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Social dominance, seasonal movements, and spatial segregation in African elephants: a contribution to conservation behavior

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Abstract The structure of dominance relationships among individuals in a population is known to influence their fitness, access to resources, risk of predation, and even energy budgets. Recent advances in global positioning system radio telemetry provide data to evaluate the influence of social relationships on population spatial structure and ranging tactics. Using current models of socio-ecology as a framework, we explore the spatial behaviors relating to the maintenance of transitive (i.e., linear) dominance hierarchies between elephant social groups despite the infrequent occurrence of contests over resources and lack of territorial behavior. Data collected from seven families of different rank demonstrate that dominant groups disproportionately use preferred habitats, limit their exposure to predation/conflict with humans by avoiding unprotected areas, and expend less energy than subordinate groups during the dry season. Hence, our data provide strong evidence of rank derived spatial partitioning in this migratory species. These behaviors, however, were not found during the wet season, indicating that spatial segregation of elephants is related to resource availability. Our results indicate the importance of protecting preexisting social mechanisms for mitigating the ecological impacts of high density in this species. This analysis provides an exemplar of how behavioral research in a socio-ecological framework can serve to identify factors salient to the persistence and management of at risk species or populations.

Keywords Animal movement · Spatial organization · Dominance

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Introduction

The formation of dominance hierarchies in mammals is a function of competition for resources and serves to minimize the frequency of potentially costly disputes between individuals (Rowell 1974). Differentiation among individuals in dominance rank can influence skew in reproductive success (Pusey et al. 1997; von Holst et al. 2002), resource access (Clutton-Brock 1982; Krebs and Davies 1987), territory quality (Fox et al. 1981), predation risk (Hall and Fedigan 1997), and energy budgets (Isbell and Young 1993; Koenig 2000). The framework of socio-ecological theory, originally developed to explore the relationship between ecological variables and the diversity of social systems among primates (Wrangham 1980; van Schaik 1989; Isbell 1991), which predicts transitivity in dominance hierarchies among conspecific females, is related to the type of competitive interactions (contest or scramble; Nicholson 1954). Well-established hierarchies occur in species experiencing contest competition as a function of reliance on monopolizable resources, whereas weak or nonexistent hierarchies occur in species competing through scramble interactions as a function of widely distributed resources (Sterck et al. 1997). The competitive regime in a population impacts its spatial organization; group (or individual in solitary species) defense of territories indicates contest competition between groups (or individuals), whereas spatial properties of scramble competitors are thought to be related to density (van Schaik 1989; Isbell 1991; Sterck et al. 1997). Transitive dominance hierarchies, however, are common to females of many large, non-territorial herbivores typically thought to predominantly experience scramble competition (Barrette and Vandal 1986; Rutberg 1986; Prins 1989; Dennehy 2001; Holand et al. 2004; Archie et al. 2006), potentially as a function of the high costs (risk of injury) associated with agonistic interactions in these well armed, large species. In this paper, we explore spatial behavioral differences that may drive transitive relationships between groups in one such species, the African elephant.

African elephants are generalist herbivores that are relatively nonselective and reliant on widely distributed resources (Laws 1970; Owen-Smith 1988). Agonistic interactions occur at very low frequency (0.05±0.01 per hour in non-first order relationships in the Amboseli ecosystem, see Archie et al. 2006), and between-group agonistic interactions occur as frequently in relation to point (contestable) resources as for social reasons not associated with any resource (Wittemyer and Getz 2007). Despite being infrequent and often of little immediate benefit, agonistic interactions among elephants do lead to the formation of transitive dominance hierarchies both within and between groups (Archie et al. 2006; Wittemyer and Getz 2007). The benefit of maintaining transitive relationships between groups is not obvious in relation to their infrequent contests over low value point resources. If between-group dominance hierarchies in elephants were a function of competition over salient, spatially limited resources, as proposed by socio-ecological models (Wrangham 1980; van Schaik 1989; Isbell 1991; Sterck et al. 1997), then we would expect to see rank-related differentiation in spatial behavior among groups, which in turn should enable dominant groups to access superior resources or minimize energetic costs. Alternatively, between-group dominance hierarchies may simply result from rare contests amidst predominantly scramble competitive interactions where the formation of transitive relationships based on matriarch rank is driven more by winner/loser effects (initial winners tend to continue winning) and less by derived benefits (Chase et al. 2002). Such a hypothesis is supported by the fact that the transitive dominance hierarchy between group matriarchs is age based and not based on group size or the physical size of a matriarch (Wittemyer and Getz 2007). Under such circumstances, differentiation in spatial behavior may be driven by scramble competition between groups and should be a function of group size, where bigger groups will utilize larger range (Isbell 1991). In addition, seasonal variation in resource distribution may also affect the temporal expression of any dominance related differentiation in behavior patterns.

Using movement data recorded with global positioning system (GPS) telemetry and observational data on dyadic agonistic interactions, we analyze the relationships between resource distribution, competitive interactions, and spatial behavioral differentiation across seven social groups in a free ranging population of African elephants (*Loxodonta africana*). We assess the hypothesis that transitive between-group dominance relations are driven by resource competition by testing four predictions relating social dominance to fitness benefits. These predictions are tested across the seven groups both during the dry season, when resources are limited and potentially monopolizable, and the wet season, when resources are ubiquitous and less monopolizable. Our analyses allow conclusions regarding the influence of spatial properties of resources on dominance structuring. If transitivity in between-group dominance relations relates to competition over spatially limited resources, then assuming that high ranking groups can translate their dominance into increased fitness, we hypothesize that: (a) High ranking groups move less, expending less energy, than low ranking groups; (b) high ranking groups use smaller areas than low ranking groups, where range size serves inversely as a proxy for home range quality; (c) high ranking groups access areas in close proximity to permanent water (a critical resource in the study area) to a greater extent than low ranking groups; and (d) high ranking groups spend a greater proportion of time within protected areas, where human-based threats are minimal, than low ranking groups.

