# Hierarchical dominance structure and social organization in African elephants, *Loxodonta africana*

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According to the socioecological framework, transitivity (or linearity) in dominance relationships is related to competition over critical resources. When a population is structured into groups, the intensity of between-versus within-group competition influences the form and function of its social organization. Few studies have compared the type and relative intensity of competition at these two levels. African elephants have well-structured social relations, providing an exemplary system for such a study. We report on dominance hierarchies among free-ranging elephants and evaluate the factors that drive their socioecological structure to lie in a region of the three-dimensional nepotism/despotism/tolerance space rarely observed among social species; namely, where non-nepotistic, transitive dominance hierarchies within groups emerge despite kin-based philopatry and infrequent agonistic interactions over widely distributed resources. We found significant transitivity in dominance hierarchies between groups. Dominance relations among the matriarchs of different social groups were primarily age based, rather than driven by physical or group size, and group matriarch rank influenced the dominance relationships among nonmatriarchal females in the population. Our results suggest that between-group dominance relationships induce tolerance among group members, which in combination with high group relatedness, reduces the benefits of nepotism. We postulate that cognitive abilities and high risk of injury in contests enhance winner and loser effects, facilitating the formation of transitive dominance relationships, despite widely distributed resources over which infrequent competition occurs. The interplay of cognitive abilities, winner and loser effects, resource distribution, and within- and between-group dominance relationships may produce behaviour in other strongly social mammals that differs from that predicted by a superficial application of current socioecological models.

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Agonistic interactions resulting from competition among females serve as a strong organizational feature of social groups (Emlen & Oring 1977; Wrangham 1980). In socioecological models (originally focused on primates but applicable to other taxa), dominance relations are described as varying along three dimensions (Sterck et al. 1997): degree of despotism (egalitarian to despotic), degree of nepotism (individualistic to nepotistic) and degree of

tolerance. In egalitarian societies, agonistic interactions are not necessarily unidirectional and dominance relationships are fuzzy and nontransitive (i.e. contain circular relationships where A dominates B, B dominates C, and C dominates A). In contrast, in despotic societies, transitive (also called linear) dominance hierarchies are clearly established. Dominance hierarchies can be individualistic, where female ranks are independent, or nepotistic, with kin tending to rank close together. Finally, tolerance is typically inversely related to aggression and is a function of the degree to which dominant individuals accept challenges (de Waal 1989). Different combinations of these attributes relate to the three major competitive expressions typically found in social animals: within-group contest

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(WGC), within-group scramble (WGS) and between-group contest (BGC) (van Schaik 1989; Sterck et al. 1997).

In combination with predation pressure and the cost of dispersal (and infanticide for some species), the distribution of critical resources constrains the form of agonistic interactions inducing WGS, WGC or BGC. Species dependent on monopolizable resources (e.g. clumped or patchy) will tend to evolve strict, transitive dominance relationships (characteristics of despotic societies associated with WGC and BGC). In contrast, those reliant on uniformly distributed, nonmonopolizable resources will tend to have poorly defined dominance relationships (characteristics of egalitarian societies associated with WGS). Statistical tests of the degree of transitivity in the dominance relationships among individuals and groups are typically used to assess the dominance structure of a species (van Schaik 1989; Isbell 1991; Sterck et al. 1997; Isbell & Young 2002), although such tests assume that competitive abilities define dominance relationships, simplifying recognized complexity in dominance interactions (Hemelrijk et al. 2005).

The form of transitive hierarchies, when found, also indicates characteristics of the competitive regime impacting a species. Nepotistic hierarchies, in which related individuals support each other in dominance interactions leading to increases in rank, are typical in kin-based philopatric species, where individuals remain in natal groups and receive inclusive fitness benefits from aid to their relatives (Wrangham 1980; van Schaik 1989; Isbell 1991; Sterck et al. 1997; Isbell & Young 2002). Individualistic hierarchies, commonly based on individual size or strength, are more common in species without kin-based group structure (Wrangham 1980; van Schaik 1989; Isbell 1991; Sterck et al. 1997; Isbell & Young 2002).

The complex sociality found among African elephants, entailing multiple hierarchical social levels maintained by fission and fusion processes (Douglas-Hamilton 1972; Moss & Poole 1983; Wittemyer et al. 2005), makes them an interesting nonprimate species for the investigation of the relationship between dominance hierarchy structure and social and ecological factors influencing competition. Female African elephants are philopatric and closely bonded to their relatives, generally remaining in natal groups for life (Moss 1988). Thus, core female social groups are kin based (Archie et al. 2006b). Elephants are generalist herbivores that are relatively nonselective and reliant on widely distributed resources (Laws 1970; Owen-Smith 1988). Seasonal diet switches occur between widely spaced, poor-quality shrubs (dry season) and uniformly distributed grass (wet season; Cerling et al. 2006), although neither of these food sources appear to be monopolizable. Agonistic interactions among elephants, however, do occur in relation to infrequent use of point resources like fruiting trees and water holes (Archie et al. 2006a). Thus, elephants have characteristics pertaining to both egalitarian and despotic social systems.

In a study of how these apparently conflicting characteristics affect dominance relationships, Archie et al. (2006a) found that within-group dominance hierarchies were significantly transitive but not nepotistic. This atypical combination of traits was interpreted as indicating the importance of infrequent contest competition to elephant sociality and that direct or indirect benefits from assisting kin to attain resources were weak or not experienced (Archie et al. 2006a). Transitive female hierarchies lacking the influence of nepotism have been observed in other species (e.g. mantled howlers, *Alouatta palliatta*: Glander 1992; some hanuman langurs, *Presbytis entellus*: Borries 1993). The socioecological framework predicts that such intermediate organizations may occur under a narrow range of conditions where resources lead to contest but benefits derived from dominance are low, although philopatry is not expected under such circumstances (Sterck et al. 1997). Assessment of competition both within and between groups, the dynamics of which are recognized as influential to sociality (van Schaik 1989), offer important insight into the evolution of intermediate characteristics like philopatry without nepotism. Such studies are few (Sterck et al. 1997), and the present study, pertaining to measured levels of between-group competition in the free-ranging Samburu elephant population in northern Kenya, thus provides novel insight into the co-occurrence of social traits not typically thought to occur in mammalian societies.

