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Dominance rank relationships among wild female African elephants, *Loxodonta africana*

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Socioecological models of the evolution of female-bonded societies predict a relation between resource distribution and the nature of female affiliative and dominance relationships. Species that mainly rely on abundant, widely distributed resources, like African savanna elephants, are predicted to have unresolved dominance hierarchies and poorly differentiated female social relationships. Contrary to this prediction, female elephants have well-differentiated social relationships; however, little is known about the nature of their dominance rank relationships. Here we present the first quantitative analysis of dominance relationships within 'family' groups of adult female elephants in two wild populations: one in Amboseli National Park, Kenya, and another in Tarangire National Park, Tanzania. We tested three possibilities, that female elephants: (1) are egalitarian, (2) have linear, nepotistic hierarchies, or (3) have linear age/size-ordered hierarchies. Our results best support the third outcome: dominance rank relationships were transitive within families and highly asymmetrical within dyads, such that older, larger females consistently dominated smaller, younger females. We discuss the implications of this result for understanding the evolution of female social relationships.

The evolution of social organization is thought to reflect both the costs and benefits of group living (Alexander 1974). For example, individuals may cooperate to find food or mates, but they may also compete for those same resources. How these costs and benefits are distributed among group members is partially determined by dominance rank relationships; in societies where dominance rank relationships are poorly resolved, the costs and benefits tend to be divided relatively equally among group members, but in societies with strong linear hierarchies, a few individuals reap the majority of benefits or pay the majority of costs (Vehrencamp 1983).

Socioecological models of the evolution of female social relationships have been developed with primates in mind (Wrangham 1980; van Schaik 1989; Isbell 1991; Sterck et al. 1997; Isbell & Young 2002). These models represent a diverse set of approaches to the problem of how and why highly differentiated female social relationships evolved, but all address the possibility that predation pressure, intergroup competition and intragroup competition are important selective forces favouring such relationships. These models posit that a society's location along the continuum from weak to strong dominance hierarchies is partially determined by how its critical resources are distributed (Wrangham 1980; van Schaik 1989; Sterck et al. 1997; Isbell & Young 2002). One predominant view is that predation pressures force female mammals of many species to live in groups, and the distribution of resources subsequently determines the strength of within-group competition and the nature of female social relationships. For instance, species that exploit dispersed, abundant resources will tend to live in egalitarian societies with poorly differentiated social relationships among females (i.e. females will have no special affiliative bonds). This is because, when food is abundant and widely dispersed, coalitions with other group members offer few advantages in gaining access to resources, making it unlikely that long-term affiliative alliances will evolve (Wrangham 1980; van Schaik 1989; Sterck et al. 1997; Isbell & Young 2002). In contrast, species that exploit clumped resources

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that can be usurped by single individuals will tend to live in despotic societies with well-differentiated relationships and strong linear dominance hierarchies. In this case, high dominance rank confers fitness benefits because it improves access to resources. Nepotistic hierarchies (hierarchies in which relatives aid each other in agonistic interactions and hence obtain similar rank positions in the hierarchy) may evolve in such societies if related individuals gain direct or inclusive fitness benefits from mutual aid with their relatives (Wrangham 1980; van Schaik 1989; Isbell 1991; Sterck et al. 1997; Isbell & Young 2002). Such nepotistic, female-bonded societies are common among primates (Wrangham 1980; Gouzoules & Gouzoules 1987; van Schaik 1989; Sterck et al. 1997).

Hence, these models predict a relation between (1) how resources are distributed (clumped and 'usurpable' versus dispersed), (2) whether the society is female bonded and (3) whether the society has a strong linear dominance hierarchy. Within this framework, here we present the first quantitative investigation of dominance rank relationships among wild adult female African savanna elephants.

African elephants seem to have a combination of characteristics that are unexpected under the models described above. They are typically characterized as generalist herbivores whose food resources (grass, shrubs and trees) are abundant and widely dispersed: 60–95% of elephant diets are composed of grasses; elephants forage less selectively than other large herbivores, including rhinoceros and giraffe; they eat a much wider range of vegetation than do smaller ungulates (Laws 1970, 1975; Owens-Smith 1988). Under the socioecological models, this foraging pattern and resource distribution should result in an egalitarian society with poorly defined rank relationships. However, unlike most egalitarian species, elephant societies are 'female bonded' (Wrangham 1980) in the sense that females remain near female relatives throughout their lives (Archie et al., in press), and show extensive affiliative and cooperative behaviour with female kin (Douglas-Hamilton 1972; Dublin 1983; Moss & Poole 1983; Lee 1987; Moss 1988; Archie et al., in press). Such female-bonded relationships are typically associated with strongly linear, nepotistic hierarchies and intense within-group competition, because female coalitions are thought to be important in maintaining access to resources (Wrangham 1980; van Schaik 1989; Isbell 1991; Sterck et al. 1997; Isbell & Young 2002).