This study provides novel insights into the relationship between social behavior and spatial organization. It also adds important information on the spatial organization (and needs) of a threatened species. Hence, this study offers an exemplar to the growing field of conservation behavior (Caro 1998; Festa-Bianchet and Apollonio 2003) of the power of socio-ecological focused analysis for the management of threatened species. Range constriction increasingly confines elephant populations to ever shrinking safe areas. Our study offers a rare and timely insight into the use of space in a population of elephants that still range relatively unconstrained. Our results demonstrate that social relationships among elephants can serve to mitigate the impacts of high population density and highlight the importance of dispersal regions for the conservation and the future management of this species. Securing these regions must be at the forefront of discussions when land use planning is being formulated across most of the elephant's range.

Materials and methods

Study of the relationship between rank and spatial use was conducted on the elephants inhabiting the Samburu and Buffalo Springs National Reserves in northern Kenya. This semi-arid region is dominated by *Acacia–Commiphora* savanna and scrub bush, and the reserves are focused on the major permanent water source in the region, the Ewaso N'giro River (Barkham and Rainy 1976). Rainfall averages approximately 350 mm per year and occurs during biannual rainy seasons generally taking place in April and November. For a more detailed description of the ecology of the study area, see Wittemyer (2001).

The elephants using these reserves are largely habituated to the presence of vehicles, enabling easy observation of behavior. These elephants are individually identified using their distinct ear morphology and physical characteristics, enabling individual based monitoring of the population, which has been conducted since 1997 (Wittemyer 2001; Wittemyer et al. 2005a). More than 900 elephants have been observed within the reserves over the course of the 9-year monitoring project. Fine-scaled social delineations have been defined quantitatively from an analysis of 5 years of individually based association data (Wittemyer et al. 2005b).

Communal areas managed by multiple pastoralist tribes surround the national reserves. As a result, the reserves are not fenced and the study population of elephants is free ranging. The parks have been found to comprise less than 10% of the area used by the study population (Wittemyer et al. 2005a) and are part of a complex spatial arrangement of patches connected by corridors in the ecosystem (Douglas-Hamilton et al. 2005). Elephants move in and out of the reserve continually and no elephants stay within the park year round (pers. obs.). Thus, the movements and range reported here are assumed to be relatively natural, as neither fences nor other hard boundaries impact the spatial use of the study elephants. This combination of factors makes Samburu an excellent population in which to study the spatial structure of free-ranging elephants.

Dominance analysis

For this study, the rank of social group matriarchs is considered representative of the group rank, as conspecifics following a high ranking matriarch will benefit from her rank (see discussion in Wittemyer and Getz 2007). Matriarchs of elephant groups are repositories of social knowledge whose behavior impacts on the behavior and fitness of all group members (McComb et al. 2001). Because of the properties of elephant social structure, individual group members take on the spatial behavior of their matriarch as they are generally in close proximity (metric presented below in radio tracking data analyses). We recognize, however, our assumption that matriarch rank equates to group rank simplifies the true complexity of dominance relationships (Hemelrijk et al. 2005).

Dominance rank relationships are calculated from an analysis of dyadic, agonistic interaction data collected between July 2001 and December 2003 within the study area. We recorded agonistic interactions using ad libitum sampling (Altmann 1974); that is, the initiator and recipient of agonistic interactions were recorded opportunistically. Dominance relationships were characterized from observations of overt interactions that were both physical (tusk pokes, trunk slaps, and physical nudges) and nonphysical (supplants where individual A moves directly toward individual B typically with ears flared, B then moves away from A). The role of each individual recorded during agonistic interactions was clear because the individual defined as the loser of the interaction would usually move away while looking over its shoulder at the winner (for a more detailed description of this dominance interaction data set, see Wittemyer and Getz 2007). Interactions in which dominance relationships were not obvious were not included in analyses. Dominance interactions were predominantly dyadic. When full groups interacted, interactions typically occurred between matriarchs.

During the study period, 419 agonistic interactions were observed across 39 family groups involving 73 different individuals resident to the study area (as defined in Wittemyer 2001). Each individual interacted with an average±SE of 3.8±0.42 individuals outside her family unit and was observed in an average of 5.7±0.53 agonistic interactions, excluding within-group interactions. Individuals not observed in agonistic interactions were not included in analyses. These observations were used to formulate the "most likely rank order" among resident elephants using methodology specifically developed to resolve dominance hierarchies in systems with multiple unknown relationships (Wittemyer and Getz 2006). This method is an extension of de Vries (1998) I&SI method, following the same procedure of minimizing the number and strength of inconsistent dominance relationship, i.e., those interactions against the dominance rank order. The ranks of all individuals were determined by, first, sorting dominance matrices to minimize circular relationships and, second, ordering individuals by their dominance strength metrics (shown in Table S1), where dominance strengths were calculated as the sum of each individual's row (wins) subtracted from the sum of its column (losses) in the dominance matrix (Wittemyer and Getz 2006). Individual and group dominance ranks and the degree and significance of transitivity (i.e., linearity) in the dominance hierarchy were defined previously (Wittemyer and Getz 2007) for an analysis of two dominance matrices containing (a) only group matriarchs (n=20 with 37% of relationships known) and (b) all individuals (including the 20 group matriarchs) seen to interact with at least two individuals outside their social group (n=73 with 13% of relationships known). Both matrices were significantly transitive as assessed using the directional consistency index (Noë et al. 1980) and Landau's linearity index h (Landau 1951). Individual ranks of the focal groups' matriarchs derived from both analyses (matrices composed of matriarch and all females) are similar (Table 1). Because of the relative sparseness of our interaction data, we categorized the assigned ranks, including the seven focal groups in this study, into three broad categories (Table 1) to ensure the robustness of our rank definitions (Wittemyer and Getz 2006).