Three characteristics of elephant dominance relationships lead us to predict that between-group relationships among elephants are egalitarian. First, the resources over which elephants compete are widely distributed, causing elephants to experience predominantly scramble competition with infrequent contests over point resources. While this may drive transitivity in dominance relationships among individuals within closely associated core groups, in order to evoke BGC, these infrequent point resources need to be sufficiently clumped (Isbell 1991) and large (van Schaik 1989), such that monopolization can occur and bestow salient benefits to all group members. These conditions are not obviously met from descriptions of contests by Archie et al. (2006a). Second, transitivity among individuals within groups is not typically associated with transitivity in relations between groups. Group defence of resources requires group cohesion that can cause relationships within groups to be less despotic than what would be predicted by the distribution of resources alone (de Waal 1989; 'resident nepotistic tolerant': van Schaik 1989). Therefore, BGC is typically associated with unexpressed or weak WGC (van Schaik 1989), not strong WGC as found in elephants. Finally, since territoriality is a common manifestation of BGC (Isbell 1991; Sterck et al. 1997), and elephants do not demonstrate territorial behaviour (Douglas-Hamilton 1972; Moss 1988), the general assumption has been that between-group dominance relationships in elephants are probably not well established.

We tested the prediction that between-group dominance relationships are egalitarian by assessing the degree of transitivity in dominance relations among the matriarchs of different social units, recognizing that such an analysis simplifies the true complexity of dominance relationships (Hemelrijk et al. 2005). In addition, we investigated the relationship between a matriarch's rank and the rank of her social group counterparts to understand the role of nepotism in elephant social organization.

We discuss our results and the effect of the interaction of within- and between-group dominance relationships on the social organization of African elephants.

## METHODS

Data were collected on the population inhabiting the Samburu and Buffalo Springs National Reserves in northern Kenya. The elephants using these reserves are largely habituated to the presence of vehicles, enabling easy observation of behaviour, and are individually identified, following well-established methodology (Moss 1996). They have been closely monitored since 1997 (Wittemyer 2001). For a description of the ecology of the study area see Wittemyer (2001).

Fine-scale social delineations in the study population were defined quantitatively using cluster analysis on individually based association data collected over 5 years (Wittemyer et al. 2005). A breeding female and her sexually immature offspring were defined as the base social unit for the analysis, termed tier 1 associates. Four hierarchical social tiers stemming from association behaviour among first-tier units were defined, where multiple first-tier units (mother–calf units) compose second-tier groups (at least two breeding females; 'families'), which coalesce to form third-tier social groups ('bond groups') and finally fourth-tier groups ('clans'; Fig. 1). We defined 'within-group dominance' as dominance relationships among individuals within second-tier groups and 'between-group dominance' as dominance relationships among individuals (matriarchs) from different second-tier groups. Also, our second-tier groups appear to be equivalent to the core social groups analysed for dominance relationships by Archie et al. (2006a). Comparisons of rank and group sizes were designated using the quantitative definitions of second-tier social groups (Wittemyer et al. 2005). Dominance relationships within second-tier groups were clearly transitive (i.e. no circular relationships), supporting the conclusions of Archie et al. (2006a). The most dominant individual in either second- or third-tier groups was defined as that group's matriarch. This definition of matriarch was used in analysis of the effect of both second- and third-tier matriarchs' rank on the rank of other group members in our assessment of nepotistic effects on rank order (see Statistical Analysis).

Weight measurements of elephants are not possible in the wild. Rather, we used measurements of the shoulder height of individuals to compare the sizes of individuals. Shoulder heights were measured using an Impulse 200 Laser Range Finder, which is accurate up to 3 cm within 50 m. Measurements from which shoulder heights were calculated were generally made within 20 m of each elephant and included the angles from the observer to where the elephant's foot met the ground and to the shoulder blade, as well as the distance from the observer to the elephant. All individuals were measured in the same manner. The average $\pm$ SD difference in shoulder height measurements, calculated from repeated measurements (minimum $= 3$) of the same individual ($N = 125$), was $2.9 \pm 1.1$ mm.

Age estimates of elephants were conducted using well-established techniques developed on known-aged individuals (Moss 1996, 2001). The accuracy of ageing has been established as $\pm 3$ years with 80% confidence in studies that compared estimates to ages derived from molar progression (Laws 1966; Jachmann 1985), assessed during immobilization operations (Rasmussen et al. 2005). This level of accuracy, together with evidence that young elephants can be aged more accurately with greater confidence, prompted us to bin the elephants in our study into 5-year age classes.

### Dominance Analysis

Agonistic interaction data were collected between July 2001 and December 2003 within the study area using ad libitum sampling (Altmann 1974), where the initiator and recipient of agonistic interactions were recorded opportunistically. Only overt agonistic interactions between elephants were included. Two types of overt interactions were observed, physical and nonphysical. We defined physical interactions as chases (A runs in the direction of B, B then runs away from A), pokes (A contacts B with a tusk, B then moves away from A) and pushes (A contacts B using a body part other than a tusk, B then moves away from A). We defined nonphysical interactions
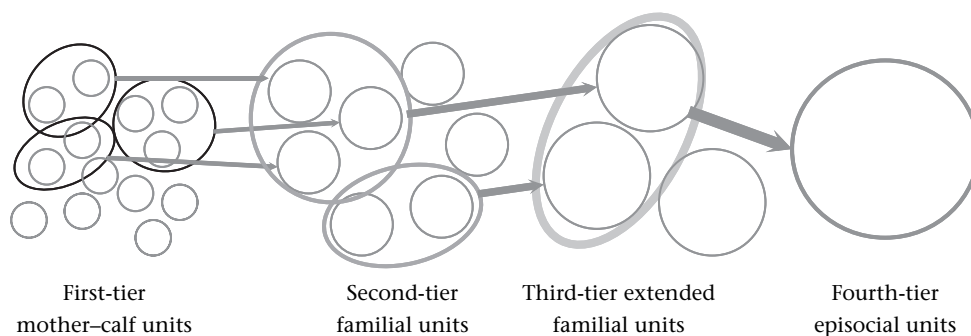