In showing this combination of characteristics, elephants present something of a puzzle: a female-bonded social system in a species that exploits abundant, widely dispersed food resources is unexpected under established socioecological models of the evolution of social systems. In our view, these models are essentially correct, but the apparent disparity with elephants rests in either (1) an incomplete current understanding of elephant social structure or resource use, or (2) an incomplete model that describes only one of several possible relations between resource distribution and female social relationships. We attempted to explain why elephants appear to contradict the current models and to shed light on the selective forces that have influenced female elephant social organization by investigating the nature of dominance rank relationships within 'family' groups of wild female elephants.

Given that elephants are female bonded yet apparently use abundant, widely distributed resources, how might dominance rank relationships be structured within groups of female elephants? There are three possibilities (Table 1), and each one generates a slightly different set of inferences about the evolution of female elephant social relationships.

First, dominance relationships among adult female elephants may be poorly resolved with few agonistic interactions and many reversals (i.e. interactions below the diagonal of the dominance matrix). This hypothesis would accord well with the general view that most resources used by elephants are abundant and widely distributed, and that competition among group members should therefore be low. In this scenario, the well-differentiated social relationships that occur among female elephants may exist, not because of resource acquisition, but because individuals rely on social partners for

Table 1. Possible ways in which dominance rank relationships are structured in elephant societies, and resulting inferences about the strength of competition and the function of female relationships

Possible dominance rank relationships	Inference regarding competition for resources	Inference regarding the function of female relationships	Evidence
Egalitarian	Resources are abundant and widely distributed and competition for them is minimal	Primary function is cooperative offspring care or defence against predation; no direct or inclusive fitness benefits accrue from mutual aid in competition	Linear dominance hierarchies are sometimes difficult to construct (Lee 1987)
Linear, nepotistic	Clumped, usurpable resources are more important for elephants than has been previously suggested	Direct or inclusive fitness benefits of mutual aid are central to female relationships, but other forms of cooperation may also be important	Fission–fusion nature of elephant societies may be a strategy to reduce competition (e.g. Chapman 1990)
Linear, not nepotistic	Most resources are widely distributed and abundant, but some usurpable resources create competition; linear hierarchies reduce the risk of conflict	Primary function is cooperative offspring care or defence against predation; few to no direct or inclusive fitness benefits accrue from mutual aid in competition	Age/size-based linear hierarchies have been suggested for elephants (Douglas-Hamilton 1972; Dublin 1983)

cooperative offspring care, protection against predation or to share knowledge about resource distribution (Douglas-Hamilton 1972; Dublin 1983; Moss & Poole 1983; Lee 1987; Moss 1988; McComb et al. 2001; Foley 2002). In support of this prediction, Lee (1987) was unable to construct linear hierarchies within female elephant groups because agonistic interactions were too infrequent in her 18-month study.

Second, elephant dominance hierarchies may be linear and nepotistic (Fig. 1a, Table 1). This hypothesis suggests that female elephants gain direct or inclusive fitness benefits from helping kin to attain rank and acquire resources, and could explain the well-differentiated relationships observed among females (but would not exclude the importance of cooperation for other reasons). A linear, nepotistic dominance hierarchy in elephants would lead us to strongly question the claim that critical resources for elephants are abundant and widely distributed and that competition is therefore uncommon within groups. In fact, some resources for female elephants, including water holes, mineral resources, rubbing posts or high-quality foods, are sometimes clumped or rare (e.g. *Acacia xanthophloea* bark, palm flowers, balanites seeds; Weir 1972; Dublin 1983; Western & Lindsay 1984; Owens-Smith 1988). It is possible that these resources are important enough to create a competitive environment that shapes elephant social relationships. This hypothesis is further supported by the observation that elephants live in fission–fusion societies, which are thought to be an adaptive response to minimize competition, because groups divide and reform depending on resource availability (Moss & Poole 1983; Chapman 1990; Dunbar 1992; Takahata et al. 1994; Kummer 1995; van Schaik 1999; Shimooka 2003).

Third, female elephant dominance rank relationships may be linear but ordered by size or age, rather than nepotistic (Fig. 1b, Table 1). This hypothesis suggests that individuals receive few direct or indirect fitness benefits for assisting kin in attaining rank. However, competition for resources may be moderate, because some resources are usurpable, and linear dominance hierarchies would allow individuals to predict the outcome of agonistic interactions and thereby reduce overall rates of aggression (Rowell 1974). In this case, we would not expect dominance rank to be strongly predictive of fitness, and other sources of variance in fitness should be more important. Furthermore, other forms of cooperation (e.g. against predators, for offspring care) may explain the female bonding and well-differentiated female relationships in female elephants. In support of these predictions, researchers have suggested that such age/size-based linear hierarchies exist for elephants (Douglas-Hamilton 1972; Dublin 1983; Moss 1988).