Radio tracking data analyses

To assess the degree to which rank relations affect spatial use, we analyzed data from GPS collars fitted on seven different individuals representing distinct family groups (previously defined in Wittemyer et al. 2005b) in the Samburu elephant population. The rank of the matriarch of each family, defined as the most dominant individual in a family group, was used for rank based intergroup comparisons, because the matriarch primarily directs family movement and spatial use (Moss 1988). The ranks of these families were not known at the time of collaring. The collared families differed in respect to their rank status within the population (Table 1), but were of similar sizes (range 9–13 individuals) and all lead by mature matriarchs estimated to be over the age of 35 years (Wittemyer et al. 2005b). Age estimates of all elephants were conducted using physical characteristics such as shoulder height and back length and verified from dental impressions during immobilization operations (Rasmussen et al. 2005). Individuals were radio collared by a Kenya Wildlife Service (KWS) veterinarian following the protocol established by KWS and Save the Elephants. The data used in this study are part of an ecosystem wide assessment of elephant ranging behavior being conducted on the Samburu/Laikipia elephant population by Save the Elephants. Non-matriarchal breeding females in four of the focal groups (the three most dominant groups and one of the lowest ranking groups) were fitted with radio collars rather than the matriarch to avoid unnecessary stress on families and older-aged individuals. The within-group ranks of the collared females did not reflect the between-group ranks of the groups matriarchs. We assumed that the range and movement patterns of all individuals in a group are essentially the same, as the individuals comprising these quantitatively defined groups were observed between 85–100% of the time together (Wittemyer et al. 2005b) and maintain close cohesion with their matriarchs. It is likely that group members are in close spatial proximity even when not observed in direct proximity by field biologists (individuals separated may not both be observed). We assessed actual distances between two radio-tracked breeding females from the same group, finding that they spent over 95% of a 6-month tracking period within 1 km of each other (80% within 250 m), using nearly identical ranges, and moving similar daily distances (unpublished data). It is important to note that such differences are within the range of infrasonic communicative abilities of elephants; therefore, it is likely that dyads separated by such small distances (relative to elephant home ranges) are still able to coordinate movement (Langbauer et al. 1991; McComb et al. 2003). Therefore, we assume core group members maintain similar movement behavior.

Table 1 The ranks of family group matriarchs (Table S1) were defined from analysis of two dominance matrices (containing 20 matriarchs with relationships in 37% of dyads known and 73 breeding females with relationships in 13% of dyads known) analyzed in Wittemyer and Getz (2007)

Collared female	Group matriarch rank		
	Relative rank	Absolute rank among 20 known matriarchs	Absolute rank among 73 known breeding females
M54	High	1	1
M5	High	2	3
R28	High	4	2
M31	Mid	9	12
R22	Mid	11	15
M46	Mid-low	14	29
R37	Mid-low	13	28

The ranks of collared females' matriarchs were used to classify the seven focal groups into three categories of relative ranks (high, mid, and mid-low) used in analyses.

Data quality

Dry season data analyzed in this study were collected from the seven focal individuals between July 10 and October 1, 2001, a total of 84 days. We initiated our analysis on July 10th because all seven focal individuals had been collared for at least 24 h by this date and rainfall had not occurred in the study area for over 30 days (a definition previously used to define dry seasons). We ended our analysis on October 2 because the first rain of the "November" 2001 wet season occurred on this date. Thus, our dry season study period incorporated movement and spatial information carried out by the study elephants during a period without rainfall in the study area, and as a result, localized rainfall was not a potential factor impacting the recorded movements and spatial use.

Wet season data analyzed in this study were collected between November 1, 2001 and January 2, 2002, a total of 62 days. This period was defined using normalized differential vegetation index (NDVI) data: An increase in the mean NDVI values greater than or equal to one standard deviations above the baseline for the whole year (the mode of the distribution of NDVI values) marked the onset of the wet season, and a decrease in NDVI values below this demarcation defined the cessation of the wet season (Rasmussen et al. 2006). Thus, our wet season study period incorporated movement and spatial information carried out by the study elephants during the seasonal period of increased primary productivity as measured by NDVI (Sellers et al. 1992; Pettorelli et al. 2005).

During the dry season, GPS radio collars were programmed to record the positions of the collared individual on an hourly basis. Failure to obtain fixes occurred infrequently in each of the collars during the 3-month dry season, with a median of 11 (range 4–56) failures per collar during the 2,016-hour period. Collar performance and the resulting data set were not as good during the wet season period of the study. Two of the seven collars were programmed to record GPS data at 3-h intervals during this period. One collar failed on December 15, 2001 spanning the last 17 days (415 h) of the 1,488-h wet season period, and another collar failed for an 8-day (196-h) period between December 12th and 19th 2001, after which it operated normally. The remaining three collars performed well with failures ranging from 5–16 h. Although wet season data have more failures than those collected during the dry season, data for all individuals were recorded for at least 45 days during the wet season. Analyses of wet season data were collated on a 3-h basis to ensure similar sample sizes among the seven individuals during this period.

Calculation of distances traveled

Distances traveled were calculated in the Animal Movement extension (Hooge and Eichenlaub 1997) of ArcView 3.2© (Environmental Systems Research Institute) using GPS data. Hourly distances were determined for each individual for all possible hours where successful fixes were taken. Hours for which the GPS failed to get a position were not included in analysis of hourly distances. Likewise, 3-h distances were calculated for wet season data sets using consecutive 3 hourly GPS fixes. Daily movement distances (covering a 24-h period) were calculated by summing hourly, during the dry season, or 3 hourly, during the wet season, distances. Where GPS fix failures occurred in the data sets, distances moved during 2-h periods, dry season, or 6-h periods, wet season, were used in calculation of daily movement distances. Where dry and wet season data were directly compared, dry season data was collated on a 3 hourly basis.

Home range estimation

Three types of home range estimation techniques were used to analyze the data: minimum convex polygons (MCPs), fixed kernel estimates (Worton 1995), and fixed point or *k* method local (nearest-neighbor) convex-hull construction (LoCoH; Getz et al. 2007). MCP home ranges and kernel home ranges were calculated using the Animal Movement Extension (Hooge and Eichenlaub 1997) in ArcView 3.2©. The fixed kernel method was used to create density isopleths, as described by Worton (1995). Although the kernel least squares cross-validation technique is preferred (Seaman et al. 1998), the amount of data collected for each individual made such estimation unwieldy. Therefore, we defined the smoothing parameter used for all individuals on a 1-m grid as $h=1{,}000$. Both 50 and 95% density isopleths were calculated. The local convex-hull construction in LoCoH depends on a user-selected parameter *k*, the number of nearest neighbors to be included in hulls, which we calculated to be 20 for dry and 15 for wet season data sets following procedures in Getz and Wilmers (2004). The spatial analyst extension of ArcView 3.2© (Environmental Systems Research Institute [ESRI]) was then used to calculate the areas of different isopleths.

