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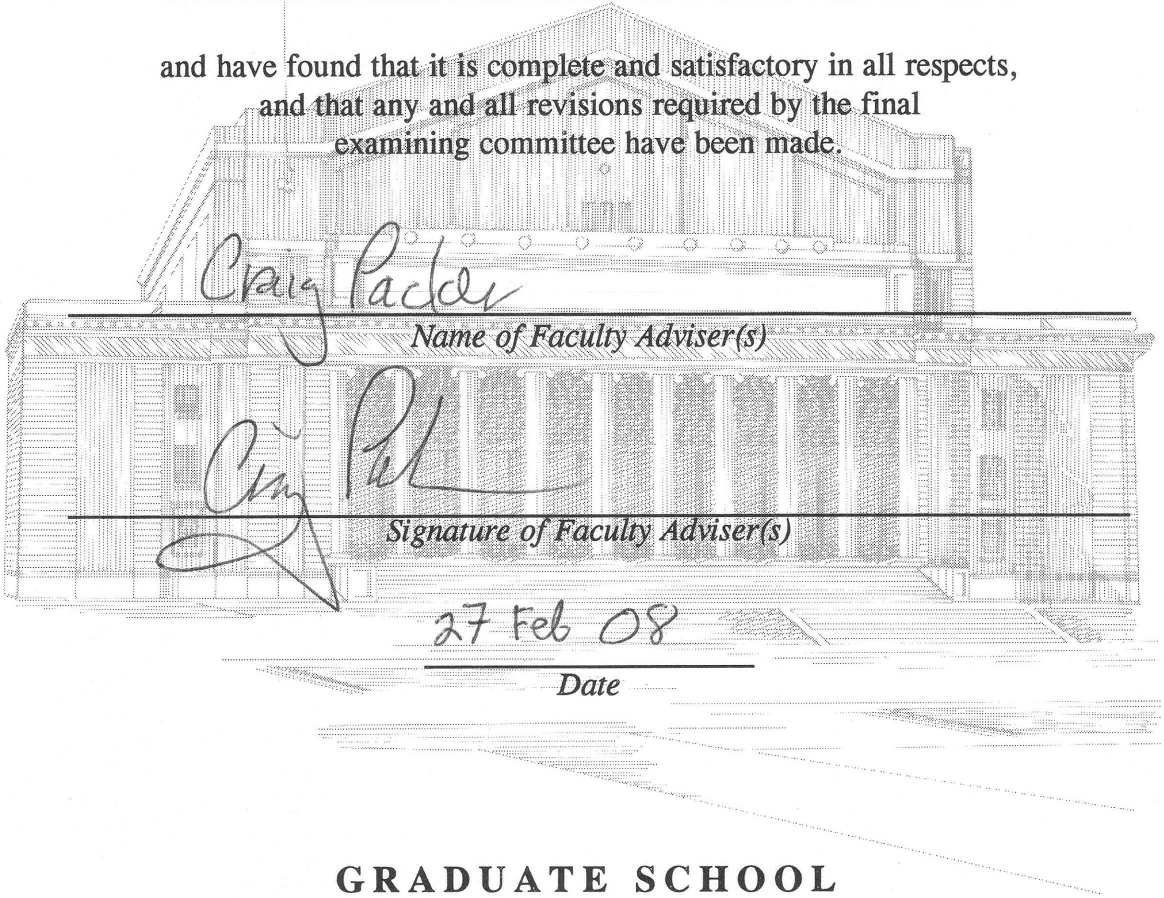

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GRADUATE SCHOOL

Group territoriality of the African lion: behavioral adaptation in a heterogeneous landscape

A DISSERTATION
SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL
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Anna Alice Mosser

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This dissertation is dedicated to my parents,
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ABSTRACT

This thesis examines the evolution of group territoriality – a compelling form of social behavior marked by notable levels of cooperation and violence. My research focuses on the evolution of social behavior in African lions and places numerical advantage in territorial competition at the foundation of the lion social group. Results also suggest how group-territorial behavior was shaped by a heterogeneous savanna landscape.

This research required, above all, an understanding of how lion's view their habitat, as territoriality is an ongoing effort to gain and maintain exclusive access to a valuable share of real estate. Using a 38-year dataset on lions in the Serengeti National Park, Tanzania, I determined that a fitness-based (as opposed to density-based) measure is a superior gauge of lion habitat quality. Average female per capita reproductive success was significantly correlated with proximity to river confluences. This single landscape feature, which provides food, water and shelter, best describes the value of Serengeti lion real estate.

With this information, I estimated pride territory quality and established that larger prides do indeed maintain control of the highest value habitat. In addition, neighbors had a significant negative impact on female reproductive success and survival, indicating that inter-group competition strongly affects fitness. Pride subgroups were also significantly larger when a pride had more neighbors, suggesting sensitivity to risk of encounter. Males played a more important role in group-territorial competition than expected, and female mortality was strongly associated with male neighbors, suggesting that males may exhibit adaptive lethal aggression, which tips the balance of power in favor of their own pride.

Simulation modeling demonstrates that group territoriality may be an emergent property, which evolves due to the synergistic effects of landscape structure and advantages of forming territorial social groups. The model also shows that group territoriality is more likely to evolve in high density populations and that rates of inter-group conflict are significantly higher in heterogeneous landscapes. These results help us to understand how lions became social as a result of adaptation to the heterogeneous savanna landscape, and also provide insight into the evolution of other group-territorial species, including humans.

TABLE OF CONTENTS

Chapter 1 – Serengeti real estate: a lion's-eye view of the savanna landscape

Chapter 2 – Group territoriality of the African lion

Chapter 3 – The evolution of group territoriality: balance of power in a heterogeneous landscape

TABLES & FIGURES

Introduction

Chapter 1 – Serengeti real estate: a lion's-eye view of the savanna landscape

Chapter 2 – Group territoriality of the African lion

Chapter 3 – The evolution of group territoriality: balance of power in a heterogeneous landscape

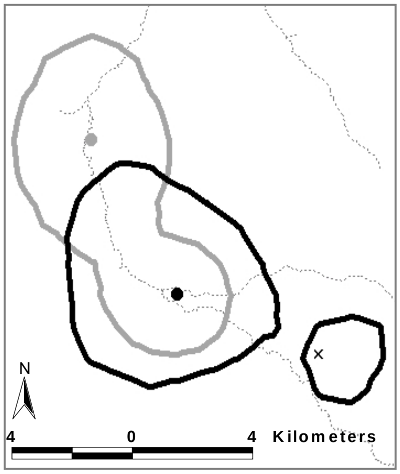
INTRODUCTION

Lions are the most social of all the felids, and understanding the basis of their gregarious nature has long been a central topic of research for this charismatic species. Past research has ruled out the infamous group hunt and defense of cubs from infanticide as sole drivers in the evolution of lion sociality (Packer et al. 1990), but has demonstrated that cooperative territorial defense plays an important role in lion social life (McComb et al. 1994, Heinsohn and Packer 1995, Heinsohn 1997). Lion sociality is also likely the result of behavioral adaptation to the savanna habitat (Kleiman and Eisenberg 1973, Packer 1986, Mattern and McLennan 2000). Thus, the focus of my thesis has been to address this question: Do lions live in groups in order to out-compete their neighbors for control of the highest value real estate on the heterogeneous savanna landscape?

In his book, *The Serengeti Lion* (1972, pp. 51-2), George Schaller describes this interaction between the neighboring Masai and Seronera prides (Fig. 1):

> *At 0655, on December 27, 1968, five Masai pride lionesses walked through the central part of their area obviously searching for the rest of the pride as one or another roared, then stopped, as if waiting for an answer. Filing across the skyline, barely visible in the high grass .6 km away, were seven lionesses and six cubs of the Seronera pride. When the Masai pride females spotted them, they trotted closer, apparently thinking that these were members of their own pride. The Seronera pride lionesses became aware of the other at 60 m; the cubs scattered and several lionesses growled, yet the Masai pride females still did not discover their mistake. One ran up to a Seronera pride female as if to rub heads in greeting. But suddenly she stopped, with noses almost touching, snarled and slapped at the other. For 15 seconds the lionesses milled around growling and snarling and roaring and several tussled briefly. One snarling lioness chased a Masai pride female and clawed her deeply in the rump, an injury which caused the thigh to wither in the following months until she could only hobble on three legs. Two Masai pride lionesses fled at the beginning of the melee and two more did so at the end. Only one remained. She walked for nearly a minute among the other lionesses with her canines exposed, snarling, then followed unharmed those that had fled. Although the Seronera pride females had driven four of the five others away, they now moved toward their own pride area, traveling 5km in 65 minutes.*

Figure 1: Territories of the Masai (black outline) and Seronera (gray outline) prides, 1967-68. Circles indicate the territory centers for each pride. Gray dotted lines are main rivers. The X marks the location of the interaction described.



Schaller did not stress the role of territoriality in the social behavior of lions, but this description largely captures the main aspects of group-territorial competition: a need to maintain contact with pride-mates, aggressive encounters with neighboring prides, severe wounding, an imbalance of power (5 lionesses in the Masai pride sub-group vs. 7 in the Seronera sub-group) and retreat by the smaller group despite the location of the interaction, and finally retreat by the intruders indicating a recognition of which pride currently owns the area. This anecdote also brings to mind a larger issue; why risk such an intrusion into a neighbor's territory? My research poses that it is what is at stake in these interactions (exclusive use of high quality habitat), combined with the pressure that landscape heterogeneity places on such competitive interactions, that has provided the foundation for the evolution of lion social behavior.

Addressing the question

Complete analysis of this hypothesis requires an integration of several components: empirical information describing both the lion population and the savanna landscape, concepts from different disciplines, and new technical analytic tools.

The backbone of my research is the continuous long-term observations on lions in the Serengeti National Park, Tanzania, started by George Schaller in the mid 1960's. This dataset provides a large enough sample size to assess the relationship between relative group size and individuals fitness, a feature lacking in most studies of group-territorial species. The long-term lion data, combined with a wealth of ecological data describing the study system (e.g. river locations and prey abundance), allows for a unique fine-scale analysis of habitat quality, furnishing us with a definition of lion real estate, the object of inter-group territorial competition.

This dissertation brings together concepts from three related disciplines: animal behavior, ecology, and landscape ecology. Most broadly, my research draws from the study of the evolution of social behavior, and examines patterns of phylogenetic inertia and ecological constraints that favor to the development of territorial animal groups (Wilson 1975). Behavioral analysis of group territoriality began, for the most part, with studies of cooperatively breeding birds (e.g. Brown 1964, Gaston 1978, Woolfenden and Fitzpatrick 1984). These studies focus on the trade-off between the costs of delayed reproduction versus the potential benefits of delaying dispersal and remaining to help at the nest. They stress factors that constrain dispersal, such as habitat saturation, and consider the potential benefits of forming a social group, such a cooperative territorial defense. Various other studies have addressed the evolution of group territoriality - such as the remarkable study by Davies and Houston (1981) that illustrates tolerance of a territorial intruder, which can assist in territorial defense, dependent upon rates of resource availability – but there has been little integration of this research. The most development has occurred in the study of group-territorial behavior in chimpanzees and humans (e.g. Wadley 2003, Wilson and Wrangham 2003). The study of territoriality, in general, also began with birds (e.g. Howard 1948), and is an area of research that has enjoyed a strong development that continues as new research tools are made available (Stamps 1994, Adams 2001). The evolution of territorial behavior, and thus group territoriality as well, depends upon resource distribution and abundance (Davies and Houston 1984). An understanding of territorial behavior therefore necessitates an understanding of an animal's basic resource requirements, that is, its ecology.

Ecology is concerned with the factors that determine the distribution and abundance of organisms (Andrewartha 1961), and resources (food, water, and shelter) are among the most important of these factors. Without an understanding of how and where the landscape provides these resources, we cannot define the parameters that determine landscape value and territory quality, which is required to evaluate the outcome of group-territorial competition. Using the detailed spatial and demographic records on lions in the Serengeti, we build upon and challenge the established ecological methods of determining habitat quality, which assume an ideal free distribution and a direct relationship between consumer density and resource density (Fretwell and Lucas 1969, Fretwell 1972, VanHorne 1983). Given their territorial behavior, lions conform instead to an ideal despotic distribution, where densities may not relate directly to habitat quality (Fretwell and Lucas 1969, Fretwell 1972), and we therefore use a fitness related measure to determine habitat quality. We view demographic data from a unique landscape perspective and on a scale smaller than most studies - a scale that we expect is closer to how lions use their landscape and more relevant to understanding territorial competition.