METHODS

Study Areas and Populations

Behavioural data were collected from free-ranging habituated adult female elephants in and around Amboseli National Park, Kenya, between 1999 and 2003, and in Tarangire National Park, Tanzania between 1993 and 2000. The Amboseli and Tarangire elephants represent two of the best-studied wild elephant populations in Africa and both have been subjects of long-term research projects. The two parks are several hundred kilometres

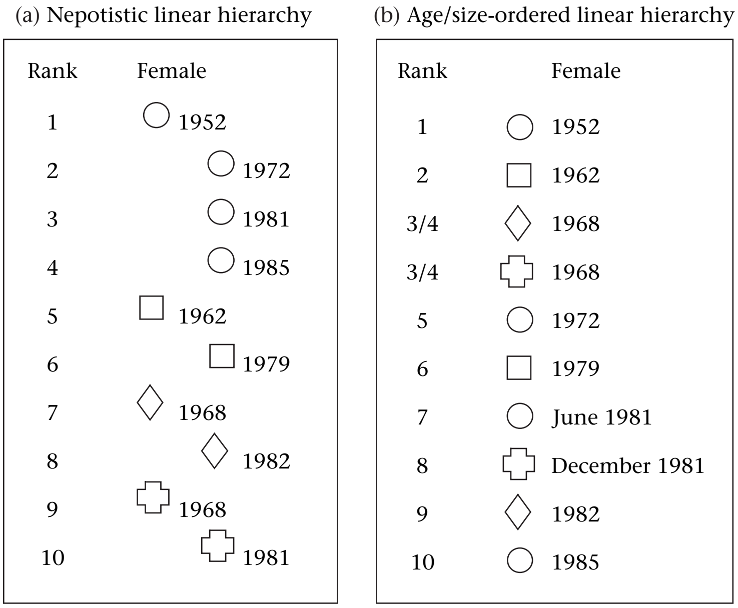

Figure 1. Diagram of contrasting predictions for how individual ranks would differ among adult females in the AA elephant family in Amboseli, depending on whether the rank relationships are (a) linear and nepotistic, such that females inherit the rank just below their mother, or (b) linear and age/size-based, such that older, larger females outrank younger, smaller females. Each female is represented by a shape, followed by her known or estimated birth year. Different shapes reflect different known matrilines; genetic relationships between females born before 1972 are unknown.

apart and are home to distinct sets of individuals. However, genetic analyses have indicated fairly extensive gene flow among elephant 'populations' across the African continent (Georgiadis et al. 1994; Nyakaana & Arctander 1999; Comstock et al. 2002; Eggert et al. 2002; Nyakaana et al. 2002), indicating that Tarangire and Amboseli should not be considered genetically distinct populations. The Amboseli basin supports a population of approximately 1200 elephants (Moss 2001) and Tarangire supports approximately 2000 elephants (Foley et al. 2001). Although Amboseli's population has been relatively unaffected by hunting and poaching (Moss 1988, 2001), the poaching of many older elephants, of both sexes, in Tarangire has altered the age structure, although not the mean group size (Foley 2002).

Data collection took place during daytime hours in all months of the year and all seasons (dry and wet). The ecosystem of each park is characterized by semiarid mixed savanna and woodlands; mean annual rainfall is 346 mm in Amboseli (Altmann et al. 2002) and 620 mm in Tarangire (van de Vijver et al. 1999). In both parks, most precipitation falls during biannual rainy seasons from March to May and November to December (van de Vijver et al. 1999; Altmann et al. 2002). Permanent springs provide Amboseli with a continuous source of water (Altmann et al. 2002). In Tarangire, wildlife rely on the Tarangire River, particularly in the dry season when it becomes the main source of water in the 35 000 km^2 Masai ecosystem (Prins 1987).

Identification of 'Family' Units and Kin Composition of Families

Consistent social groupings can be challenging to identify in fission–fusion societies. However, for female elephants, 'families' represent one of the most predictable levels of social association. Families are composed of around 2–20 adult females and their immature offspring. We chose to analyse dominance at the level of the family because most social interactions, both competitive and affiliative, occur within family groups, indicating that most of the relevant forces shaping female relationships occur there. We focused on 10 families each in Amboseli and Taragire (20 total families). The Amboseli Elephant Research Project defined families through observations of consistent association patterns over the past 30 years (mean ± SD number of adult females per focal family from Amboseli = 8.2 ± 2.04, $N = 10$). The Tarangire Elephant Project defined families as groups of females that were seen together on more than 70% of sightings (mean ± SD number of adult females per focal family from Tarangire = 4.6 ± 1.70, $N = 10$). Furthermore, families in both populations could be easily recognized because females in the same family associated consistently, moved in a coordinated manner and directed affiliative behaviour almost exclusively towards each other (Moss & Poole 1983).

