Original Article

The influence of forage, protected areas, and mating prospects on grouping patterns of male elephants

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Factors affecting social group size in mammals are relatively well studied for females, but less is known about determinants of group size for males, particularly in species that live in sexually segregated groups. Male grouping patterns are thought to be driven more by spatial and temporal dispersion of mating opportunities than by food resources or predation risk. We evaluated the influence of 3 factors on male group sizes and number of males in mixed-sex groups in African elephants; forage availability (using Normalized Difference Vegetation Index, a satellite-based indicator of primary productivity), anthropogenic mortality risk (using distance of elephants from a protected area center), and mating opportunities (using the number of males in mixed-sex groups with and without estrous females). Using zero-truncated negative binomial regressions and a model-selection approach, we found that male elephants occurred in larger groups where primary productivity was higher and where they were further from a protected area center. However, we found an interaction between primary productivity and anthropogenic mortality risk: at low primary productivity, elephants formed larger groups further away from a protected area center, but did less so at higher primary productivity. This pattern suggests that male elephants are sensitive to seasonal variation in potential anthropogenic mortality risk, by remaining in smaller groups when risk is low, but forming larger groups when risk is high. Mating opportunities also led to an increase in male numbers in mixed-sex groups, but its relative influence on male grouping was less important because mating opportunities were rare.

Key words: **Amboseli, anthropogenic mortality risk, estrous, group size, NDVI, sociality.**

INTRODUCTION

Understanding the mechanisms that drive variation in social group size is crucial for gaining insight into the evolution of sociality (Alexander 1974). However, the mechanisms that influence group size may affect males and females differently, especially in sexually segregated species (e.g., mountain sheep, Bleich et al. 1997; fallow deer, Ciuti et al. 2004; Alpine ibex, Grignolio et al. 2007; African buffalo, Hay et al. 2008). For instance, predation risk, social and reproductive opportunities, and the distribution and abundance of forage may have a profound influence on group sizes in a number of mammalian systems (Baird and Dill 1996; Clutton-Brock et al.

1999; Hebblewhite and Pletscher 2002), but their specific influence on male group size in sexually segregated species has received limited empirical attention (e.g., Waterman 1997; Fischhoff et al. 2009). Generally, male social behavior and grouping patterns are thought to be driven more by spatial and temporal dispersion of mating opportunities than by dispersion of food resources or by variation in predation risk (Mitani et al. 1996; Nunn 1999; Sánchez-Prieto et al. 2004).

In African savannah elephants (*Loxodonta africana*), in common with many ungulates (reviewed in Conradt 1998), males and females frequently aggregate in same-sex groups (Shannon et al. 2006; Evans and Harris 2008). Elephants also show extreme variation in group sizes, both in single-sex groupings and in mixed-sex aggregations (Lee et al. 2011b; Moss and Lee 2011). Specifically, female African

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elephants can be found in family social groups, which may consist of as few as 2 or as many as 50 (mean = 7, standard deviation [SD] = 4) adult females and their immature offspring (Archie et al. 2006; Moss and Lee 2011). Over the course of hours, days, or weeks, families may fission into smaller groups or fuse into larger groups, generating a large range of experienced group sizes (Archie et al. 2006). At maturity, males disperse from their natal family, after which they spend their time either alone, in aggregations with other males ranging in size from 2 to 40 (mean = 3, SD = 2) individuals, or with groups of females that are not their natal families (Chiyo et al. 2011; Lee et al. 2011b; Poole et al. 2011); these latter associations are most likely to occur when females are in estrus (Poole 1989b; Poole and Moss 1989). The probability of seeing a male elephant alone versus in a group varies with age; the percentage of sightings in which males are alone ranges from 5% in males aged up to 19 years, to 25% in adult males aged 50 years and older (Lee et al. 2011b). The particularly fluid fission–fusion social system of male elephants and the large range of group sizes they exhibit make them an especially interesting system in which to examine determinants of group size.

Predictions

Here, we investigated the effects of 1) the abundance or quality and dispersion of food resources, 2) predation risk, and 3) mating opportunities on male grouping patterns in the African elephant. We specifically tested the following predictions.

(1) We predicted that male elephants would occur in larger groups in areas with high Normalized Difference Vegetation Index (NDVI), a simple graphical indicator that relies on satellite images to assess the extent of live green vegetation in a geographical area. NDVI is strongly positively correlated with primary production (Prince 1991), forage quality (Hamel et al. 2009; Ryan et al. 2012), and plant phenology (Reed et al. 1994). In many mammalian species, abundant or clumped food resources are known to encourage aggregation (Skogland 1989; Symington 1988; Basabose 2004; Atwood 2006). Access to high-quality forage is especially important for males of most polygynous mammalian species as their reproductive efforts often entail substantial energetic costs (e.g., Poole 1989a; Deutsch et al. 1990; Forsyth et al. 2005; Lane et al. 2010; Garel et al. 2011; Crocker et al. 2012). For male elephants, access to high-quality forage is important because their reproductive success depends on their body size and condition, and they exhibit nearly indeterminate growth, gaining stature and body mass throughout most of their lives (Roth 1984; Poole 1989b; Lee and Moss 1995; Hollister-Smith et al. 2007; Lee et al. 2013).