First-tier
mother–calf units

Second-tier
familial units

Third-tier extended
familial units

Fourth-tier
episocial units

**Figure 1.** The hierarchical social structure of elephants is characterized by two or more regularly associating mother–calf units (tier 1) coalescing into 'familial' units (tier 2), which, in turn, coalesce with other familial units into 'extended familial units' (tier 3, or bond groups); several of these units again coalesce to create 'episocial units' (tier 4, or clans; Wittemyer et al. 2005).

as supplants (A moves without running directly towards B, typically with ears flared, B then moves away from A). The role of each individual during agonistic interactions was clear because the individual defined as the loser of the interaction typically moved away while looking at the winner over its shoulder. Rank relationships that were not obvious, such as occasionally occurred when two individuals faced off and both moved off in opposite directions, were noted but not included in this analysis. The context of agonistic interactions was recorded when possible (283 of 419 interactions). Agonistic interactions occurred in relation to point resources (e.g. water holes, fruiting trees, shade) as well as for social reasons, defined as encounters between individuals moving together in the same aggregation but in the absence of a contested point resource.

We focused on agonistic interactions among breeding females in different second-tier social units in an attempt to understand between-group dominance relationships. Low agonistic interaction rates have been found among elephants within the same second-tier family group (Lee 1987; Archie et al. 2006a), where individuals spend over 80% of their time in close association. In the Amboseli ecosystem, an ecologically similar area to Samburu, Archie et al. (2006a) calculated that such interactions occurred an average ± SE of 0.14 ± 0.02 times per hour in mother−calf pairs and 0.05 ± 0.01 times per hour in non-first-order pairs. Both Amboseli and Samburu receive similar levels of rainfall (∼350 mm) during biannual rainy seasons and are characterized by similar vegetative communities, predominantly dominated by acacia (*Acacia* spp.) scrub bush. In relation to the hierarchical fission−fusion social organization of elephants, contacts between individuals from different social groups occur at significantly lower rates than those within social groups (Wittemyer et al. 2005). Thus, nonfamilial agonistic interactions are rare, and the numbers of agonistic interactions observed within second-tier groups are greater than those between groups. Individuals not observed in at least two between-group interactions were excluded from this analysis. Matriarch females are more commonly observed in between-group agonistic interactions since they tend to lead moving groups and may have a predisposition to assert their rank. As a result, the total data set consisted of 73 breeding females observed in 419 agonistic interactions across second-tier groups. Each individual in this data set interacted with an average ± SE of 3.8 ± 0.42 individuals outside her second-tier unit. Including interactions within and between second-tier groups among the 73 individuals, each individual was observed, on average, in 9.6 ± 0.72 agonistic interactions.

We conducted two analyses, the first on a matrix containing a subsample of the most frequently observed 20 matriarchs of second-tier groups and the second on a matrix containing the complete set of 73 breeding females (both matriarchs and nonmatriarchs). For pairs with ambiguous (two-way) dominance relations, where A sometimes beat B and vice versa, we assigned a dominance probability of 0.5 for both individuals. This occurred in less than 3% of known dyads. For pairs where the winner or loser was consistent across observations or only a single observation occurred (one-way), the dominance probability of the winner was 1 and that of the loser was 0. The first matrix contained our best data set of 20 second-tier group matriarchs in which 37% of dyads were known (Table 1). The second matrix was composed of 73 females (representing 39 second-tier groups) that were observed interacting with at least two females outside their second-tier group, in which 13% of dyads were known (not shown).

Observations were used to formulate the 'most likely rank order' among the study elephants using methodology specifically developed to resolve dominance hierarchies in systems with multiple unknown relationships (Wittemyer & Getz 2006). This method minimizes the number and strength of inconsistent dominance relationship following de Vries's (1998) inconsistencies and sum of inconsistencies (I&SI) method, where inconsistent dyads are defined as a lower-ranking individual that dominates a higher-ranking individual, and the strength of an inconsistent dyad is its element's distance from the matrix diagonal. The solution of the I&SI method is achieved by switching the relative positions of individuals in the dominance order until the numbers of I&SI below the matrix diagonal are minimized (de Vries 1998). An interpolated value determined from the difference in relative ranks of dyad members is calculated for unknown relationships (i.e. the matrix element $a_{ij}$, where no interactions were observed between $i$ and $j$, is assigned):

$$\hat{a}_{ij} = 0.5 - (i-j)/2n,$$

where $i$ and $j$ are the rankings after completion of de Vries's (1998) I&SI method and $n$ is the number of individuals in the dominance matrix. Interpolated values (proportional entries in Table 1) are incorporated into a dominance strength metric, derived from subtracting the sum of wins from the sum of losses for each individual, and then used to solve the relative ranks of individuals with unknown relationships (Wittemyer & Getz 2006). This dominance strength metric, modelled off the calculation of David's (1987) Score in that unknown relationships are weighted by the relative difference in ranks of the opponents, can be used in parametric statistical analyses.

