

Group territoriality and the benefits of sociality in the African lion, *Panthera leo*

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We analysed 38 years of data on 46 lion prides in the Serengeti National Park, Tanzania, and found that territorial competition directly affected critical components of female fitness and that larger prides gained and maintained access to the highest-quality habitat. Neighbours had a significant negative effect on female reproductive success and survival, and larger prides were significantly more likely to maintain control of disputed areas and to improve the quality of their territories. Adult females were significantly less likely to be alone when a pride had more neighbours, suggesting sensitivity to risk of encounter. In most cases, the effects of intergroup territorial competition were associated only with prides that had not recently split (i.e. that were not closely related). Overall, males were more important in group-territorial competition than expected, and female mortality and wounding rates were significantly associated with male neighbours, suggesting that males may use lethal aggression to tip the balance of power in favour of their prides. Within the Felidae, only lions are consistently gregarious, and our research illustrates that numerical advantage in territorial competition is a primary benefit of group living in lions and may have been important in the evolution of lion sociality.

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Species ranging from social insects to primates are group-territorial. For these animals, numerical advantage in intergroup competition may be an important benefit of social grouping, but the precise relationship between group size and differential access to limiting resources has never been formally tested. Experimental work has shown that weakened groups lose territory to larger neighbours (Carlson 1986; Adams 1990) and that territory owners assess intruding groups based on relative group size (McComb et al. 1994; Heinsohn 1997; Wilson et al. 2001). Some evidence, largely anecdotal, also suggests that larger groups generally have a competitive advantage in territorial competition (e.g. Woolfenden & Fitzpatrick 1984; Grinnell et al. 1995; Mech et al. 1998; Wilson & Wrangham 2003). Although numerical advantage is often implicit in studies of group-territorial animals (e.g. Stacey & Ligon 1991; Lazaro-Perea 2001; Campbell et al. 2005), past research has not actually confirmed whether larger groups are more successful in territorial competition, primary because samples sizes have been too small (too few groups) and study periods have been too short.

Using 38 years of data on 46 lion prides in the Serengeti National Park, Tanzania, we present the first comprehensive analysis of the role of group size in territorial competition and demonstrate the long-term advantages of sociality in a territorial species. A lion pride is composed of 1–21 adult females (mean \pm SE = 4.64 ± 0.18), their dependent offspring, and a temporary coalition of 1–9 adult males. Although the pride is a stable social unit, it is a fission–fusion social group, in which individuals are typically found in a range of subgroup sizes and compositions. Lions are matrilineal, although roughly one-third of Serengeti females disperse to form a new pride (Pusey & Packer 1987). Males leave their natal pride by the age of 4 years and remain solo or form a coalition with other males (Pusey & Packer 1987). Male coalitions challenge one another for pride residency, and incoming males kill or evict dependent offspring sired by the previous coalition, so as to accelerate the mothers' return to sexual receptivity (Packer 2001). Females pool their cubs together into crèche groups (Packer et al. 2001). Litter size ranges from one to six cubs, and 98% of litters contain one to four cubs (Packer & Pusey 1987). Females live up to 18 years and males live up to 14 years (Packer et al. 1988).

Serengeti lions defend territories of a mean size of 56 km², with a range of 15–219 km² (Mosser 2008). Core areas are generally exclusive, with some overlap during the first years following pride fission (VanderWaal et al. 2009) or sharing of a male coalition. Territories shift slightly with the seasons and the associated shifts

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in prey density, but site fidelity is strong from one year to the next (Schaller 1972). Territories are defended through roaring, patrolling, scent marking and direct aggressive encounters. Previous research showed that lions are sensitive to relative group size in interpride territorial interactions. In playback experiments, females were more likely to approach (McComb et al. 1994; Heinsohn 1997) and responded more quickly (Spong & Creel 2004) to intruders (a loudspeaker) if their group outnumbered the intruders. Females also roared more often if they were in a subgroup that did not include all adult females in the pride (McComb et al. 1994; Heinsohn 1997; Spong & Creel 2004), potentially in an effort to recruit the distant pride mates.

We tested five hypotheses that examined the role of group size in territorial competition. First, in order for group-territorial behaviour to be subject to selective pressure, there must be fitness costs associated with territorial competition. We therefore predicted that prides faced with competition from larger neighbouring prides would suffer reduced per capita female reproductive success (i.e. lower per capita recruitment of surviving cubs), higher mortality and more frequent wounding.

Grouping patterns within a pride are not associated with foraging efficiency (Packer et al. 1990), thus our second hypothesis examined whether potential risks from neighbouring prides may account for the grouping patterns within each pride. Male chimpanzees form larger party sizes in territory border areas where they may encounter opposing groups (Bauer 1980; Wilson 2001), and group sizes of primates and ungulates are often larger in open habitat (Jarman 1974; Clutton-Brock & Harvey 1977), where animals are more visible and more vulnerable to attack (Watts 1990). Female lions gain direct reproductive benefits through the mutual defence of their cubs against the threat of infanticide, and crèche formation accounts for the most consistent grouping patterns within each pride (Pusey & Packer 1994). We therefore restricted our analysis to females without dependent cubs.

Larger subgroups usually 'win' isolated interpride encounters (Packer et al. 1990; Grinnell et al. 1995). Territory is probably gained or lost partly as a result of a series of such encounters, and our third and fourth hypotheses examined whether group size influences the outcome of territorial competition. We analysed the relationship between pride size and territory size, expecting that larger prides would defend larger territories. Next, we predicted that the larger of two prides would be more likely to gain contested space in areas of territorial overlap.

Finally, we predicted that group size determines access to resources. In the Serengeti, larger prides are located in higher-quality habitat (Mosser 2008), but this may simply reflect pride growth and success in productive areas and not necessarily preferential access to such habitat. We therefore examined the dynamics of territorial competition and predicted that larger groups would be associated with improvements in territory quality.

For each analysis, we also examined the roles of sex and relatedness in territorial behaviour. We expected intergroup territorial competition to be most intense between unrelated adult females. Lionesses are philopatric and presumably have the most at stake in long-term territorial competition; thus, females in opposing groups are expected to be especially hostile towards each other (Wrangham 1980; Cheney 1987; Boydston et al. 2001). Dispersing daughters establish territories adjacent to their natal pride (Pusey & Packer 1987), and thus, neighbours are often closely related. Genetic analysis has shown that relatedness can initially be as high between neighbouring prides as within the same pride, before declining as each pride breeds independently of each other (Packer et al. 1991). We therefore expected kin selection and inclusive fitness (Hamilton 1964) to influence patterns of intergroup competition.

METHODS

Study System

The 2700 km² study area is located in the Serengeti National Park, Tanzania, at the centre of the Serengeti–Mara ecosystem (Fig. 1a). The study area is transected by rivers and tributaries, and a southeast-to-northwest gradient of rainfall and soil type (Norton-Griffiths et al. 1975; Sinclair 1979) creates a transition from short-grass plains in the southeast to woodlands in the north (Packer et al. 2005). Serengeti lions have been studied continuously since 1966 (Schaller 1972; Bertram 1973; Hanby & Bygott 1979; Packer et al. 2005). The size of the study population has ranged between roughly 50 and 300 individuals in 5–30 prides. Observations taken during 1966–1983 were opportunistic and, beginning in 1984, one member of each study pride was radiocollared, and all subsequent monitoring has relied on both radiotelemetry and opportunistic sightings. Study prides were generally located at least once every 2 weeks, and individual lions were identified from natural markings. Research was conducted under Institutional Animal Care and Use Committee permit no. 0107A04903 from the University of Minnesota.