Spatial proximity analyses

The number of fixes occurring in different regions of the study area was calculated using the assign attribute feature in the spatial analyst tool box of ArcGIS 9.0© (ESRI). The proportions of fixes located within 1 km, between 1 and 5 km, and greater than 5 km from permanent water were calculated using the assign attribute function to buffer shape files created for these distances from permanent water. The protective status of areas within the study region varies from national reserves (established over 20 years ago), to community or private conservancies (established in the last 5–10 years), to unprotected communal areas. To determine how differently ranked individuals used space in relation to these different protective designations, the proportion of fixes occurring within each land use type were also calculated.

Hard boundaries do not exist in the study region, making explicit study area definitions difficult. We defined the study area as the MCP range of the combined data from the seven tracked elephants during the dry season. When testing for selectivity, defined as when elephants use areas with certain spatial properties to a greater extent than expected from the total area available with that property, we calculated the available area within this MCP-defined study area. The proportion of the MCP area occupied by different habitat criteria was then compared to the amount of time spent in each habitat (Neu et al. 1974). Wet season data were analyzed for preferences only within the dry season-defined study area where individual ranges overlapped, as wet season ranges did not overlap in outlying regions. A greater proportion of area within 1 km of water occurred outside protected areas than within protected areas; therefore, it is unlikely preferences for protected areas drive preferences for areas within 1 km of water or vice versa (see Fig. 3).

Statistical analysis

Habitat selection in relation to proximity to permanent water (four classes described above) and protected status (two classes protected and not protected) was conducted using the Neu method (Neu et al. 1974; Alldredge and Ratti 1992). χ^2 goodness of fit statistics were Bonferroni corrected to account for multiple comparisons. Selectivity was assessed for each individual elephant, as well as across the pooled data of the seven tracked individuals. Comparisons between the wet and dry season were conducted.

To collate data sets to the 3-h interval used for analysis of wet season spatial behavior and comparisons between wet and dry season movements, we subsampled each data set so that the GPS fixes matched those of the 3-h interval collars, collected at 0000, 0300,..., 2100 hours. Comparisons between seasons (dry vs wet) were conducted on 3-h data using paired Wilcoxon rank sums tests. Analyses of movement and spatial use exclusively within the dry season were conducted using data collected at hourly intervals to utilize the maximum amount of information available (Rooney et al. 1998).

Analyses of movement data were conducted using nonparametric techniques, as both hourly and daily data sets were not normally distributed across all individuals. Within season pair-wise comparisons of hourly and 3 hourly distances moved were conducted across all pairs using Kruskal–Wallis rank sums tests. Thus, 21 tests were conducted within each season among the seven individuals. Significance of p values was assessed after Bonferroni correction for multiple comparisons of the alpha level, resulting in significance being assigned to p values<0.0028 (Zar 1999). Comparisons of differences across multiple individuals were conducted using Kruskal–Wallis tests. The correlation between social rank and movement and spatial use was conducted with Spearman rank correlations. All comparisons to rank were conducted on ordinal groupings where the rank of each of the seven groups matriarchs was categorized as 1 (high), 2 (mid-high), or 3 (mid-low) to ensure the robustness of the rank relationships (Wittemyer and Getz 2006). Data within categories were not pooled but analyzed as independent samples. Thus, the data from the seven groups in three rank categories were used in Spearman rank correlations. The group matriarchs of M54, M5, and R28 were the highest ranking in the population because they were dominant in all of their recorded interactions (interestingly, contests among these groups were not observed when they associated). The groups led by M31 and R22 were categorized as mid-high ranking because they were grouped together in analyses of both dominance data sets (i.e., dominance matrices containing 20 matriarchs and 73 adult females). Finally, M46 and R37 were grouped as mid-low ranking because they were also consistently grouped together and below M31 and R22 in both analyses of dominance relationships.

Weekly proportions of time spent in protected areas during the dry season were calculated for both dominant groups (n=3) and lower-ranking groups (n=4) and normalized using arcsine transformation to allow analysis of trends over time in protected area use. We examined the residual autocorrelation from an ordinary least squares (OLS) regression model of the time series to ensure independent distribution of the data (Fox 2002). The partial autocorrelation function for both analyses demonstrated residuals were not significantly correlated at any lag; therefore, OLS regression results are reported.

Due to the high temporal resolution of the data set, individual data are not statistically independent. Our analysis is conducted on a close approximation of real time spatial properties over a seasonally defined study period, following the recommendations of previous research concluding that the use of the shortest possible sampling interval over biologically relevant temporal periods is the best strategy for home range size estimates, spatial use intensity and quantification of fine-scale behavioral decisions (Swihart and Slade 1985; Rooney et al. 1998). The inferences presented here on spatial behavior are limited to the temporal and spatial scope of the study (Otis and White 1999). All statistical analyses were conducted using S-Plus (Venables and Ripley 1999).

Results

General and seasonal characteristics of spatial behavior among elephant groups

During the study period, GPS tracking data pooled for the seven focal groups revealed that, on average, the studied elephants preferred to be in areas that were (1) protected and (2) in close proximity to water (Table S2). However, these preferences showed seasonal differences, particularly in relation to use of areas in close proximity to water (Fig. 1). In the dry (but not in the wet) season, selective use of areas near permanent water (<1 km) was found. Significant selection of areas within protected areas and avoidance of unprotected areas occurred during both the wet and dry season, but use of protected areas generally decreased during the wet season (Table S2). Groups differed in their use of protected areas with only five of the seven groups showing a significant preference for such