Statistical significance of linearity for the dominance matrices was tested using the randomization method developed by de Vries (1995), which is based on Landau's (1951) linearity index $h$:

$$h = \frac{12}{N^3 - N} \sum_{i=1}^{N} [V_i - (n-1)/2]^2,$$

where $N$ is the number of individuals in the matrix and $V_i$ is the sum of row $i$. This method is designed to deal with data sets containing unknown relationships (de Vries 1995). In this method, Landau's $h$ is calculated after all unknown relationships in the matrix are randomly assigned 1 or 0, such that dyad elements are the opposite value. This is then compared with a calculation of Landau's $h$ for a matrix in which all dyads are randomized. The number of times that the completely randomized matrix $h$ is greater than the observed matrix $h$ is summed across 10 000 permutations and divided by the number of

**Table 1.** Dominance matrices used to resolve between-group dominance rank strengths of female African elephants, based on the observed number of wins in agonistic interactions ($N = 103$) and on derived individual dominance strength metrics from categorical interaction data

| Rank | ID | M52 | M2 | M33 | R27 | R17 | M8 | M3 | M24 | M31 | R10 | R22 | S30 | R37 | M45 | M63 | M65 | R1 | M73 | R25 | M30 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Number of wins*** | | | | | | | | | | | | | | | | | | | | | |
| 1 | M52 | — | | | | 2 | | | 1 | | 1 | 1 | 6 | 2 | 1 | | | 1 | | 2 | |
| 2 | M2 | | — | **1** | | | 5 | 4 | | 1 | | 1 | 1 | | 2 | | | | 1 | | |
| 3 | M33 | | **2** | — | | | 1 | 2 | | 1 | | 1 | | | 1 | | | | | 1 | 1 |
| 4 | R27 | | | | — | 1 | | | | | | 1 | | 2 | | | 1 | 1 | | 1 | |
| 5 | R17 | 0 | | | 0 | — | | | 1 | 1 | | | | | 2 | | | 1 | | | |
| 6 | M8 | | 0 | 0 | | | — | **1** | | 1 | | | | | | 1 | | | | | 3 |
| 7 | M3 | | 0 | 0 | | | **1** | — | | | | | | 2 | | | | | | | |
| 8 | M24 | 0 | | | | 0 | | | — | 1 | | 1 | | 0 | 1 | | | | | | |
| 9 | M31 | | 0 | 0 | | 0 | 0 | | 0 | — | 1 | 2 | | | 1 | | | | 1 | | 1 |
| 10 | R10 | 0 | | | | | | | | 0 | — | | 1 | | | | | 1 | | 1 | |
| 11 | R22 | 0 | 0 | 0 | 0 | | | | 0 | 0 | | — | **1** | 1 | 1 | | 1 | | 1 | 1 | |
| 12 | S30 | 0 | 0 | | | | | | | | 0 | **1** | — | | | 1 | | | | 1 | |
| 13 | R37 | 0 | | | 0 | | | 0 | 1 | | | 0 | | — | 1 | 0 | | 1 | | | |
| 14 | M45 | 0 | 0 | 0 | | 0 | | | 0 | 0 | | 0 | | 0 | — | 1 | | | 1 | | 1 |
| 15 | M63 | | | | | | 0 | | | | | | 0 | 1 | 0 | — | | 1 | | 2 | 1 |
| 16 | M65 | | | | 0 | | | | | | | 0 | | | | | — | | | 4 | 1 |
| 17 | R1 | 0 | | | 0 | 0 | | | | | 0 | | | 0 | | 0 | | — | | | 2 |
| 18 | M73 | | 0 | | | | | | | 0 | | 0 | | | 0 | | | | — | | |
| 19 | R25 | 0 | | 0 | 0 | | | | | | 0 | 0 | 0 | | | 0 | 0 | | | — | |
| 20 | M30 | | | 0 | | | 0 | | | 0 | | | | | 0 | 0 | 0 | 0 | | | — |
| **Dominance strength metric†** | | | | | | | | | | | | | | | | | | | | | |
| 1 | M52 | — | 0.52 | 0.55 | 0.57 | 1 | 0.62 | 0.64 | 1 | 0.69 | 1 | 1 | 1 | 1 | 1 | 0.83 | 0.86 | 1 | 0.90 | 1 | 0.95 |
| 2 | M2 | 0.48 | — | **0.5** | 0.55 | 0.57 | 1 | 1 | 0.64 | 1 | 0.69 | 1 | 1 | 0.76 | 1 | 0.81 | 0.83 | 0.86 | 1 | 0.90 | 0.93 |
| 3 | M33 | 0.45 | **0.5** | — | 0.52 | 0.55 | 1 | 1 | 0.62 | 1 | 0.67 | 1 | 0.71 | 0.74 | 1 | 0.79 | 0.81 | 0.83 | 0.86 | 1 | 1 |
| 4 | R27 | 0.43 | 0.45 | 0.48 | — | 1 | 0.55 | 0.57 | 0.60 | 0.62 | 0.64 | 1 | 0.69 | 1 | 0.74 | 0.76 | 1 | 1 | 0.83 | 1 | 0.88 |
| 5 | R17 | 0 | 0.43 | 0.45 | 0 | — | 0.52 | 0.55 | 1 | 1 | 0.62 | 0.64 | 0.67 | 0.69 | 1 | 0.74 | 0.76 | 1 | 0.81 | 0.83 | 0.86 |
| 6 | M8 | 0.38 | 0 | 0 | 0.45 | 0.48 | — | **0.5** | 0.55 | 1 | 0.60 | 0.62 | 0.64 | 0.67 | 0.69 | 1 | 0.74 | 0.76 | 0.79 | 0.81 | 1 |
| 7 | M3 | 0.36 | 0 | 0 | 0.43 | 0.45 | **0.5** | — | 0.52 | 0.55 | 0.57 | 0.60 | 0.62 | 1 | 0.67 | 0.69 | 0.71 | 0.74 | 0.76 | 0.79 | 0.81 |
| 8 | M24 | 0 | 0.36 | 0.38 | 0.40 | 0 | 0.45 | 0.48 | — | 1 | 0.55 | 1 | 0.60 | 0 | 1 | 0.67 | 0.69 | 0.71 | 0.74 | 0.76 | 0.79 |
| 9 | M31 | 0.31 | 0 | 0 | 0.38 | 0 | 0 | 0.45 | 0 | — | 1 | 1 | 0.57 | 0.60 | 1 | 0.64 | 0.67 | 0.69 | 1 | 0.74 | 1 |
| 10 | R10 | 0 | 0.31 | 0.33 | 0.36 | 0.38 | 0.40 | 0.43 | 0.45 | 0 | — | 0.52 | 1 | 0.57 | 0.60 | 0.62 | 0.64 | 1 | 0.69 | 1 | 0.74 |
| 11 | R22 | 0 | 0 | 0 | 0 | 0.36 | 0.38 | 0.40 | 0 | 0 | 0.48 | — | **0.5** | 1 | 1 | 0.60 | 1 | 0.64 | 1 | 1 | 0.71 |
| 12 | S30 | 0 | 0 | 0.29 | 0.31 | 0.33 | 0.36 | 0.38 | 0.40 | 0.43 | 0 | **0.5** | — | 0.52 | 0.55 | 1 | 0.60 | 0.62 | 0.64 | 1 | 0.69 |
| 13 | R37 | 0 | 0.24 | 0.26 | 0 | 0.31 | 0.33 | 0 | 1 | 0.40 | 0.43 | 0 | 0.48 | — | 1 | 0 | 0.57 | 1 | 0.62 | 0.64 | 0.67 |
| 14 | M45 | 0 | 0 | 0 | 0.26 | 0 | 0.31 | 0.33 | 0 | 0 | 0.40 | 0 | 0.45 | 0 | — | 1 | 0.55 | 0.57 | 1 | 0.62 | 1 |
| 15 | M63 | 0.17 | 0.19 | 0.21 | 0.24 | 0.26 | 0 | 0.31 | 0.33 | 0.36 | 0.38 | 0.40 | 0 | 1 | 0 | — | 0.52 | 1 | 0.57 | 1 | 1 |
| 16 | M65 | 0.14 | 0.17 | 0.19 | 0 | 0.24 | 0.26 | 0.29 | 0.31 | 0.33 | 0.36 | 0 | 0.40 | 0.43 | 0.45 | 0.48 | — | 0.52 | 0.55 | 1 | 1 |
| 17 | R1 | 0 | 0.14 | 0.17 | 0 | 0 | 0.24 | 0.26 | 0.29 | 0.31 | 0 | 0.36 | 0.38 | 0 | 0.43 | 0 | 0.48 | — | 0.48 | 0.55 | 1 |
| 18 | M73 | 0.10 | 0 | 0.14 | 0.17 | 0.19 | 0.21 | 0.24 | 0.26 | 0 | 0.31 | 0 | 0.36 | 0.38 | 0 | 0.43 | 0.45 | 0.48 | — | 0.52 | 0.55 |
| 19 | R25 | 0 | 0.10 | 0 | 0 | 0.17 | 0.19 | 0.21 | 0.24 | 0.26 | 0 | 0 | 0 | 0.36 | 0.38 | 0 | 0 | 0.45 | 0.48 | — | 0.52 |
| 20 | M30 | 0.05 | 0.07 | 0 | 0.12 | 0.14 | 0 | 0.19 | 0.21 | 0 | 0.26 | 0.29 | 0.31 | 0.33 | 0 | 0 | 0 | 0 | 0.45 | 0.48 | — |