Mapping Territories

Pride territories were mapped from the sightings of adult females, and each observation of a female group was treated as a single observation. Adults females were defined as those at least 3 years of age, the age at which females first reproduce (Packer et al. 1988). Analyses were separated into 2-year time steps; 2 years is the average interbirth interval as well as the average tenure length for resident males (Packer et al. 1988) and 2-year periods increased the sample size per time step. Intervals started in November, the start of the wet season. Observations collected from radiotracking and opportunistic sightings were pooled together, as pride ranges derived from the different data types were similar (with an average overlap of 75%, $N = 25$ in 2003–2004). Prides that had been observed on at least 5 days in each year of a time step were included in the analysis. About 20% of the 2-year ranges were based on fewer than 20 observations, representing a trade-off between accuracy and biasing against less frequently observed prides that occupied fringe areas of low-quality habitat. To test for effects of small sample size, we randomly subsampled (6 random subsets of 15 observations each) from the 2-year data sets of 10 well-observed prides. The ranges based on the subsets differed little from those based on the full data set (on average, subset ranges were 2% larger and overlapped with the full-data range by 93%). Thus, including pride ranges based on relatively small sample sizes did not introduce significant biases into the pride-range estimates.

Using ArcView version 3.2 (Environmental Systems Research Institute, Inc., Redlands, CA, U.S.A.), we determined pride ranges from utilization-distribution maps of lion sightings, created using a fixed kernel with a smoothing parameter (h) of 3000 m, which is the mean distance moved by a lion in 1 day plus one standard deviation. Territory boundaries were defined as the 75% contour (kernel density isopleth), and core area boundaries were defined as the 50% contour. Because of the potential sensitivity of kernel density estimates to sample size (Anderson 1982; Worton 1987, 1989; Harris et al. 1990; Hemson et al. 2005), we chose a 75% contour as a less biased estimate of territory area and location. We also calculated the area (km²) of the 75% kernel as well as the coordinates of the centre of activity for each pride's 2-year territory. For some analyses, territory maps were converted to grid maps of 1 km resolution.

Territory Quality

Mosser (2008) used these same data to determine the landscape characteristics that best define the fitness value of the Serengeti landscape. This analysis examined the spatial correlations between female 2-year reproductive success and six landscape variables (distance to rivers, distance to river confluences, distance to kopjes, vegetation type, prey density and rainfall). Proximity to river

confluences was significantly correlated with reproductive success, to the exclusion of all other explanatory variables in a multivariate model. This result corroborated the findings of Hopcraft *et al.* (2005), which revealed the relationship between landscape characteristics (rather than prey abundance) and hunting success. We therefore based landscape value on proximity to confluences and mapped the distance to nearest confluence on a scale of 0–100 within the study area (Fig. 1c), where 100 corresponds to grid cells

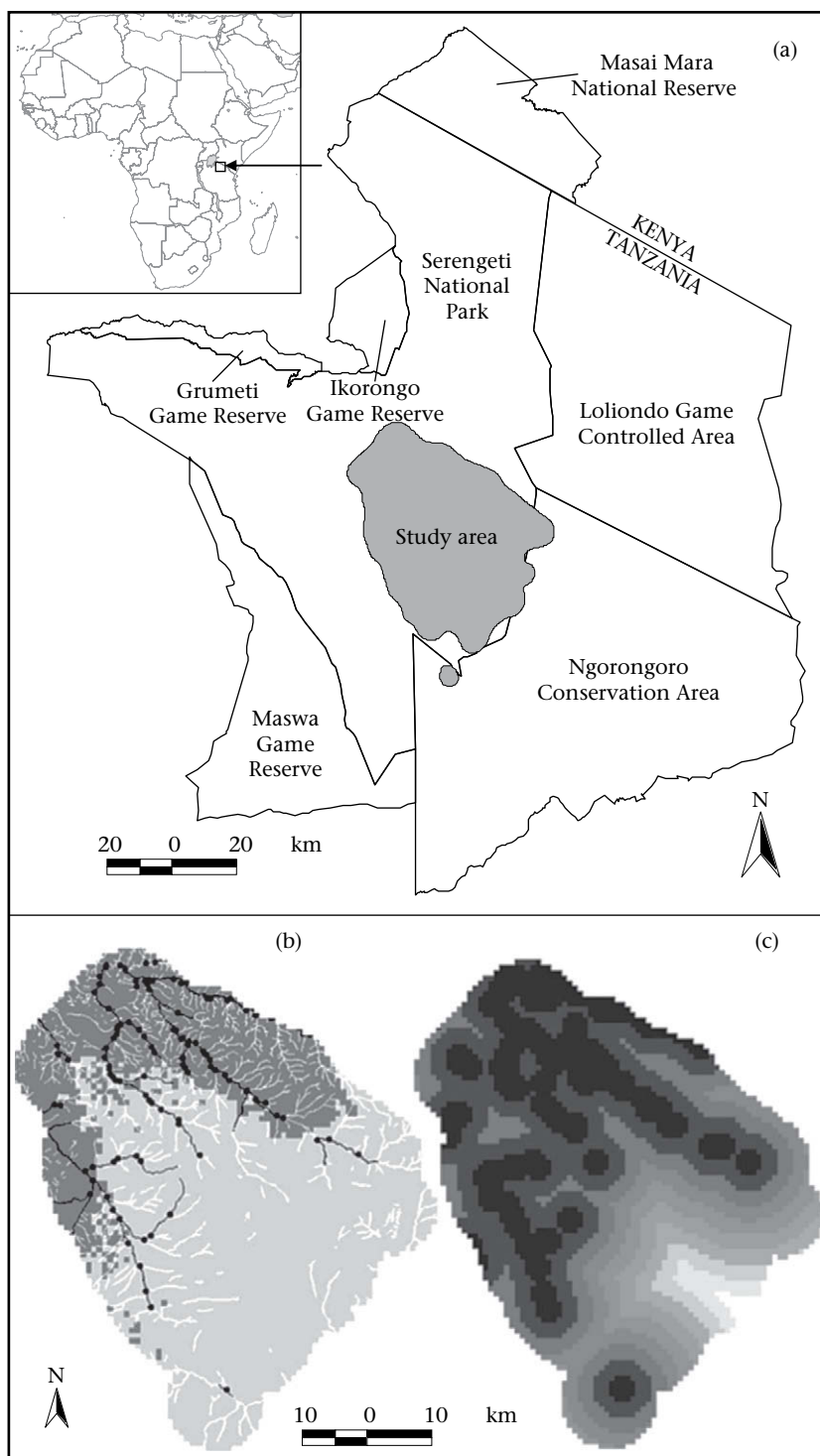


Figure 1. (a) The Serengeti–Mara ecosystem and the lion study area (grey fill). (b) Landscape features: major rivers (black lines), confluences (black circles), tributaries (white lines) and habitat type (light grey: plains, dark grey: woodlands). (c) Landscape quality, based upon distance from nearest confluence, scaled from 0 to 100 within the study area.

that contain river confluences and 0 corresponds to the maximum distance (28 km) from a confluence. Territory quality was calculated as the average value of the grid cells within a 75% territory contour.

Neighbour Variables

Prides were defined as neighbours if their core area boundaries were within 3 km of each other, which is the average distance moved per day (plus one standard deviation) and supports a reasonable possibility of interpride interaction and competition. We calculated the total number of adult female, adult male and adult neighbours for each pride for each 2-year time step. Males were not counted as 'neighbours' if they were resident in both the focal and a neighbouring pride.

For each pair of neighbouring prides, we determined whether the two prides had split within 2 or 10 years. This was used as a proxy for relatedness. Prides that have split within 2 years (in the previous or current time step) are closely related, whereas neighbours that have split within 10 years are still more closely related to each other than they are to the general population (Packer et al. 1991).

Prides at the edge of the study area were identified, as we lacked an accurate estimate of neighbours for these prides, and this factor was included in our statistical models. Finally, 17% of pride time steps were excluded from the analyses because the prides ranged, in multiple forays, more than 20 km from their long-term core areas.