Through the resource dispersion hypothesis (RDH) (Macdonald 1983, Kruuk and Macdonald 1985), group-territoriality was linked to concepts that are addressed by landscape ecology. RDH was developed in an effort to understand the social behavior of European badgers, which appear to enjoy no obvious benefit from grouping and were thought be social by due to patterns of resource dispersion alone. In a patchy landscape, a territory that supports a solitary individual or breeding pair may very well support additional individuals at little cost to that original individual or pair. Beginning in the 1970's, patchiness, or landscape heterogeneity, has been increasingly recognized as a significant factor affecting many ecological processes (Forman and Godron 1986, May and Southwood 1990). The role of landscape structure is well established in the discipline of ecology and is the defining principle of landscape ecology. Although landscape heterogeneity is addressed when appropriate in behavioral studies (e.g. dispersal patterns in acorn woodpeckers, Stacey and Ligon 1987), it is yet to play a clear role in the discipline of animal behavior. There is undoubtedly much potential in the integration of concepts from landscape ecology and animal behavior.

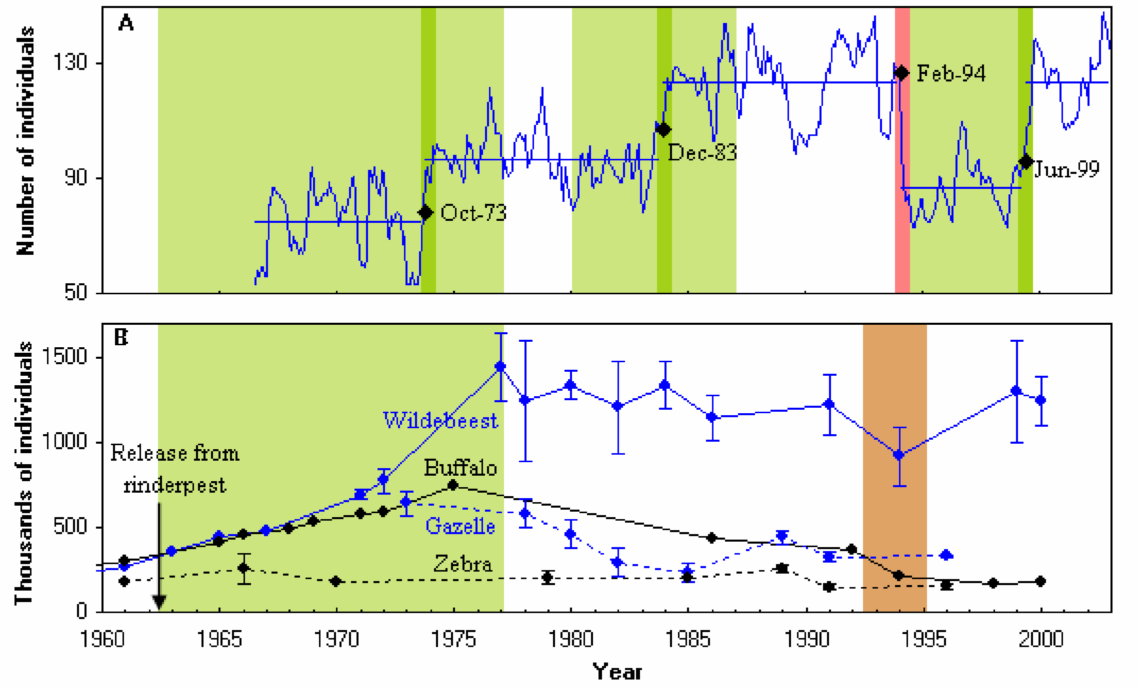
Broader significance

The evolution of social behavior is an exceptional but consequential transition in evolutionary history, sharing significance and similarities with the development of the chromosome, the eukaryote, and sexual reproduction (Maynard Smith and Szathmary 1995). In contrast to solitary species, social animals secure fitness benefits through mutually dependent intraspecific relationships. Via these relationships, the formation of social groups becomes a stepping stone to complex characteristics such as cooperative behavior (e.g. African wild dogs, Creel 2001), division of labor (e.g. ants, Blanchard et al. 2000), and, in many cases, enhanced cognitive ability (e.g. Pinyon jays, Bond et al. 2003). Defining the ecological selective pressures that lay the foundation for social relationships has therefore been the primary focus of numerous research studies in behavioral ecology.

Our concern for preserving biological diversity demands that we increase our understanding of how population dynamics are linked to landscape structure. The sustainability of threatened populations depends upon detailing how a species utilizes the resources in its habitat (Fahrig and Merriam 1994). In the aptly titled paper, *Finding the Missing Link between Landscape Structure and Population Dynamics: A Spatially Explicit Perspective*, the authors use a modeling approach to demonstrate that incorporation of individual space use (such as dispersal and habitat selection) is essential to understanding population and metapopulation phenomena. This, in turn, helps to forecast how populations will respond to an ever changing heterogeneous and unfortunately fragmented landscape. This type of research arms us with knowledge and tools applicable in effective wildlife conservation.

In recently published work (Packer et al. 2005) we demonstrate the profound effects that social structure can have on population dynamics. Rapid population increases in the Serengeti lion population (Fig. 2a) only occur when specific demographic, social and ecological conditions coincide. Despite gradual changes in resource availability (Fig. 2b), the lion population dynamics are abrupt, because they are mediated by the lion's social use of the landscape. Commentary on this work notes the significance of the influence of social behavior and suggests that "behavioral-based population models… will ultimately find their way into the analytical toolbox of population ecologists" (Ranta & Kaitala 2005). *Behavior* describes how an animal exploits the resources in its habitat and plays a key role in understanding that elusive link between landscapes and animal population dynamics.

Figure 2: a) Woodland lion population each month. Horizontal lines indicate periods where population sizes were statistically homogeneous but different from adjacent periods. Diamonds designate change points. Pale green blocks highlight times when the populations were below local equilibrium density; dark green lines demarcate years within these periods with favorable rainfall. Red line shows the canine distemper virus die-off in 1994. b) Serengeti herbivore population sizes. Vertical bars show SE. Green box highlights recovery from rinderpest; brown box highlights drought-related die-off in the wildebeest (adapted from Packer et al. 2005).



In two respects, the study of lion social behavior provides insight into the evolution human society. Some have argued that the natural history of hominid evolution is better understood thorough analysis of animals that are also adapted to life on the savanna landscape.(Schaller and Lowther 1969, Alberts et al. 2006). We also share with lions the trait of group territoriality, which has profoundly shaped the characteristics of our culture and social life (Tinbergen 1968, Toft 2006, Wrangham 2006). Thus an understanding of the basis of lion social behavior will undoubtedly provide us with some insight into the forces that have shaped our own evolution.

Thesis overview

In chapter 1, I determine the ecological parameters that define the value of the landscape for Serengeti lions. I present a new method of analysis, which analyzes the spatial relationships between demographic parameters and landscape features and yields a fine-scale picture of lion real estate value, over short and long time scales. I also compare the use of density versus fitness-based measures of habitat quality, and use this information to determine source and sink habitat. The information gained from this analysis is applied in chapter 2, as a measure of territory quality.

In chapter 2, I examine the patterns of inter-group competition and test whether pride size confers a territorial competitive advantage in Serengeti lions. The impact of neighbors on fitness-related demographic parameters and sub-grouping patterns within the pride is used to assess the degree and effects of inter-group resource competition. The effect of pride size on the outcome of territorial competition and territory quality is analyzed to determine the long-term advantages of grouping in lions.

In chapter 3, I use a spatially explicit, individual-based, simulation model to examine the conditions that lead to the evolution of group territoriality. I focus on the roles of landscape heterogeneity (testing the ideas developed in the resource dispersion hypothesis), three potential advantages of forming territorial groups, and population density. This model also provides for an analysis of the relationship between heterogeneity and inter-group conflict.

CHAPTER 1

Serengeti real estate:
a lion's-eye view of the savanna landscape

(with John Fryxell[1], Lynn Eberly[2], and Craig Packer)

INTRODUCTION

Measurement of consumer distribution and abundance is the most common means of determining habitat quality. Established methods include habitat suitability indices (U.S. Fish and Wildlife Service 1981), resource selection functions (Boyce and McDonald 1999, Buskirk and Millspaugh 2006), and niche parameter estimation (Hirzel et al. 2002, Peterson 2006). When applied at a local scale of second-order selection (Johnson 1980), these methods rely upon a key prediction of density-dependent habitat selection (e.g. the ideal free distribution; Fretwell and Lucas 1969): consumer density reflects resource abundance and habitat quality.

Although distribution- and abundance-based methods do generally detect relative habitat quality for a broad range of species (Bock and Jones 2004), the accuracy and predictive utility of these methods has been questioned (VanHorne 1983). Several authors have recommended including fitness parameters in the determination of habitat quality (VanHorne 1983, Murphy and Noon 1991, Hall et al. 1997), as these measures should better predict the factors that support the long-term persistence of a population. This recommendation is especially important for species unlikely to conform to an ideal free distribution.

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Territorial animals are expected to fit an ideal despotic distribution (Fretwell and Lucas 1969, Fretwell 1972), in which superior individuals exclude conspecifics from high quality habitat. This distribution predicts that individual fitness will correlate positively with resource abundance and habitat quality, but makes no precise predictions of how density will vary across the landscape. Source-sink dynamics are traditionally associated with the closely related preemptive distribution (Pulliam 1988, Pulliam and Danielson 1991), but such dynamics will also result from a despotic distribution if the degree of despotism forces some individuals into poor habitat that does not support successful reproduction. In a source-sink system, only demographic parameters can reveal the sources, while density patterns may correlate with a set of parameters that support short-term local persistence but not necessarily reproduction.

We tested whether a fitness-related measure is superior to density in gauging habitat quality and in identifying source locations for a population that exhibits source-sink dynamics. Patterns of per capita reproductive success and density were mapped for adult female lions (*Panthera leo*) studied over a continuous 38-year period in the Serengeti National Park, Tanzania (Packer et al. 2005). Short-term and long-term average patterns of reproductive success and density were analyzed with respect to fine-scale landscape features associated with the availability of basic resources. Such correlative analyses, however, can only generate inductive conclusions about the relationship between a species and its landscape; it is also important to consider physiological and behavioral mechanisms in analyses of habitat quality (Hobbs and Hanley 1990, Morrison 2001). We therefore also compared reproductive success and density to a mechanism-based map of habitat quality (termed a niche map; Pulliam 2000, Kearney 2006), derived from an empirical understanding of the availability of food, water, and shelter for lions.

Across Africa, lion densities are highest in ecosystems with the highest biomass of resident prey (VanOrsdol et al. 1985), and a similar pattern is observed within large ecosystems such as the Serengeti (Schaller 1972). However, no prior study has examined the relationship between fitness, density, and habitat quality at the scale that individual lions use the landscape – the scale most relevant to testing the predictions of Fretwell & Lucas (1969), Pulliam (1988), and Pulliam and Danielson (1991). The territorial patterns of Serengeti lions are consistent with a despotic distribution; larger prides out-compete smaller prides for high quality habitat (they are the despots) and the degree of despotism decreases with population density (greater territory overlap with increasing population density), indicating that this is not a density independent preemptive distribution (chapter 2). We expect the spatial patterns of reproductive success to identify the source areas of high fitness value. Given the despotic distribution and that local heterogeneities support larger prides, we also expect adult female density to be greater in high quality habitat. Despite the expected positive association between reproductive success and population density, non-reproductive individuals are likely to aggregate in "refuges" with merely adequate resources, so fine-scale population density is likely to correlate with a broader set of landscape variables and may fail to identify the source areas that support the long-term persistence of the population.

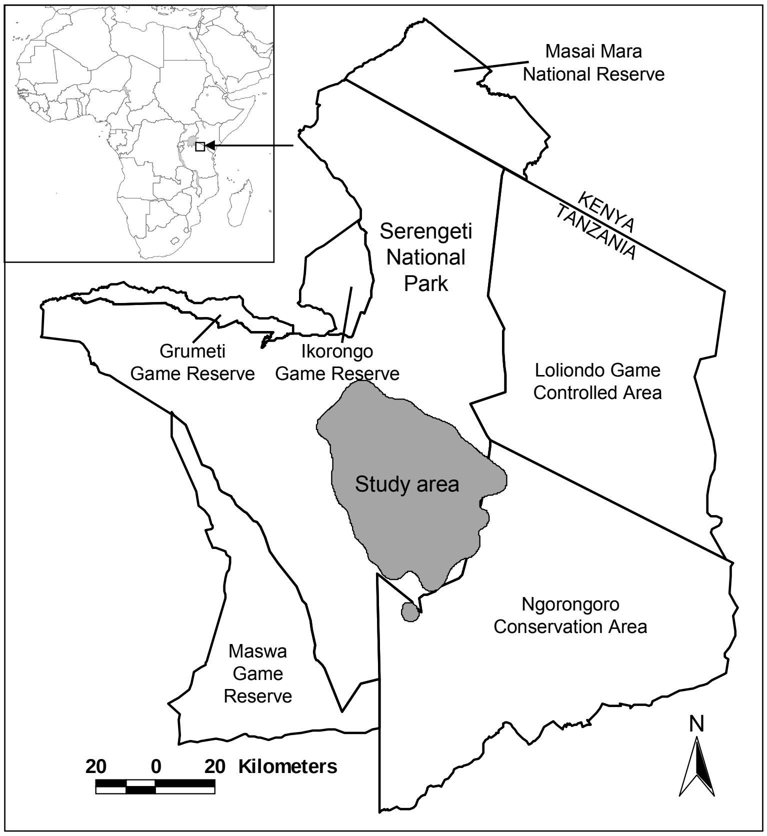
Variation in fitness is traditionally analyzed using an individual-based approach, but we developed a method of analysis with a distinct landscape perspective. The unit of our analysis is a location (a grid cell), rather than individuals or their territories (cf. Breininger et al. 1985, Langen and Vehrencamp 1998, Delahay et al. 2006, Kerbiriou et al. 2006). This method shares similarities with spatial epidemiology (Elliott and Wartenberg 2004) and hedonic analysis of real estate values (e.g. Geoghegan et al. 1997). The grid-cell method also averages out individual variation and stochasticity, facilitates comparison with density patterns, and allows for patterns to be mapped at any spatial or temporal scale within the limits of the available data. We determine the *value* of each grid cell by averaging, across individuals and over time, the reproductive output associated with the occupancy of that location. The result is a "real estate map" of average reproductive rates.