(2) We predicted that male elephants would occur in larger groups the further away they were from protected areas, as a result of increased anthropogenic mortality risk. We also predicted that the formation of larger groups of male elephants when NDVI is high (prediction 1, mentioned previously) and preference of males for high NDVI locations would be attenuated outside of protected areas, particularly in the dry season when such areas tend to be associated with human and livestock presence (Kioko et al. 2006). Specifically we, i) examined the influence of the interaction between distance from a protected area and NDVI on group size, to test whether males' responses to anthropogenic risk moderated their response to NDVI and ii) examined whether selection for locations with higher than average NDVI inside and outside protected areas by elephants was influenced by the anthropogenic mortality risk.

Individuals of many species aggregate into groups when in open habitats to minimize predation risk through improved predator detection (Ebensperger et al. 2006), cooperative defense (Dublin

1983; Griffith 1988; Shank 1977), and reduction in an individual's probability of being attacked once detected (Foster and Treherne 1981; Hebblewhite and Pletscher 2002; Childress and Lung 2003). Predation risk may encourage individuals to remain solitary or in smaller groups in order to minimize detection by predators in habitats with adequate cover (Hebblewhite and Pletscher 2002). Individuals and groups can also minimize predation risk by changing their spatial and temporal ranging patterns to minimize encounters with predators (Heithaus and Dill 2002; Eldegard et al. 2012), sometimes at the cost of reduced forage quality (Hebblewhite and Merrill 2009).

Humans are currently the major "predator" of adult elephants, killing them for ivory or meat, or causing retaliatory wounding or killing of elephants that raid cultivated crops or compete with livestock for forage and water (Haigh et al. 1979; Douglas-Hamilton 1987; Prins et al. 1994). In Amboseli, hostile elephant–human interactions resulting from crop-raiding or competition with livestock for water is a major cause of adult elephant mortality, accounting for 67% of deaths (Moss 2001). These hostile interactions are primarily restricted to land outside the protected areas or at their boundaries because livestock and human presence inside the protected areas (other than tourists) are quite limited (Kangwana 2011). In addition, elephants show strong avoidance of sounds and odors associated with local Maasai and their livestock, indicating that they perceive local people and their livestock as a direct threat to their safety (Bates et al. 2007; Kangwana 2011). Further, evidence from studies within Amboseli and elsewhere suggests that elephants perceive locations further away from a protected area as risky (Douglas-Hamilton et al. 2005; Galanti et al. 2006; Graham et al. 2009); similar behavior has been observed in Nubian ibex, (Iribarren and Kotler 2012), Dall's sheep (Frid 1997), and Eurasian lynx (Bunnefeld et al. 2006) in relation to human hunters.

(3) We predicted that male elephants in mixed-sex groups would occur in larger numbers when the group contained an estrous female than when the group did not contain an estrous female. When reproductive opportunities are spatially or temporally rare, temporary breeding aggregations may form, as in sperm whales (Christal and Whitehead 1997) and Cape ground squirrel (Waterman 1998). Female elephants in estrus are scarce because each female is in estrus for only 3–6 days every 3–9 years (Moss 1983), and females are mobile and may range widely (Thouless 1996). Intrasexual competition for access to estrous females is, therefore, intense among male elephants. Male African savannah elephants employ a roving male reproductive strategy in which males contact multiple groups of conspecifics in search of mating opportunities in order to increase their chance of locating receptive females; this roving strategy is intensified when males are in musth (Poole and Moss 1981, 1989; Barnes 1982). Among mammals, similar roving strategies are seen in Cape ground squirrels (Waterman 1997), American red squirrels (Lane et al. 2009), African buffalo (Prins 1989; Turner et al. 2005), American bison (Komers et al. 1992), and sperm whales (Whitehead and Arnbom 1987; Whitehead 1993).

MATERIALS AND METHODS
Study area and study population

The Amboseli elephant population, which consists of approximately 1400 elephants, has been intensively studied by the Amboseli Elephant Research Project (AERP) since 1972. These

elephants roam the Amboseli ecosystem (size: ca., 8000 km²) that stretches from the Amboseli National Park in southern Kenya to the northern slopes of Mt. Kilimanjaro, Tanzania, and includes 2 protected areas that are in close proximity to each other, Amboseli National Park and Kimana Wildlife Sanctuary (see Figure 1). "Protected" here is used to refer to wildlife conservation areas in which the presence of local humans and their livestock is illegal or severely limited. The land surrounding the protected areas of Amboseli National Park and Kimana Wildlife Sanctuary includes small local conservancies promoting ecotourism, but these conservancies, and the majority of the land that has remained under communal ownership in a group ranch model, allow livestock and wildlife movements throughout the area (Browne-Nunez 2011). Agriculture is concentrated around human settlements that occur near the villages of Namelok and Kimana (not to be confused with Kimana Wildlife Sanctuary, a protected area), and near the town of Oloitokitok. Namelok and Kimana represent small fenced agricultural pockets that were excised from the group ranches in the 1990s (Kangwana 1993). All 3 of these agricultural areas are within approximately 20 km of Amboseli National Park (Figure 1).