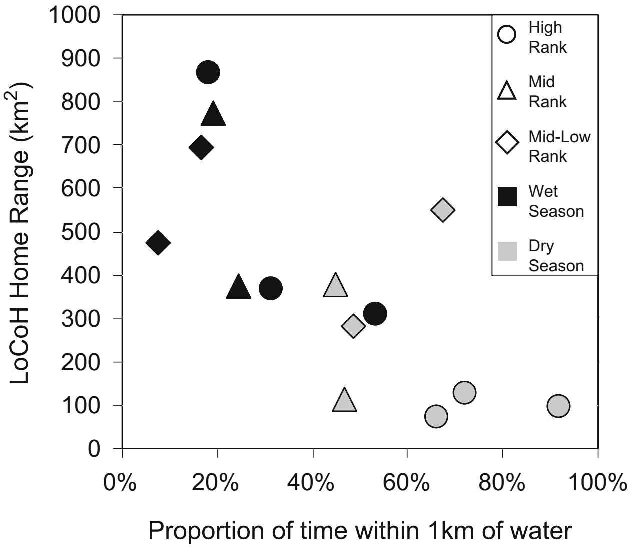

Fig. 1 LoCoH home range sizes are smaller and use of areas in close proximity to permanent water sources decreases during the wet season across social groups regardless of rank. Dominant groups during the dry season (*gray circles*) tend to use smaller home ranges that are closer to permanent water sources than lower ranking groups (*lower right of graph*). Rank-related differentiation in range size and proximity to permanent water, however, is not apparent during the wet season (*black symbols*)

areas (Table 2; R37 demonstrates a significant avoidance, see below for relation of this result to rank). Regardless of the home range estimation method, home ranges varied among groups during the dry season (Table S3). LoCoH home ranges were significantly larger during the wet season (Wilcoxon rank sums $W=35$, $n=7$, $m=7$, $p=0.026$), although range size did not change between seasons for one of the lower-ranked groups (Fig. 1). Group size and home range size were not significantly correlated (Spearman's $\rho=-0.505$, $n=7$, $p=0.245$), as might be expected if home range size was mediated by the effects of dominance rank on home range quality (see our prediction B, that high ranking groups use smaller areas than low ranking groups; results below).

Table 2 Selection for areas in relation to protected status was tested across groups during the dry season

Elephant	Within obs	Within exp	χ^2 *p* value
M54	1,939	429	*<0.001*
M5	984	419	*<0.001*
R28	2,016	429	*<0.001*
M31	638	430	*<0.01*
R22	1,691	428	*<0.001*
M46	400	427	>0.60
R37	168	420	*<0.001*

Five of seven groups demonstrated significant preference, and one group (R37) demonstrated significant avoidance of protected areas. Significant *p* values are italicized.

Travel distances differed among the seven focal groups both within and between seasons (Fig. 2). Hourly and daily travel distances differed significantly across groups during the dry season (Kruskal–Wallis rank sums: $\chi^2=519.39$, $df=6$, $p<0.0001$ and $\chi^2=287.24$, $df=6$, $p<0.0001$, respectively) and wet season (Kruskal–Wallis rank sums: $\chi^2=80.93$, $df=6$, $p<0.0001$ and $\chi^2=60.22$, $df=6$, $p<0.0001$, respectively; Table S4a and b). And daily travel distances were significantly greater during the wet season (exact Wilcoxon rank sums: $W=32$, $n=7$, $m=7$, $p=0.007$, Fig. 2). Pair-wise comparisons of hourly (dry season) and 3 hourly (wet season) travel distances between all pairs of groups demonstrated greater differentiation during the dry season, when 15 of the 21 pairs differed significantly (after Bonferroni correction of alpha levels; Table S5). Significant differences were typical between groups of different rank but not between groups of similar rank, i.e., between two of the three top ranked and three of the four bottom-ranked groups. During the wet season, only seven of the 21-paired comparisons were significantly different—six of these resulted from comparisons to a single group (a dominant) with the lowest travel distances recorded (Table S5).

Influence of social rank on spatial behavior

In support of our hypothesis that fitness expressed through transitive dominance relationships among groups is driven by resource competition, differences in spatial behavior among groups during this study were related to dominance relationships albeit with a significant seasonal dependence (Table 3). In support of prediction A, analysis of dry season data demonstrated that hourly and daily travel distances were

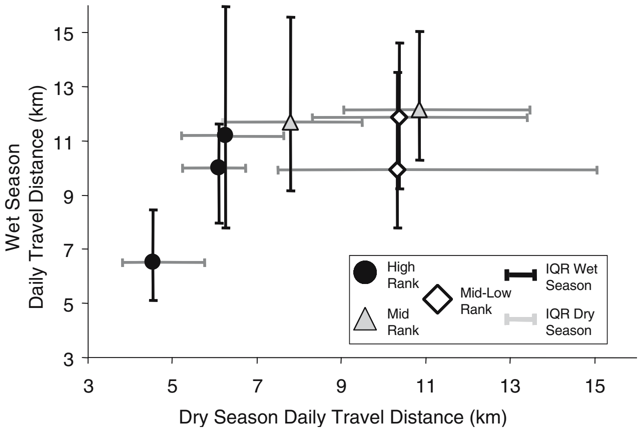

Fig. 2 Daily travel distances, median values with interquartile range (*IQR*) error bars, for both the dry and wet seasons. Travel distances of dominant groups are significantly shorter than those of lower ranked groups (note *gray error bars* representing IQR during the dry season) during the dry season when resources are limited. Rank-related differentiation in travel distances, however, does not occur during the wet season when competition for resources decreases (note *overlap in black error bars* representing IQR during the wet season)

Table 3 Spearman rank correlations comparing ranks of the seven radio collared groups (categorized as high [n=3], medium [n=2] and low [n=2]) with various measurements of movement, home range (HR) size, and spatial use behavior (N.R. refers to National Reserves)

Season		3 Hour dist	Daily dist	Total dist	Time in N.R.	MCP HR	LoCoH HR	K95 HR	K50 HR	K50 in N.R.	1 km water	1–5 km water	>5 km water
Dry[a]	Spearman's rho	***0.808***	***0.794***	***0.869***	***−0.850***	***0.775***	***0.775***	0.699	−0.227	***−0.784***	−0.473	0.473	***0.760***
	p value	***0.028***	***0.033***	***0.011***	***0.015***	***0.041***	***0.041***	0.080	0.625	***0.037***	0.284	0.284	***0.047***
Wet[b]	Spearman's rho	0.302	0.378	−0.264	−0.246	0.265	0.265	0.113	0.302	***−0.775***	−0.756	0.265	0.699
	p value	0.510	0.403	0.668	0.595	0.566	0.556	0.809	0.510	***0.041***	0.044	0.566	0.080

Correlations significant at the $\alpha<0.05$ are italicized and bolded.