METHODS

Study area

The Serengeti study area (Fig. 1), located at the center of the Serengeti-Mara ecosystem, reflects the heterogeneities characteristic of this savanna ecosystem. Most of the total annual rainfall occurs during the wet season, but there is an increasing rainfall gradient from southeast to northwest (Norton-Griffiths et al. 1975). Vegetation follows a similar gradient, from short to tall grassland to woodland, as determined by rainfall and changing soil type (Sinclair 1979, Packer et al. 2005). Woody vegetation is also denser along rivers (Herlocker 1975) and kopjes (rocky inselburgs) are dispersed throughout the study area. The study area does not directly border areas of dense human settlement.

Figure 1: Serengeti-Mara ecosystem, located in east Africa (inset), spans the border between Tanzania and Kenya. The lion study area (grey) is determined by the ranges of the current 26 study prides.



Large herds of migratory wildebeest (*Connochaetes taurinus*), zebra (*Equus burchelli*), and Thomson's gazelle (*Gazella thomsoni*) move on to the southeastern short-grass plains during the wet season, passing through the woodlands portion of the study area at the start and end of each season. Resident prey include buffalo (*Syncerus caffer*), warthog (*Phacochoerus aethiopicus*), topi (*Damaliscus korrigum*), kongoni (*Alcelaphus buselaphus*), giraffe (*Giraffa camelopardalis*), Grant's gazelle (*Gazella granti*), impala (*Aepyceros melampus*), and reedbuck (*Redunca redunca*). During the dry season months, the resident prey species are more abundant in the woodlands than on the plains.

Study population

Serengeti lions have been studied since 1966 (Schaller 1972, Bertram 1973, Hanby and Bygott 1979, Packer et al. 1988, Packer et al. 2005). The woodland lions have been monitored continuously over this entire period, but the plains lions were not studied from Nov. 1969 until Oct. 1974. The size of the study population has ranged between roughly 50 and 300 known individuals living in 5 to 30 prides, with the lowest numbers corresponding to periods when the study area only included the woodlands. Observations between 1966 and 1983 were opportunistic. Beginning in 1984, one member of each study pride was radio collared and all subsequent monitoring relied on a combination of radio telemetry and opportunistic sightings. Study prides were generally located at least once every two weeks, and the lions were almost always observed directly. All observations include date, time, GPS (Geographic Positioning System) coordinates, pride membership, group composition, individual identification, prey consumed, and reproductive status/behavior. Demographic records for the population (individual birth, death, and pride immigration/emigration dates) were maintained on an ongoing basis.

Mapping reproductive success and density

Reproductive success and density were calculated for each pride on a 2-year time-step, which is the average inter-birth interval for these lions (Packer and Pusey 1983). Time-steps begin in November (the start of wet season), and are labeled for the years that comprise the majority of the time-step (e.g. Nov. 1966 – Oct. 1968 was labeled as "1967–1968"). The number of adult females (3 years and older) in a pride was determined for each month and then averaged over each 2-year period. Per capita reproductive success was defined as the total number of cubs born within each time-step that survived to 1 year of age divided by the average number of adult females in the pride over the same 2-year period. Adult female density was calculated as the average number of adult females in the pride divided by the size (km^2) of the pride's territory for each 2-year time-step (see mapping details below).

Cub survival varies considerably between prides and is the primary determinant of lion population growth (Packer et al. 2005), whereas birth rates cannot be estimated accurately (due to early mortality of unseen cubs) but appear to be relatively constant. Adult mortality primarily results from density independent disease (Packer et al. 1999, Kissui and Packer 2004) and intraspecific aggression (Packer *et al.* 1988). Per capita reproductive success was therefore chosen as the main response variable and the best proxy for individual fitness in this analysis. There is little within-pride variation in female reproductive success (Packer et al. 2001) and individual ranging patterns, so per capita reproductive success was analyzed at the level of the pride rather than for specific individuals. Thus, within each time-step, each adult female in a pride was assigned the same value for reproductive success and was associated with the same territorial range.

The lion ranging data included records on 45 prides and 1102 adult female lions collected from Nov. 1966 to Oct. 2004. Observations collected from both radio-tracking and opportunistic sightings were pooled together; pride ranges based on the two methodologies were similar (range estimates of 25 prides in 2003–4 overlapped by an average of 75%). Territory boundaries were determined from utilization-distribution curves calculated from the lion sightings (in ESRI ArcView GIS 3.2), using a fixed kernel with a smoothing parameter (*h*) of 3000 meters, roughly the mean distance moved by a lion each day plus one standard deviation (Kirkby unpublished). Due to the potential sensitivity of kernel density estimates to sample size (Anderson 1982, Worton 1987, 1989, Harris et al. 1999), a 75% kernel was chosen as a potentially less biased estimate of territory area and location. Larger 95% kernels tend to overestimate the area used while smaller 50% kernels can incorrectly identify the location used. The average territory size was 57 km^2 (57 grid cells), ranging from 15-220 km^2, with the larger territories located in open grassland habitat.

A pride was included in the analysis if it had been observed at least five times in each year of a time-step. About 20% of the 2-year ranges had <20 observations, representing a trade-off between accuracy and biasing our results against less frequently observed prides that occupy fringe areas of lower quality habitat. To test for effects of small sample size, we randomly sub-sampled 10 well observed prides (6 random subsets of 15 observations each). The 75% kernel ranges derived from these subsets differed little from those based on the full dataset (subset kernels were 2% larger on average and overlapped with the full dataset kernel by an average of 93%), thus small sample sizes were unlikely to introduce systematic error into the analysis.

Each pride's 2-year reproductive success was assigned to each grid cell in the pride's 2-year territory. Pride maps were merged across the study area to create a reproductive success map for each time-step. In areas of territory overlap, reproductive success was averaged, weighting by the number of adult females in the respective prides. The merged short-term maps contained 79-1123 grid cells. We controlled for density dependence in reproductive success by scaling the values from 0-1 within each time-step. Thus each pride's success was measured relative to the success of the other prides in each year and population-wide effects of changes in density over time were minimized. Absolute measures, however, were used in the initial analysis of average overall reproductive rates and source-sink dynamics. To construct a long-term picture of lion real estate values, all nineteen 2-year time-step maps were overlaid, and average relative reproductive success was calculated for each grid square, again weighting by the number of females. Grid cells were excluded from the final map if fewer than three 2-year maps contributed to the overall average. The long-term map contained 1424 grid cells. Note that the real estate maps are left-truncated; we did not quantify the reproductive value of grid cells that fell outside estimated pride ranges and are probably of the lowest reproductive value. The same method was used to map female density, but density was not scaled to relative values within each time-step.

Source-sink dynamics

Reproductive rates required to replace adult females were determined from age-specific mortality rates estimated for the Serengeti and nearby Ngorongoro Crater lion populations (Packer et al. 1998). Per capita reproductive success rates of 0.66, 0.84, and 0.99 were estimated to replace females of ages 4, 6, and 8 years. Sinks were defined as areas with average 2-year reproductive rates below 0.66 cubs per adult female; areas unable to support replacement of reproductive adults. Sources (weak to strong) were defined as areas with average reproductive rates above 0.66.

Landscape variables

The GIS (Geographic Information System) maps detailing the landscape characteristics of the study area included: rivers, river confluences, tree cover, kopjes, seasonal prey distribution, and seasonal rainfall. The first five landscape variables were used in the niche map (see below). Rainfall was included as a surrogate variable for water availability and prey abundance because of the impact of precipitation on herbivore migratory patterns (Hanby and Bygott 1979). All data were projected into UTM coordinates (zone 36S, datum Clarke 1880) and the scale of analysis was limited by the data set with the coarsest resolution (rainfall maps at 1000 m). For discrete landscape features (rivers, confluences, tree cover, and kopjes), grid cell values equal the distance (km) of that cell's centroid to the nearest landscape feature of a particular type.

Rainfall maps were generated on a seasonal basis through spatial interpolation of data collected from rain gauges located across the ecosystem. Dry season rainfall maps were averaged within each 2-year period and over the whole 38-year time span.

The vegetation map was a simplified version of a map created by Herlocker (1975), and designated two vegetation types: areas of greater or less than 2% canopy cover. The map distinguished between woodland and plains and identified areas of thicker vegetation near rivers. This 2% tree cover designation corresponds closely to that used by Hopcraft (2002) and Hopcraft et al. (2005) in analyses of Serengeti lion hunting success (see below). Although, the vegetation patterns within the study area have changed over the four decades of the study (Packer et al. 2005), the two general categories represented in our map have not changed considerably and do represent the basic environment experienced by lions over the full time-span.

Prey distribution was estimated from monthly herbivore counts collected in the dry season of 2004 (July – Oct.). The same two observers (Joseph Masoy and John Mchetto) drove a predetermined 404 km track every month and counted all large mammals <100 m from the vehicle. Spatial position was monitored to the nearest 0.1 km on the odometer, with UTM coordinates interpolated from GPS readings taken along the tracks at 1 km intervals. Only the most common lion prey species (as listed above) were included here. Monthly maps of prey density were interpolated from prey counts totaled within hexagonal regions of roughly 100 km^2. Dry season prey density was averaged over the four months. This prey distribution only represents a single season, thus we have also included annual rainfall as a surrogate measure of prey abundance (see above).

Niche map

A niche map was created to represent expected patterns of per capita reproductive success. Cub survival is largely determined by the harsh conditions of the dry season months (Schaller 1972, Bertram 1973, Packer et al. 2005). During this period, roughly May through October, rain is infrequent, water is scarce and, because the migratory herds have left the study area, prey densities are low. We evaluated each 1 km grid cell in the Serengeti study area according to its association with landscape characteristics that provide (a) food, (b) water, or (c) shelter during the dry season. Each of these three ecological components of reproductive success was determined separately, and scaled from 0-1, where a 1 indicates maximum access to that resource within the study area. These three maps were then averaged to create the final niche map, thus assuming that each component contributes similarly to reproductive success and that areas with multiple resources are most valuable. The validity of these assumptions was evaluated by testing each niche component separately and in each combination in the statistical analysis.

a) *Food* – Food intake is largely determined by prey distribution and landscape features that promote successful prey capture (Elliot et al. 1977, VanOrsdol 1984, Stander and Albon 1993, Funston et al. 2001, Hopcraft et al. 2005). A group-based type-II functional response model was used to predict per capita food intake, following the model structure and parameterization of Fryxell *et al.* (2007). Lion food intake depends on the encounter rate with herds rather than individual prey and the capture rate of the foraging group, which varies with landscape characteristics (Hopcraft et al. 2005) but not with group size (Packer et al. 1990).

Landscape-based probabilities of prey capture were derived from the resource selection functions presented in Hopcraft (2002), who found that hunting success is higher near river confluences and in areas with ≥5% woody cover (Hopcraft 2002, Hopcraft et al. 2005). Although capture probability is highly localized, the effect of access to good hunting locations was expected to be expressed at the scale of individual territories. Prey capture probabilities were thus applied to all grid cells within 4km (the average territory radius) of the landscape feature that provides the given rate of capture success. Hopcraft also found that hunting success was higher near erosion terraces, but at a finer spatial scale than could be included in this analysis. Rates of scavenging were estimated without the use of the functional response model and were based on herd density and relevant landscape features (scavenges are more frequent near confluences and kopjes; Hopcraft 2002). Rates of food intake, based on kills and scavenges, were mapped and scaled from 0-1, then averaged with kills weighted by 60%, representing their proportion in the diet of lions (Packer et al. 1990).

b) *Water* – While lions obtain some water from the bodily fluids of their prey, they depend upon free-standing water for up to half their water intake during hotter months (Green et al. 1984, Clarke and Berry 1992). For much of the year, water is only located in small pools along river courses (Wolanski and Gareta 2001), and these pools are more likely to occur at confluences (Knighton and Nanson 2000, Hopcraft 2002). Lions will travel well outside their territories in search of water, so distance to a water source was used as the measure of access to this resource. Maps of distance to rivers and confluences were scaled from 0-1 within the study area, then these two maps were averaged with a weight of 2:1 towards confluences, where water is twice as likely to occur (Hopcraft 2002).

c) *Shelter* **–** Female lions separate from their pride-mates and give birth in locations that are relatively inaccessible to other lions and predators (Schaller 1972, Hanby et al. 1995), and that also provide shelter from the heat of the sun (Bleich et al. 1996). Based upon the behavior of new mothers extracted from the long-term dataset, lion dens are typically located along rivers and in kopjes. Mothers do not travel long distances in search of dens and they return to dens on a daily basis. Shelter availability was based upon distance from rivers and kopjes, up to 2km (the estimated average mother foray distance). Landscape values were scaled from 1 to 0 between 0km and 2km from a river or kopje, and assigned a value of 0 beyond 2km.