Average annual rainfall within Amboseli National Park is 340 mm, occurring primarily during the long rainy season (March to May) and the short rainy season (November to December), but the amount of rain and its monthly distribution is highly variable from 1 year to another (Croze and Lindsay 2011). Vegetation consists of open or bushed grassland in the northern and eastern parts of our study area, *Acacia* grasslands in the south, and patches of swamps scattered throughout. Swamps form a dominant part of the landscape, constituting 12% of the area of Amboseli National Park, and represent a foraging refuge in dry seasons. Kimana Sanctuary contains a portion of swamp as well.

Determination of male group sizes and detection of estrous females

We collected data on all sightings of male elephants during near-daily drives in the study areas (Figure 1) from May 2005 to May 2008. Most sightings were made between May and December of each year. Daily drives were roughly evenly allocated to areas within and outside the protected areas. Outside protected areas, we allocated effort particularly to the east and south of Amboseli National Park where previous experience informed us elephants were likely to be located (Figure 1). During these 6–8 h long daily drives, we recorded, for each group or individual we encountered, i) the date, time, and location using a hand-held Global Positioning System (GPS), ii) the number of individual males in the group, and iii) whether females were present or not. We defined an elephant group as a spatially cohesive and behaviorally coordinated aggregation of 2 or more elephants clustered within a radius of 100 m or less (see Archie et al. 2006 for a similar definition and description of group size). Pairs or groups of elephants were considered behaviorally coordinated if they had similar activity patterns, or interacted during a 30-min observation window. For each sighting of a mixed-sex group, we counted all independent adult males and noted whether any females present were in estrus. Our study encompassed areas used by elephants originating from many geographic areas in and around Amboseli National Park (Figure 1); for elephants originating in Amboseli, we knew individual identities and ages. However, many males in this study came from outside the Amboseli study population; for these males, we created individual identities and determined whether they were adult by using well-developed morphological and behavioral criteria (Moss 1996).

Our knowledge of elephant IDs enabled us to avoid double counting of elephant social groups each day we were in the field. All males that were found alone or in an all-male group were also considered independent adults because they had dispersed from their natal family. Estrus in females is easily detectable and manifests as a specific set of female behaviors (wariness, "estrous walk," and consorts; Moss 1983) that occur only during estrus and when males are present.

Estimation of distance of elephant sightings from a protected area boundary

GPS locations for most elephant sightings ($N = 2200$) were taken as close to the elephants as was feasible given the terrain and the goal of avoiding disturbance to the animals. In practice, this meant that readings were usually taken within 10–30 m of the animals, but sometimes as much as approximately 50–100 m away from the animals. Using ArcGIS software (Version 9.3.1, ESRI, Redlands, CA), we created a boundary feature for each of the protected areas in our study site (Amboseli National Park and Kimana Wildlife Sanctuary) and plotted elephant sightings within and outside protected areas. For each elephant sighting that we had a GPS record for, we determined its distance to the nearest protected area boundary feature using ArcGIS.

Spatial and temporal variation in NDVI

We determined primary productivity patterns, assessed using the NDVI for Amboseli National Park, Kimana Sanctuary, and adjacent areas that we monitored in order to locate elephants (Figure 1). All locations of elephant sightings were allocated to a 1-km grid square, so we could determine primary productivity around each sighting. We therefore obtained, from 16-day composite images at the 1-km resolution (http://www.vito-eodata.be), 3 sets of monthly NDVI values: 1) individual NDVI values in the 1-km grid square around each elephant sighting during the calendar month the observation was made; 2) mean NVDI values across Amboseli National Park, for each month of all the study years; and 3) mean NDVI values for the area outside of protected areas that we monitored for elephant sightings (Figure 1), for each month during the years of the study.

Statistical analyses

Before testing our 3 main predictions, we performed 2 tests. First, we validated that NDVI measures reflected the patterns of plant growth expected for the rainfall regime within the region (see Supplement 1 and Supplementary Figure S1). Second, we evaluated our predictors for multicollinearity by estimating their variance inflation factors (VIF; Graham 2003) because previous studies have shown that primary productivity and the occurrence of estrous females, 2 of our predictor variables, are correlated (Lee et al. 2011a; Poole et al. 2011). However, we did not observe evidence of significant multicollinearity in our data set as all VIF were less than 2 (results are not shown).

