

Optimal group size, dispersal decisions and postdispersal relationships in female African lions

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We used 40 years of long-term data to test whether dispersal decisions of female African lions, *Panthera leo*, are sensitive to variations in pride size, interpride competition and the quality of their natal territory. Per capita reproductive success reached a maximum at 3–6 females on the open grass plains of the Serengeti and at 3–11 females in the woodlands. Approximately 50% of female cohorts dispersed when potential pride size exceeded the habitat-specific optimum, whereas only 9% of cohorts dispersed at smaller pride sizes. Cohorts of one to two females rarely dispersed, especially in high-density habitats. Thus, pride size typically remained within the range that maximized individual reproductive success. In the high-density woodland habitat, females were less likely to disperse from prides that were surrounded by large numbers of unrelated females, as would be predicted on the basis of habitat saturation. However, the number of unrelated neighbours did not affect dispersal decisions of females living in the sparsely occupied plains habitat. After pride fission, daughters settled closer to their mothers in areas where there were greater numbers of unrelated female neighbours, but territories were just as exclusive as between unrelated neighbouring prides. Maternal prides in high-quality areas shared a greater percentage of their territory with descendant prides, but this tolerance diminished as relatedness declined through time.

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The evolution of sociality involves a fundamental trade-off between the benefits and costs of group living (Alexander 1974; Hoogland 1979; Wrangham et al. 1993; Waterman 2002). As group size grows, the costs of remaining in the group are expected to increase until they outweigh the benefits, and groups will either cease growing or undergo a permanent division into two descendent groups. Per capita reproductive success generally declines with increasing group size (Hoogland 1981; Armitage 1986; Packer et al. 1988), and large social groups are more likely to divide (e.g. Ménard & Vallet 1993; Henzi et al. 1997; Kuester & Paul 1997; Vucetich & Creel 1999; Okamoto & Matsumura 2001; Bayart & Simmen 2005; Manno et al. 2007).

Environmental factors also influence dispersal and group fission. In territorial species, philopatry is favoured by high costs of dispersal in saturated habitats (Emlen 1982). Dispersal is less common when natal territory quality is high (Stacey & Ligon 1987; Komdeur et al. 1995; Luck 2001; Pasinelli & Walters 2002) and in saturated habitats with a shortage of breeding opportunities (Jones et al. 1988; Walters et al. 1992; Holekamp et al. 1993; Sillero-Zubiri et al. 1996; Pasinelli & Walters 2002). Previous studies relating

dispersal to territory quality and availability have largely been confined to species with high reproductive skew. Individuals may gain inclusive fitness by helping their parents, but they do not usually breed until they disperse or inherit the territory; thus, dispersal decisions largely reflect breeding opportunities. In species with little to no reproductive skew, including lions, *Panthera leo*, all individuals of the philopatric sex have equal breeding opportunities (Packer et al. 2001); thus, dispersal is not due to subordinates seeking breeding status.

Dispersing females usually settle within or near their natal range (Pusey & Packer 1987), hence involving some degree of accommodation or tolerance by the parental pride. Many solitary species tolerate offspring remaining in their territory (Waser & Jones 1983; Zedrosser et al. 2007), even subdividing their original territory with their offspring (Rogers 1987). However, tolerance of recently divided social groups has not been well studied in any mammalian species.

The Serengeti lion project has documented 41 pride fissions between 1966 and 2006, providing a unique opportunity to examine dispersal decisions. Lions are characterized by female philopatry, but up to one-third of subadult females disperse as groups and establish new prides (Pusey & Packer 1987). Dispersal is of considerable interest in lions because population size is highly correlated with the number of prides; the size of each pride is

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limited by within-group density dependence, and the only way the lion population can increase is through the formation of new breeding units (Packer et al. 2005). Here, we explore how pride fission regulates pride size and how habitat saturation and territory quality influence dispersal decisions. We predicted that female dispersal would be more likely when (1) pride size was large, (2) intergroup competition was low and (3) territory quality was low. Among factors influencing the degree to which descendant prides are tolerated by their original pride, we expected prides to remain in closest proximity when (1) dispersing females faced high levels of interpride competition and (2) when natal territory quality was high.