Individual matriarchs are identified by letter–number combination and by rank, although rank was an outcome of (not input into) the analysis.

*Cell values in bold denote unresolved dyads, where both individuals won and lost against each other.

†Cell values: 0 = loss; 1 = win; 0.5 = unresolved dyads (in bold); all other proportions = interpolated values for unknown relationships (see Methods).

permutations to get a $P$ value (de Vries 1995). As a result of this permutation test where matrix elements below the diagonal may be randomly assigned a value of 1, nonlinearity (i.e. circularity) in randomized matrices increases with the number of unknown relationships. This causes estimated Landau's $h$ values to be low.

Additional metrics describing the linearity (i.e. the extent of transitivity) of the dominance relationships were calculated including the number of one-way relationships (winner always wins and loser always loses) and two-way relationships (both dyads members were observed winning at least once). This information can be used to calculate the degree of symmetry in dyadic agonistic interactions (with more than a single agonistic interaction observed) using the directional consistency (DC) index (Noë et al. 1980; van Hooff & Wensing 1987). The number of times that interactions occur in the higher-frequency direction ($H$) is subtracted from the number of times that agonistic interactions occur in the lower-frequency direction ($L$) and then divided by the total number of interactions: $DC = (H - L)/(H + L)$. The DC index is scaled between 1 and 0, where a high DC index, approaching 1, indicates a high degree of consistency in the directionality of dyadic interactions (i.e. winners consistently win) and a low DC index, approaching 0, indicates little consistency across dyadic interactions.

## Statistical Analysis

Statistical analyses were conducted on rank strengths, calculated as described in Wittemyer & Getz (2006). Initial investigation into dominance relationships between groups was conducted by running linear regressions between second-tier matriarch dominance strength as the response variable, determined from analysis of our matriarch dominance matrix (Table 1), and independent variables of the matriarch's age class, shoulder height and second-tier unit group size. Generalized linear models (GLM), incorporating significant variables from linear models, were run to compare the combined effects of independent variables. Using our matrix containing 73 females, we assessed nepotistic impacts on the dominance strengths of nonmatriarchs by incorporating the matriarch rank for each nonmatriarchal female's social group in a GLM. Because of the hierarchical social structure found in this species, independent variables included the dominance strength from the matriarchs of second- and third-tier units, second- and third-tier social unit group sizes, and individual-specific characteristics of age class and shoulder height. We conducted stepwise elimination of nonsignificant variables and compared the full model to the reduced model, which contained only significant variables using the $F$ statistic, as calculated in the model comparison function of S-PLUS (Venables & Ripley 1999). Model residuals were assessed for homoscedasticity. Because dominance strengths were scaled between 0 and 1, we used arcsine transformation to normalize strength metrics in all analyses (Zar 1999). All statistical analyses were conducted using S-PLUS 6.0.