Hypothesis Testing

First, we examined the impact of territorial competition on major components of fitness (Packer et al. 1988) by modelling female reproductive success, mortality and wounding rates against pride size, the number of take-over events, territory quality and neighbour variables, over 2-year intervals. Per capita female reproductive success was defined as the total number of cubs surviving to 1 year within a 2-year period divided by the number of adult females, for each pride. Because females pool their cubs into crèche groups, it is often difficult to know maternity; however, previous analyses showed that reproductive success does not significantly differ across the pride (Packer et al. 2001), thus averaging reproductive success is not problematic. Adult female per capita mortality and wounding rates were calculated as the number of adult females that died (based upon the date that an individual was last seen) or were wounded during a given month divided by the number of adult females present in the pride during that month. The monthly mortality and wounding rates were then averaged over the 2-year time step. In the analysis of wounding rates, we also controlled for the total number of observations for each pride in each time step. Pride size was measured in three ways: the number of adult females, the number of resident males and the number of adults. Pride size was calculated for each month, then averaged over all months within a 2-year time step. The number of resident male take-over events was totalled for each time step.

Our second hypothesis explored the risk of interpride encounter on female subgrouping patterns. We included only sightings of radiocollared adult females without dependent cubs, also excluding cases where they were with other pride mothers or resident males, or were at a kill. The location of each sighting was characterized by habitat type (woodland or plains) and distance to the pride's territory centre. Females without dependent offspring were alone 48% of the time; thus, we modelled group size as a binomial variable (lone female versus group). We examined the probability of being alone against variables representing potential risk (habitat type, distance from centre of territory and number of

neighbours), after excluding prides with only a single non-mother and controlling for the total number of non-mothers in the pride.

For our third hypothesis, we modelled territory size against the three measures of pride size (number of adult females, number of males and number of adults). We also examined whether these relationships differed by habitat type.

Our fourth hypothesis analysed the outcome of direct territorial competition. For each 2-year time step, we identified all overlap areas between adjacent prides. Grid cells were then identified as 'gained' if only the focal pride 'owned' the cell (it fell within the 75% contour) in the next time step. The proximity of the cell to the territory border was identified by using the kernel utilization values (1–75), where cells with lower values were located near the territory centre and cells with values of 75 were located on the territory boundary. Prides that overlapped because of a pride split within the time step or because they shared a male coalition were excluded. The gain of grid cells was modelled against the cell's proximity to the territory boundary and relative pride sizes (natural log of focal pride size/neighbour pride size). For each case, grid cells within the area of overlap were randomly assigned, in equal proportions, to each of the two neighbouring prides.

Our final hypothesis considered the role of group size in determining differential access to resources, as measured by the quality of the landscape. Change in territory quality was calculated for each pride with a sufficient number of observations (≥ 10) in consecutive

Table 1

Per capita adult female reproductive success in African lions versus pride and neighbour variables ($N = 217$ pride 2-year time steps)

Variable	Estimate	SE	Z	P	R ² _{margin}
Intercept	0.0911	0.3381	0.27	0.788	0.100
Number of adult females	0.1313	0.3381	3.46	0.001	
Number of adult females ²	-0.0076	0.0019	-4.03	<0.001	
Number of take-overs	-0.2185	0.0705	-3.10	0.002	
Territory quality	0.0063	0.0034	1.86	0.064	
Intercept	0.0816	0.3424	0.24	0.812	0.159
Number of adult females	0.0645	0.0424	1.52	0.128	
Number of adult females ²	-0.0041	0.0020	-2.02	0.043	
Number of take-overs	-0.2003	0.0654	-3.06	0.002	
Territory quality	0.0123	0.0040	3.10	0.002	
Number of neighbours: adult females	-0.0219	0.0068	-3.23	0.001	
Intercept	0.1668	0.3727	0.45	0.656	0.143
Number of adult females	0.0911	0.0397	2.30	0.022	
Number of adult females ²	-0.0053	0.0019	-2.84	0.005	
Number of take-overs	-0.1971	0.0697	-2.83	0.005	
Territory quality	0.0091	0.0039	2.34	0.019	
Number of neighbours: adult males	-0.0483	0.0155	-3.11	0.002	
Intercept	0.1240	0.3553	0.35	0.727	0.168
Number of adult females	0.0619	0.0417	1.49	0.137	
Number of adult females ²	-0.0039	0.0020	-1.98	0.048	
Number of take-overs	-0.1974	0.0658	-3.00	0.003	
Territory quality	0.0123	0.0039	3.12	0.002	
Number of neighbours: adults	-0.0201	0.0056	-3.60	<0.001	
Intercept	0.1075	0.3493	0.31	0.758	0.170
Number of adult females	0.0585	0.0424	1.38	0.167	
Number of adult females ²	-0.0038	0.0020	-1.88	0.060	
Number of take-overs	-0.2031	0.0658	-3.09	0.002	
Territory quality	0.0127	0.0038	3.36	0.001	
Neighbours: no split within 2 years	-0.0277	0.0078	-3.56	<0.001	
Neighbours: split within 2 years	-0.0121	0.0206	-0.59	0.556	
Intercept	0.1179	0.3470	0.34	0.734	0.175
Number of adult females	0.0596	0.0423	1.41	0.159	
Number of adult females ²	-0.0035	0.0020	-1.77	0.077	
Number of take-overs	-0.2102	0.0677	-3.11	0.002	
Territory quality	0.0126	0.0039	3.27	0.001	
Neighbours: no split within 10 years	-0.0232	0.0079	-2.94	0.003	
Neighbours: split within 10 years	-0.0478	0.0195	-2.45	0.014	

2-year time steps. We modelled change in territory quality against pride demography and neighbour variables.

Statistical Analysis

We used generalized estimating equations (GEE) to analyse the relationships between the dependent and independent variables (PROC GENMOD, SAS 9.1, SAS Institute Inc., Cary, NC, U.S.A.) (Zeger et al. 1988; Ballinger 2004). We accounted for multiple observations of the same pride over time by including a repeated statement in the model. We first analysed pride variables in a multivariate model, and retained statistically significant ($P \leq 0.05$) variables. Next, neighbour effects were considered independently in a model including the significant pride variables. In all analyses of neighbour effects, 'edge' was included as an interaction variable, and results are presented for the non-edge interactions only. We report coefficient estimates, standard errors, Z values and P values for each independent parameter. Robust model-fit statistics are not yet available for GEE models, but we calculated marginal R^2 values (R^2_{marg}), which estimate improvement in model fit by comparing a parameterized model to the null (intercept-only) model (Zheng

2000), with larger values indicating a greater improvement in model fit. The R^2_{marg} value compares the sum of squared deviations between the predicted and actual values for the two models, and, as with a traditional R^2 value, can be interpreted as an estimate of the variance explained by a particular model.

All models were linear regressions, with the exception of the analysis of subgrouping patterns and the gain of disputed territory, where we used logistic regression. In the analysis of subgrouping patterns, we plotted the data in a semivariogram, and we found no significant spatial autocorrelation (PROC VARIOGRAM, SAS 9.1). For analysing gain of disputed territory, we used a nested repeated statement to account for multiple observations on the same pride as well as for multiple cells and spatial autocorrelations for each case of overlap.