Statistical analysis

Statistical relationships were analyzed using a linear mixed model (PROC MIXED, SAS 9.1, SAS Institute Inc., Cary, NC; Littell *et al.* 2002). Spatial structure was built into the model, using a repeated-measures statement, to account for spatial autocorrelation as a decreasing function of increasing distance between grid cells. We expected autocorrelation to be generated by a pride using multiple grid cells (Lichstein et al. 2002), so the extent of expected autocorrelation was fixed at 4.2 km (the average territory radius).

Maps of reproductive success and adult female density were modeled as a function of each landscape variable, the overall niche model, and each component of the niche model (food, water, or shelter). We expected negative correlations between the dependent variables and the discrete landscape features (e.g. reproductive success will decline with increasing distance from rivers) and positive correlations in all other cases. The niche model and its components represent our best *a priori* understanding of the relationships between the demographic patterns and the landscape, thus complex multivariate models including interactions between the landscape variables were not tested. Akaike Information Criterion (AIC) values were used to evaluate the strength of alternative models (Akaike 1974, Burnham and Anderson 2002). For a set of candidate models, information-theoretic weights were calculated from the ΔAIC values, comparing each model to the model with the lowest AIC value. AIC weights ranged from 0-1, and the model with the highest weight was interpreted as providing the best fit to the data. Significance tests were also reported and used where applicable.

RESULTS

The short-term (2-year) and long-term (38-year) spatial patterns of per capita reproductive success and adult female density were consistent with a despotic distribution (Fretwell and Lucas 1969, Fretwell 1972). Both reproductive success and density were greater in areas of higher habitat quality (Tables 1 and 2; Figs. 2, 3, 5, and 6); reproductive success and density decreased with increasing distance from rivers, for example. Accordingly, reproductive success was strongly correlated with female density in the short-term maps (68% of the 2-year reproductive success maps were significantly ($p \leq 0.001$) correlated with density) and in the long-term map (effect = 1.18, SE = 0.13, $p < 0.001$). Also consistent with a despotic distribution, there was increased use of poorer habitat at higher population densities (average annual distance from confluence vs. average annual density: effect = -27.61, SE = 5.81, $p < 0.001$) and greater variance in reproductive success in higher quality habitat, although this trend was not significant (variance in reproductive success vs. distance from confluence: effect = -0.01, SE = 0.01, $p = 0.15$).

Analysis of the average absolute reproductive success revealed clear source-sink dynamics (Fig. 4). Based upon reproductive rates estimated to balance the rates of adult mortality, 52% of the study area was identified as a potential sink. Analysis of female dispersal (when cohorts of females establish a new pride) confirms that the sink areas are largely supported by immigration from the sources. Of the sink-area prides of known origin, 69% (9 out of 13) were the result of dispersal from a source-area pride. The rate of source-to-sink dispersal was low, with roughly one such dispersal event every three years. In contrast, no source-area prides of known origin had a natal pride located in a sink.

While short-term patterns of reproduction and density followed the expected directional relationship with landscape (Table 1, Figs. 2 and 3), there were few significant correlations for either dependent variable. In a given set of 19 correlations, at best 42%

were significant at a 0.001 level. However, the overall trends were significant when the 19 two-year maps were considered in aggregate (e.g. dry season rainfall was positively correlated with reproductive success in 74% of the 2-year maps). To some extent, stronger patterns of correlation were observed between short-term density and the independent variables.

Long-term average reproductive success (Table 2, Fig. 5) was significantly correlated with proximity to rivers and confluences, and, according to the AIC weight and the multivariate model, confluence was the stronger of these two explanatory variables. Reproductive success correlated significantly with only the food and water components of the niche model (Fig. 7). Of the niche components, inclusion of water alone or food and water together provided the best fit to the data. Of all models, proximity to confluence provided the best fit to the long-term pattern of reproductive success. The significant correlation between reproductive success and confluences remains if we also control for adult female density in a multivariate model.

Long-term average adult female density (Table 2, Fig. 6) was significantly correlated with all the landscape variables but dry season rainfall provided the strongest fit (according to AIC weight). Density was significantly correlated with all niche models, with the exception of the food component, and water was the strongest of the niche models. Overall, dry season rainfall was the strongest univariate variable explaining patterns of adult female density. In the multivariate model, rainfall and proximity to rivers and kopjes were significant, while confluences, tree cover, and herd density were dropped.

Table 1: Univariate analysis of short-term (2-year) reproductive success and adult female density with respect to each landscape variable and niche model. Results were separated by positive (+) vs. negative (−) estimated association. Explanatory variables were considered significant if, using a Bonferroni correction, p-values were less than 0.001. *A significant pattern of association ($p<0.05$) was seen across all 19 maps in a positive or negative direction using a chi-square test for goodness of fit to a binomial ($n=19$, expected probability of 50%).

Variable	% maps w/+ effect	% sig. (p≤0.001)	% maps w/− effect	% sig. (p≤0.001)	Majority effect
Reproductive success:					
Distance to river (km)	26	0	74	11	−*
Distance to confluence	16	0	84	5	−*
Distance to tree cover	47	16	58	11	−
Distance to kopje	42	0	58	0	−
Herd density – dry season	63	11	37	0	+
Rainfall – dry season	74	11	26	11	+*
Niche model	58	0	42	0	+
Food	79	5	21	0	+*
Water	79	11	21	0	+*
Shelter	53	0	47	0	+
Food & water	84	5	16	0	+*
Food & shelter	58	5	42	0	+
Water & shelter	53	0	47	0	+
Density:					
Distance to river (km)	0	0	100	21	−*
Distance to confluence	0	0	100	37	−*
Distance to tree cover	11	0	89	26	−*
Distance to kopje	26	0	74	0	−*
Herd density – dry season	84	32	16	0	+*
Rainfall – dry season	89	42	11	0	+*
Niche model	84	16	16	0	+*
Food	84	21	16	0	+*
Water	100	32	0	0	+*
Shelter	84	5	16	0	+*
Food & water	95	32	5	0	+*
Food & shelter	79	11	21	0	+*
Water & shelter	89	5	11	0	+*

Table 2: Univariate analysis of long-term (38-year) average reproductive success and adult female density with respect to each landscape variable and niche model. [1]AIC weights within model types (landscape variable or niche). [2]AIC weights across all 13 alternative models. *Landscape variables significant in the multivariate model.

Variable	Effect	Standard error	P-value	AIC weight[1]	AIC weight[2]
Reproductive success:					
Distance to river	-0.0105	0.0036	0.004	0.2183	0.1708
Dist. to confluence	-0.0114	0.0034	0.001*	**0.7620**	**0.5961**
Dist. to tree cover	-0.0043	0.0027	0.114	0.0109	0.0085
Distance to kopje	-0.0011	0.0045	0.813	0.0031	0.0024
Herd density	0.0384	0.0493	0.436	0.0003	0.0003
Rainfall	0.0009	0.0008	0.281	0.0054	0.0042
Niche model	-0.0080	0.0267	0.765	0.0118	0.0026
Food	0.0639	0.0296	0.031	0.1116	0.0243
Water	0.2586	0.0959	0.007	**0.4095**	0.0892
Shelter	-0.0126	0.0097	0.194	0.0262	0.0057
Food & water	0.1440	0.0534	0.007	**0.4095**	0.0892
Food & shelter	-0.0103	0.0183	0.574	0.0130	0.0028
Water & shelter	-0.0190	0.0189	0.315	0.0184	0.0040
Density:					
Distance to river	-0.0035	0.0007	<0.001*	0.2722	0.2610
Dist. to confluence	-0.0032	0.0007	<0.001	0.0578	0.0554
Dist. to tree cover	-0.0019	0.0005	<0.001	0.0003	0.0003
Distance to kopje	-0.0029	0.0009	0.001*	0.0002	0.0002
Herd density	0.0227	0.0095	0.017	0.0000	0.0000
Rainfall	0.0008	0.0002	<0.001*	**0.6695**	**0.6420**
Niche model	0.0230	0.0052	<0.001	0.3013	0.0124
Food	0.0098	0.0058	0.092	0.0001	0.0000
Water	0.0849	0.0187	<0.001	**0.4968**	0.0204
Shelter	0.0072	0.0019	<0.001	0.0235	0.0010
Food & water	0.0290	0.0105	0.006	0.0008	0.0000
Food & shelter	0.0147	0.0036	<0.001	0.0821	0.0034
Water & shelter	0.0153	0.0037	<0.001	0.0954	0.0039

Figure 2: Short-term (2-year) relative per capita reproductive success. Note that lion ranging data were only available for the northwestern quarter of the study area in 1971-74. White areas are outside the estimated pride ranges.

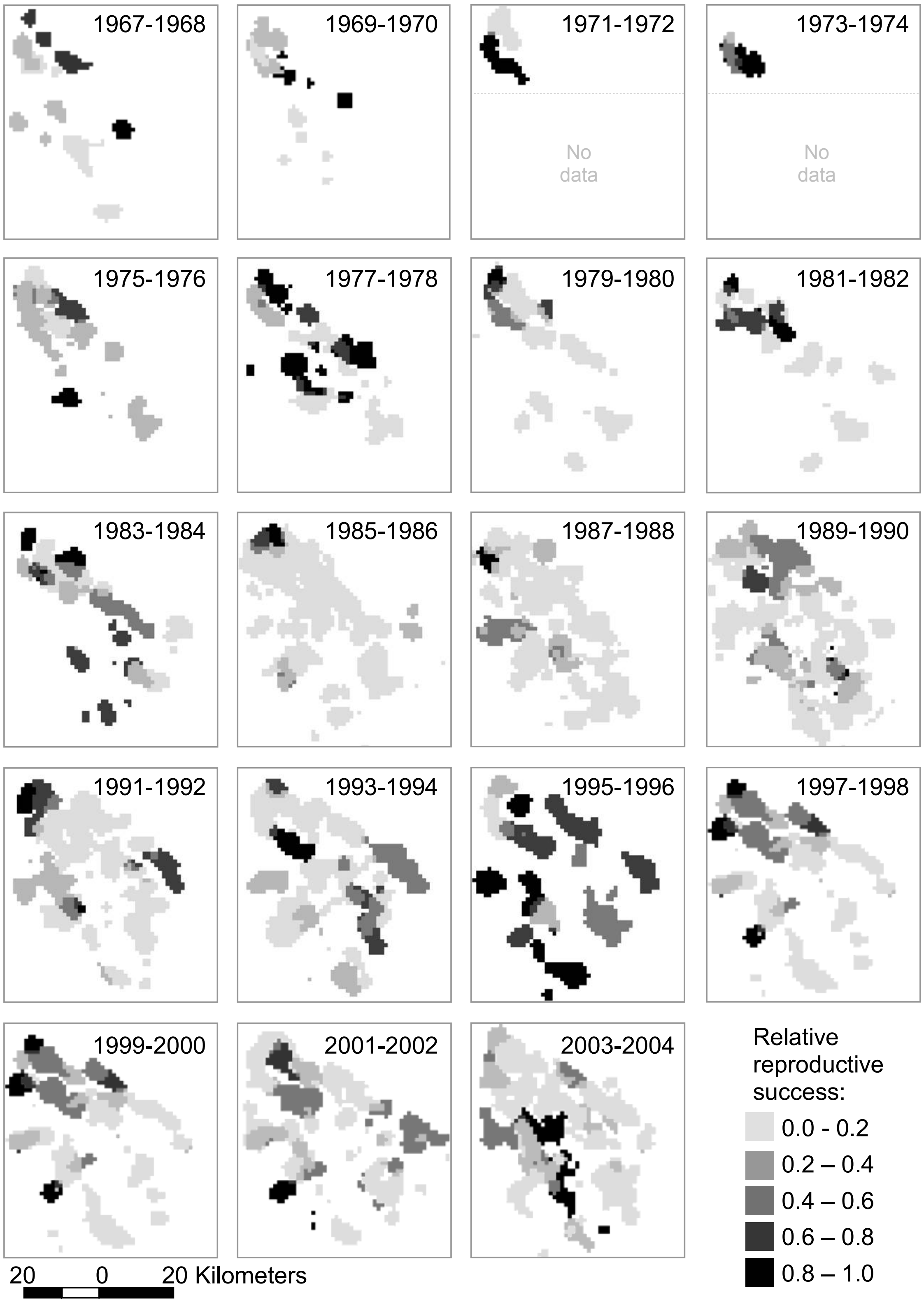


Figure 3: Short-term (2-year) adult female density. Note that lion ranging data were only available for the northwestern quarter of the study area in 1971-74. White areas are outside the estimated pride ranges.