METHODS

Study Area and Population

Our study area encompassed a 2000 km² area of the Serengeti National Park, Tanzania. The area was located within the 25 000 km² Serengeti–Mara ecosystem, which contains ~3500 lions. Population density of lions is largely limited by food availability in the dry season when prey biomass is at an annual low (Schaller 1972; Bertram 1975; Van Orsdol et al. 1985; Packer et al. 2005; Mosser 2008). Our study population typically included about 200–300 lions, each recognized individually by natural facial markings (Packer & Pusey 1993). The population has been monitored continuously since 1974 (Bygott et al. 1979; Packer et al. 2001), and several prides have been monitored since 1966 (Schaller 1972). From 1966 to 1983, all observations were opportunistic. Beginning in 1984, one female per pride was radiocollared, and lions were found opportunistically or by radio telemetry; each pride is usually located at least once every 2 weeks. Demographic events (births, deaths, immigration and emigration) are based on direct observation and reproductive behaviour/status. Dispersal is defined as the permanent emigration of one or more females, resulting in the establishment of a new pride. Pride locations have been recorded using GPS (Global Positioning System) since 1991; Universal Transverse Mercator (UTM) coordinates of earlier ranging data were taken from 1:50 000 topographic maps.

The study area consisted of two habitat types: acacia woodland and open-grassland plains. The annual rainfall-driven migration of wildebeest, *Connochaetes taurinus*, zebra, *Equus burchelli*, and Thomson's gazelle, *Gazella thomsoni*, moves through both habitats (McNaughton 1979), but the woodlands habitat hosts resident herds of buffalo, *Syncerus caffer*, antelope and giraffe, *Giraffa camelopardalis*; thus, the lions are typically found at higher densities in the woodlands than in the plains (Hanby & Bygott 1979). The woodlands habitat is also more homogeneous compared to the open grass plains, which are sparsely punctuated by waterholes and rocky outcrops.

Basic Lion Behaviour

Lions live in fission–fusion social groups consisting of 1–21 related females, their dependent offspring, and a coalition of immigrant males. We classified immatures less than 18 months old as cubs and those 18–48 months old as subadults. Four years (48 months) is the median age at which females have their first litter (Packer et al. 1988); therefore, we considered all females that were at least 4 years old or that were known to be pregnant to be 'adult females'. Female lions with similarly aged cubs pool their cubs in a crèche and rear them communally (Schaller 1972; Rudnai 1974; Bertram 1975; Pusey & Packer 1994; Packer et al. 2001). Male coalitions compete for control of prides and kill or evict unrelated cubs when they first enter a new pride (Bertram 1975; Packer &

Pusey 1983a, b, 1984; Hanby & Bygott 1987; Packer et al. 2001). Subadult females are generally recruited into their mothers' prides, although up to a one-third may disperse as cohorts and establish new prides, sometimes accompanied by an adult female (Pusey & Packer 1987).

Pusey & Packer (1987) identified four main social contexts for the formation of new prides. (1) Incoming male coalitions may evict subadult females that are too young to breed. (2) Mothers may remove themselves and their cubs from the rest of the pride during a male take-over, thereby avoiding the risks of infanticide (Bertram 1975; Packer & Pusey 1983a, b, 1984; Packer et al. 1988). (3) Prides occasionally split because of a loss of familiarity between crèche females and females without cubs; the latter tend to avoid crèches because of the low rate of food intake experienced by females in large crèches (Packer 1986; Packer et al. 1990). (4) Subadult females may disperse if they reach sexual maturity when their fathers' coalition is still resident, thereby avoiding close inbreeding.

Demographic Analysis

We followed the fates of 140 subadult female cohorts born in 32 prides. A cohort was defined as all subadult females whose consecutive births were less than 18 months apart during the tenure of the same male coalition. We calculated the proportion of females (0 to 1) that dispersed from each cohort. Entire cohorts usually dispersed together (33 of 43 cases); when only a subset of females dispersed, the remaining females were treated as a separate cohort, because they often dispersed independently.

Independent variables included pride size (as measured by the number of breeding females), number of subadult females, number of unrelated female neighbours (total number of adult females in all neighbouring prides) and quality of the territory (75% kernel). Since dispersal events were typically triggered by male take-overs, explanatory variables were measured during the year when each cohort experienced its first male take-over. The average age at first take-over (2.29 ± 0.10 years, $N = 151$ cohorts) was very close to the average age of dispersal (2.76 ± 0.24 years, $N = 43$ cohorts), and the average time elapsed between dates of male take-overs and dispersal was 4.70 ± 1.15 months.