Multivariate models of elephant group size

For our multivariate models, we used group size as the dependent variable. As predictor variables, we used 1) primary productivity (NDVI) at each elephant sighting, 2) distance of elephant sightings from the nearest protected area center (Amboseli National Park or Kimana Sanctuary), and 3) group type, defined as i) all-male groups, including single males, ii) mixed-sex groups without
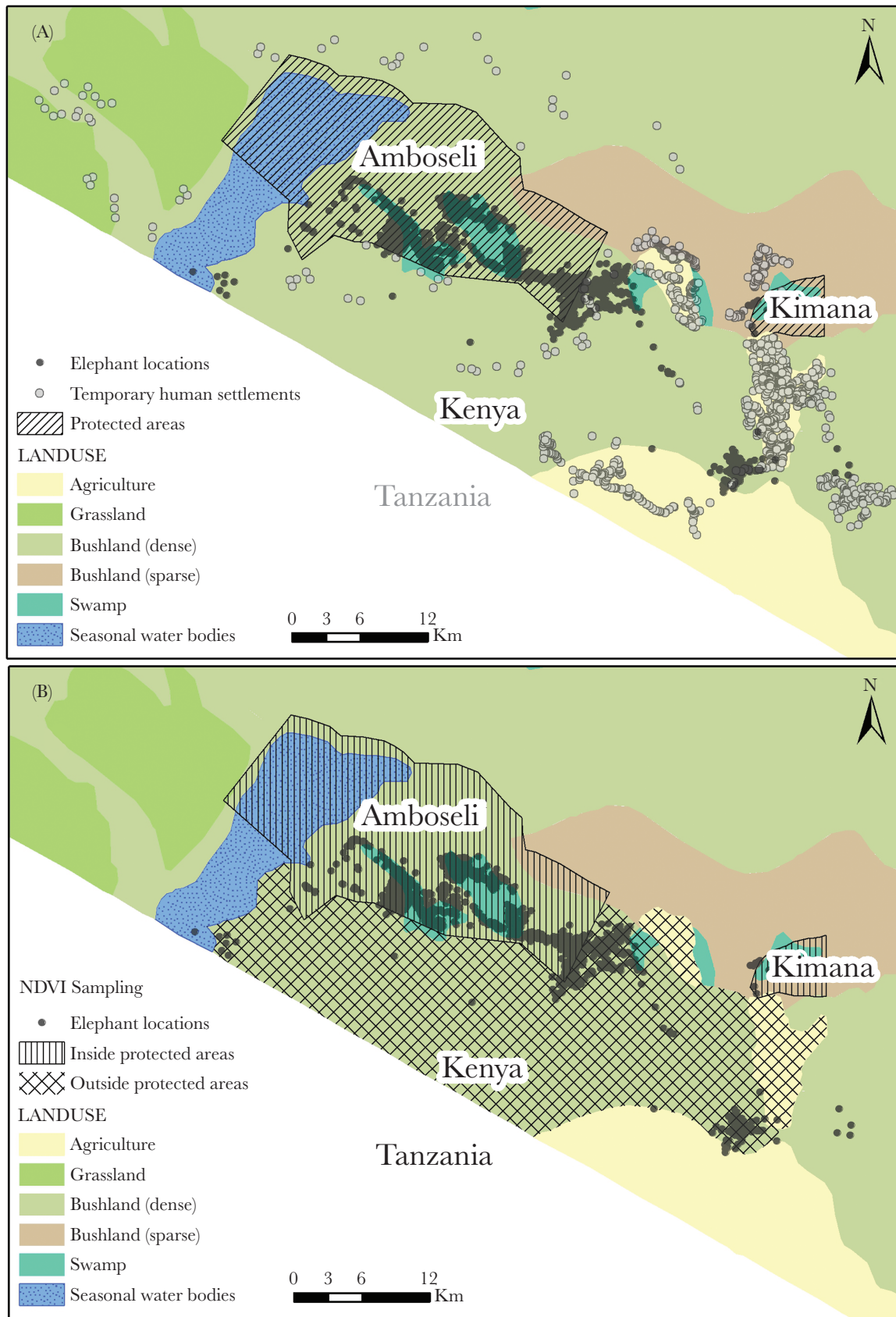
Figure 1
Map of the Amboseli ecosystem depicting (A) the locations of temporary human settlements and (B) the regions inside and outside of protected areas where NDVI was estimated. Both panels show the locations of elephant sightings, general patterns of land use, and habitat type.

an estrous female, and iii) mixed-sex groups with an estrous female. After exploring a variety of regression models, we selected a zero-truncated negative binomial regression model with the variance parameterized as a linear function of the mean (neg.binom1) as the best fitting model based on Bayesian Information Criteria (BIC; Supplementary Table S1, Schwarz 1978). Using this zero-truncated negative binomial regression approach, we then created a set of 15 models that consisted of an intercept-only model, models with each single predictor variable only, and then models that had a unique combination of 2 or 3 variables and their interactions. We considered the model with the smallest BIC to be our best model.

We also compared 3 representations of distance in a multivariate model of group size to evaluate "risk perception" of locations by elephants with respect to a protected area boundary (Supplement 2). First, we treated locations within and outside of a protected area as differentially "safe," or as a function of distance from a center of the protected area. Second, we treated all locations inside a protected area as equivalent in terms of risk and locations outside as differentially risky or as a function of distance from a protected area boundary. Third, we treated all locations inside protected areas as equivalently safe and all locations outside as equivalently risky. The best expression of distance, based on a BIC, was the one in which we treated distance in and out of protected areas as differentially "safe," that is, as a function of distance from a center of the protected area (Supplementary Table S2). Specifically, distances for locations inside and outside the protected area with respect to a protected area boundary were assigned negative and positive values, respectively, whereas locations at the boundary were assigned a value of 0. Hereafter, we describe our distance measures as "distance from a protected area center" to indicate that the animals were sensitive to distance from boundaries both inside and outside the protected areas.