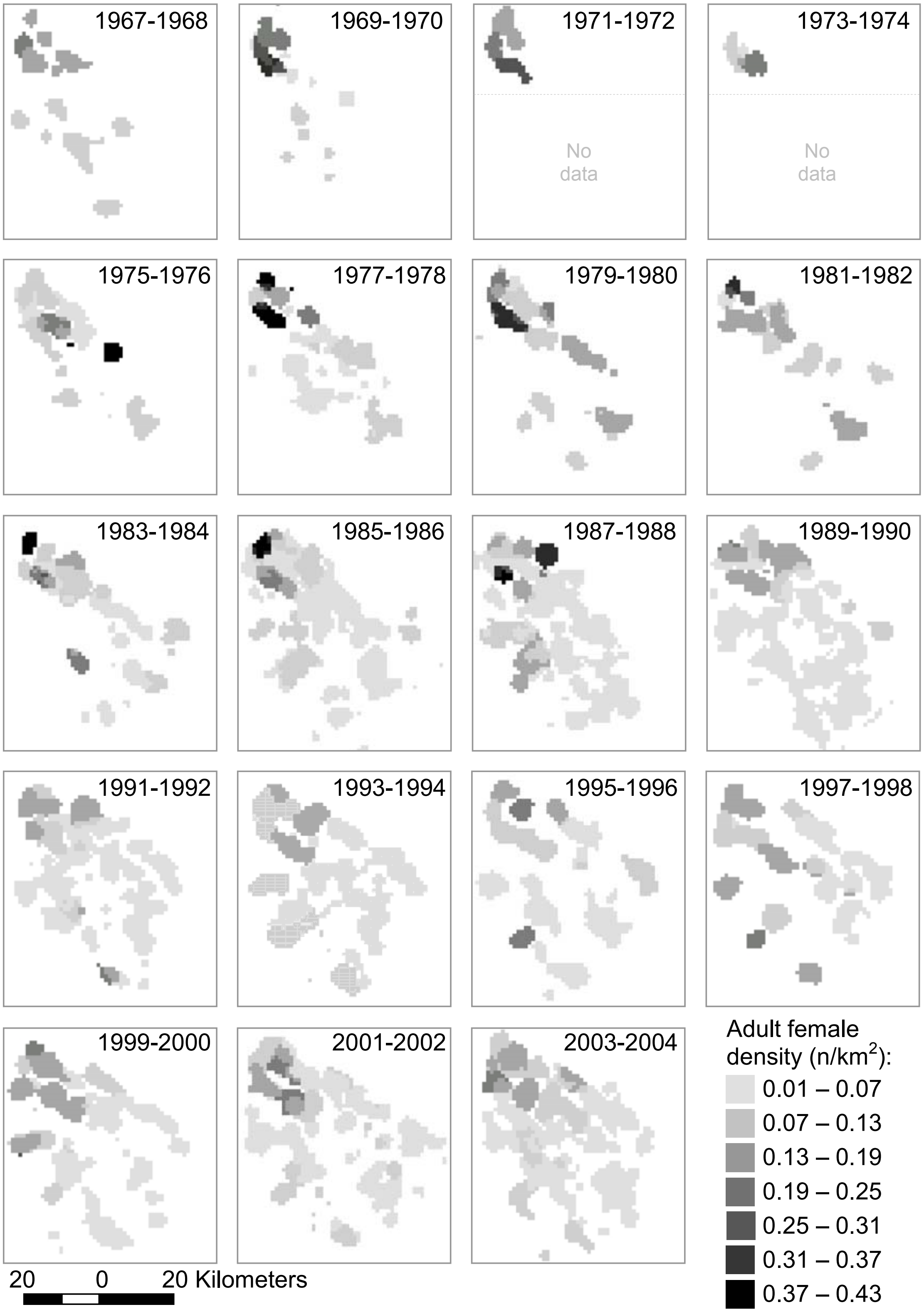


Figure 4: Source and sink areas were based upon the 38-year average of absolute (not relative) reproductive success. Sinks supported a low reproductive rate that is not expected to replace 4-yr old females. Weak sources support a reproductive rate capable of replacing 4-yr old females, sources support replacement of 6-yr old females and strong sources support replacement of 8-yr old females (the average age of adult females in the Serengeti is 7.7 yrs). White areas indicate grid squares with insufficient ranging data.

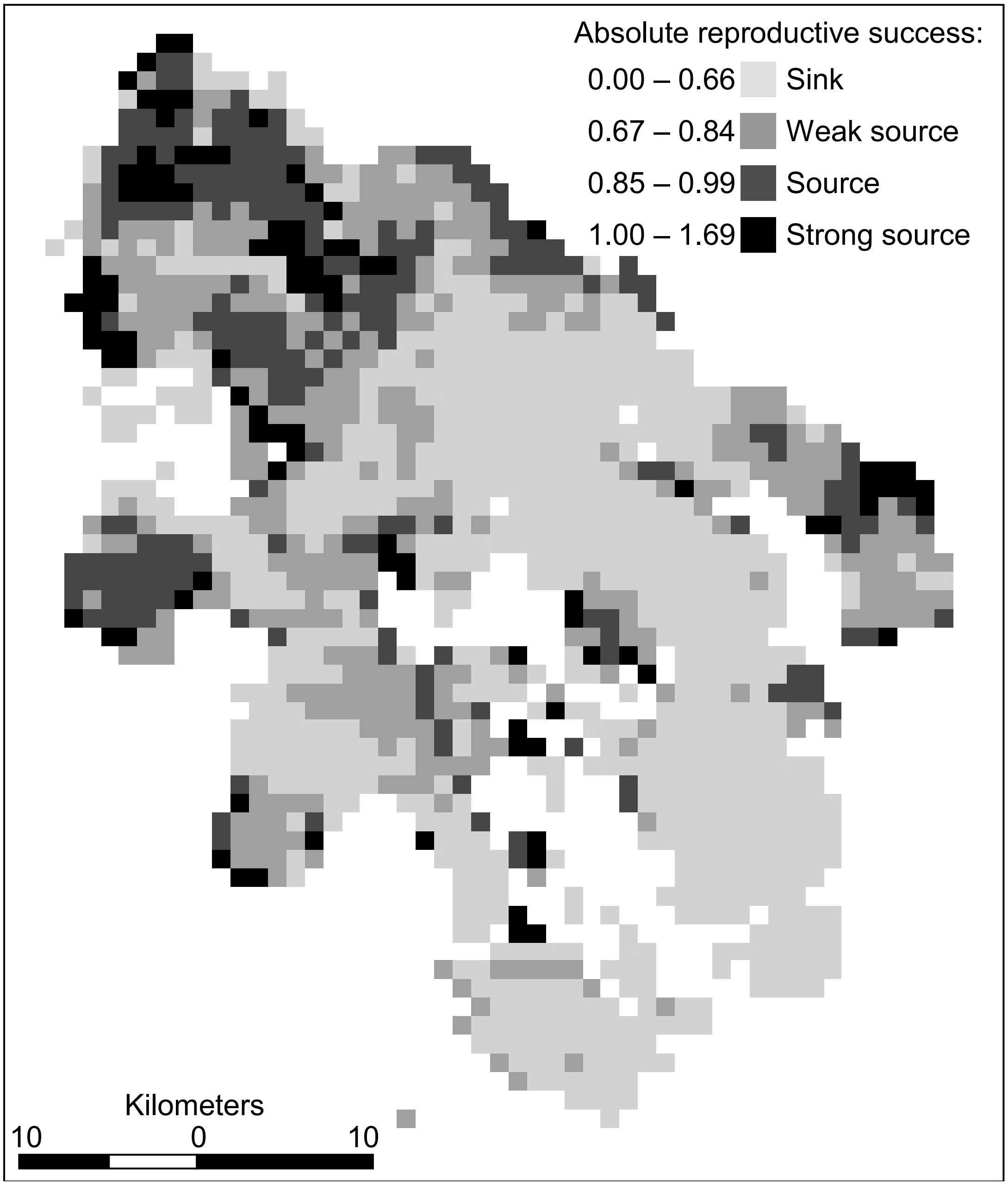


Figure 5: Long-term (38-year) average relative reproductive success. Major rivers are shown in black, tributaries are light gray, and confluences are white open circles. White areas indicate grid squares with insufficient ranging data. Note that the legend scale is not evenly distributed and is extended for the lower values to better illustrate the observed patterns.

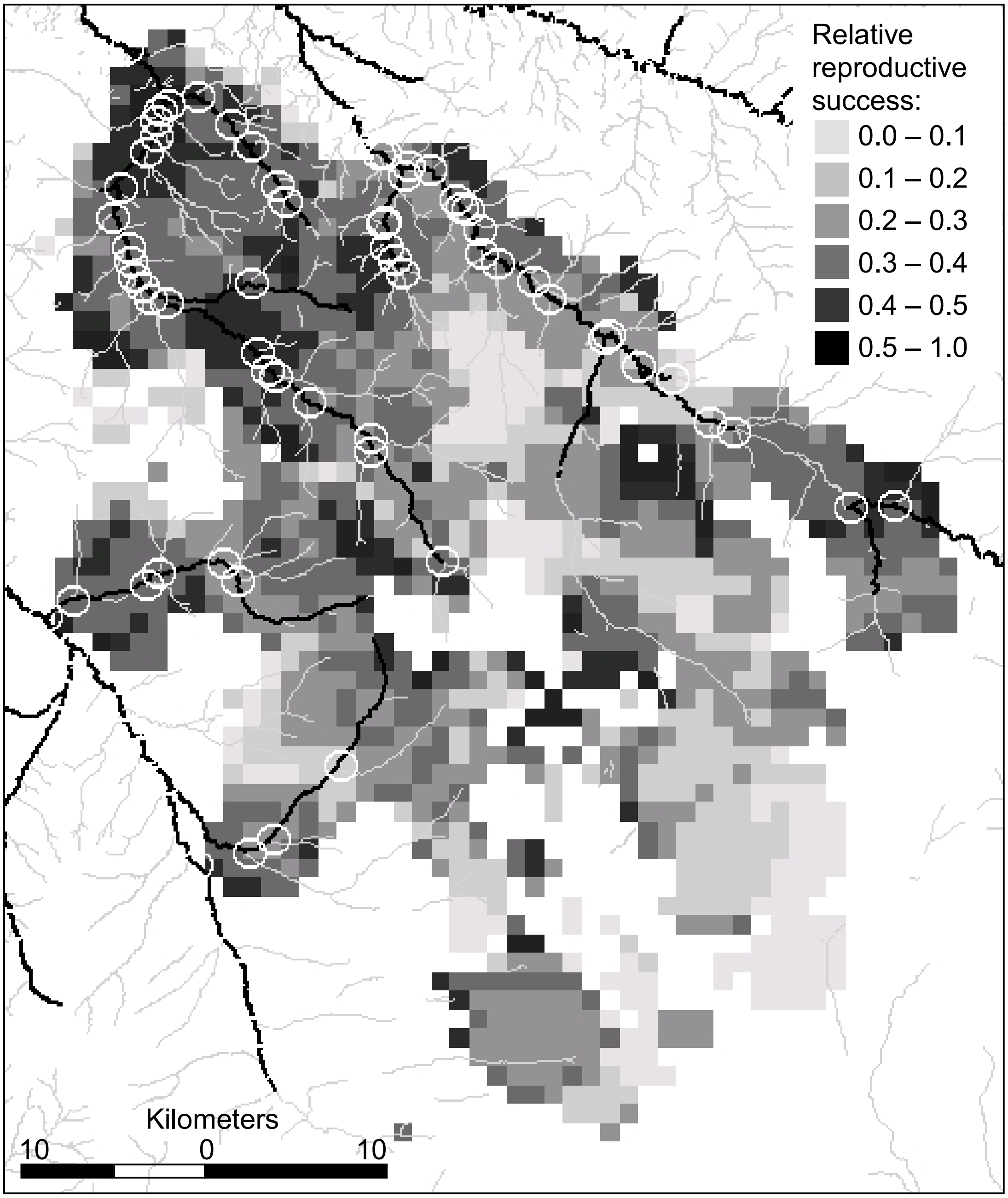


Figure 6: Long-term (38-year) average adult female density. White areas indicate grid squares with insufficient ranging data. Note that the legend scale is not evenly distributed and is extended for the lower values to better illustrate the observed patterns.