Annual pride territories were mapped from a fixed-kernel utilization-distribution of sightings of adult females, using ArcView (version 3.2, ESRI, Redlands, CA, U.S.A.). The territory boundary was defined as the 75% contour (kernel density isopleth), and the core area boundary was defined as the 50% contour. Further details can be found in Mosser (2008). Prides were considered to be neighbours if their territory cores (50% kernel) were within 3 km of each other, which is the mean daily movement distance for adult females plus one standard deviation (Mosser 2008). Unrelated prides were defined as prides that did not share maternal lineage or that split from the focal pride more than 5 years earlier. Genetic relatedness between prides remains high 5 years after a split (Packer et al. 1991), but prides have established autonomy and distinct territories by this point (Mosser 2008).

Territory quality was defined as the average landscape value of each 1 km grid cell within the pride's overall territory (75% kernel). Landscape value was determined by proximity to river confluences, which is significantly correlated with the spatial pattern of per capita female reproductive success and best describes the fitness value of the landscape (Mosser 2008). We performed separate analyses for the woodlands and plains habitats because of the large-scale differences in population density and habitat heterogeneity. Data were analysed in univariate generalized linear models, specifying a binomial distribution and logit-link function to account for the proportional nature of the data (R, R Foundation for Statistical Computing, Vienna, Austria).

Table 1

Univariate generalized linear models predicting the proportion of subadult cohorts dispersing from their natal prides

Variable	Effect	SE	Z	P
Plains (N=64)				
Adult females	0.4037	0.1564	2.582	0.0098
Subadult females	0.1677	0.1322	1.269	0.2046
Potential pride size	0.2523	0.1010	2.498	0.0125
Unrelated female neighbours	-0.0676	0.0573	-1.430	0.1526
Territory quality	-0.0075	0.0166	-0.452	0.6510
Woodlands (N=76)				
Adult females	0.3665	0.1005	3.648	0.0003
Subadult females	0.2309	0.0857	2.694	0.0071
Projected pride size	0.2502	0.0681	3.676	0.0002
Unrelated female neighbours	-0.1059	0.0501	-2.113	0.0346
Territory quality	0.1518	0.1652	0.918	0.3580
Overall (N=140)				
Adult females	0.3228	0.0755	4.273	<0.0001
Subadult females	0.1952	0.0681	2.864	0.0042
Projected pride size	0.2016	0.0470	4.289	<0.0001
Unrelated female neighbours	-0.071	0.0294	-2.415	0.0157
Territory quality	-0.0052	0.0140	-0.370	0.7110

Spatial patterns of dispersal were measured in two ways: the distance between the focal and neighbouring prides' territory centres and the percentage overlap between territories. 'Distance' was measured as the absolute distance between territory centres, and as a scaled distance relative to the mean of all neighbours to control for habitat. Thus, relative distance to a related neighbour = $(\text{distance}_{\text{related}} - \text{distance}_{\text{mean}}) / \text{distance}_{\text{mean}}$. Percentage overlap is the number of 1 km grid squares shared by both prides divided by the area of the focal pride's territory (75% kernel).

We performed linear regressions to examine the effects of years since pride division, number of unrelated neighbours and territory quality on distance/overlap. We analysed distances/overlaps between neighbouring prides, regardless of relatedness, and also between 'related neighbours' that had separated no more than 10, 5 or 2 years earlier. In these latter analyses, the maternal pride was always the focal pride, since we were measuring the extent to

which parental prides shared territory with dispersing groups. Depending on the analysis, unrelated neighbours were considered females from any neighbouring pride that had split more than 10, 5 or 2 years earlier, respectively.