Finally, we observed a larger proportion of mixed-sex groups inside than outside protected areas: 340 of 352 mixed-sex groups *without* estrous females and 32 of 33 mixed-sex groups *with* estrous females, were inside a protected area. Such social and spatial segregation (i.e., variation in spatial locations according to social group type) could potentially cause a spurious effect of distance from a protected area center or social group type on elephant group size. We, therefore, tested for this potential bias by conducting 3 post hoc analyses. Specifically, we divided the data into 3 subsets: 1) only all-male social groups, 2) only mixed-sex groups, and 3) all sightings inside a protected area. Then, for each subset, we repeated our models of group size, including the predictor variables from our best model; distance from a protected area center, NDVI, the interaction between NDVI and distance from a protected area center and social group category whenever applicable (see Results). These data sets were homogenous with respect to spatial segregation by group type, and we expected that in the absence of bias in our final model due to spatial segregation by group type, their results should be similar to those of our final model (combining all subsets of data).

Influence of anthropogenic mortality risk on elephant selection for highly productive locations

We compared values of mean primary productivity associated with each elephant sighting inside Amboseli National Park with the average primary productivity across the entire area of Amboseli National Park during the same month as the sighting. We used a sign test for matched pairs to test the hypothesis that male elephants seek higher than average areas of productivity. We repeated this

analysis 3 times: 1) over the entire study period regardless of season, (2) for the wet season months only, and (3) for the dry season months only. We also repeated this analysis outside protected areas by comparing the primary productivity value for each elephant sighting outside of a protected area with the mean primary productivity over the entire region we monitored outside of protected areas, during the same period.

All statistical tests were performed using R statistical software (R Core Team 2012). We used glmmADMB package, Version: 0.7.2.12 (Fournier et al. 2012; Skaug et al. 2012) for multivariate statistical analyses. Means are reported with 1 SD as mean ± SD unless otherwise stated.

RESULTS

Variation in the number of males in elephant groups

We recorded 2281 sightings of male elephants in 32 months between May 2005 and May 2008; we obtained GPS locations for 2200 of these sightings. The 81 sightings for which we missed GPS location data consisted of 71 all-male sightings and 10 mixed-sex sightings and occurred in a range of locations scattered throughout the study area. Male elephants were observed as solitary individuals ($n = 836$ sightings, 37% of observations), in all-male groups ($n = 1050$ sightings, 46%), and in mixed-sex groups ($n = 395$ sightings, 17%, Figure 2). In a simple bivariate analysis, male groups tended to be somewhat larger in the wet season than in the dry season (wet season mean = 3.1 ± 3.1, $n = 557$ sightings; dry season mean = 2.2 ± 1.7 males, $n = 1724$ sightings). Male groups also tended to be larger outside a protected area than inside a protected area (bivariate analysis: outside mean = 3.5 ± 3.0 males, $n = 546$ sightings; inside mean = 2.1 ± 1.7 males, $n = 1654$ sightings).

Male group sizes were similar in all-male groups and in mixed groups without estrous females (bivariate analysis: mean for all-male groups, including lone males = 2.5 ± 2.2, $n = 1886$ sightings; mean for groups without estrous females = 2.2 ± 2.1, $n = 362$ sightings). Male group sizes tended to be somewhat larger when an estrous female was present in the group (mean = 3.1 ± 1.9, $n = 33$ sightings). The mean number of males in mixed-sex groups without estrous females was 2.2 ± 2.0 inside a protected area ($n = 340$) and 3.7 ± 4.1 outside a protected area ($n = 12$). In mixed-sex groups with estrous females, all but one of our sightings was inside a protected area (mean = 3.1 ± 1.9, $n = 32$); the single sighting with an estrous female outside a protected area included 4 adult males.

NDVI, anthropogenic mortality risk, and estrous females influenced elephant group sizes

In our multivariate models, we used the 2200 sightings for which we had GPS locations and excluded 81 sightings without GPS locations. The most parsimonious model predicting group size in male elephants indicated that male elephants aggregated in larger groups when farther away from a protected area center, when primary productivity was high, and when estrous females were present (Table 1, Figure 3). This model explained significantly more deviance than the intercept-only model (deviance = 619, df = 5, $P < 0.001$). This model also included a negative interaction between primary productivity and distance from a protected area center, indicating that elephants formed larger groups further away from a park center when primary productivity was low, but this effect was weaker
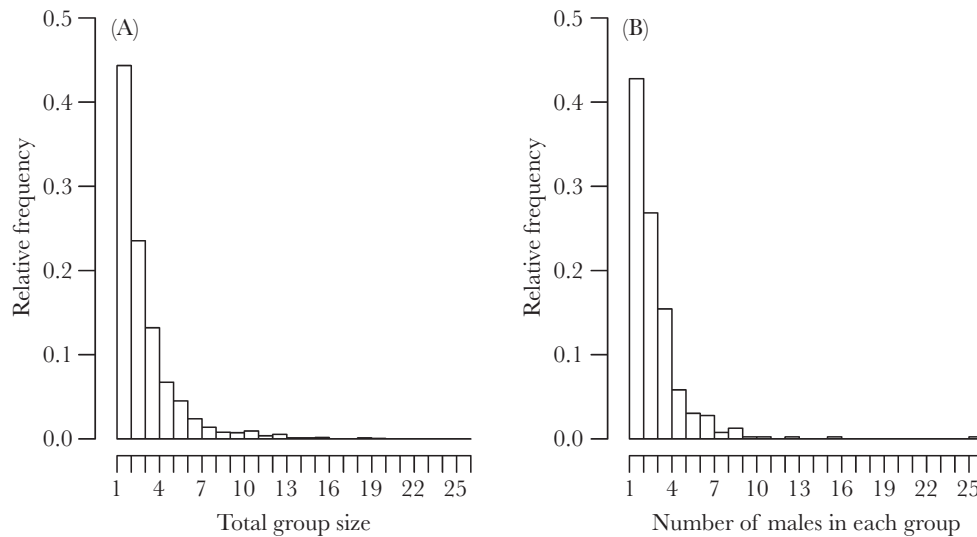
Figure 2
The distribution of (A) the sizes of all-male groups, including lone males (N = 1886 sightings) and (B) the numbers of adult males in mixed-sex groups (N = 395 sightings) in Amboseli National Park and the surrounding areas during May 2005–June 2008.