RESULTS

Territorial Behaviour Inflicts Costs on Neighbours

Mean \pm SE reproductive success was 0.75 ± 0.05 yearling cubs per adult female per 2-year time step (range 0–3.88). As in previous

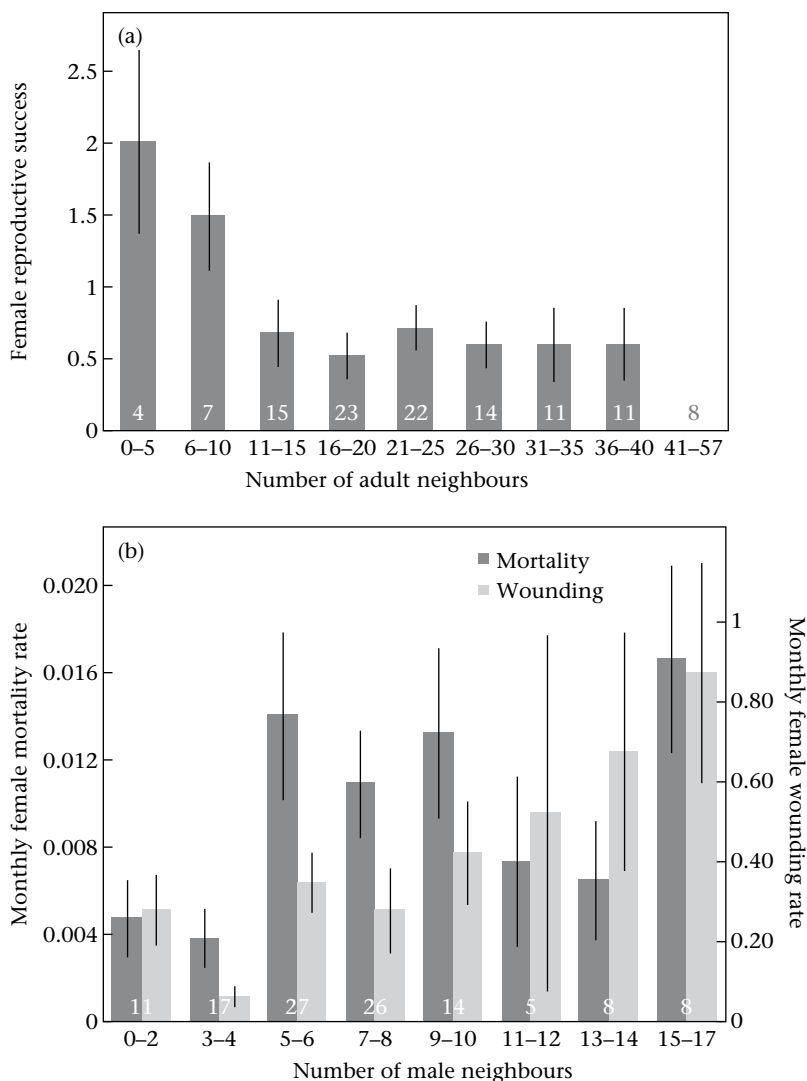


Figure 2. (a) Per capita adult female reproductive success versus total number of adult neighbours and (b) average adult female monthly mortality and wounding rates versus number of male neighbours ($N = 115$, non-edge prides only, numbers at the base of each bar denote sample sizes).

analyses (Packer et al. 1988), we found a quadratic relationship between the number of adult females in the pride and reproductive success (Table 1). Prides of 1–4, 5–11 and 12–19 adult females had a mean \pm SE of 0.63 ± 0.07 , 0.94 ± 0.08 and 0.46 ± 0.13 cubs per female per 2-year interval, respectively. In addition, prides with fewer male take-overs and those in higher-quality habitat had higher rates of reproductive success. After controlling for these pride variables, we found strong negative effects of neighbours on reproductive success, with the total number of adult neighbours having the strongest effect (see Z and R^2_{marg} values in Table 1). A univariate analysis revealed that female reproductive success was 65% lower in prides with more than 10 adult neighbours than in prides with 10 or fewer adult neighbours (Fig. 2a). Neighbours that split within 2 years had no significant effect on reproductive success.

Mean \pm SE adult female mortality rate was 0.01 ± 0.001 deaths per month, and individual females suffered a mean \pm SE of 0.23 ± 0.03 wounds per month. Larger prides had lower rates of adult female mortality and wounding, and prides that experienced multiple take-overs had higher rates of mortality (Tables 2, 3). The positive correlation between mortality and territory quality suggests that territorial competition is more intense in higher-quality areas, which also have higher lion densities (Mosser 2008). The number of neighbours is a direct measure of density; thus, the effects of territory quality and neighbours are co-linear and confound one another. When territory quality was removed from the model, mortality was significantly correlated with the number of male neighbours (effect = 0.0004, SE = 0.0002, $Z = 2.21$, $P = 0.027$, $R^2_{\text{marg}} = 0.078$, after controlling for number of pride females and number of take-overs). Of the neighbour effects, mortality and wounding were most strongly associated with the number of adult male neighbours, according to the R^2_{marg} values. Female mortality and wounding rates were three times higher in prides that had the most male neighbours than in prides that had the fewest male neighbours (Fig. 2b).

Risk Influences Subgrouping Patterns

Mean \pm SE subgroup size of non-mothers (for prides with > 1 non-mother) was 1.87 ± 0.03 females (range 1–9), compared with an overall mean \pm SE of 2.46 ± 0.02 adult females (range 1–12). Overall, females in smaller prides (2–3 adult females) were significantly less likely to be alone than females in larger prides (small versus large prides: effect = -0.4395 , SE = 0.1960, $Z = -2.24$, $P = 0.025$). For small prides, however, females were more likely to be sighted alone in risky locations (open plains habitat and when further from their territory centre, although the latter effect was only marginally significant), in contrast to larger prides, where females were less likely to be alone in risky locations (Table 4, Fig. 3a, b).

Females were less likely to be alone when their pride was surrounded by more neighbours, although the effects depended on pride size. Small prides were not significantly affected by any measure of the number of neighbours, whereas large prides were most strongly affected by the number of male neighbours, according to the Z and R^2_{marg} values in Table 4. When all pride sizes were analysed together, the total number of adult neighbours had the strongest correlation with the probability of being alone (effect = -0.0251 , SE = 0.0060, $Z = -4.16$, $P < 0.0001$, $R^2_{\text{marg}} = 0.034$, after controlling for habitat type and distance from territory centre; Fig. 3c). Only neighbours that were not associated with a recent pride split significantly affected the probability of being alone, and we present the results only for neighbours that had not split within 10 years. The results were qualitatively identical for splits considered within 2 years.

Table 2

Per capita monthly adult female mortality rate in African lions versus pride and neighbour variables ($N = 217$ pride 2-year time steps)

Variable	Estimate	SE	Z	P	R^2_{marg}
Intercept	0.0006	0.0026	0.22	0.823	0.078
Number of adult females	-0.0007	0.0002	-2.95	0.003	
Number of take-overs	0.0028	0.0010	2.97	0.003	
Territory quality	0.0001	0.0000	4.11	<0.001	
Intercept	0.0006	0.0026	0.22	0.824	0.079
Number of adult females	-0.0007	0.0002	-2.83	0.005	
Number of take-overs	0.0029	0.0010	2.98	0.003	
Territory quality	0.0001	0.0000	3.77	<0.001	
Number of neighbours: adult females	-0.0000	0.0001	-0.30	0.765	
Intercept	0.0007	0.0027	0.26	0.798	0.089
Number of adult females	-0.0006	0.0002	-2.92	0.004	
Number of take-overs	0.0027	0.0010	2.77	0.006	
Territory quality	0.0001	0.0000	2.96	0.003	
Number of neighbours: adult males	0.0003	0.0002	1.71	0.087	
Intercept	0.0008	0.0026	0.30	0.766	0.079
Number of adult females	-0.0007	0.0002	-2.79	0.005	
Number of take-overs	0.0029	0.0010	2.94	0.003	
Territory quality	0.0001	0.0000	3.37	0.001	
Number of neighbours: adults	0.0000	0.0000	0.63	0.526	
Intercept	-0.0001	0.0026	-0.04	0.970	0.083
Number of adult females	-0.0007	0.0003	-2.31	0.021	
Number of take-overs	0.0029	0.0010	2.95	0.003	
Territory quality	0.0001	0.0000	3.54	<0.001	
Neighbours: no split within 2 years	-0.0000	0.0001	-0.41	0.685	
Neighbours: split within 2 years	0.0000	0.0005	0.08	0.934	
Intercept	0.0007	0.0026	0.26	0.796	0.082
Number of adult females	-0.0007	0.0003	-2.54	0.011	
Number of take-overs	0.0030	0.0010	2.93	0.003	
Territory quality	0.0001	0.0000	3.44	0.001	
Neighbours: no split within 10 years	-0.0000	0.0001	-0.48	0.632	
Neighbours: split within 10 years	0.0002	0.0004	0.61	0.544	