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RESULTS

The probability of female dispersal increased with increasing pride size. A larger proportion of each cohort dispersed as the number of breeding females in each pride increased (Table 1), and this pattern clearly reflected the greater within-group competition in larger prides. Reproductive success declined when pride size exceeded 11 adult females in the woodlands and 6 females on the plains (Fig. 1). Only 23.2% of woodlands cohorts and 30.2% of plains cohorts dispersed when pride size was below these respective thresholds. However, 66.7% of woodlands cohorts and 63.6% of plains cohorts dispersed when pride size exceeded these thresholds. This pattern was even more striking when considering 'potential pride size' (number of adult females + number of recruited subadult females). Only 11.5% of plains cohorts dispersed when potential pride size was at most 6 females, whereas 52.6% dispersed when potential pride size exceeded 6 females (chi-square test: $\chi^2_1 = 11.32$, $P = 0.0008$). Similarly, only 7.1% of woodlands cohorts dispersed when potential pride size was at most 11, whereas 51.5% dispersed when potential pride size exceeded 11 (chi-square test: $\chi^2_1 = 18.61$, $df = 1$, $P < 0.0001$). Prides almost never split unless further recruitment increased pride size to a point where individual reproductive success was reduced.

Female cohorts were sensitive to the different pride-size-specific reproductive rates on the plains and in the woodlands (Fig. 2). Prides of 3–6 females showed favourable reproductive rates in both habitats, and when potential pride size was in this range, only 3 of 26 (11.5%) plains cohorts and 0 of 22 woodlands cohorts dispersed. However, plains prides of 7–11 females suffered substantially lower reproduction than their woodlands

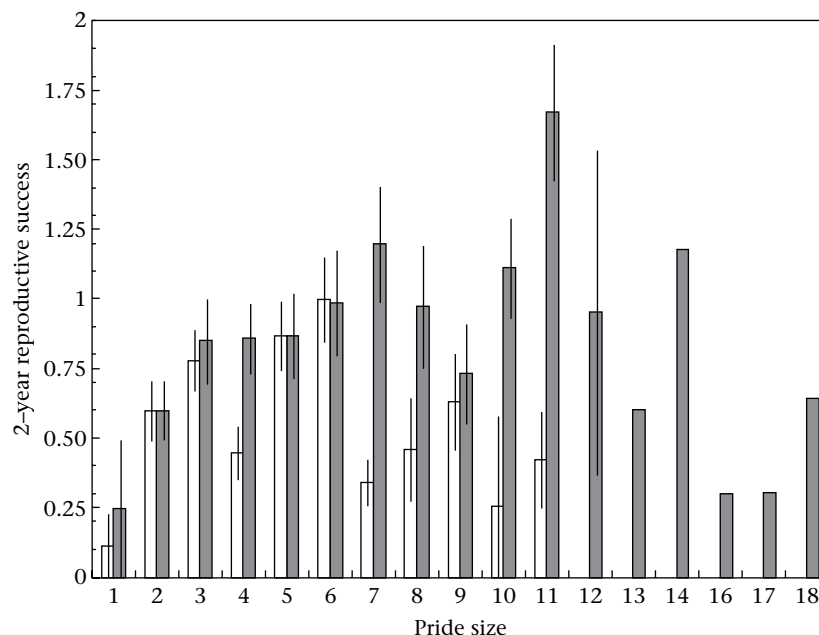


Figure 1. Two-year per capita reproductive success of females in woodlands (grey bars) and plains (white bars) prides. Pride size is the number of adult females in each pride.

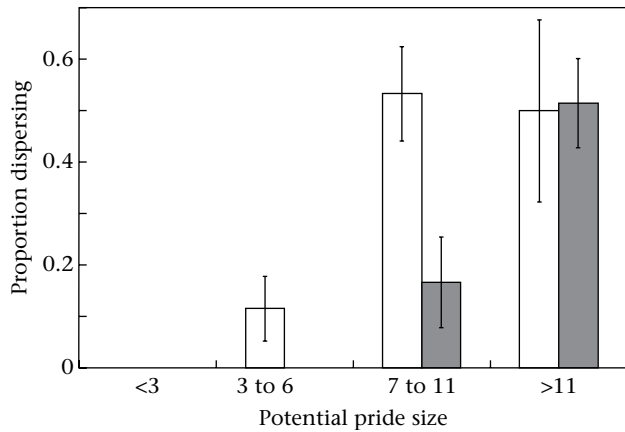


Figure 2. Proportion of plains (white bars) and woodlands (grey bars) cohorts dispersing versus the potential size of the natal pride when the subadult cohort was recruited.

counterparts, and 16 of 30 plains cohorts dispersed when potential pride size climbed within this size range compared to only 3 of 18 woodlands cohorts (chi-square test: $\chi^2_1 = 6.32$, $P = 0.0119$).