MCP Minimum convex polygon, *LoCoH* local convex hull, *K95* 95% kernel, *K50* 50% kernel

[a] Dry season GPS data were analyzed at an hourly interval

[b] Wet season GPS data were analyzed at a 3 hourly interval in relation to data collected for two of the seven elephants (see "Materials and methods")

significantly correlated with rank category (Spearman's ρ= 0.808, n=7, p=0.028, and ρ=0.794, n=7, p=0.033, respectively; Table 3), with high ranking groups (category 1) moving less than low ranking groups (categories 2 and 3, Fig. 2). By ranking high groups as 1 and low groups as 2 or 3, a positive correlation coefficient result implies high have shorter travel distances than low. Combined, the three highest ranking groups averaged 0.25 km/h and 5.93 km/day, approaching half the average distances moved by the four lower ranking groups, which averaged 0.46 km/h and 10.78 km/day. Cumulative distances moved during the dry season, calculated by summing all distances from consecutive GPS fixes regardless of interval, were also significantly correlated with the three rank categories (Spearman's ρ= 0.869, n=7, p=0.011).

In support of prediction B, dry season MCP and LoCoH range estimates were significantly correlated with rank (MCP: Spearman's ρ=0.775, n=7, p=0.044; LoCoH: Spearman's ρ=0.775, n=7, p=0.044). Specifically, lower-ranked groups (categories 2 and 3) had larger ranges than the groups in rank category 1 (Fig. 1). Similarly, the sizes of the 95% kernel density isopleth demonstrated rank-related differences (Fig. 3), although not significantly (Spearman's ρ=0.699, n=7, p=0.080; Table 3). Interestingly, the sizes of the 50% kernel density isopleth, used to define an individual's core range, were similar across groups and not significantly correlated with rank (Spearman's ρ=−0.227, n=7, p= 0.625). The location of the 50% density kernel, however, was related to rank (Fig. 3), with higher ranking groups having a greater proportion of their "core" range located within protected areas (Spearman's ρ=−0.784, n=7, p= 0.037; Table 3).

In support of prediction C, dominant groups generally spent more time near water (Fig. 1), although rank was not significantly correlated with use of areas less than 5 km from permanent water. Rank was significantly correlated with use of areas greater than 5 km from water with lower-ranked groups using such areas more than high-ranked groups (Table 3). In support of prediction D, the proportion of fixes occurring within protected national reserves during the dry season was significantly correlated with rank with dominance groups spending more time in protected areas than their counterparts (Spearman's ρ=−0.850, n=7, p=0.015; Table 3). Only the lowest two ranking groups did not demonstrate significant selection for protected areas (Table 2). Interestingly, we found that the four lower ranking groups significantly decreased their use of the national reserve as the dry season progressed (R^2=0.460, p=0.015), whereas the three high ranking groups showed no change (R^2=0.113, p= 0.285; Fig. 4). Time spent in the national reserves was calculated (as percentage on a weekly basis) for each group and normalized for this analysis using arcsine transformation; residuals were not significantly autocorrelated; thus, OLS results are reported here (see "Materials and methods").

Further support for our hypothesis that fitness expressed through competition for resources drives transitivity in rank relationships was provided by a lack of rank-related spatial behavior during the wet season, a period when competition decreases in relation to widely distributed, higher quality resources. During the wet season, rank did not correlate significantly with (1) time spent in or out of protected areas, (2) travel distances, (3) MCP, (4) LoCoH, or (5) kernel home range size (Table 3 and Fig. 1). The proportion of "core" range located in the national reserves, however, remained correlated with rank, although the contiguity of core ranges decreased for dominant groups, from single adjoining 50% isopleths during the dry season to multiple, separated isopleths during the wet season. Further, the proportion of time spent within 1 km of permanent water was significantly correlated with rank (Table 3), although use of areas in close proximity to water decreased for all individuals (Fig. 1). But rank was not significantly correlated to use of areas 1–5 km or greater than 5 km from permanent water during the dry season.

Discussion

The elephants we studied demonstrate the characteristic spatial structuring associated with scramble competitive