Table 3

Per capita adult female wounding rate versus pride and neighbour variables ($N = 217$ pride 2-year time steps)

Variable	Estimate	SE	Z	P	R^2_{marg}
Intercept	0.2325	0.0924	2.52	0.012	0.073
Number of observations	0.0018	0.0006	3.03	0.003	
Number of adult females	-0.0252	0.0103	-2.45	0.014	
Intercept	0.0969	0.0687	1.41	0.159	0.126
Number of observations	0.0015	0.0006	2.76	0.006	
Number of adult females	-0.0185	0.0082	-2.25	0.024	
Number of neighbours: adult females	0.0111	0.0047	2.39	0.017	
Intercept	0.0518	0.0664	0.78	0.435	0.165
Number of observations	0.0016	0.0005	3.06	0.002	
Number of adult females	-0.0214	0.0069	-3.08	0.002	
Number of neighbours: adult males	0.0362	0.0101	3.59	<0.001	
Intercept	0.0609	0.0697	0.87	0.383	0.142
Number of observations	0.0015	0.0005	2.83	0.005	
Number of adult females	-0.0183	0.0077	-2.38	0.017	
Number of neighbours: adults	0.0097	0.0034	2.81	0.005	
Intercept	0.0924	0.0644	1.43	0.152	0.125
Number of observations	0.0016	0.0006	2.81	0.005	
Number of adult females	-0.0167	0.0077	-2.17	0.032	
Neighbours: no split within 2 years	0.0110	0.0051	2.15	0.030	
Neighbours: split within 2 years	0.0018	0.0113	0.16	0.871	
Intercept	0.0746	0.0631	1.18	0.237	0.138
Number of observations	0.0015	0.0006	2.67	0.008	
Number of adult females	-0.0146	0.0066	-2.21	0.027	
Neighbours: no split within 10 years	0.0126	0.0061	2.06	0.039	
Neighbours: split within 10 years	0.0062	0.0125	0.50	0.620	

Group Size Determines Outcome of Territorial Competition

Territory size was not significantly correlated with pride size when all data were pooled together, but we did find a difference when data were separated by habitat (Fig. 4). Woodland territories were significantly smaller than plains territories (woodlands average = $38.12 \pm 1.59 \text{ km}^2$, plains average = $70.31 \pm 3.06 \text{ km}^2$; ANOVA: $F_{142,117} = 76.97, P < 0.0001$). In woodlands habitat, territory size was significantly correlated with the number of adult females in the pride (territory size versus number of adult females: estimate = 1.3626, SE = 0.4644, Z = 2.93, P = 0.003, $R^2_{\text{marg}} = 0.084$) but not the number of males (territory size versus number of adult males: estimate = 0.5099, SE = 0.8162, Z = 0.62, P = 0.532, $R^2_{\text{marg}} = 0.002$). In contrast, for plains prides, no measure of pride size was significantly correlated with territory size (e.g. territory size versus number of adult females: estimate = 0.2109, SE = 1.8233, Z = 0.12, P = 0.908, $R^2_{\text{marg}} = 0.0002$).

For the analysis of gain of disputed territory (Table 5), we controlled for the location of the disputed grid cells within each pride's territory because grid cells nearer to a pride's territory

Table 4
Probability of being alone for females with no dependent offspring versus risk factors (small prides: N = 568 sightings, larger prides: N = 1222 sightings)

Variable	Estimate	SE	Z	P	R^2_{marg}
Prides of 2–3 adult females					
Intercept	0.0454	0.7112	0.06	0.949	0.044
Number of females with no cubs	-0.3979	0.2667	-1.49	0.137	
Plains vs woodlands	0.4960	0.2005	2.47	0.013	
Distance from territory centre	0.0379	0.0230	1.65	0.099	
Intercept	0.5764	0.7302	0.79	0.430	0.055
Number of females with no cubs	-0.4133	0.2606	-1.59	0.113	
Plains vs woodlands	0.3764	0.1534	2.45	0.014	
Distance from territory centre	0.0362	0.0245	1.48	0.139	
Number of neighbours: adult females*	-0.0216	0.0131	-1.65	0.099	
Intercept	-0.0720	0.7443	-0.10	0.923	0.046
Number of females with no cubs	-0.3874	0.2687	-1.44	0.149	
Plains vs woodlands	0.5029	0.2130	2.36	0.018	
Distance from territory centre	0.0370	0.0244	1.51	0.130	
Number of neighbours: adult males	0.0148	0.0229	0.64	0.519	
Intercept	0.4125	0.7367	0.56	0.576	0.050
Number of females with no cubs	-0.4009	0.2639	-1.52	0.129	
Plains vs woodlands	0.4206	0.1782	2.36	0.018	
Distance from territory centre	0.0390	0.0241	1.62	0.106	
Number of neighbours: adults*	-0.0117	0.0089	-1.31	0.192	
Prides of 4 or more adult females					
Intercept	1.0803	0.2081	5.19	<0.001	0.025
Number of females with no cubs	-0.1174	0.0434	-2.70	0.007	
Plains vs woodlands	-0.4765	0.1990	-2.39	<0.017	
Distance from territory centre	-0.0361	0.0136	-2.66	0.008	
Intercept	1.3297	0.3270	4.07	<0.001	0.036
Number of females with no cubs	-0.1157	0.0474	-2.44	0.015	
Plains vs woodlands	-0.5883	0.2460	-2.39	0.017	
Distance from territory centre	-0.0367	0.0143	-2.56	0.010	
Number of neighbours: adult females*	-0.0226	0.0124	-1.82	0.068	
Intercept	1.4573	0.2001	7.28	<0.001	0.044
Number of females with no cubs	-0.0978	0.0417	-2.34	0.019	
Plains vs woodlands	-0.5726	0.1844	-3.10	0.002	
Distance from territory centre	-0.0365	0.0141	-2.58	0.010	
Number of neighbours: adult males	-0.0922	0.0259	-3.55	<0.001	
Intercept	1.4255	0.2869	4.97	<0.001	0.040
Number of females with no cubs	-0.1120	0.0469	-2.39	0.017	
Plains vs woodlands	-0.6119	0.2311	-2.65	0.008	
Distance from territory centre	-0.0370	0.0144	-2.57	0.010	
Number of neighbours: adults*	-0.0220	0.0081	-2.72	0.007	

* All results presented in this table are for neighbouring prides that had not split within 10 years.

border were less likely to be retained by that pride. Prides with more adult females were significantly more likely to gain a disputed area (Fig. 5). Prides that gained disputed cells were on average 24% larger than their neighbour. Prides that were one to two times larger than the neighbour pride were about 50% more likely to gain a disputed cell than were prides that were smaller than the neighbour pride; prides that were three to nine times larger than a neighbouring pride were 69% more likely to gain the disputed area than were prides that were one to two times as large as the neighbouring pride. Relative pride size had no significant effect on gain of disputed cells for prides that had split within 2 years.