Elephant families are genetic units as well as social units. Like many social mammals, female elephants are usually matrilocal (females remain with their relatives), and thus families are often composed of close maternal kin. However, many family members are not first-order maternal relatives and a range of kin relationships occur within families (Archie et al., in press). This is because, like all long-lived mammals with female matrilocality, demographic events (births and deaths) that occur over time within groups create multiple distinct clusters of maternal relatives within most families (e.g. Fig. 1a). In Amboseli, the maternal identities of all calves born since 1972 are known. From these we were able to identify 30 mother–offspring and 16 maternal sibling pairs in our focal families (range of known mother–offspring pairs per family = 1–6; range of known maternal sister pairs per family = 0–5). In addition, each of these families had two to five females who were born before 1972. The genetic relationships between these females were unknown, but may include mothers and offspring, maternal siblings, cousins, or more distant kin relationships. In Tarangire, kin relationships were unknown for most of the females in our data set.

Age Estimation

All data were collected on adult female elephants of known or estimated age. In Amboseli, adults were those who had given birth at least once (mean age at first birth = 14.1 years; Moss 2001); in Tarangire, adults were at least 10 years old. Since the inception of the Amboseli Elephant Research Project in 1972, dates of birth (month and year) have been recorded or estimated for all individually recognized elephants. Those born after 1972 were positively known, and dates of birth for individuals born before the study began were estimated using multiple ageing methods, including footprint length, back length, shoulder height, or visual estimates based on head morphology (Laws 1975; Moss 2001).

In Tarangire, the ages of 374 females and infants were initially estimated by C.J.M., which provided a direct comparison of ageing in the two populations (Moss 1990). The ages of all other Tarangire females were subsequently estimated at the beginning of the Tarangire Elephant Project (in 1993) using standard morphological measures (shoulder height, back length, tusk size and head shape). Females over 15 years were placed into 5-year age classes up until 35 years of age, and into 15-year age classes thereafter. Age estimates from body dimensions were later checked against tooth eruption and wear (Laws 1966) for 12 females that had either died or been darted, and all were found to be accurate to within 5 years, with all females under the age of 25 accurate to within 3 years.

Collection of Agonistic Interactions

Elephants range widely and unpredictably; therefore, our behavioural sampling scheme was opportunistic rather than systematic. Each day we searched for elephants, and when we encountered them, we collected data on their association patterns (see Predicting patterns of aggression, below) and social interactions. Social interactions between adult females were recorded in two ways: (1) all-occurrence records during 20-min focal animal samples and (2) ad libitum sampling during observation sessions on family groups (Altmann 1974). In Amboseli, these two types of samples were collected concurrently by two separate observers in the same research vehicle; in Tarangire, these samples were collected during separate time periods. In both studies, focal samples recorded all agonistic social interactions between the focal and any other adult female and only included periods of time when the focal animal was visible. Ad libitum interactions recorded any agonistic interaction that we observed between any two adult females, but were not 'all-occurrence' samples in the sense that some interactions were missed, and hence, these samples were not used to calculate rates of interactions. Results are derived from 478 h and 488 h of sampling in Amboseli and Tarangire, respectively.

Although the data were initially part of two separate studies, the agonistic interactions that we collected encompassed the same behaviours, and outcomes were scored in the same way. Specifically, at both sites we collected the most overt forms of aggression, including charges, chases, pokes and pushes, as well as milder forms of aggression, including displacements and supplants. Displacements and supplants occurred when the aggressor moved directly towards the loser in a line to intercept it, then either remained in the site formerly occupied by the loser (a supplant), or continued moving through the point of intersection while the loser moved away (a displacement). In both cases, the loser often retreated while looking over its shoulder at the approaching individual.

These behaviours were the only agonistic interactions that we used to evaluate dominance rank relationships. We chose these for two reasons: first, they are all measures of competition that relate to the functional significance of dominance in that the loser faced potential injury or loss of resources. Second, it is unknown whether elephants engage in other behaviours that are accurate signals of status, because rank relationships are as yet uncharacterized. In this study, agonistic interactions were deemed 'decided', and were therefore included in the analysis only if the loser (subordinate) physically retreated in response to the action of the aggressor and made no aggressive behaviours in response to the aggressor (Rowell 1974; Drews 1993). In our analyses, we excluded all instances in which there were multiple possible winners in a given agonistic interaction. However, decided agonistic interactions could involve one winner and multiple losers; these were scored as decided dyadic interactions between the winner and each of the losers. Within a dyad, an individual was considered dominant if it won more than 50% of the agonistic interactions against the other dyad member (Jackson & Winnegrad 1988).

Measuring Linearity within Families

Linear dominance hierarchies are ones in which dyadic relationships are asymmetric, and triadic relationships are transitive. Asymmetry occurs when one animal in a dyad consistently wins a disproportionate number of interactions. Transitivity occurs when, for any three individuals within a social group, animal A dominates animal B, B dominates C and A dominates C. We described female rank relationships using two measures: (1) transitivity of relationships across multiple dyads, measured as the number of circular dominance relationships within families and (2) the degree of symmetry within dyadic relationships across two or more agonistic interactions, measured with the 'directional consistency index' (DC index; Noë et al. 1980; van Hooff & Wensing 1987; Isbell & Young 2002). The DC index ranges from 0 to 1 and is calculated as: $(H - L)/(H + L)$, where H is the total number of times that agonistic interactions were seen in the higher-frequency direction and L is the total number of times that agonistic interactions were seen in the lower-frequency direction (e.g. van Hooff & Wensing 1987). A high directional consistency index indicates that, among pairs of females who are observed to interact multiple times, wins are highly asymmetrical.