## RESULTS

Dominance relationships among matriarchs in the Samburu elephant population were well resolved and significantly linear (i.e. had more transitive relationships than expected at random; average $h = 0.2428$, $P = 0.030$, as calculated using de Vries's 1995 randomization test; Table 2). The best rank order among the study population's 20 most frequently observed matriarchs, in which 37% of dyads were resolved, contained two inconsistencies (see Methods). Of the 71 known relationships, three dyads were found with two-way relationships (i.e. both dyad members won interactions). The DC index for matriarchs (0.882) also showed that the majority of relationships were transitive. Analysis of an expanded data set, containing 73 individuals with 13% of dyads known, showed stronger transitivity (average $h = 0.050$, $P < 0.001$, DC index $= 0.905$).

Dominance strengths of matriarchs were significantly correlated with the matriarch's age class (linear regression: $R^2 = 0.587$, $P < 0.001$; Fig. 2a), shoulder height ($R^2 = 0.463$, $P = 0.0026$; Fig. 2b) and group size of the matriarch's second-tier unit ($R^2 = 0.257$, $P = 0.0224$; Fig. 2c). The relation between each matriarch's dominance strength and the size of her third-tier group was nonsignificant ($R^2 = 0.176$, $P = 0.0659$). Stepwise elimination in a GLM, in which the response variable was the dominance strength of the matriarch and the independent variables were age class, shoulder height and second-tier group size, showed that neither group size nor shoulder height added significant explanatory power to the model of matriarch dominance strength (Table 3). A reduced model containing only matriarch age was not significantly different from the full model (Table 4).

To determine the effect of matriarch dominance strength on that of nonmatriarchal females, we compared the dominance strength of nonmatriarchal females to their age class, shoulder height, second- and third-tier group

**Table 2.** Analysis of transitivity (or linearity) in between-group dominance hierarchies of female African elephants, based on interactions among all females and among a subset of second-tier matriarchs

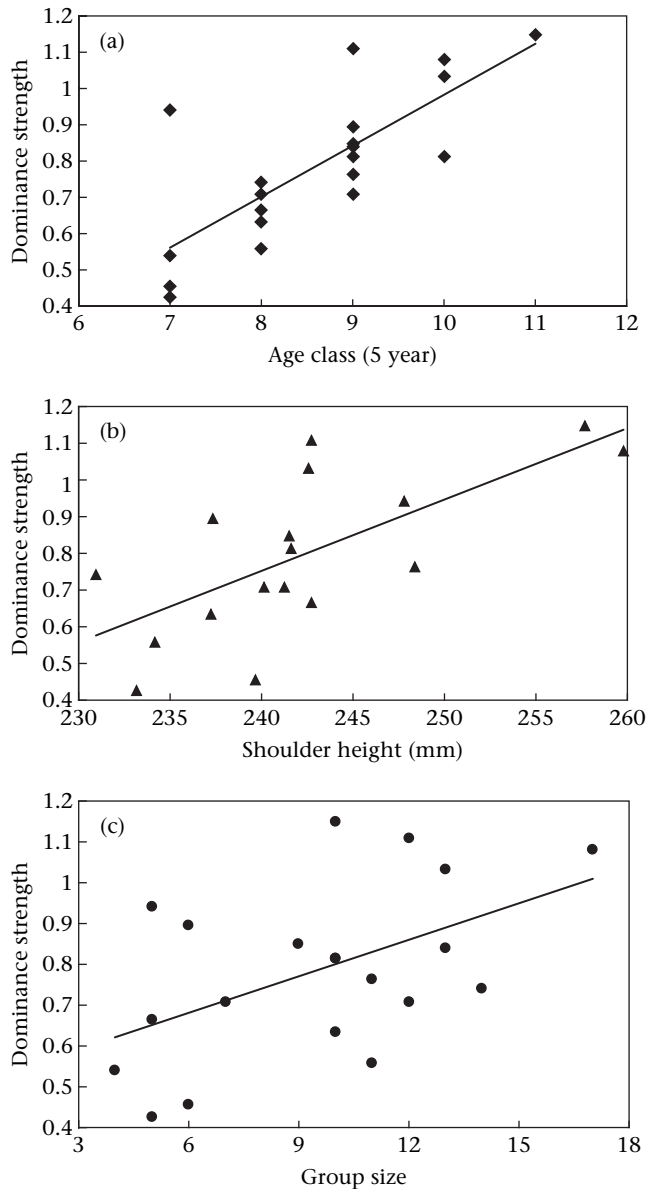| | All females ($N=73$) | Second-tier matriarchs ($N=20$) |
|---|---|---|
| Number of interactions | 419 | 103 |
| Observed linearity index ($h'$) | 0.050 | 0.242 |
| Expected linearity index ($h'$) | 0.024 | 0.146 |
| $P$ | >0.001 | 0.030 |
| DC index | 0.905 | 0.882 |
| Number (%) of known relationships | 279 (11%) | 71 (37%) |
| Number of one-way relationships | 272 | 68 |
| Number of two-way relationships | 7 | 3 |
| Number (%) of relationships against rank order | 41 (1%) | 2 (3%) |

**Figure 2.** Correlations between matriarch rank ($N = 20$ second-tier social units) and (a) matriarch age class (partitioned into 5-year classes), (b) matriarch shoulder height (measured using a laser range finder) and (c) second-tier group size.

sizes, and the dominance strength of their second- and third-tier unit's matriarchs. Dominance strengths of non-matriarchal females were correlated with the dominance strength of their second-tier group's matriarch (linear regression: $R^2 = 0.1204$, $P = 0.0517$) and that of their third-tier group's matriarch ($R^2 = 0.0925$, $P = 0.0398$). Most matriarchs were relatively high ranking, particularly at the third-tier group level, so more data were available for higher-ranked matriarchs than lower-ranked ones, causing residuals to be skewed in simple linear regressions (see Fig. 3). A multivariate GLM was used to determine the effect of matriarch dominance strength on dominance strength of nonmatriarchal females while controlling for other covariates. Age class and shoulder height were