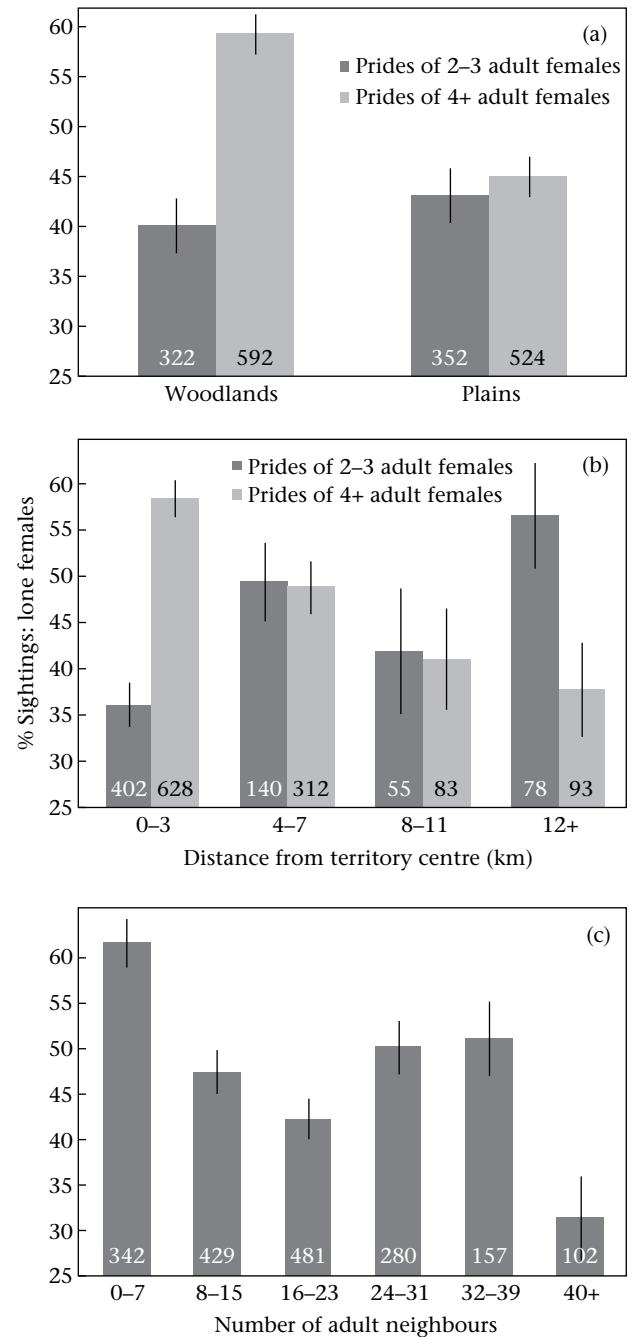


Figure 3. For adult females with no dependent cubs, the percentage of sightings of alone versus risk factors: (a) habitat type, (b) distance from territory centre and (c) the number of adult neighbours (N = 1791 subgroup sightings, samples sizes are indicated at the base of each bar).

Group Size Influences Access to Resources

Mean \pm SE territory quality was 84.75 ± 1.00 (range 26–97, scale 0–100), corresponding to a territory with a mean \pm SE distance of 4.5 km from a river confluence. Change in territory quality from one time step to the next was positively and significantly correlated with change in the number of adult females and the relative number of males in the pride (Table 6, Fig. 6). The R^2_{marg} value, however, suggested that this effect was not particularly strong. Statistical analysis also showed that an increase in the number of females was more strongly associated with improvement in territory quality than a decrease was associated with a loss in territory quality (controlling for the relative number of males, increase in the number of females: effect = 1.2184, SE = 0.6277, $Z = 1.94$, $P = 0.05$; decrease: effect = 0.2018, SE = 0.6332, $Z = 0.32$, $P = 0.75$), indicating that adult female recruitment is particularly important to gaining and maintaining access to high-quality habitat. Prides with an increase in the number of females improved their territory quality, on average, by 0.41, representing a territory shift of roughly 115 m closer to a confluence, and prides that lost adult females suffered losses in territory quality, on average, by 0.21, or 58 m. Prides with more males than their neighbours experienced territory shifts that were, on average, 160 m closer to a river confluence, while prides with fewer males experienced territory shifts that were, on average, 275 m away from a confluence. There were no differences associated with time since pride split in these analyses.

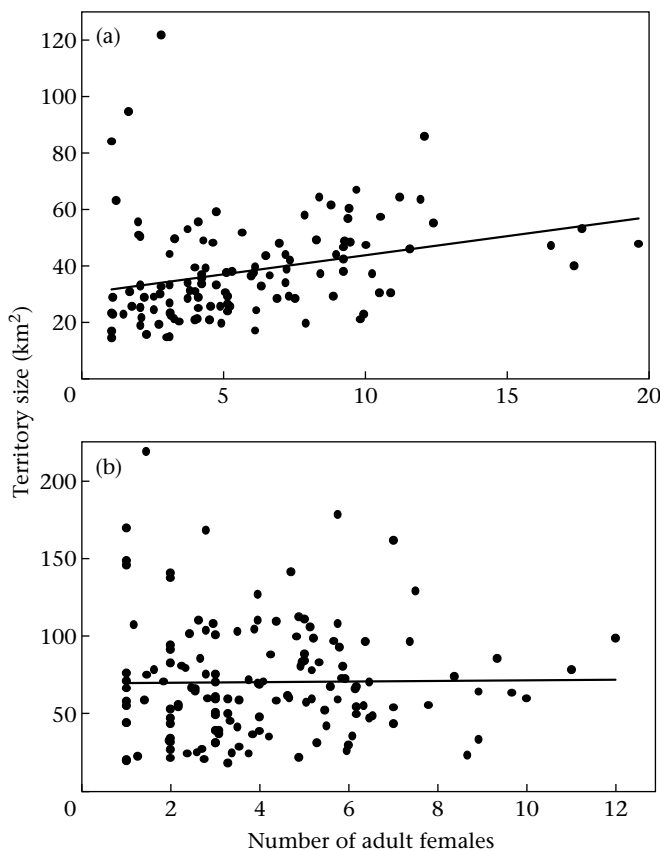


Figure 4. Territory size versus pride size for (a) woodlands and (b) plains habitat. Trendlines illustrate the coefficient estimates of the GEE models presented in the text, which account for repeated measures of the same pride over time.

DISCUSSION

Our results illustrate that intergroup competition in African lions significantly affects female reproductive success and mortality, suggesting that territorial behaviour is subject to substantial selection pressure and that larger prides have a broad competitive advantage in intergroup competition. Prides with more adult females had higher rates of reproductive success and lower rates of mortality and wounding, and formed larger subgroups when in potentially risky situations. In woodland habitat, larger prides had significantly larger territories, although the sparse distribution of resources in the plains habitat may make it unprofitable for prides to expand their range with increasing pride size. Prides with more females were also more likely to gain control of disputed areas, and prides that recruited additional adult females improved the quality of their territories. Surprisingly, males had measurable effects on females in neighbouring prides, impacting their reproductive success, mortality and wounding. Neighbouring resident males also influenced the female grouping patterns within larger prides and improved the quality of their own pride's territory.

Most of the analyses supported the expectation that territorial competition would be most intense between unrelated neighbours; negative effects on reproductive success, wounding rates, subgrouping patterns and gain of disputed territory were associated only with neighbours that had not recently split. Tolerance between prides was strongest within 2 years of a pride split but diminished for neighbours that had split within 10 years, suggesting that mothers do not interfere with the establishment of their daughters' new pride territories, but treat them as any other neighbour after the first 2 years (also see VanderWaal et al. 2009).

Mortality and Aggression

Females with more adult male neighbours had higher rates of mortality and wounding, although the effect was marginally

Table 5

Gain of disputed territory versus location variables and relative pride size ($N = 1539$ grid cells from 349 pride pairs)