The degree of linearity is often measured with the Landau index (h) or de Vries's corrected index (h'), both of which range from 0 to 1, where 0 is a completely nonlinear system and 1 is completely linear (Landau 1951; de Vries 1995). However, some researchers have advocated using the DC index and transitivity, instead of h and h', because the former are more reliable indicators of the strength of competition (Isbell & Young 2002; Koenig et al. 2004). We also chose not to use h and h' because, for these indexes, it is not mathematically possible to construct a significantly linear hierarchy ($P < 0.05$) in groups with less than six members (Appleby 1983), and nine of the family groups in our study had five or fewer members. Furthermore, in many species, some pairs of individuals in a group interact at relatively low frequencies so that researchers cannot detect the direction of their relationship without many hours of observation. When this is true, as it is for elephants, both h, and to a lesser extent h', provide inaccurate estimates of linearity, and yield misleadingly low linearity index values (e.g. Rutberg 1986; Isbell & Pruetz 1998; Isbell & Young 2002).

Differentiating between Nepotistic and Age-based Hierarchies

If elephants have age-ordered dominance hierarchies, they cannot also have nepotistic hierarchies because these two models give a different set of predictions for how the females in our study families should be ranked relative to each other (Fig. 1). In nepotistic hierarchies, daughters inherit a rank near their mother and therefore outrank females that are (1) older than themselves, (2) lower ranking than their mother and (3) not first-order relatives of their mother. This pattern of rank inheritance makes an age-ordered hierarchy impossible except in groups composed of a single mother and her adult daughters but no granddaughters, of which there were none in our study. In age-based hierarchies, daughters of even high-ranking mothers attain ranks below their mothers' age peers. For each family in Amboseli, we constructed two predicted hierarchies, one based on a nepotistic model and one based on an age-ordered model, and compared the predicted hierarchies with the observed ones. We did not know kin relationships in Tarangire and so were only able to do this for the Amboseli population.

Predicting Patterns of Aggression

Even if hierarchies were observed to be age-ordered, we might expect to detect some nepotistic bias in patterns of aggression. Using focal sampling data from Amboseli, we tested whether the rate of aggression and proportion of reversals in a given dyad were affected by closeness in maternal relationship. Closeness of maternal relationship was determined by categorizing dyads into one of the following three categories: known mother–daughter pairs ($N = 30$), known maternal sibling pairs ($N = 16$) or other family members ($N = 182$). Rates of aggression were calculated by dividing the total number of agonistic interactions that occurred within a dyad by the total amount of time (in hours) that those two individuals were together in the same group. This period was calculated for each dyad by multiplying the total number of hours that each animal was focal-sampled by the association index for that dyad. Association indexes were measured between October 1999 and July 2003 via scan sampling. Briefly, when a focal family was encountered, we recorded the identity of all adult females in the same group at 10-min intervals. An individual or a group of females was considered to constitute a distinct subgroup when the nearest neighbouring adult female(s) was greater than 100 m away. Association indexes were calculated using the ‘simple ratio’ index (Ginsberg & Young 1992), where the association index is: $N_{AB}/N_A + N_B + N_{AB}$. Here, N_A and N_B are the total number of times either individual (or family) A or B was seen alone and N_{AB} is the total number of times that A and B were seen together. Analyses are in the form of analysis of variance; all statistical tests use two-tailed probabilities (JMP, version 4, SAS Institute Inc., Cary, North Carolina, U.S.A.).

RESULTS

Linear Dominance Hierarchies within Families

There was no evidence that elephants are egalitarian. Instead, rank relationships among female elephants were well resolved, and hierarchies among adult females in the same family appear to be linear (Fig. 2). Intrafamily dyads were highly unidirectional and dominance hierarchies were transitive. In Amboseli, we did not observe any circularities among the 160 intrafamily dyads in which we observed at least one agonistic interaction, excluding two ties. In Tarangire, we observed only two circular triads, excluding one tie, among the 88 intrafamily dyads where we observed at least one agonistic interaction. The total DC index was 0.90 in Amboseli and 0.97 in Tarangire, reflecting highly asymmetric relationships. Hence, the high degree of transitivity and unidirectionality within dyads demonstrate that the outcome (although not the intensity) of all agonistic encounters between individuals familiar to each other will be largely predictable to both observers and elephants.