The minimum pride size for optimal per capita reproduction was three females in both habitats (Fig. 1), and only 2 of 33 (6.1%) singletons and pairs dispersed in the woodlands and 5 of 32 (14.3%) in the plains. However, 10 singletons/pairs split off from 33 larger cohorts on the plains compared to only 1 of 33 larger cohorts in the woodlands (chi-square test: $\chi^2_1 = 14.05$, $P = 0.0002$). Taken together, these results suggest a general tendency for plains females to disperse in suboptimal group sizes.

The probability of dispersal declined with increasing intensity of intergroup competition, as measured by the number of females in unrelated neighbouring prides (Table 1). This result was statistically significant in the overall data set and in the woodlands data set, but not in the plains data set. We found no evidence that territory quality influenced dispersal decisions. Thus, subadult females were most likely to disperse when intragroup competition was high (large pride size) and intergroup competition was low (fewer neighbouring females in high-density habitat).

In the first few years after dispersal, prides showed considerable territorial overlap with their mothers' pride and centred their range close to the midpoint of their mothers' range (Table 2). Proximity between mother and daughter prides did not change significantly with time between the first 2 to 5 years after dispersal, but decreased significantly by 10 years, when proximity was the same as for unrelated prides (Fig. 3). As the numbers of unrelated neighbours increased, daughter prides ranged increasingly closer to their mothers' pride than to unrelated neighbouring prides (Table 2, Fig. 4), although the degree of territorial overlap was unaffected by the number of unrelated neighbours. High territory quality led to closer proximity between all neighbouring prides but only increased overlap between related prides (Fig. 5).

DISCUSSION

Female lions showed a clear habitat-specific threshold for dispersal, corresponding to the pride size at which within-group competition reduced per capita reproductive success. Roughly 50% (37 of 71) of subadult female cohorts dispersed when pride size would exceed this threshold if the cohort were recruited into the pride. Only 6 of 68 (~9%) cohorts dispersed when projected pride size was below the threshold. Pusey & Packer (1987) also showed that dispersal was much more likely if prides would have exceeded

Table 2

Results of univariate regressions on spatial relations between all prides, and between prides that split no more than 10, 5 and 2 years earlier

	df	Effect	SE	t	P
All prides					
<i>Distance (m)</i>					
Unrelated neighbours	1181	-95.481	20.279	-4.7083	<0.0001
Territory quality	1212	-195.57	13.591	-14.390	<0.0001
<i>% Overlap</i>					
Unrelated neighbours	1203	-0.0008	0.0005	-1.5103	0.1312
Territory quality	1234	0.0006	0.0004	1.633	0.1069
Pride split ≤10 years					
<i>Distance (m)</i>					
Years since fission	91	452.45	228.87	1.9769	0.0512
Unrelated neighbours	91	-176.17	79.352	-2.2201	0.0289
Territory quality	91	-73.094	44.638	-1.6375	0.1050
<i>Relative distance (proportion)</i>					
Years since fission	83	0.0925	0.0334	2.7669	0.0070
Unrelated neighbours	83	-0.0273	0.0122	-2.2454	0.0274
Territory quality	83	0.0072	0.0084	0.8549	0.3951
<i>% Overlap</i>					
Years since fission	98	-0.0302	0.0096	-3.1575	0.0021
Unrelated neighbours	98	<0.0001	0.0035	-0.0184	0.9854
Territory quality	98	0.0034	0.0019	1.8342	0.0697
Pride split ≤5 years					
<i>Distance (m)</i>					
Years since fission	66	-103.72	421.14	-0.2463	0.8062
Unrelated neighbours	66	-157.97	82.464	-1.9156	0.0598
Territory quality	66	-74.724	49.018	-1.5244	0.1322
<i>Relative distance (proportion)</i>					
Years since fission	58	-0.0008	0.0423	-0.0186	0.9852
Unrelated neighbours	58	-0.0247	0.0082	-3.0094	0.0039
Territory quality	58	0.0040	0.0076	0.5348	0.5948
<i>% Overlap</i>					
Years since fission	72	-0.0135	0.0211	-0.6410	0.5237
Unrelated neighbours	72	-0.0012	0.0042	-0.3043	0.7618
Territory quality	72	0.0047	0.0023	2.0281	0.0463
Pride split ≤2 years					
<i>Distance (m)</i>					
Years since fission	33	598.66	1326.3	0.4514	0.6547
Unrelated neighbours	33	-91.406	112.02	-0.8160	0.4204
Territory quality	33	-60.108	67.490	-0.8906	0.3796
<i>Relative distance (proportion)</i>					
Years since fission	28	-0.0874	0.1211	-0.7214	0.4767
Unrelated neighbours	28	-0.0223	0.0104	-2.1506	0.0403
Territory quality	28	-0.0080	0.0126	-0.6360	0.5299
<i>% Overlap</i>					
Years since fission	39	-0.0230	0.0500	-0.4396	0.6627
Unrelated neighbours	39	-0.0007	0.0045	-0.1620	0.8721
Territory quality	39	0.0056	0.0027	2.0372	0.0485