Variable	Estimate	SE	Z	P	R^2_{marg}
Intercept	-1.0930	0.4253	-2.57	0.010	0.046
Proximity to territory border: focal pride	-0.0140	0.0047	-2.99	0.003	
Proximity to territory border: neighbour	0.0147	0.0052	2.80	0.005	
Intercept	-1.2031	0.4284	-2.81	0.005	0.070
Proximity to territory border: focal pride	-0.0143	0.0048	-2.97	0.003	
Proximity to territory border: neighbour	0.0162	0.0052	3.11	0.002	
Relative pride size: adult females	0.4637	0.1415	3.28	0.001	
Intercept	-1.3369	0.5256	-2.54	0.011	0.055
Proximity to territory border: focal pride	-0.0189	0.0060	-3.14	0.002	
Proximity to territory border: neighbour	0.0203	0.0066	3.07	0.002	
Relative pride size: adult males	0.0781	0.2038	0.38	0.702	
Intercept	-1.5667	0.4827	-3.25	0.001	0.060
Proximity to territory border: focal pride	-0.0132	0.0053	-2.50	0.012	
Proximity to territory border: neighbour	0.0214	0.0060	3.56	<0.001	
Relative pride size: adults	0.2021	0.1815	1.11	0.265	
Intercept	-1.2053	0.4292	-2.81	0.005	0.070
Proximity to territory border: focal pride	-0.0142	0.0049	-2.91	0.004	
Proximity to territory border: neighbour	0.0163	0.0052	3.10	0.002	
Relative pride size: no split within 2 years	0.4552	0.1541	2.95	0.003	
Relative pride size: split within 2 years	0.4378	0.3026	1.78	0.076	
Intercept	-1.2266	0.4213	-2.91	0.004	0.067
Proximity to territory border: focal pride	-0.0140	0.0048	-2.91	0.004	
Proximity to territory border: neighbour	0.0163	0.0052	3.15	0.002	
Relative pride size: no split within 10 years	0.4240	0.1554	2.73	0.006	
Relative pride size: split within 10 years	0.6511	0.2684	2.43	0.015	

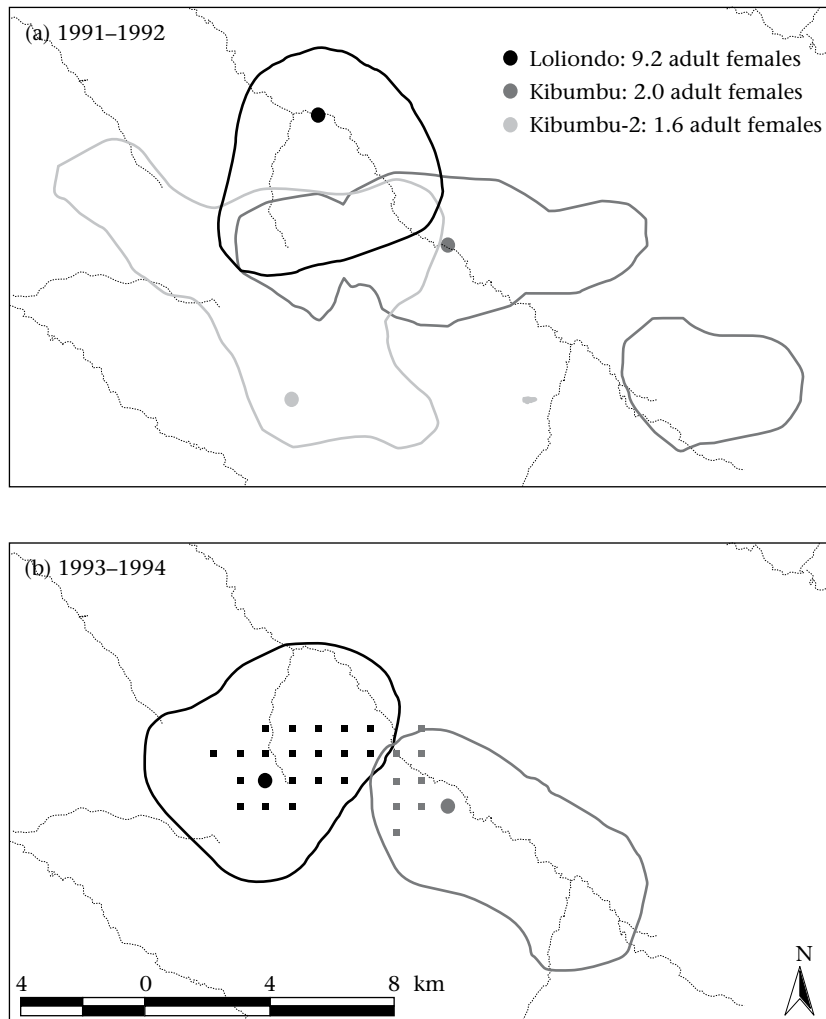


Figure 5. Illustration of the outcome of territorial competition for overlapping territory. The larger pride (Loliondo) gained the majority of the area that was disputed with the Kibumbu and Kibumbu-2 prides. The Kibumbu-2 pride went extinct in the following time step. (a) Territory boundaries for the three prides in 1991–1992. Circles indicate the centre of activity within the territory for each pride. Dotted grey lines show major rivers. (b) Territory boundaries for the two surviving prides in 1993–1994. Circles indicate the centres of activity. Squares are the centres of the grid cells that were in dispute during the previous time step and gained by one of the two prides.

significant for mortality. Females have been killed while defending their cubs from extrapride males (C. Packer, personal observation; K. Skinner, personal communication), and although we found a positive relationship between the number of take-overs and mortality, female mortality was not exclusively associated with females caring for cubs at the time of a take-over. Between the ages of 3 and 10 years, females have dependent offspring (cubs age 2 years or younger) during 53% (± 24 standard deviation) of months; of the females that died within this age range (180 total), 45% were caring for cubs at the time of their death and 59% were caring for cubs within 3 months of their death. Neither of these values was significantly lower or higher than expected. Also, the probability of an adult female dying in any given month was significantly lower when there were more mothers in the pride (estimate = -0.5450 , $\bar{X} \pm SE = -3.63 \pm 0.1501$, $Z = -3.63$, $P = 0.004$).

Why might a male attack and potentially kill a neighbouring female, given the possibility of eventually mating with her? Our results show that there are distinct advantages to reducing the number of neighbours and altering the balance of power in territorial competition through adaptive lethal aggression (Manson & Wrangham 1991). A handful of accounts have described lethal male attacks on females that were not associated with infanticide (e.g. Schenkel 1966, page 20; Schaller 1972, page 159). Male chimpanzees sometimes attack and kill sexually unreceptive adult females

Table 6

Change in territory quality versus pride and neighbour variables ($N = 169$ pride 2-year time steps)

Variable	Estimate	SE	Z	P	R_{margin}^2
Intercept	0.0209	0.3269	0.06	0.949	0.006
Change in pride size: adult females	0.1765	0.0855	2.06	0.039	
Intercept	-0.0051	0.3546	-0.01	0.989	-0.001
Change in pride size: adult females	0.2021	0.0990	2.04	0.041	
Relative pride size: adult females	0.9004	0.7207	1.25	0.212	
Intercept	-0.2294	0.3274	-0.70	0.484	0.074
Change in pride size: adult females	0.1692	0.0888	1.90	0.057	
Relative pride size: adult males	2.8380	1.3688	2.07	0.038	
Intercept	-0.1168	0.3481	-0.34	0.737	0.023
Change in pride size: adult females	0.2067	0.0925	2.23	0.026	
Relative pride size: adults	1.0708	0.9915	1.79	0.073	
Intercept	-0.7004	1.3271	-0.53	0.598	-0.093
Change in pride size: adult females	0.2616	0.1741	1.50	0.133	
Relative pride size: no split within 2 years	0.2025	1.1282	0.18	0.858	
Relative pride size: split within 2 years	1.1799	1.7437	0.68	0.499	
Intercept	-0.8404	0.6773	-1.24	0.215	-0.058
Change in pride size: adult females	0.3269	0.2395	1.36	0.172	
Relative pride size: no split within 10 years	-0.5395	0.6767	-0.80	0.425	
Relative pride size: split within 10 years	1.9969	1.4731	1.36	0.175	