Table 1

Standardized coefficients for the independent variables from our best zero-truncated negative binomial regression model (N = 2200 elephant sightings with GPS locations, inside and outside the park combined)

Independent covariates	Estimate	Standard error	Z value	P value
Intercept	0.749	0.044	17.17	<0.001
Primary productivity	0.209	0.016	12.75	<0.001
Distance to a protected area center	0.311	0.015	20.45	<0.001
All-male groups relative to mixed-sexed groups without estrous females	−0.111	0.048	−2.31	0.021
Estrous females present relative to estrous females absent (mixed-sex groups)	0.489	0.117	4.17	<0.001
Primary productivity × distance to a protected area center	−0.053	0.009	−6.15	<0.001

when primary productivity was high (Figure 3). The interaction between productivity and distance away from safety was largely driven by males in all-male social groups: we inferred this pattern from the fact that the strongest interaction effect was at distances greater than 10 km from a protected area center (Figure 3), but we never observed a mixed-sex group further than 9.5 km from a protected area center (Table 2). In contrast, the furthest distance male elephants were recorded from a protected area center was 21.6 km, reflecting the limits of our surveillance of the ecosystem; it is likely that male elephants traveled further than this from protected area centers.

Finally, we also obtained similar results when we tested for bias that would result if certain group types only occurred in certain locations, that is, when we divided the data into 3 subsets (only all-male social groups, only mixed-sex groups, and all sightings inside a protected area). Specifically, we found that primary productivity, distance to a protected area center, and group type still predicted group size even when we controlled for the influence of spatial location and social segregation (Table 2), suggesting no confounding effect of spatial location or social segregation on our best model. However, the interaction between productivity and distance from a park center was not statistically significant for data from only sightings inside the park, perhaps because of limited variation in risk and productivity gradients in this data

set (however, the effect signal was in the expected direction; Table 2).

Elephants were less selective of highly productive locations in the presence of anthropogenic mortality risk

Primary productivity was higher, on average, outside protected areas (which included croplands) than inside, and this pattern persisted regardless of whether we combined wet and dry season data (mean outside NDVI = 0.341; mean inside NDVI = 0.230; N = 41, t_{64} = 4.318, P < 0.001), or whether we considered wet season productivity only (mean inside NDVI = 0.255, mean outside Park NDVI = 0.365, N = 18, t_{32} = 3.573, P = 0.001) or dry season productivity only (mean inside NDVI = 0.211, mean outside NDVI = 0.323, N = 23, t_{32} = −2.888, P = 0.007). Both inside and outside of protected areas, elephants generally chose areas of higher productivity (Table 3). Inside protected areas, elephants were much more likely to be found in areas with higher than average productivity; such areas tended to overlap with the large, permanent swamps. This pattern was especially true during the dry season: elephants were less selective of highly productive locations during the wet season than during the dry season (Table 3). Outside protected areas, the opposite pattern was seen: elephants were less

selective of highly productive locations during the dry season than during the wet season (Table 3).

DISCUSSION

We found strong support for the prediction that male African elephants would aggregate into larger groups in areas with high primary productivity compared with areas with low productivity. This result shows that forage quality and abundance are major drivers of sociality in male elephants (see also, Leuthold 1976; Western and Lindsay 1984) as in many other large mammals (Underwood 1982; Basabose 2004; Isvaran 2007; Winnie et al. 2008).