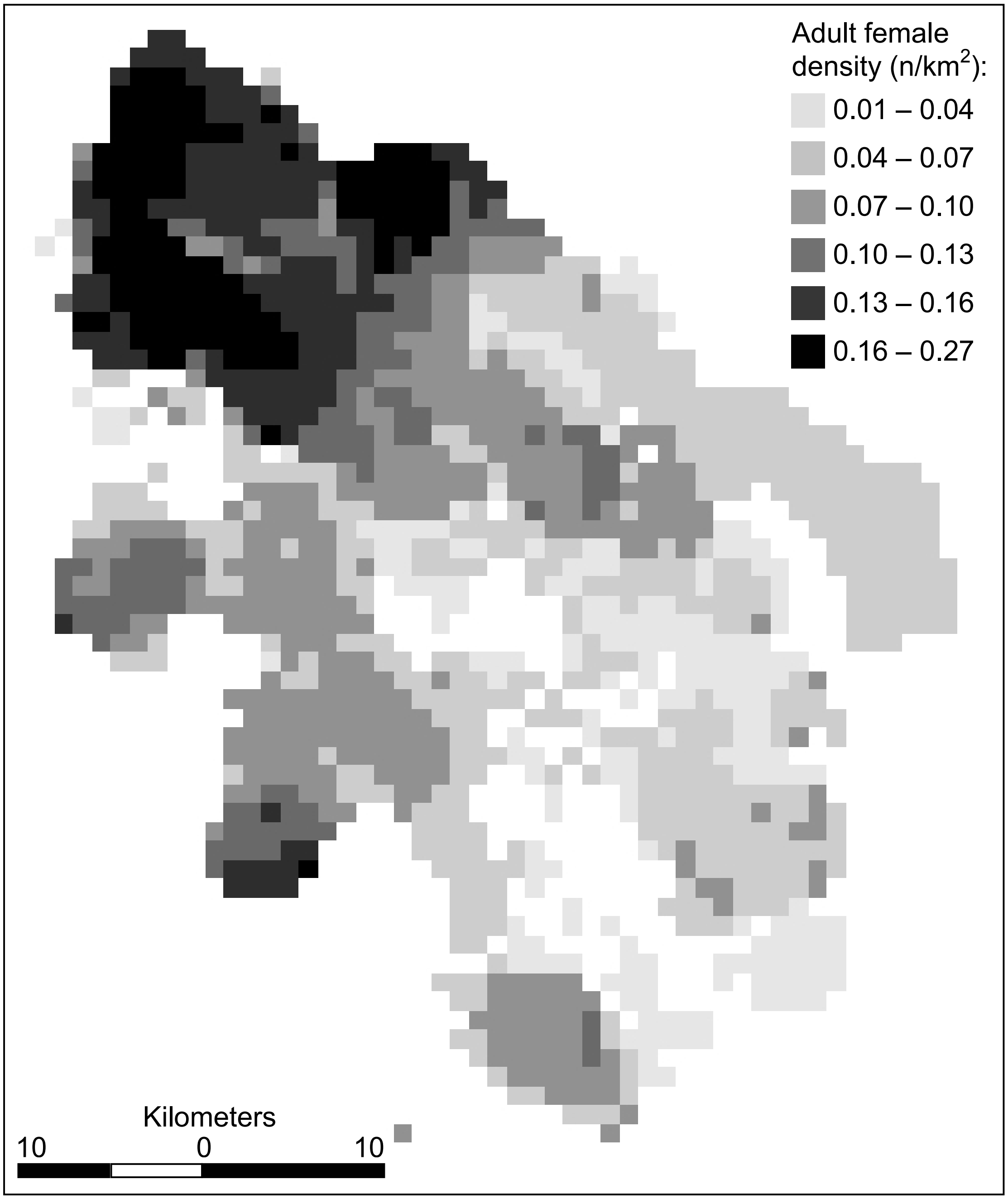
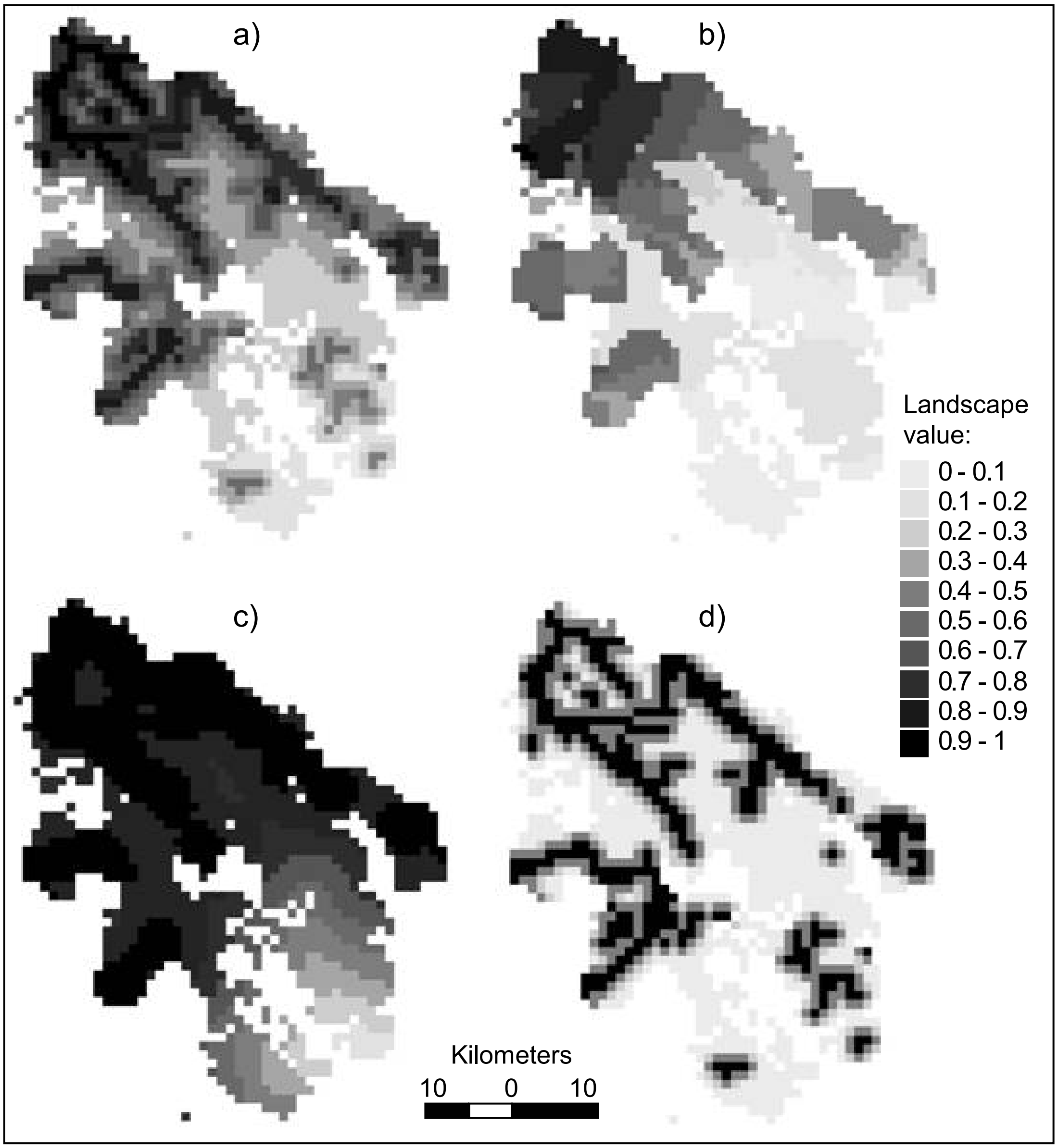


Figure 7: Full niche map (a), and niche components food (b), water (c), and shelter (d).



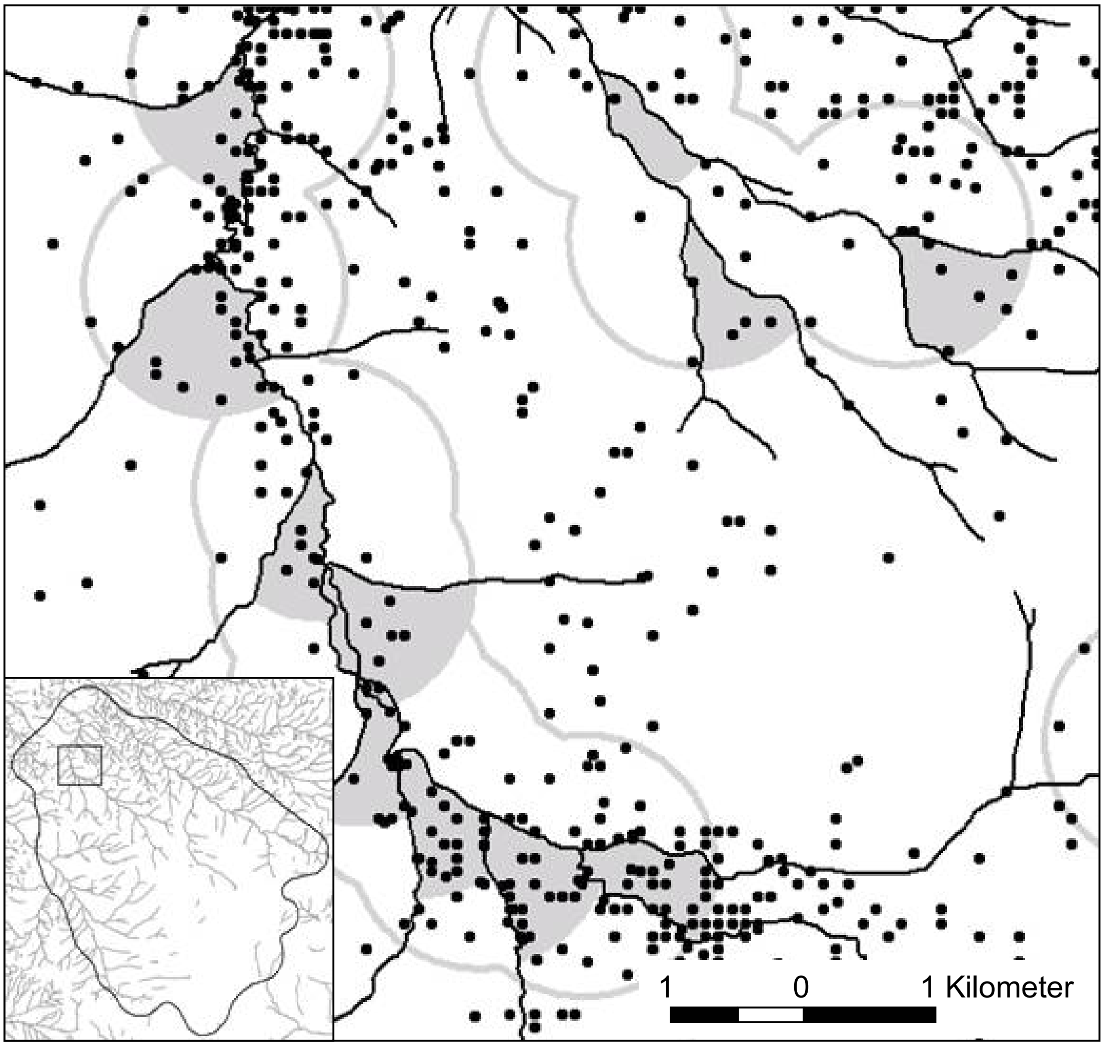
DISCUSSION

Areas near river confluences were identified as sources, owing to the strong significant correlation between this landscape feature and long-term average reproductive success (Table 2, Fig. 5). Confluences are associated with open water and high probabilities of prey capture, and additional analysis of kill locations (Fig. 8) suggests that herbivores, wary of crossing rivers or dry river beds, may get funneled into and trapped at confluence locations (Hopcraft 2002, Sinclair personal communication). River confluences provide the most consistent access to food and water on this savanna landscape, explaining their prominent role in the success of female Serengeti lions.

Analysis of reproductive success and the niche maps showed that access to food and water, but not shelter, contributes significantly to relative fitness. Our conception of the full niche model, giving equal weight to each niche component, was not accurate. Shelter for dens is provided by vegetation near rivers and in kopjes – but kopjes are located across the study area, including areas of low reproductive success, which accounts for the resulting negative correlation. Although water was the strongest niche component, because availability of water and food are highly correlated, our data cannot determine which is more important to cub survival. Previous research on the Serengeti population suggested, however, that starvation is a major cause of cub mortality (Bertram 1973).