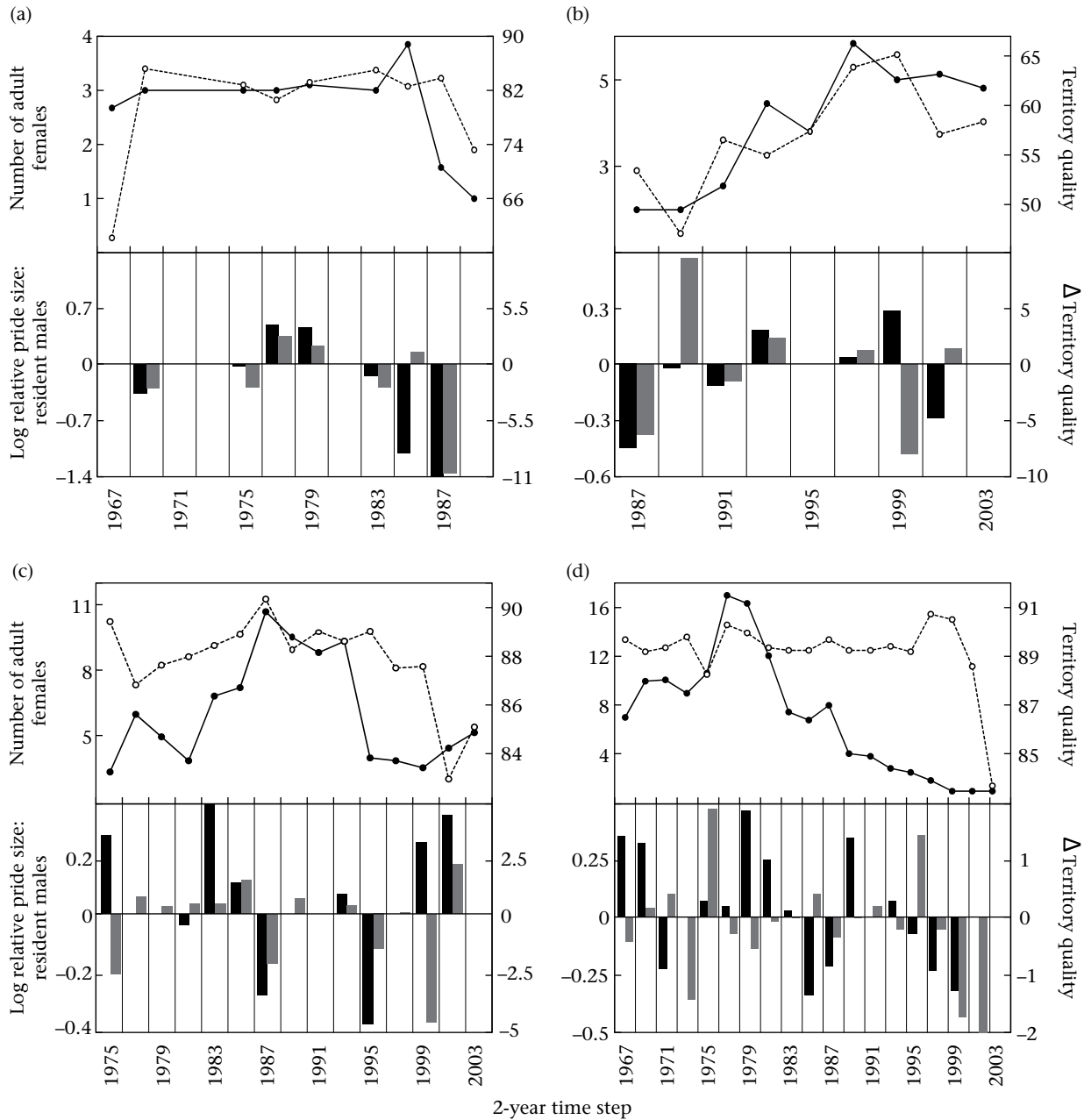


Figure 6. Upper plots: number of adult females (solid lines) and territory quality (dashed lines) over time. Lower plots: log relative pride size (resident males, black bars) and change in territory quality (grey bars) over time. The patterns here illustrate the statistical results in Table 6. Plots are for (a) Boma, (b) Gol United, (c) Loliondo and (d) Maasai prides.

in neighbouring communities (Wilson & Wrangham 2003; Williams et al. 2004). A neighbouring lioness, if not receptive to mating, may be viewed by males as a competitor for scarce resources (see Williams et al. 2004) and as potentially infanticidal, since females sometimes kill cubs of neighbouring prides (Packer & Pusey 1984). Thus, male lions may actively seek opportunities to attack, wound and kill neighbouring females to enhance the current success of their pride.

Fission–Fusion Grouping Patterns

Our analysis of subgroups of non-mothers shows that grouping patterns within prides are affected by the number of neighbours and probably serve a territorial function. Prides with

many neighbours are at greater risk of losing territory and are possibly at greater risk of attack and so form larger groups to counter such threat. When faced with location-based risk (further from the territory centre or in open habitat) non-mothers in small prides were more likely to be found alone, perhaps to evade detection in risky environments. Females in larger prides were less likely to be alone in risky locations and thus may reduce individual risk through safety in numbers. Alternative strategies in response to risk was predicted by Jarman (1974), and a similar pattern was seen for elk under threat of attack by wolves (Hebblewhite & Pletscher 2002). Still, the R^2_{marg} values for these analyses were small, suggesting that factors unrelated to group territoriality may influence fission–fusion patterns within each pride.

Benefits of Grouping in African Lions

The sociality of male lions is attributed to numerical advantage in intercoalition competition; larger coalitions have greater success in pride take-overs and longer tenure times (Bygott et al. 1979; Packer 1986). Our results also indicate that numerical advantage may additionally benefit large male coalitions by reducing levels of interpride competition for their females. All the same, it is the sociality of female lions, forming long-term matrilineal social groups, that has remained an unresolved question.

Cooperative hunting was a leading explanation for female lion sociality (Schaller 1972; Macdonald 1983; Turner 1997), but empirical evidence has failed to support this hypothesis. Social grouping patterns in lions are not strongly associated with increased food intake (Caraco & Wolf 1975; Packer 1986; Packer et al. 1990). Although hunting success increases slightly with the size of the hunting group (Schaller 1972; Elliot et al. 1977; Van Orsdol 1984; Stander & Albon 1993; Funston et al. 2001), lions often opt out of a group-hunt (Scheel & Packer 1991) and actual hunting success, for groups of more than two, fails to match the capture rates predicted by full cooperation (Packer & Rutten 1988). More importantly, detailed analyses (Packer et al. 1990) showed that during periods of prey scarcity, subgroups of two to four adult females had the lowest rates of food intake, compared with lone females or subgroups of at least five females. During periods of prey abundance, food intake did not significantly differ with group size.

Our analyses show that females in small prides (2–3 females), without dependent cubs, were significantly less likely to be alone, despite the feeding disadvantage. These results held when observations were restricted to the dry season (the period of prey scarcity). After controlling for other risk factors, the subgrouping patterns for all pride sizes were significantly affected by the number of neighbours in either season. These results are all consistent with the hypothesis that grouping patterns reflect the threat of territorial competition rather than the effects of group foraging.

An additional benefit of grouping in lions is the defence of carcasses from scavenging spotted hyenas, *Crocuta crocuta* (Cooper 1991; Mills & Biggs 1993). However, in the Serengeti and Ngorongoro Crater, Tanzania, lions rarely lose carcasses before they have been able to consume a significant proportion of the meat (Packer 1986; Kissui & Packer 2004).

Cooperative defence against infanticide is a major benefit of grouping for female lions (Pusey & Packer 1994), but it is difficult to tease apart the relative importance of cub defence from territorial defence, as the threat posed by conspecifics leads to larger group sizes in both cases. Playback experiments, however, have shown that crèche groups typically retreat from extrapride males but that mothers approach female intruders and they do so more often than females without dependent cubs (McComb et al. 1993, 1994). Leaving cubs unprotected puts them at considerable risk, suggesting that the need to respond to territorial threat may often override the value of protecting cubs.

Our analyses show a strong long-term individual advantage to group territoriality in lions and explain why individuals in larger groups have higher rates of reproductive success than do individuals in smaller groups. Larger groups are the successful despots on the savanna landscape, gaining access to the best reproductive real estate near river confluences. The effects of intergroup competition between females are direct and immediate, so much so that male coalitions attempt to modify the dynamics of territorial competition. Group-territorial competition therefore provides strong selection for cooperative territorial defence and a clear benefit to grouping in lions.

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