Distance from a protected area center, a proxy for potential anthropogenic mortality risk, also predicted male elephant group sizes. This result suggests that elephants perceive areas further from the core of protected areas as increasingly risky. Humans are a major cause of mortality and injury to adult elephants (Moss 2001; Obanda et al. 2008). The nomadic pastoralists in Amboseli shift their settlements periodically and also shift fine-scale grazing locations for their livestock on a daily basis, creating a dynamic mosaic of risk from anthropogenic mortality during the day. Under such a complex and dynamic anthropogenic mortality risk, elephants may treat varying distances from protected areas as differentially risky because the probability of escaping swiftly into a safe refuge to
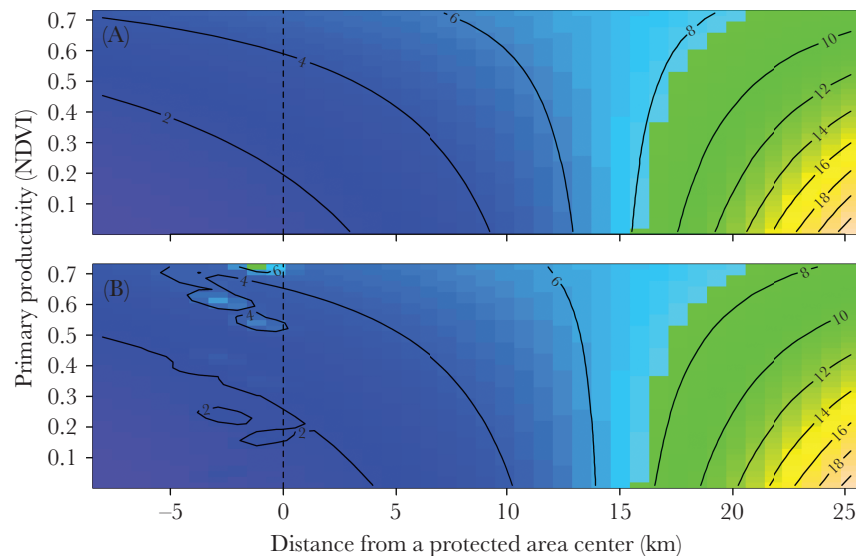

Figure 3

A multivariate model of elephant group size as a function of NDVI and distance from protected area centers; the protected area boundary is indicated by the dashed line at zero distance from a protected area and group size is represented by contour lines and changing color intensities. In panel A, the model assumes equal frequency of all social groups; in panel B, the perturbations on the contour lines indicate the effect of estrous females on group size; these effects are restricted to areas near the protected area boundary.

Table 2

Comparison of standardized coefficients for independent variables predicting the number of males in elephant groups from different subsets of the data

Independent covariates	Estimate	Standard error	z value	P value
Mixed-sex groups ($N = 385$ elephant sightings with GPS locations)				
Intercept	0.588	0.044	13.4	<0.001
Primary productivity	0.199	0.039	5.06	<0.001
Distance to a protected area center	0.101	0.041	2.49	0.013
Estrous females present relative to estrous females absent	0.530	0.116	4.58	<0.001
Primary productivity × distance to a protected area center	0.180	0.039	4.57	<0.001
All-male groups ($N = 1815$ elephant sightings)				
Intercept	0.676	0.020	34.06	<0.001
Primary productivity	0.192	0.018	10.59	<0.001
Distance to a protected area center	0.326	0.016	20.21	<0.001
Primary productivity × distance to a protected area center	−0.055	0.010	−5.61	<0.001
Inside the park ($N = 1654$ elephant sightings)				
Intercept	0.650	0.043	14.97	<0.001
Primary productivity	0.103	0.020	5.05	<0.001
Distance to a protected area center	0.256	0.025	10.14	<0.001
All-male groups relative to mixed-sex groups (estrous females absent)	−0.189	0.050	−3.76	<0.001
Estrous females present relative to estrous females absent (mixed-sex groups)	0.481	0.117	4.1	<0.001
Primary productivity × distance to a protected area center	−0.022	0.025	−0.86	0.392

Table 3

Average productivity in the Amboseli ecosystem compared with average productivity of locations where elephants were sighted

Season	Mean ± SD NDVI for the entire area monitored	Mean ± SD NDVI for elephant locations only	Number of months (N)	Sign test (positive)	P value
Inside the park					
All year round	0.182 ± 0.051	0.263 ± 0.053	17	0	<0.001
Wet season	0.212 ± 0.081	0.294 ± 0.079	5	0	0.063
Dry season	0.170 ± 0.031	0.250 ± 0.034	12	0	<0.001
Outside the park					
All year round	0.307 ± 0.117	0.341 ± 0.162	30	10	0.099
Wet season	0.349 ± 0.108	0.414 ± 0.166	12	2	0.039
Dry season	0.279 ± 0.116	0.292 ± 0.143	18	8	0.815

Only data for months when elephants were sighted are shown, and data for primary productivity inside and outside the park are shown separately.

minimize anthropogenic mortality risk diminishes with increasing distance from a protected area core.

This result is also generally consistent with observations in other species showing increases in group size in response to increased risk of mortality from anthropogenic causes (e.g., Jedrzejewski et al. 2006; Wilson et al. 2007) or from predation by carnivores (Tambling et al. 2012). Specific support for the idea that predation risk increases with increasing distance from a safe refuge comes from studies of Dall's sheep, *Ovis dalli* and Nubian ibex, *Capra nubiana*. In Dall's sheep, group size increased with distance from cliffs that were safe from predators (Frid 1997), whereas in Nubian ibex, the "giving up density" or the amount of food left in a patch after exploitation—a measure of predation risk—was positively correlated with distance from predator safe cliffs and slopes (Iribarren and Kotler 2012). Further indirect support specific to elephants comes from elephant movement studies in protected areas interspersed within human-dominated landscapes. In these landscapes, elephants often move between protected areas in haste or at night, preferring areas with vegetation cover for concealment (Galanti et al. 2006; Graham et al. 2009). Similar nocturnal movement behavior through human-dominated landscapes has been observed in elephants moving between Amboseli and Kimana Wildlife Sanctuary (Douglas-Hamilton et al. 2005).