Dominance Rank Relationships are Age-ordered and Not Nepotistic

Age determined the outcome of nearly all agonistic encounters in both populations. In Amboseli, older adult females won 94.4% of intrafamily agonistic interactions (339 of 363), and in Tarangire, older/larger individuals won 98.2% (328 of 334) of agonistic interactions (see also Lee 1987). We observed only two dyads in Amboseli in which the older and younger individuals won an equal number of interactions, and eight dyads in which a younger animal consistently dominated an older animal (5.0% of 160 dyads; Fig. 2, grey boxes), but for five of these eight dyads, we observed only one interaction. In Tarangire, females appeared to adhere to the age/size hierarchy even more strictly, because only two dyads (2.3% of 88 dyads for which we observed at least one agonistic interaction) were inconsistent with the age hierarchy, and both of these caused rank circularities. The differences between the two populations may result from stochastic sampling effects, because we observed fewer interactions per dyad in Amboseli (average of all dyads = 1.16) than in Tarangire (average of all dyads = 3.28).

Dominance rank relationships were not nepotistic in Amboseli. For each family, we compared the hierarchy that was predicted based on nepotism with the hierarchy ordered by age (Table 2, Fig. 1). The age-ordered hierarchy better described the observed hierarchy in every family. Furthermore, of 30 known mother–offspring pairs, in only two cases did mother and offspring rank adjacently as adults; in one case the daughter was higher ranking, and in the other the mother was higher ranking. Although kin relationships were unknown in Tarangire, the observed linear dominance hierarchies exactly fit our predictions for age-ordered hierarchies, except for the two circularities described above.

Even though elephants do not have nepotistic hierarchies in the sense that daughters inherit a rank close to their mother, they might still show some form of nepotistic bias in their agonistic interactions. In particular, individuals may have lower rates of aggression and a higher proportion of rank reversals with first-order maternal relatives than with other family group members. To test this possibility, we analysed dyads consisting of each focal animal in our data set and each other adult female member of her family. We found no evidence for this sort of nepotism: first-order maternal relatives (mother–daughter pairs or maternal sister pairs) were actually more likely to engage in aggression with each other than were pairs of non-first-order maternal relatives, probably because they spent more time in close proximity (mean ± SE rate of aggression per hour spent in the same

