

Forty-one of 77 core groups behaved in an affiliative manner with other core groups (Table 1). Group size was the best predictor of the affiliation index (Welch's ANOVA: $F_{3,73} = 6.1$, $P = 0.01$). Core groups with two adults showed the highest frequency of affiliation, although variance in this measure was also greatest for the two adult groups (Levene's test: $F_{3,73} = 4.5$, $P = 0.01$). Frequent and nearly mutually exclusive affiliation among bond group members had the potential to mask the influence of other factors. After excluding bond group affiliations, location and its interaction with relatedness were significant predictors of affiliation index (GLMM: adjusted $R^2 = 0.20$, $\chi^2_{11} = 23.1$, $P = 0.02$; location: $\chi^2_{11} = 17.7$, $P = 0.003$; location*relatedness: $\chi^2_{11} = 12.1$, $P = 0.03$). Core groups in location MG were most frequently affiliative. In contrast, core groups in location K were least frequently affiliative, with high-relatedness core groups having the lowest frequency of affiliation with other core groups (Table 2). No other factors tested were significant.

Forty-one of 77 core groups interacted agonistically with others; agonism was the least frequent response observed (Table 1). Agonism index was predicted by location and relatedness (GLMM:

Table 1

Frequency of between-group responses during 503 pairwise core group interactions among 77 Mikumi elephant groups across 346 multigroup sightings (groups were observed to be alone during 223 of 569 sightings)

Response	Tolerance	Affiliation	Agonism
Sightings	213	194	96
<i>N</i> core groups	63	41	41
Mean \pm SE number of responses per core group	3.13 \pm 0.21	2.85 \pm 0.20	1.41 \pm 0.14

Table 2
Significant predictors of between-group responses for 77 elephant core groups in Mikumi National Park

Predictors	Tolerance	Affiliation (all groups)	Affiliation (without bond groups)*	Agonism*
Location	K		MG, K	MG, MW
Composition factors	First-order relatives × location	Group size	Relatedness	Relatedness
Behaviour cross-reactions				Tolerance

MG = M'goda; MW = Mwanamboga; K = Kikaboga.

* Excludes core groups that were not categorized by relatedness.

adjusted $R^2 = 0.20$, $\chi^2_7 = 25.7$, $P = 0.0006$; location: $\chi^2_7 = 16.5$, $P = 0.006$; relatedness: $\chi^2_7 = 4.5$, $P = 0.03$; tolerance: $\chi^2_7 = 5.2$, $P = 0.02$. Core groups were more agonistic than expected in location MG and were less agonistic than expected in location MW. Agonism was significantly more likely to occur in low-relatedness core groups than in high-relatedness core groups, as expected (Table 2). Surprisingly, tolerance was a significant predictor of agonism, suggesting that a number of Mikumi groups purposefully accompanied each other to waterholes, although contests often ensued. No other factors tested were significant.

The presence of kin influenced behaviour, as demonstrated by our separate analyses on each response index. Trends were difficult to discern because of low sample size and statistical power. However, a general pattern emerged when all affiliative responses were included, with high-relatedness core groups opting to be either alone or affiliated with related core groups that were apart of their bond group (Fig. 2). In contrast, low-relatedness core groups responded to others in an agonistic or tolerant manner relatively more often than did highly related core groups (Fig. 2). When affiliation among bond groups was removed, this pattern dramatically changed. Without their bond groups, high-relatedness core groups displayed affiliation relatively less often than low-relatedness core groups.

DISCUSSION

Our results demonstrate that the behaviour of an elephant core group in Mikumi is influenced by its composition. No single core group characteristic fully explains all of the observed within- and

between-group variance in behaviour. Presence of an old matriarch, which strongly covaried with high relatedness, and age class influenced how cohesively an adult female bonded to her core group. Furthermore, relatedness among females within a core group had a significant effect on how the core group responded as a unit to other core groups.