As expected, density was correlated with a larger set of landscape variables than was reproductive success. If reproductive success represents the fundamental niche and density patterns reflect the realized niche (Hutchinson 1957), the greater size of the lions' realized niche is consistent with source-sink dynamics (Pulliam 1988). More importantly, however, the patterns of long-term average density resulted in a very different set of conclusions. By solely using a density-based measure, we would have concluded that habitat quality is determined primarily by dry season rainfall, followed by proximity to rivers and kopjes. Rainfall is a surrogate summary variable that correlates with all the landscape variables (except kopjes), and therefore is not an entirely inaccurate measure of

Figure 8: Position of lion kills (black circles) with respect to river confluences. Of kills recorded <1 km of a confluence (grey circles), more prey were captured between the converging tributaries (grey shaded areas) than expected by chance (χ^2=96.8, n=1141, p<0.001). The map shown here is just a portion of the full study area (inset).



habitat quality in the Serengeti. The same can be said for proximity to rivers. The association with kopjes, however, is misleading; kopjes are one of the few refuges in the sink areas of open plains and they correlate with a localized density pattern of effectively non-reproductive adults. Analysis of density did identify water as the strongest niche component, but also suggested that shelter, and not food, was an important factor in habitat quality, inconsistent with the results based upon reproductive success.

Two-year snapshots of reproductive performance and of population density were poor indicators of lion habitat quality. Additional analyses show that reproductive success in the short-term is more strongly correlated with pride demography (especially infanticide by incoming males (Packer et al. 1988)) and territorial competition (chapter 2). Short-term reproductive success is also susceptible to environmental stochasticity and factors that could not be measured consistently, such as severe disease outbreaks. Density was marginally better at gauging habitat quality in the short-term, given that a higher proportion of the nineteen 2-year maps were significantly correlated with the landscape variables, but short-term analyses should be interpreted with caution.

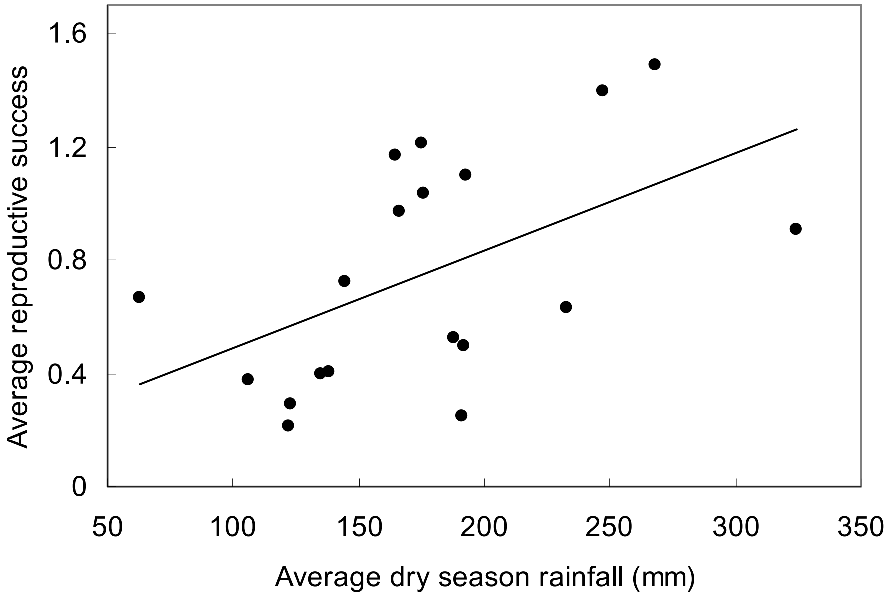
Reproductive success and population density became more robust measures of habitat quality once patterns were averaged over longer time periods (Table 3). For example, when reproductive success was averaged over 6-year periods, 59% of the maps showed a significant ($p \leq 0.05$) negative correlation with distance to river confluence. The short-term variability in reproductive success was dampened when localized patterns were averaged over at least 14 years, at which point reproductive success becomes a reliable measure of habitat quality.

The short-term patterns of reproductive success and density showed consistent positive associations with dry season rainfall, but rainfall was not significantly correlated with long-term reproductive success. Analysis of temporal patterns revealed that average 2-year reproductive success was significantly correlated with average dry season rainfall (Fig. 9). Migratory herds tend to remain in the study area during wetter dry seasons

Table 3: Reproductive success and density as averaged over increasing time-scales vs. distance to river confluence. Only the negative correlations are quantified (decreasing reproductive success or density with increasing distance from confluence) and the significance level was relaxed to $p \leq 0.05$ with no Bonferroni correction, to suggest what might be expected if any given isolated time-step were measured.

	Distance to confluence			
	Repr. success		Density	
Time-step	% − effect	% sig. p≤0.05	% − effect	% sig. p≤0.05
2-year	84	32	100	68
4-year	83	44	100	72
6-year	88	59	94	71
8-year	94	63	100	69
10-year	100	53	100	73
12-year	100	64	100	79
14-year	100	85	100	77
16-year	100	67	100	75
18-year	100	82	100	82
20-year	100	80	100	90

Figure 9: Linear regression of reproductive success vs. dry season rainfall, both averaged across the study area within 2-year periods (n = 19 biennial time-steps, adjusted-$R^2 = 0.23$, $p = 0.02$).



(Hanby and Bygott 1979), which reduces the risk of cub starvation and boosts the average reproductive success of the population as a whole. Thus, although the spatial rainfall patterns do not contribute to relative fitness and habitat quality, annual variation in rainfall strongly affects growth rates and has an important effect on the dynamics of Serengeti lion population (Packer et al. 2005).

Our results highlight the importance of forming an animal's-eye view (Altmann and Altmann 2003) of the landscape – derived from long-term individual-based monitoring. The variability in short-term patterns of reproductive success emphasized that a lioness's view of her immediate environment is tempered by stochastic events, individual variation, and current demographic conditions. The long-term patterns of average reproductive success revealed a despotic territorial system with source-sink dynamics, reflecting evolutionary adaptation of habitat selection (Southwood 1977) to a heterogeneous pattern of Darwinian real estate. Although identification and conservation of source areas is critical, preservation of the whole system – sources and sinks – will likely support a larger and more stable metapopulation (Pulliam 1988, Howe and Davis 1991, Pulliam and Danielson 1991). A long-term fitness-related measure was required to identify the ecological characteristics of a source, while density patterns revealed the resources within the realized niche that were valuable to adult survival. Long-term studies are indispensable in clarifying the linkages between landscape and population dynamics and in informing effective management decisions.

CHAPTER 2

Group territoriality of the African lion

(with Craig Packer)

INTRODUCTION

Group territoriality sets the stage for a complex dynamic of intergroup resource competition based on relative numerical strength. Species ranging from social insects to chimpanzees are group-territorial, but the precise relationship between group size and differential access to limiting resources has never been formally tested. Experimental work has demonstrated that weakened groups lose territory to larger neighbors (Carlson 1986, Adams 1990), that larger groups win staged intergroup encounters (Adams 1990), and that territory owners assess intruding groups based on relative group size (McComb et al. 1994, Heinsohn 1997, Wilson et al. 2001), and a range of largely anecdotal evidence suggests that larger groups have a general competitive advantage in territorial competition (Woolfenden and Fitzpatrick 1984, Mech et al. 1998, Wilson and Wrangham 2003). Indeed, numerical advantage is often implicit in studies of group-territorial animals (e.g. Stacey and Ligon 1991, Lazaro-Perea 2001, Campbell et al. 2005). But, due to small sample sizes (too few groups) and short study periods, past studies have not confirmed whether larger groups win out over smaller groups in controlling the best habitat and consequently enjoy greater individual fitness.

Here we present the first complete example of the long-term benefits of group territoriality. Analysis of 38 years of data on 46 lion prides in the Serengeti National Park, Tanzania, demonstrates that territorial competition directly affects critical components of fitness in lions (reproductive success and survival, Packer et al. 1988), and that larger prides gain and maintain access to the highest quality habitat.

In addition, lions provide a prime example of social evolution driven by the economics of group-territoriality. The lion stands out within the family Felidae as being the only consistently social cat, diverging from its non-social relatives roughly three million years ago (Turner 1997). Lion sociality is commonly viewed as an adaptation a heterogeneous savanna landscape (e.g. Kleiman and Eisenberg 1973, Mattern and McLennan 2000) and high population densities (Packer 1986). Spatial analyses of female per capita reproductive success (chapter 1) define the parameters that determine lion real estate value and thus provide the framework for evaluating the consequences of territorial competition. We explore the roles of landscape heterogeneity, population density, and cooperative defense in the evolution of group territoriality in chapter 3.

Background

A lion pride is a fission-fusion social group of 1-18 adult females, their dependent offspring, and a temporary coalition of 1-9 adult males. Lions are matrilineal, although roughly one third of females disperse to form a new pride, usually at a nearby location (Pusey and Packer 1987). Males typically leave their natal pride by the age of four, and after a 1-2 year nomadic phase, either remain solo or form a coalition with other males (Pusey and Packer 1987). These males challenge current pride males for residency, and if successful, remain in a pride for an average of two years (average: 2.16 years, range: 0.01-8.12 years). Incoming males kill or evict dependent offspring from the previous coalition, so as to accelerate the mothers' return to sexual receptivity (Packer 2001). Coalitions can be resident in more than one pride (usually neighboring prides) at the same time. Females are solitary at parturition and hide newborn cubs until they are at least four weeks old, when they pool their cubs together with current mothers into crèche groups (Packer *et al.* 1988). Females live up to 18 years, males to 14 years (Packer *et al.* 1988).

Social grouping in lions is not strongly associated with increased food intake (Packer 1986, Packer et al. 1990). Cooperative hunting was a leading explanation for lion sociality (Schaller 1972, Macdonald 1983, Turner 1997), but empirical evidence has failed to support this hypothesis. Although hunting success is associated with the size of the hunting group (Schaller 1972, Elliot et al. 1977, VanOrsdol 1984, Stander and Albon 1993, Funston et al. 2001), lions often opt out of a group-hunt (Scheel and Packer 1991) and actual hunting success, for groups of more than two, fails to match the capture rates predicted by full cooperation (Packer and Ruttan 1988). More importantly, detailed analyses of per capita food intake per day showed that grouping patterns within the pride were not associated with maximized foraging efficiency (Packer et al. 1990). During periods of prey scarcity solitaries and subgroups of five to seven do equally well, while subgroups of two to four suffer in terms of food intake; despite this disadvantage, lion prides of two to four females remained in the largest group size possible.

Female lions do gain direct reproductive benefits through the mutual defense of their cubs against the threat of infanticide, but this is not the sole basis for sociality in lions (Pusey and Packer 1994). Prides of two or more are more successful in defending their cubs from infanticidal males, and crèche groups largely account for the grouping patterns of mothers within a pride. When cubs are not present, however, in times of prey scarcity smaller prides are still found in the largest group size possible (Packer et al. 1990), again despite the feeding disadvantage. While protection of cubs is a benefit of grouping in lions, it still does not account for the fission-fusion grouping patterns observed.

Other research pointed to a numerical advantage in intergroup interactions and territorial defense. Playback experiments, in which roars of varying numbers of females were played to groups of females, revealed that the females were more likely to respond and approach intruders (the loudspeaker) if their group outnumbered the simulated intruders (McComb et al. 1994, Heinsohn 1997). Females also roared more often if they were in a subgroup that did not include all adult females in the pride, potentially in an effort to recruit the other pride mates. These findings showed that lions are highly sensitive to relative group size and suggested that lion social behavior may be tightly linked to territorial defense.