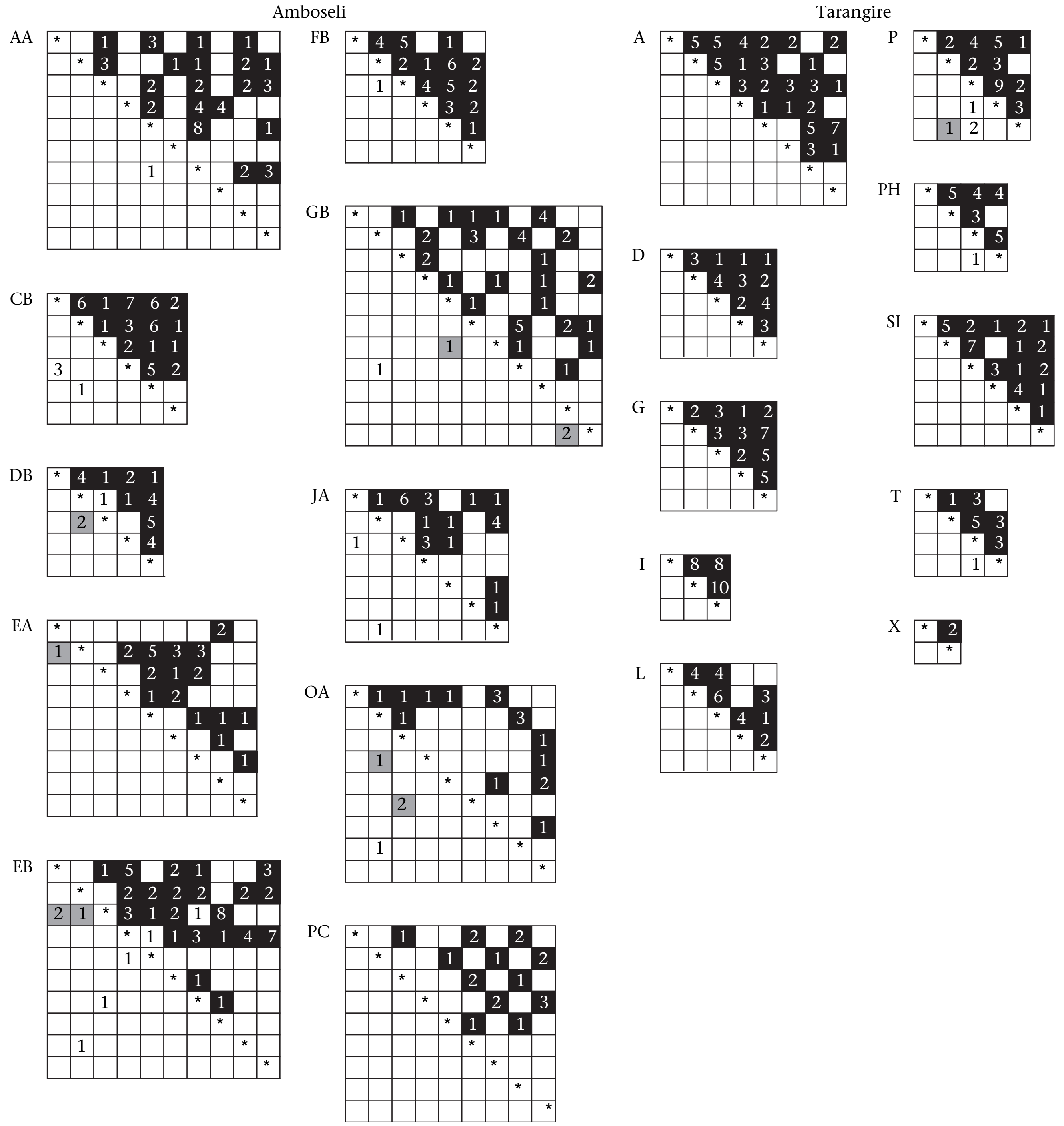

Figure 2. Dominance matrices between adult females within 10 families each in Amboseli and Tarangire. Each matrix is symmetrical, with each row in the matrix representing one individual in the family. At the intersection of each row (the aggressor) and column (the loser), a cell shows the number of agonistic interactions won by the aggressor against the loser. Individuals are ordered by size/age, with the largest/oldest female in each family represented in the top row and far left column of each matrix. Black squares: dyads for which the older/larger female won the majority of agonistic interactions; grey squares: dyads for which the younger female won the majority of agonistic interactions; white squares: dyads for which an equal number or no agonistic interactions were observed. Family identification symbols are shown to the left of each matrix.

group: mother–daughter pairs: 0.14 ± 0.02, $N = 30$; maternal sisters: 0.14 ± 0.03, $N = 16$; non-first-order maternal relatives: 0.05 ± 0.01, $N = 182$; ANOVA: $F_{2,227} = 12.26$, $P < 0.0001$). Furthermore, there was no significant difference in the proportion of reversals among these relationship categories (mean ± SE proportion of reversed interactions: mothers–daughter pairs: 0.09 ± 0.05, $N = 22$; maternal sisters: 0.02 ± 0.08, $N = 10$; non-first-order maternal relatives: 0.09 ± 0.04, $N = 50$; $F_{2,81} = 0.33$, $P = 0.723$).

Table 2. Observed and expected age-based and nepotistic dominance hierarchies within the AA elephant family from Amboseli

Female ID	Birth date	Mother	Observed hierarchy	Expected age-ordered hierarchy	Expected nepotistic hierarchy
Amy	1952	Unknown	1	1	1
Alison	1962	Unknown	2	2	5
Agatha	1968	Unknown	3–4 (tie)	3/4	7
Amelia	1968	Unknown	3–4 (tie)	3/4	9
Audrey	1972	Amy	5	5	2
Astrid	1979	Alison	6	6	6
Amber	1981 (June)	Amy	7	7	3
Anghared	1981 (December)	Amelia	8	8	10
Althea	1982	Agatha	9	9	8
Angelina	1985	Amy	10	10	4

DISCUSSION

Dominance Rank Relationships and Competition within Elephant Families

The socioecological model for the evolution of female social relationships (Wrangham 1980; van Schaik 1989; Isbell 1991; Sterck et al. 1997; Isbell & Young 2002) has become a well-established and sometimes controversial conceptual framework (Isbell & Young 2002; Koenig et al. 2004). While most of the research on this set of socioecological models has focused on primate social systems, these models assume that social behaviour is adaptive and that its predictions should therefore be broadly applicable to a range of group-living species. A key prediction of these models is that species that exploit dispersed, abundant resources will have low within-group competition, and thus dominance rank relationships will be poorly differentiated. In contrast, species that exploit limited, usurpable resources will have high within-group contest competition and strong linear dominance hierarchies (Wrangham 1980; van Schaik 1989; Sterck et al. 1997; Isbell & Young 2002).

We used this framework to investigate dominance rank relationships among wild adult female elephants, and to make inferences about the strength of within-group competition and the function of female relationships. Our results best support the third outcome described in Table 1, that dominance hierarchies among adult female family members are transitive and age-ordered but not nepotistic. We found that dyadic relationships were strongly asymmetric such that older, larger females consistently dominated smaller, younger females. Furthermore, reversals (i.e. dyadic interactions that went against this hierarchy) were uncommon (4–6%), and indeed were less common than those observed in female savanna baboons, *Papio cynocephalus*, which are characterized as having strong, well-resolved, linear dominance relationships (11%, Samuels et al. 1987). In our study, the DC index ranged from 0.90 in Amboseli to 0.97 in Tarangire; these values are more asymmetric than those observed for female Phayre's leaf monkeys, *Trachypithecus phayrei* (Koenig et al. 2004) and wild horses, *Equus scandinavicus* (van Dierendonck et al. 1995), are similar to those observed among captive wolves, *Canis lupus* (van Hooff & Wensing 1987) and stumptail macaques, *Macaca arctoides* (de Waal & Luttrell 1989), but are less extreme than those observed in rhesus macaques, *Macaca mulatta* (de Waal & Luttrell 1989).