Our model revealed an interaction between distance from protected areas and forage abundance. When male elephants were distant from a protected area, they formed larger groups when primary productivity was low (dry season) than when primary productivity was high (wet season). This pattern suggests that elephants are sensitive to seasonal variation in potential anthropogenic mortality risk because hostile human–elephant interactions in the Amboseli ecosystem are usually higher in the dry season than in the wet season (Kioko et al. 2006; Kangwana 2011). A high number of elephant injuries in the dry compared with the wet season from hostile human–elephant interactions has also been observed elsewhere in Kenya (Mijele et al. 2013). Elephants in our study were likely responding to increased potential anthropogenic mortality risk in the dry season by forming larger groups because large group size may enhance cooperative defense against predation as observed elsewhere (Dublin 1983; Barnes et al. 1991; Buij et al. 2007). Alternatively, they may have been responding to dry season resource distribution, which is likely to consist of a few, discrete foraging patches, for example, around swamps, water sources, and patchily distributed *Acacia* browse (Stokke and du Toit 2002). However, this later explanation is very unlikely given that elephants did not appear to select highly productive patches in the dry season when outside of protected areas (see below regarding elephant selection

of locations that are more productive). In the wet season, elephants may avoid areas where humans or livestock are present because the benefits of preferentially using such areas are lower when forage and water are generally abundant everywhere. Elephants may then remain in groups that are smaller than expected based on productivity to minimize detection by humans.

The interaction between distance from a protected area center and primary productivity was largely driven by males in all-male groups, and not males in mixed-sex groups. One reason for this is that families may be more risk averse than are all-male groups. In support, in this study, it was not common to observe mixed-sex groups more than 10 km from a protected area boundary. Similar patterns were observed in a recent study by Kioko et al (2013), which found that male elephant groups were more likely than mixed-sexed groups to be found outside Lake Manyara National Park where the risk of poaching was high. On the other hand, female groups were more likely than all-male groups to be located inside the relative safety of protected areas (for detailed analysis of female group movements, see Croze and Moss 2011).

When male elephants were outside a protected area, they were more selective of areas with high primary productivity in the wet season than in the dry season. We hypothesize that selection for highly productive locations in the dry season was constrained by the fact that anthropogenic mortality risk from conflict over croplands (areas of high productivity) is higher in the dry season than the wet season (Kioko et al. 2006; Kangwana 2011). Inside protected areas, where males experience a lower risk of mortality from hostile interactions with humans, elephants were indeed selective of locations with higher productivity all year round, as we predicted. Similar patterns of selectivity for high NDVI locations in the absence of predators has been reported in other species (e.g., Hansen et al. 2009; Smallidge et al. 2010) and selection of areas with lower food quality or abundance to minimize predation risk has also been observed in a number of species (guanaco, Acebes et al. 2013; Eurasian lynx, Basille et al. 2009; elk, Hebblewhite and Merrill 2009).

The number of adult males in elephant groups with estrous females was larger than the number of males in mixed-sex groups without estrous females. The roving male reproductive strategy employed by male African elephants should lead to male aggregation around estrous females (Poole et al. 2011). Although male elephants guard estrous females, competitive musth males seem to tolerate the presence of younger adult males, but do not tolerate the presence of other competitive musth males around estrous females (see also: Poole 1989b; Rasmussen 2005; Poole et al. 2011). This tolerance for younger males may account for the male aggregation

around estrous females that we observed in this study. A similar pattern of males aggregating around estrous females, leading to larger group sizes, is found in another nonseasonal African mammal, the Cape ground squirrel (e.g., Waterman 1998).

When food resources are positively correlated with predation risk, animals will trade-off predation risk for abundant forage (Lima and Dill 1990). We extend this result for male elephants by showing that males manage this trade-off by changing their grouping patterns in response to changes in the relationship between forage abundance and predation risk. In addition, forage abundance had a greater influence on male group size than the presence of mating opportunities, perhaps because mating opportunities were relatively rare events and appeared to be restricted in space. We also revealed a significant contribution of potential anthropogenic mortality risk on male group dynamics and corroborate an increasing influence of humans on behavior in wild animal populations (Palumbi 2001; Coltman et al. 2003). With diminishing wild habitats and expanding opportunities for elephant–human encounters, humans are likely to play an increasing role in the social evolution of elephants and perhaps many wildlife populations.

Finally, we have shown in earlier work on the Amboseli elephant population that male African elephants show mild preferences for associating with kin (i.e., with males to whom they are related; Chiyo et al. 2011) and that elephants also avoid mating with both maternal and paternal relatives (Archie et al. 2007). In combination with our current findings, these results demonstrate that male elephants choose social groupings in response to a range of nuanced and diverse predictors that include mating opportunities, forage abundance, kin relationships, and the risk of mortality caused by hostile interactions with humans.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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