10 females. Our larger data set enabled us to partition the analysis, revealing that female dispersal was sensitive to the pride size that conferred maximum reproduction in each habitat (11 females in the woodlands and 6 in the plains). The woodlands lions experience more consistent levels of prey availability and access to large-bodied prey species (Cape buffalo and giraffe) that reduce the level of within-group feeding competition, allowing for larger prides.

Pride size increases with increasing territory quality but so does the number of unrelated neighbours (Mosser 2008). Thus, it is difficult to evaluate the effect of territory quality on dispersal decisions. High territory quality leads to conditions where subadult females are not only more likely to disperse (large pride size) but also less likely to disperse (high number of neighbours).

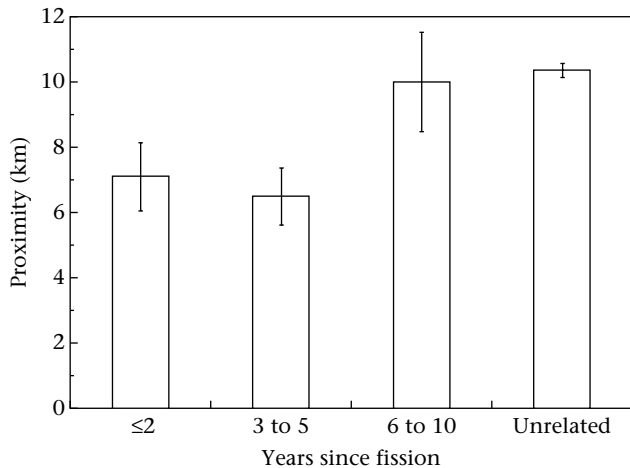


Figure 3. Proximity between maternal and descendant prides after dispersal (see Table 2 for statistics).

Similar to numerous other studies (e.g. Jones et al. 1988; Walters et al. 1992; Holekamp et al. 1993; Sillero-Zubiri et al. 1996; Pasinelli & Walters 2002), subadult female lions were less likely to disperse when their natal pride was surrounded by more unrelated neighbours (especially in the woodlands, Table 1). The high prey abundance of the woodland habitat allows lions to live at higher densities than on the plains (Hanby & Bygott 1979), perhaps making the number of neighbours more important for dispersal decisions by woodlands subadults. Plains females also showed a greater tendency to disperse as solitaires or pairs, even though females in both habitats showed an aversion to dispersing in such suboptimally small groups.

How do existing prides react to their daughters' prides? Dispersing females settle near their natal range (Pusey & Packer 1987), but related prides treat each other more like nonkin as time passes and kinship declines (Packer et al. 1991). Maternal prides shared an average of $36.9 \pm 2.3\%$ of their territories with daughters that split no more than 5 years earlier compared to $18.7 \pm 3.4\%$ that split 6–10 years earlier, and $13.1 \pm 0.5\%$ with unrelated neighbours (Table 2). Proximity between prides also diminished over time (Fig. 3).