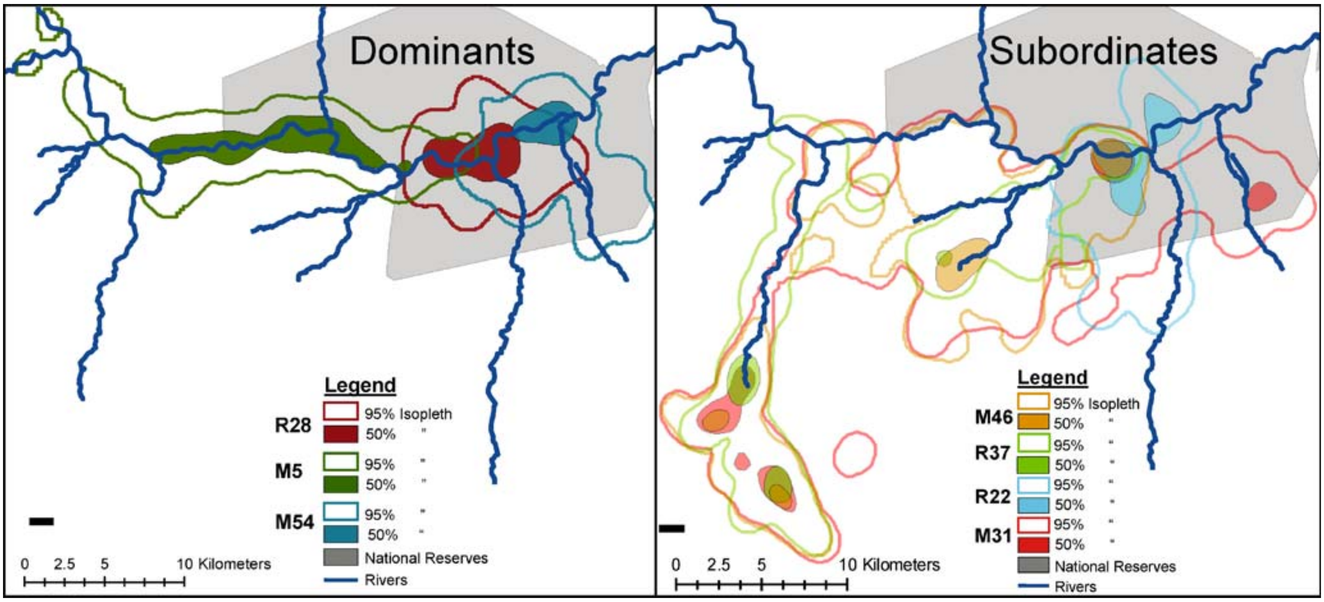

Fig. 3 Kernel home range for the three dominant groups (*left map*) and four lower ranking groups (*right map*) during the dry season. All groups with the exception of R37 have part of their core range within the boundaries of Samburu and Buffalo Springs National Reserves. The ranges of the three dominant groups are cohesive and focused on the main river in the study area, whereas ranges of the lower ranking groups are more dispersed and focused at various points within and outside the protected reserves

systems with range overlap among groups and lack of territoriality (Douglas-Hamilton 1972; Moss 1988) while concurrently maintaining social organization indicative of contest competition in which transitive dominance relationships are maintained between groups (Wittemyer and Getz 2007). Previous analysis of dominance interactions among elephant groups in our study population demonstrated that contests were often not focused on resources that could be usurped (Wittemyer and Getz 2007). Thus, before this study, the benefits of well-defined dominance relationships among groups were far from clear. The analysis presented here demonstrates that rank-derived benefits were manifested by differentiation in spatial behavior but not strict monopolization of areas. In addition, our observations demonstrate that the spatial behavior and the role of social processes in shaping the spatial structure in our study elephant population are likely to have been conditioned by the quality and distribution of resources associated with seasonal fluctuations in the ecosystem. Although the latter is expected of a migratory species, differentiation in spatial use according to social rank is not commonly associated with species that exhibit migratory behavior.

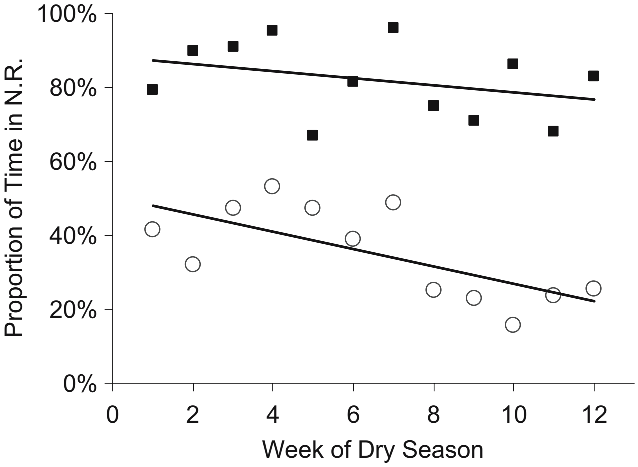

Fig. 4 Use of protected areas (national reserves—N.R.) by lower ranking groups (*open circles*) decreased significantly as the dry season progressed (arcsin normalized: R^2=0.460, p=0.015, y=−0.025x+0.525), whereas use by dominant groups (*black squares*) did not change significantly over the 12-week dry season (arcsin normalized: R^2=0.113, p=0.285, y=−0.018x+1.099). Autocovariance functions did not demonstrate significant correlation in the residuals of these linear regression models

Seasonal variation in rank-related behavior

Results from analyses of spatial behavior in relation to rank support our hypothesis that dominance relations are driven by contest competition for spatially limited resources. In support of our predictions (A–D), dominant groups traveled significantly less, had smaller home ranges, used areas within protected areas, and also closer to permanent water to a greater degree than lower ranking groups during the dry season (Figs. 1 and 2). Our results indicate foraging tactics and population spatial organization are, at least periodically, shaped by social processes. Dominance offers the benefits of decreased energy expenditure and access to preferred habitats, which is especially important when resource quality declines. Thus, we found evidence during the dry season that spatial segregation and differentiation in movement between groups was related to social rank (Table 3), as predicted to result from salient degrees of contest competition over monopolizable resources in socio-ecological models (Wrangham 1980; van Schaik 1989; Isbell 1991).

By contrast, movements in the wet season did not show differential spatial use and resource partitioning, indicating a lack of contest competition when resources are more widely available. This follows because the wet season was defined, using remotely sensed time-specific NDVI data (Rasmussen et al. 2006), as the period in the study area with increased primary productivity (Sellers et al. 1992; Pettorelli et al. 2005). The wet season period was characterized by increased availability and quality of resources (food and water). Travel distance, home-range size, and use of protected areas were not significantly correlated with social rank during the wet season (Table 3), and proximity to permanent water decreased for all groups (Fig. 1). Although core ranges of dominant groups tended to remain within protected area in the wet season (Table 3), the ranges of these groups changed from a single contiguous core region during the dry season to multiple (ranging from two to four), widely dispersed core patches. This lack of spatial partitioning during the wet season, when resources are generally of higher quality and less clumped spatially, was consistent with predictions from socio-ecological models for species experiencing scramble competition (Wrangham 1980; van Schaik 1989; Isbell 1991).

Analysis of the ratio between wet and dry season movements shows that dominant groups traveled three to four times further during the wet season and generally increased their home-range sizes to a greater degree than lower ranking groups (Fig. S6). Accordingly, the only group with larger dry season travel distances and range was one of the lowest-ranked groups of the study. Thus, our results suggest that lower-ranked groups do not alter their spatial behavior to the same degree as dominants in the face of limited resources and increasing ecological constraints. Interestingly, a cursory analysis of movement and spatial use for two of the dominant groups during successive dry seasons in which NDVI values were higher than those recorded during the 2001 dry season, found increases in distances moved and in range sizes compared to those presented here. The ratios of seasonal movements for these groups were not as extreme as those found during the 2001 dry season. Data, however, were not available for the other groups, so we were unable to explore this further with any scientific rigor. The observed increases in distances moved and range size during a relatively good dry season support the conclusion that rank-derived advantages are manifested primarily during periods when competition for resources is intense, but are not apparent when resources are sufficiently abundant to be non-limiting.