We infer from these results that competition does occur among adult female elephants in the same family group, in spite of their heavy reliance on abundant and widely distributed resources. This competition may be because some resources that are critical for elephants are rare or usurpable, including water, mineral resources, rubbing posts or high-quality foods (e.g. *Acacia xanthophloea* bark, palm flowers, balanites seeds; Weir 1972; Dublin 1983; Western & Lindsay 1984; Owens-Smith 1988). If individuals are able to monopolize access to these resources, linear hierarchies should result. Other selective forces that promote cohesion among female elephants (e.g. cooperative defence and cooperative offspring care) may also mean that group sizes are somewhat larger than can be easily supported by the resources available to a group.

Linear, Age/size-ordered Dominance Hierarchies and the Costs of Conflict

The observation that dominance hierarchies within families of female elephants are not nepotistic indicates that individuals probably do not experience direct or indirect selection to assist their kin in attaining rank or resources. Instead, elephant hierarchies are ordered by size and/or age, and this ordering may arise because such linear hierarchies may reduce rates of conflict within the group (Rowell 1974; Wilson 1975; Maynard Smith & Parker 1976; Bernstein 1981). In particular, in species where the risk of injury is high even in mild interactions, we would expect well-defined dominance relationships to arise even if direct conflict over resources is relatively rare (e.g. Crowley 2001). Female elephants are equipped with formidable weapons and continue to grow for several decades after sexual maturity (Laws 1975; Lee & Moss 1995). Furthermore, family members can differ considerably in age and hence size. In Amboseli, the age difference between the youngest and oldest adult female in the same family ranged from 24 to 53 years. Adult females within a family will therefore differ substantially in size and weaponry. Female elephants also have close social bonds, and any given female may spend an extraordinarily large proportion of her time in very close proximity (four body lengths or less) to other individuals (Archie et al., in press), creating potentially dangerous conditions if conflicts occur. Consequently, linear age/size-ordered dominance hierarchies may be selected because they reduce uncertainty about the outcome of social interactions and hence reduce the costs of sociality.

Reduced rates of conflict and injury may also explain the presence of linear dominance hierarchies in other species that are predicted to be egalitarian by socioecological models. Gelada baboons, *Theropithecus gelada*, and many ungulates including mountain goats, *Oreamnos americanus*, Barbary sheep, *Ammotragus lervia*, red deer, *Cervus elaphus*, pronghorn, *Antilocapra americana* and zebras, *Equus zebra zebra*, all exploit abundant and/or widely distributed resources that are difficult to usurp, yet none are egalitarian (Dunbar & Dunbar 1977; Dunbar 1984; Clutton-Brock et al. 1986; Thouless & Guinness 1986; Lloyd & Rasa 1989; Thouless 1990; Fairbanks 1994; van Dierendonck et al. 1995; Fournier & Fiesta-Bianchet 1995; Cassinello & Alados 1996; Ganslosser & Dellert 1997; Linklater 2000; Côté & Festa-Bianchet 2001). In ungulates, dominance hierarchies are based on traits that reflect fighting ability and the potential for inflicting injury on another individual (e.g. age, body size or horn length). In gelada baboons, female dominance rank is partly nepotistic, but individual rank within and among matrilines depends solely on individual aggressiveness (Dunbar 1984). These examples provide strong evidence that local resource abundance and distribution are not the only forces that determine whether linear dominance hierarchies arise (see also Hemelrijk 1999; Chase et al. 2002).

Nepotistic Dominance Hierarchies and Female-bonded Societies

Elephant societies resemble those of female-bonded primates in that adult females associate closely and predictably with maternal kin, and they engage in frequent affiliative interactions, such as contact rubbing or greeting behaviours (Douglas-Hamilton 1972; Laws 1975; Dublin 1983; Lee 1987; Moss 1988; Archie et al., in press). These well-differentiated relationships probably exist not because kin help each other in within-group competition, but instead because individuals benefit from cooperative and mutualistic relationships that promote cooperative defence, offspring care or sharing knowledge about resource distribution (Douglas-Hamilton 1972; Laws 1975; Dublin 1983; Lee 1987; Moss 1988; Foley 2002).

Finally, because hierarchies within elephant families are not nepotistic, we predict that dominance rank is not a predictor of female fitness in this species. This would make elephants quite different from most female-bonded species, including several primates and carnivores, in which rank appears to influence various components of fitness (e.g. Dunbar & Dunbar 1977; Packard et al. 1985; Silk 1987; Bercovitch & Strum 1993; Holekamp et al. 1996; Owens & Owens 1996; Creel & Waser 1997; Pusey et al. 1997). Furthermore, the consequences of living with close kin (rather than unrelated individuals) for female reproductive performance have been measured for only a few mammalian species, but in some cases the effects have been striking and positive (e.g. Pusenius et al. 1998; Dobson et al. 2000; Pope 2000; Pomeroy 2001; but see Dalton 2000). We predict that, in spite of the strong affiliative relationships between female relatives in elephant societies, the presence of female relatives per se will have little effect on female reproductive performance. One goal of our future analyses is to test these predictions.

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