**Table 3.** Results from generalized linear model analyses examining dominance relationships among female African elephants, based on interactions among all females and among a subset of second-tier matriarchs

|  | All females ($N=73$) | | Second-tier matriarchs ($N=20$) | |
| --- | --- | --- | --- | --- |
|  | $t$ | $P$ | $t$ | $P$ |
| **Full model** |  |  |  |  |
| Age | 4.94 | <**0.01** | 2.16 | <**0.05** |
| Height | 2.45 | <**0.05** | 1.60 | >0.05 |
| Second-tier matriarch rank | 0.41 | >0.05 |  |  |
| Second-tier group size | −0.59 | >0.05 | 0.14 | >0.05 |
| Third-tier matriarch rank | 0.73 | >0.05 |  |  |
| Third-tier group size | −2.35 | <**0.05** |  |  |
| **Reduced model** |  |  |  |  |
| Age | 5.85 | <**0.001** | 5.06 | **0.001** |
| Height | 2.74 | <**0.01** |  |  |
| Third-tier matriarch rank | 2.10 | <**0.05** |  |  |

Individual rank strength was the dependent variable; covariates for each model are listed above. Significant values are shown in bold.

significant, but stepwise elimination showed that both second- and third-tier group size did not add significant explanatory power to the total model. Dominance strength of second-tier unit matriarchs did not offer significant additional explanatory power to the model, but that of third-tier group matriarchs did (Table 3). The reduced model was not significantly different from the full model (Table 4).

## DISCUSSION

Our results show that between-group dominance structure, analysed using interactions among social group matriarchs, is not egalitarian but significantly transitive. Well-resolved dominance relationships were also found across a large sample of the population's mature females. Thus, interference competition does occur between elephant groups despite the generally widely distributed resources relied upon by individuals in this species. Values for matriarch dominance strength were significantly correlated with matriarch age class, size and second-tier group size. All these factors were partially correlated with each other, so we ran a GLM in which social group matriarch was the dependent variable. Only matriarch age class was significant, indicating that shoulder height and size of second-tier groups did not provide additional information regarding between-group dominance relationships among

**Table 4.** Comparison of the full and reduced generalized linear models from Table 3

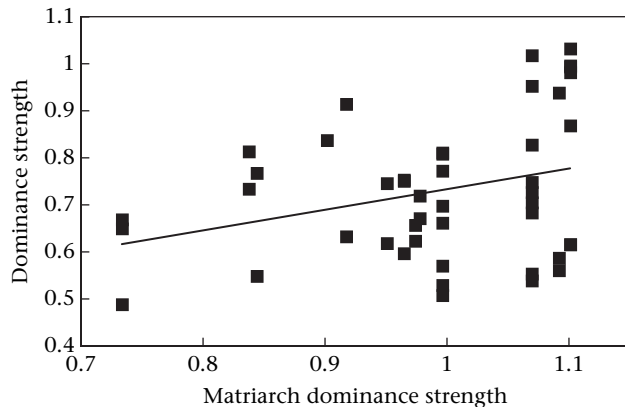|  | Deviance | $F$ | $P$ |
| --- | --- | --- | --- |
| All females | 0.092 | 1.309 | 0.288 |
| 20 matriarchs | −0.085 | −0.852 | 0.538 |

**Figure 3.** Correlation between the dominance strength of nonmatriarchal females and the dominance strength of their third-tier (bond group) matriarch.

matriarchs. Elephants have well-defined social networks (Wittemyer et al. 2005), and the age of matriarchs reflects the degree to which they are able to recognize vocalizations of other individuals (McComb et al. 2000). Thus, long-term social relations may be the foundation of dominance relations, and previously formed dominance relations may have long-term ramifications in terms of access to limited resources. These results suggest an extended winner–loser effect (Chase et al. 1994; Hsu & Wolf 1999; Rutte et al. 2006), which may only be possible in species with enhanced cognitive abilities (Crowley 2001; Chase et al. 2002).

Although within-group (Archie et al. 2006a) and between-group (this study) dominance hierarchies of elephants do not show nepotistic structuring typically found in primate groups (Hinde 1983), where kin are clustered together (van Schaik 1989), a matriarch's rank appears to influence the ranks of her group members in a less overt manner. The rank of third-tier matriarchs significantly affected dominance strengths of nonmatriarchal females regardless of the nonmatriarchal female's age or height. In contrast, a GLM including the covariates of age and height, showed that the rank of second-tier matriarchs was not significant (GLM: $t = 1.8177$, $P = 0.0827$), but the sample sizes differed in these models ($N = 37$ in the former versus 26 in the latter). Thus, the rank of second-tier matriarchs may have been significant if the population had been completely sampled. Elephants have been observed to defend second- and third-tier group members in dominance interactions in the Samburu population (G. Wittemyer, personal observation), and similar social defence has been observed among family (tier 2), bond (tier 3) and clan (tier 4) group members in a closely studied population in Tarangire National Park, Tanzania (Foley 2002).

We did not calculate rates of between-group agonistic interactions, primarily because they occur so rarely (as a function of infrequent between-group associations; Lee 1987). As a result, dominance matrices were sparse in relation to the multiple unknown relationships (Fig. 1). Average linearity indices ($h$) for both matrices were low,

although significant, as a function of the number of unknown dyads in randomization permutations (de Vries 1995). Data sparseness can cause error in rank assignment (Wittemyer & Getz 2006), although less than 3% of known relationships were inconsistent with a transitive dominance hierarchy. Further support of our results comes from other studies; data on between-group interactions collected on the Tarangire elephant population were clearly transitive, and nepotism was believed to affect dominance structure (Foley 2002).

## Transitivity Within and Between Groups Despite Infrequent Contest Competition

Low frequency of contests with dependence on widely dispersed resources, lack of territorial defence and conjecture based on the socioecological framework regarding the relationships between BGC and WGC led us to the prediction that between-group dominance relationships among elephants would be egalitarian. However, we found significant levels of transitivity in dominance relationships between groups. Where did our predictions fail, and why do elephants have transitive dominance hierarchies between groups?