Young Adult Females with Old Matriarchs form the Most Cohesive Core Groups

Cohesiveness, as measured by a proximity index, was greater in core groups with an old matriarch, with young adult females maintaining the closest proximity to their core group. This behavioural pattern may correspond to the occurrence of allomothering in African elephants. When competition for resources is high, younger, lower-ranked adult females gain access to resources from older, dominant females in exchange for providing alloparental care (Dublin 1983). Furthermore, core group structures that facilitate tight association may ensure that benefits are shared among group members, such as mutual defence from predators, dominant status, knowledge of ephemeral resources and parental care. Potentially negative social stressors are also minimized. In a previous study, we found that 84% of Mikumi females in highly related core groups are part of old matriarch–adult daughter pairs (Gobush et al. 2008). We also found that physiological stress was significantly heightened in female elephants in core groups lacking an old matriarch (Gobush et al. 2008). Together, these findings demonstrate that this core group characteristic is an important factor that positively influences both the physiology and behaviour of adult female elephants in Mikumi.

Kin Availability Influences Between-group Behaviours

In a social system where kin support is available, groups are expected to concentrate benefits and affiliative behaviour on their relatives. For example, helping behaviour is reserved for individuals above a threshold of relatedness in macaques, *Macaca fuscata* (Chapais et al. 2001). Selective support of close kin in agonistic encounters also occurs among baboons, *Papio cynocephalus* (Silk et al. 2004). Among Mikumi elephants, we found that highly related core groups affiliated less with unrelated core groups, preferring to be alone. By contrast, low-relatedness core groups interacted more frequently with other unrelated core groups. These results suggest that matrifocal behaviour serves to maintain African elephant matrilineal ties at the exclusion of close ties with unrelated groups.

The inter-relatedness of core groups appears to strongly influence their frequency of affiliation. We did not examine intergroup relatedness among all core groups participating in the 194 observed affiliative interactions. However, we previously discovered several bond groups in Mikumi, each composed of two to three core groups with one related pair of females between them (average interpair $r = 0.30 \pm 0.05$; Gobush et al. 2009). Their affiliations represented a second level of preferential bonding with kin, and their affiliation indexes were among the highest in our data set. When we excluded these bond group interactions from the analyses, highly related

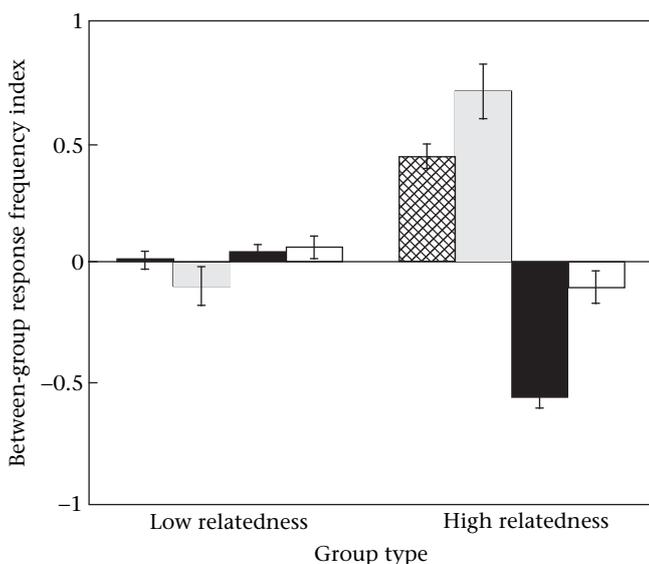


Figure 2. Mean \pm SE frequency indexes for low-relatedness ($N = 40$) and high-relatedness ($N = 29$) elephant core groups when sighted alone (▨) and when sighted with other groups and showing affiliative (□), agonistic (■) or tolerant (□) behaviour (populationwide average was zero).

core groups were less affiliative with other core groups than were low-relatedness core groups in the area near the park headquarters (location K). This area served as a refuge during the peak poaching era of the 1980s (Balozi 1989). As more nonresidents populated the area, a heightened requirement for alliances may have ensued for some elephants. Both transitory newcomers without stable groups and resident fragmented families unable to defend home ranges would mutually gain from being affiliative with others in their same situation, whereas highly related groups could afford to be more discriminating.