Additional anecdotal evidence suggests that resource depletion in preferred areas can elicit alternative spatial responses in elephants. A severe drought in the Samburu study area in 2005–2006 (the culmination of below-average rainfall for three consecutive seasons) resulted in all but a few groups completely leaving the protected areas for the majority of the dry season, including two of the dominant groups analyzed here. Decreased use of the high density protected areas as the dry season progressed, and resources became more depleted, was also observed in this study to a lesser degree for dominant groups (Fig. 4). Similarly, in Tarangire National Park, dominant groups left the protected area during an extended, severe drought and suffered lower calf mortality than those groups that remained within the depleted protected area (Foley 2002). As with the fission–fusion nature of their social organization, elephant spatial organization appears to be dynamic and subject to the unpredictability of their food distribution. Thus, spatial use strategies by elephants are adaptable to local/de facto conditions, a characteristic of migratory species.

Spatial preferences

The motivation for spatial preferences by the study elephants for protected areas is of importance to the management of this species. The national reserves are a focal area for elephant use in the study region and, thus, subject to high elephant density (Douglas-Hamilton et al. 2005; Wittemyer et al. 2005a), although the habitat types within and outside the reserves are similar, both being predominantly *Acacia–Commiphora* scrub (Barkham and Rainy 1976). With this usage, intraspecific competition for resources is expected to be higher within the reserves. Dominant groups, however, were observed to avoid non-protected areas during the dry season when competition for resources was greatest, relying almost exclusively on the national reserves during this period. This may be the result of interspecific competition between elephants and human-lead livestock herds occurring in pastoralist areas outside the protected reserves. In support of this hypothesis, we note that diurnal water use by elephants is different inside than outside the reserves during the dry season when the only permanent water in the study area is found in the Ewaso N'giro River. When in the reserves, the seven focal elephants tended to spend a greater proportion of the hotter, dry season daylight hours within 100 m of permanent water (viz., 1,128 h during the day vs 482 h at night) compared with use outside the protected areas (viz., 794 h during the day vs 675 h at night). Outside the protected areas, livestock are often on the river during midday but, as a precaution against predation, confined to corrals during the night. Thus, diurnal access to the river for elephants outside the protected areas appears to be limited and preferences for protected areas may relate to avoidance of human-dominated landscapes. Seeing that humans are one of the primary sources of mortality among adult elephants in the study area (Wittemyer et al. 2005a), such selection of protected areas is potentially a risk avoidance strategy.

Socio-ecology, conservation behavior, and elephants

The socio-ecological framework provides predictions regarding the relationship between spatial behavior and the type and strength of competition over resources. Although we did not observe the territorial behavior typically associated with linear between-group dominance relationships, we did find significant differences in range sizes and travel distances among groups. Within-group scramble competition is predicted to cause daily travel distances to be positively correlated with group size, and between-group scramble competition causes positive correlation between range and group size (Isbell 1991). In contrast, group size was not correlated with any of the spatial behavioral measurements during the dry season nor was group size correlated with rank among the seven groups (Spearman's $\rho=-0.3922$, $n=7$, $p=0.3841$). In our study, the rank-related differentiation in spatial behavior patterns mirrored differences predicted to be a function of group size in egalitarian systems; territorial behavior typical of strongly despotic societies, on the other hand, seemed to be altogether absent. The maintenance of transitive dominance relationships in the face of infrequent contest competitive interactions (and frequent scramble competition) appears to drive a spatial behavior that is hybrid to the behavior predicted for typical egalitarian or despotic societies.

As density of conspecifics increase or resources decline, intraspecific competition influences access to limited resources (Koenig et al. 1998; Hansen and Closs 2005). Thus, resource configuration in highly seasonal or patchy environments can cause periodic or locational changes from scramble to contest competition—the former being demonstrated in this study. Our results indicate that this variation impacts the expression of behavior patterns characteristic to either type of competitive regime. Because most resources in the study area are widely distributed, vary temporally in quality, and are not easily defendable even during the dry season when water and food resources are constrained, strict territorial behavior is uneconomical for elephants despite salient degrees of contest competition. This lack of strict territoriality, in addition to weakly nepotistic hierarchies in the face of transitive dominance relationships (Wittemyer and Getz 2007), indicates that elephants are relatively tolerant (de Waal 1989) of lower ranking conspecifics—possible causes for such tolerance are discussed elsewhere in detail (Wittemyer and Getz 2007). It seems unlikely that spatial defense by dominants (low tolerance) could explain the observed behavioral differentiation because the space available was large and the levels of agonistic interactions were low. Rather, similar to behavior found in common cranes (Alonso et al. 1997), subordinates may avoid areas used by dominants during periods of increased competition (Fig. 3). Such avoidance probably averts potentially costly contests (see description in Buss 1990) over relatively low quality resources, but leads to use of less preferred areas and increased movements and range sizes among subordinate groups as found among vervet monkey groups (Struhsaker 1967).

Among elephants, dominance-derived benefits are not conspicuous, and only through the detailed analysis of spatial behavioral characteristics do the forces driving transitive dominance relationships become apparent. The identification of the salient factors influencing social hierarchy formation can offer important insight into the constraints impacting a population or species. By analyzing the temporal and spatial factors driving the expression of dominance-related differentiation among elephant groups, we were able to demonstrate that resource competition during the dry season becomes critical by driving some of the population outside the high density, protected reserves. These results indicate the importance of protecting preexisting social mechanisms for mitigating the ecological impacts of high density in this species, a topic of management concern (Dublin et al. 1990; Cumming et al. 1997; Western and Maitumo 2004). In addition to the distribution of food resources, we found that spatial features of the study area, particularly proximity to water and overlap with humans/livestock, impacted elephant spatial selectivity in the Samburu ecosystem. Our results highlight the importance of open ecosystems to the social and spatial organization of elephants and indicate a mechanism whereby sociality impacts fitness in this species (as demonstrated previously in McComb et al. 2001) and acts to distribute population density across an ecosystem.

In summary, we conclude that the confinement of a migratory species like the Samburu elephants may elicit major social impacts in addition to the well-recognized ecological changes related to high animal densities. Thus, our study provides an example of the utility of behavioral research to provide information on factors vital for the conservation and management of a species.

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