The context of the observed agonistic interactions can offer insight into the factors driving the formation of transitive dominance hierarchies. Elephants rely on spatially and temporally clustered resources, such as tree bark, water points and seeds (Douglas-Hamilton 1972; Western & Lindsay 1984; Owen-Smith 1988; Foley 2002). In this study, contest interactions occurred over point resources (water holes, felled trees, shade, Duom palm fruit and *A. tortilis* seed pods) and in relation to social interaction (i.e. no resource was being contested) in almost equal proportions (47% for point resources and 53% for social). During the dry season, when resources were more constrained and localized, agonistic interactions occurred more frequently during conflicts over point resources (63%) than during social contexts (37%), but during the wet season, the opposite trend was observed (35% point resources and 65% social). Depending on the resource, contests may not cause exclusion but simply delay access of subordinates (i.e. for resources like water or shade). Contests occurring in low/no-gain situations may reinforce dominance relationships via winner and loser effects (Chase et al. 1994; Hsu & Wolf 1999), potentially curtailing escalation of later contests over beneficial resources.

In addition to elephants, other large ungulates that rely on widely distributed food resources, including cape buffalo, *Syncerus caffer* (Prins 1989), mountain goats, *Oreamnos americanus* (Fournier & Festabianchet 1995), pronghorns, *Antilocarpa americanus* (Dennehy 2001) red deer, *Cervus elaphus* (Thouless 1990), reindeer, *Rangifer tarandus* (Holand et al. 2004), and zebra, *Equus zebra zebra* (Lloyd & Rasa 1989), maintain transitive dominance hierarchies. Like elephants, other large ungulates are generally well armed, and escalated contest interactions are potentially life threatening (Rowell 1974). As such, the substantial injury risk associated with even relatively infrequent

dominance interactions may strongly shape social dynamics in these species, thereby resulting in formation of a transitive dominance hierarchy in spite of widely distributed resources. Cognitive ability, with enhanced social memory of previous agonistic interactions and their costs (winner and loser effects), may further act to extenuate transitivity in dominance relationships (Crowley 2001). Therefore, the perceived and actual costs of contest interactions may lead to a greater degree of transitivity in dominance relationships than expected by the frequency or potential benefits offered through excluding others.

## Between-group Contests, Philopatry, Kin-based Gregariousness and Non-nepotistic Dominance Relationships

Archie et al. (2006a) concluded that the non-nepotistic, transitive dominance relationships among individuals in core groups of elephants indicate that direct or indirect benefits from assisting kin to attain resources are either weak or not experienced by elephants. Our results offer an alternative explanation for the lack of nepotistic expression in within-group dominance hierarchies. Elephants maintain a kin-based, fission–fusion society where despotic behaviour among individuals can be avoided through group fissions and where relatedness between individuals probably dilutes the benefits of within-group nepotism. BGC, however, is a salient force shaping elephant sociality, as demonstrated by transitivity in between-group dominance relationships. According to the socioecological hypothesis, tolerance among individuals in social groups is often necessary to maintain group cohesion (de Waal 1989; Sterck et al. 1997). Thus, in addition to social benefits of group cohesion that are probably facilitated by relatedness, the effect of BGC may enhance tolerance among group members and suppress nepotism. Although nepotistic dominance hierarchies in the classic sense (e.g. Figure 2 in van Schaik 1989) were not found, the rank of second- and third-tier matriarchs did weakly impact the ranks of nonmatriarchal females in relation to other individuals outside their natal groups. Our findings indicate that elephant sociality acts as an extreme form of 'resident nepotistic tolerant' social organization where the expression of true nepotistic hierarchies is suppressed in part because of BGC (Sterck et al. 1997; van Schaik 1989).

The socioecological framework suggests that increased tolerance will typically be a function of advantages derived from group size in excluding other groups. Observations of BGC for seeding/fruiting tree patches (*A. tortilis* and *Hyphaene coriacea*) and of WGS while feeding in such patches support this prediction. In contrast to these predictions, however, group size did not offer significant explanatory power in addition to individual characteristics in our multiple regression models of between-group rank relationships. Among elephants, group size may not be the best metric to assess the effects of group structure on between-group dominance relationships, because the age, size and number of breeding females per group may influence between-group dominance relationships to a greater degree than group size alone. Variation in relatedness among groups (G. Wittemyer, unpublished data) also may affect the cohesion and likelihood of group cooperative defensive behaviour. Unfortunately, our data set is sparse and not all group members were observed in enough agonistic interactions to be included in this analysis; complete ensembles of breeding females were included for 22 of the 39 second-tier groups, nine of which were composed of only one breeding female. Thus, our current understanding of between-group relationships remains rudimentary, and it is likely that additional factors affect these rank relationships.

Finally, BGC is expected to be associated with territorial behaviour, but elephants are not territorial (Douglas-Hamilton 1972; Moss 1988). Lack of territoriality may partly be due to this species' dependence on widely distributed resources and partly due to interannual variation in vegetative productivity, necessitating the use of resources that are too large to be defended from others. Research on differentiation in spatial behaviour between elephant groups in relation to group size and dominance can offer insights into the form of competition that occurs within and between groups (Isbell 1991). Thus, spatial structuring may serve to drive transitivity in elephant dominance relationships, a hypothesis that we will test in future research.

Our results suggest that infrequent but potentially costly contest interactions, coupled with strong winner and loser effects, can have strong selective impacts leading to the formation of stable dominance interactions, even within species competing over widely distributed resources. Dominance relations established early in an animal's life may persist in species with cognitive abilities to discern numerous conspecifics, which could explain why matriarchal dominance structure in our study population was primarily driven by age and was independent of height or group size. Our results are conditionally supportive of the predictions offered by the socioecological framework, because our study demonstrates that semicryptic factors like (1) the interaction of WGC and BGC, (2) the impact of injury risk and related frequency of agonistic interactions and (3) winner and loser effects may generate social organizations not predicted by the form of resource competition alone.

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