An unstable hierarchy among core groups that resulted from the loss of related dominant, older matriarchs to poaching may be driving the overall reactive behaviour observed in the most vulnerable area of the park. Solitary females and small core groups consistently arrived at waterholes together, especially at one very active waterhole (location MG) in a remote area of the park that experienced historically high levels of poaching. Low-relatedness core groups participated in agonistic contests more frequently than highly related ones, as expected. However, surprisingly, these low-relatedness core groups were also more frequently tolerant of other core groups. In contrast, highly related core groups were observed to be alone more often. These findings suggest that concerns for safety place greater pressure on low-relatedness core groups to spend more time near other core groups, and this, in turn, increases opportunities for contests. In Samburu (Kenya), dominant groups disproportionately use preferred habitats, limit their exposure to predation and conflict with humans by avoiding unprotected areas, thus expending less energy than subordinate groups during the dry season (Wittemyer et al. 2007). Our results suggest that increased tolerance provides an additional way in which less dominant females without social support cope with competition for limited water.

Variation in Core Group Structures and Behavioural Plasticity

Diversity in the response of adult female elephants to unrelated conspecifics reflects behaviour plasticity in this species. Our results demonstrate preferential socializing among kin when they are available, consistent with behaviour observed in other elephant populations. Mikumi female elephants that are apart of close-knit highly related core groups primarily socialize with their own members rather than with unrelated elephants in other core groups. This behaviour is well demonstrated for protected elephant populations (Douglas-Hamilton 1972; Moss 1988; Whitehouse & Hall-Martin 2000). In playback experiments, Amboseli core groups responded with contact calls and approached calls of related females exclusively, and avoided or displayed defensive bunching to calls of unrelated females and core groups (McComb et al. 2000). For elephants in highly related core groups, the number of exchanges among members is potentially very high because of a simple function of time spent together. Alternative related groupmates are relatively few, with an effect of concentrating cooperative acts on these preferred social partners. Exceptions to this rule are elephants that also have close relatives at the next level, the bond group, which appears to be rare in Mikumi.

In contrast, cooperation, tolerance, as well as competition among a wider array of social partners occurred when kin were absent. Elephants lacking strong family bonds are expected to socialize in this manner if the cost–benefit ratio of a solitary forager is greater than that of a social forager (Mesterton-Gibbons & Dugatkin 1992). The majority of Mikumi female elephants are solitary or belong to low-relatedness core groups that are less internally cohesive. These females frequently socialize with elephants outside of their core group. Low cohesion and more frequent displays of between-group affiliation and tolerance among

females from low-relatedness core groups demonstrate an attraction of females to other adult female elephants even when kin are unavailable. Solitary foraging and its risks may be avoided by these elephants, but an increase in competitive and agonistic interactions with other core groups may contribute to downstream effects of poor stress physiology and reproductive output in this segment of the Mikumi population (Gobush et al. 2008). The use of these alternative social tactics may influence a female elephant's energy and activity budgets. The dispersal or migratory patterns of less cohesive elephant groups may similarly be altered, resulting in decreased access to limited resources, as observed in Tarangire's core groups lacking old matriarchs (Foley 2002).

Overall, the loss of adult female elephants from Mikumi, primarily caused by intense poaching in the park throughout the 1980s, has left a high percentage of the population without adult female kin, old matriarch leaders, strong social bonds and cohesive core groups. Female elephants respond with alternative social strategies when close relatives are absent, although these too come with a cost. Unfortunately, this variation in behaviour is almost certainly not unique to Mikumi. Many African elephant populations experienced heavy poaching prior to the 1989 ivory ban. This disruption in elephant social structure will continue as poaching has once again returned with a vengeance to many parts of Africa (Wasser et al. 2008).

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