High degrees of overlap are consistent with patterns in solitary species (Waser & Jones 1983; Rogers 1987; Zedrosser et al. 2007), but these studies only quantified overlap between parents and

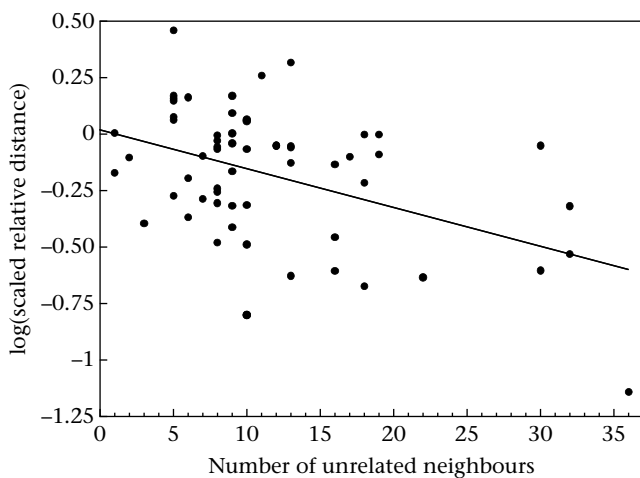


Figure 4. Effect of unrelated neighbours on the scaled relative distance between prides that split no more than 5 years earlier. A log value of -1.0 means that the related pride was $1/10$ as far from the focal pride as from its average neighbour.

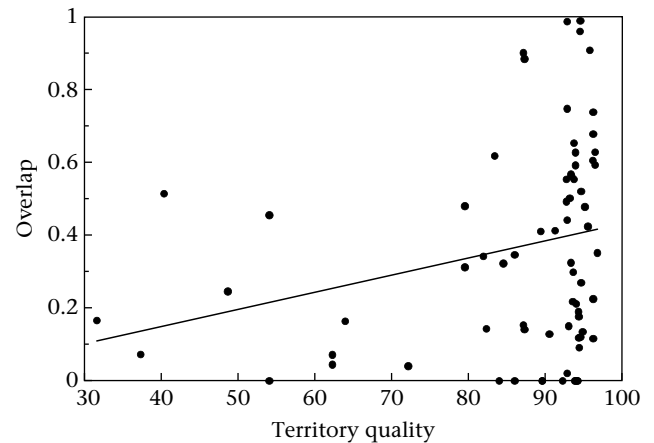


Figure 5. The effect of territory quality on the degree of territorial overlap between prides that split no more than 5 years earlier.

offspring or between siblings. Schenk et al. (1998) used DNA fingerprinting to quantify relatedness among solitary black bears, *Ursus americanus*, but found no relationship between kinship and territory overlap. Because relatedness between recently split prides declines with the recruitment of subsequent cohorts of offspring (Packer et al. 1991), we used the time that had elapsed since pride fission as a surrogate measure of kinship, and neighbouring prides ranged further apart as kinship declined.

As the number of unrelated neighbours increased, daughters settled relatively closer to their mothers' pride, but this was not accompanied by a higher degree of territory overlap. Competition may be more intense between unrelated neighbours, causing related prides to shift closer together while still excluding each other from their core areas. Exclusivity of territories increases with population density (Mazerolle & Hobson 2004), and we also found that the territories of related prides were more exclusive at higher local densities.

Increasing habitat quality usually decreases territorial overlap (Davies & Hartley 1996; Mazerolle & Hobson 2004), except when the costs of defending a territory are greater than the benefits gained by excluding others (Maher & Lott 2000; McLoughlin et al. 2001). In lions, overlap between related neighbours increased with increasing territory quality, even though the distance between territory centres did not change, suggesting that habitat quality increased tolerance of related neighbours but did not affect lions' defence of core locations against unrelated prides.

In most social mammals, dispersal decisions are highly dependent on the likelihood of an individual gaining reproductive status in a despotic group. Even though female lions are egalitarian, dispersal decisions still optimize reproductive opportunities by allowing females to live in group sizes that maximize reproductive rates. Subadults dispersed when potential pride size was larger than the habitat-specific threshold, but only when their dispersing cohort would be larger than the minimum viable pride size. These patterns also increased daughters' inclusive fitness by allowing their mothers to avoid living in excessively large prides. Further inclusive fitness benefits probably accrue from the tolerance that related prides display towards each other and from their greater proximity in areas of high intergroup competition.

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