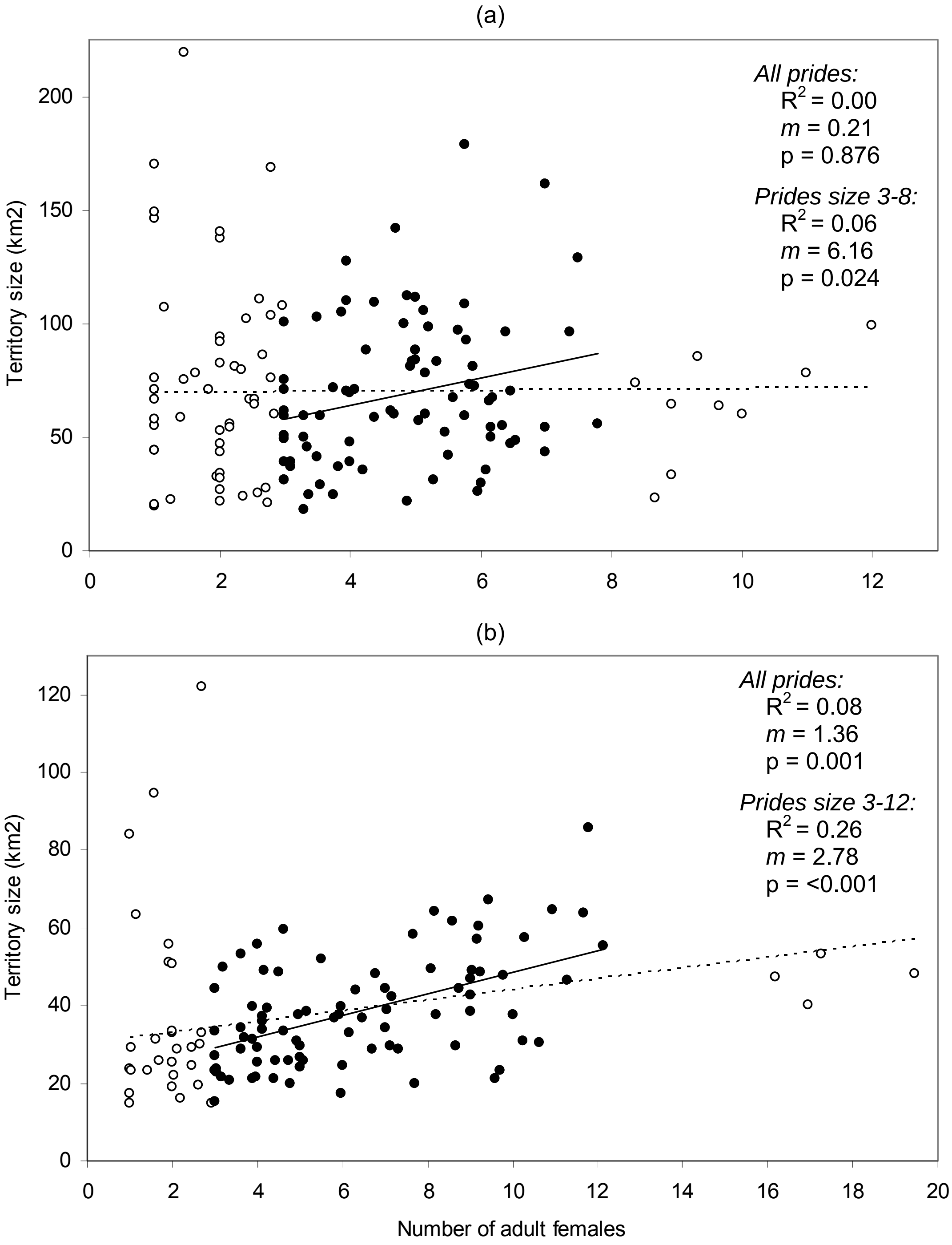
Serengeti lions defend territories of 15-150 km^2 that vary in size with habitat and pride size (Fig. 1). Core areas are generally exclusive, with some overlap often associated with periods following a pride fission or sharing of a male coalition. Territories shift slightly with the seasons and the associated shifts in prey density, but site fidelity is strong from one year to the next. Territories are defended through roaring, patrolling, scent marking, and direct aggressive encounters. Males presumably defend females, cubs, and resources, and findings from the Kruger National Park, South Africa, suggest that males devote more time than females to scent marking and territory boarder patrolling (Funston 1999). Although direct evidence is limited, lethal attacks related to intergroup aggression do occur in Serengeti lions (Schenkel 1966, Schaller 1972, Packer et al. 1988).

Hypotheses

Generally, we expect territorial competition to be most intense between unrelated adult females in neighboring prides. Lionesses are philopatric and their lifetime reproductive success is strongly impacted by the consequences of intergroup resource competition, thus females in opposing groups are expected to be especially hostile towards each other (Wrangham 1980, Cheney 1987, Boydston et al. 2001). In addition, because females do sometimes disperse and establish a territory adjacent to their natal pride, neighbors are often closely related; we therefore expect kin selection and inclusive fitness (Hamilton 1964) to influence patterns of intergroup competition. In each of the hypotheses listed below we anticipated that a ‘neighbor’, viewed as a competitor, would be best defined as an adult female that had not recently split off from the natal pride. Tests of these predictions were integrated into the analyses for all hypotheses by defining neighbors in different ways, depending upon sex, age, and time since a pride split.

These analyses focus on inter-group competition and the role of group size in this context, but in all cases the negative effects of competition within the group are also at work. In the discussion, we consider our results in reference to intra-group competition and examine the mechanisms that may limit the benefits of increasing group size.

Figure 1. Territory size vs. pride size for a) plains and b) woodlands habitat. Territory size was estimated using 75% kernel density contours. Territories are significantly larger in plains habitat (plains average = 70km^2, woodlands average = 38km^2, ANOVA: F=76.97, p<0.0001) and only vary with pride size in woodlands habitat if all pride sizes are included (dashed lines). Small prides are sometimes forced to abandon their territories and so occasionally have very large home ranges, while large prides typically gain access to the highest quality areas and need not defend very large territories. If small and large prides (open circles) are excluded from the regression model, territory size is significantly correlated with pride size in both habitats (solid lines).



H1: Territorial behavior inflicts costs on neighbors

In order for group-territorial behavior to be subject to selective pressure, there must be fitness costs and benefits associated with territorial competition. We examined the impact of neighbors on per capita female reproductive success, mortality, and food intake. We predicted that prides with more neighbors would have lower reproductive success, higher rates of mortality, and reduced food intake, after controlling for habitat quality and pride demography (e.g. the number of adult females).

H2: Risk influences sub-grouping patterns

Grouping patterns are commonly associated with individual risk: male chimpanzees move in larger party sizes in territory border areas, where they may encounter members of opposing groups (Bauer 1980, Wilson 2001), and group sizes are often larger in open habitat (Jarman 1974) where animals are more visible and thus more vulnerable to attack (Watts 1990). We analyzed female sub-grouping patterns with respect to location relative to the territory center, habitat type, and the number of neighbors. The analysis was restricted to females with no dependent cubs, to rule out crèche formation as a reason for grouping. Previous research showed that grouping patterns are not associated with foraging efficiency (Packer et al. 1990), thus here we examine whether potential risk, from neighboring conspecifics competitors, in particular, may account for the observed sub-grouping patterns within the pride. We predicted that non-mothers would form larger groups when they were more vulnerable; that is, when farther from the center of their territory, when in open plains habitat, and when they had more neighbors.

H3: Group size determines outcome of territorial competition

Larger subgroups usually ‘win’ isolated inter-pride encounters (Packer et al. 1990, Grinnell et al. 1995). Territory is likely gained or lost in part as a result of a series of such encounters, thus group size should influence the outcome of territorial competition. We predicted that the larger of two prides would be more likely to gain and less likely to lose contested space (an area overlap between territories).

H4: Group size influences access to resources

Finally, and most importantly, we predict that group size will determine access to resources. In the Serengeti, larger prides are located in higher quality habitat, 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 were associated with improvements in territory quality. Territory quality was based upon the fine-scale landscape features that were significantly associated with reproductive success in Serengeti lions (chapter 1).

METHODS

Study system

The 2700 km^2 study area is located in the Serengeti Nation Park, Tanzania, at the center of the Serengeti-Mara ecosystem (see chapter 1, Fig. 1). Within the study area, there is a southeast-to-northwest gradient of rainfall and vegetation (Norton-Griffiths et al. 1975, Sinclair 1979). Vegetation transitions from short-grass treeless plains in the southeast to woodlands in the north (Packer et al. 2005). Both grassland and woodland habitats are transected by rivers and tributaries (Fig. 2a), supporting thicker woody vegetation along the banks (Herlocker 1975).

Serengeti lions have been studied since 1966 (Schaller 1972, Bertram 1973, Hanby and Bygott 1979, Packer et al. 1988). The woodland lions have been monitored continuously over this entire period, but the plains lions were not studied from Nov. 1969 until Oct. 1974. The size of the study population has ranged between roughly 50 and 300 known individuals living in 5 to 30 prides. Observations between 1966 and 1983 were opportunistic, and, beginning in 1984, one member of each study pride was radio collared and all subsequent monitoring relied on a combination of radio telemetry and opportunistic sightings. Study prides were generally located at least once every two weeks, and the lions were almost always observed directly and identified from natural markings.

Data analysis

Pride variables

Demographic variables were calculated for each pride at 2-year intervals, which is the average inter-birth interval for female lions. Intervals started in November, the start of the wet season. Four variables reflected the size of the pride: the number of adult females, the number of resident males, the number of adults, and the total number of lions in the pride (including cubs and sub-adults). Serengeti females begin reproducing in their 3rd year (Packer et al. 1988) and start to show signs of territorial behavior at the age of two (Heinsohn et al. 1996). We therefore considered two definitions for adult female (2+ years and 3+ years). In the presentation of results, however, adult females were defined as 3 or more years unless otherwise noted. Demographic statistics were calculated for each month, and then averages were taken over all months within a 2-year time-step.

Per capita female reproductive success was defined as the total number of cubs surviving to one year within a 2-year period divided by the average number adult females (defined as 3 year-olds) in the pride during that time-step. Adult female per capita mortality was calculated as the number of adult females (age 3 years or more) that died (based upon the date an individual was last seen) during a given month divided by the number of adult females present in the pride during that month. The monthly mortality rates were then averaged over the 2-year time-step. The average age of adult females (age 3 or more years) was determined for each month and then averaged over each 2-year time-step. Finally, the number of resident male takeover events was totaled for each time-step. Average belly sizes were used as a measure of estimated food intake (Bertram 1975). The belly sizes of adult females were averaged over each 2-year time-step, and only time-steps with at least 30 belly size measurements were included.

Mapping territories

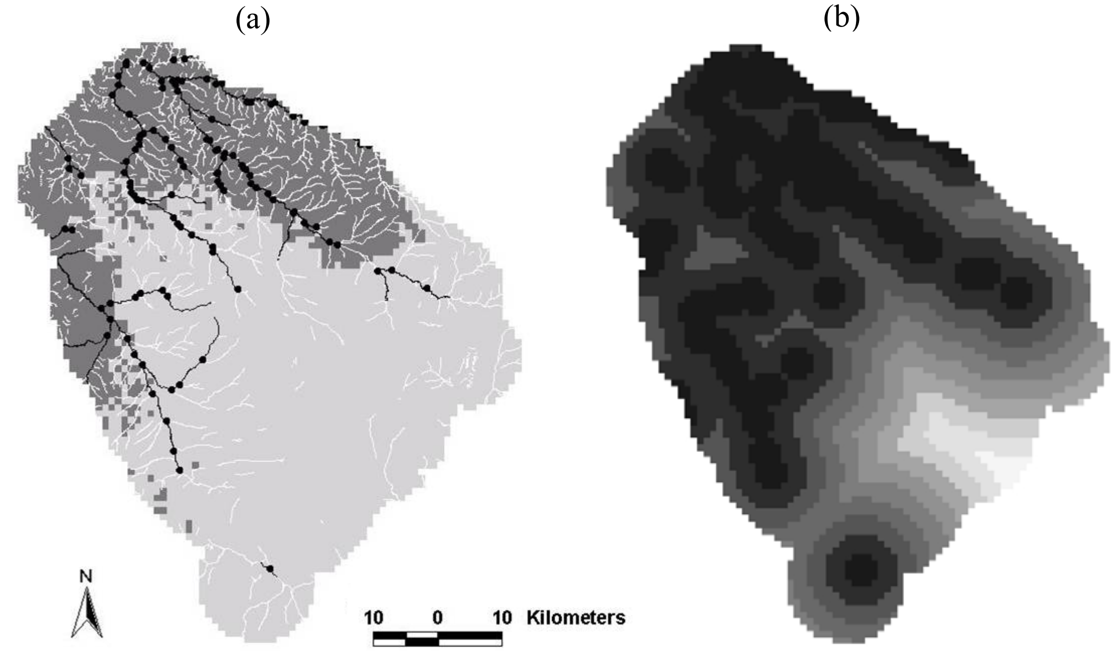
Pride territories were mapped from the ranging patterns of adult females in each 2-year time-step. Observations collected from both radio-tracking and opportunistic sightings were pooled together, as pride ranges derived from the different data types were similar (analysis of 25 prides in 2003–4 showed that ranges based on the two data types overlapped by an average of 75%). Using ArcView (version 3.2), pride ranges were determined from utilization-distribution maps of the lion sightings, created using a fixed kernel with a smoothing parameter (h) of 3000 meters, which is the mean distance moved by a lion in a day plus one standard deviation (Kirkby unpublished). The territory boundary was defined as the 75% contour (kernel density isopleth), and the core area boundary was defined as the 50% contour. Due to the potential sensitivity of kernel density estimates to sample size (Anderson 1982, Worton 1987, 1989, Harris et al. 1999, Hemson et al. 2005), a 75% contour was chosen as a less biased estimate of territory area and location and was used in most analyses. The area of the 75% kernel (km^2) and coordinates of the center of activity were also determined for each pride's 2-year territory. Territory maps were converted to grid maps of 1km resolution.

A pride was included in analysis if it had been observed at least five times in each year of a time-step. About 20% of the 2-year ranges had <20 observations, representing a trade-off between accuracy and biasing our results against less frequently observed groups located in fringe areas of lower quality habitat. To test for effects of small sample size, we randomly sub-sampled from the 2-year datasets of 10 well observed prides (6 random subsets of 15 observations each). The 75% contour territories mapped from these subsets differed little from the territory based on the full dataset (subset kernels were on average 2% larger and overlapped with the full kernel by on average 93%), and we concluded that small sample size would not introduce problematic error into the pride-range estimates.

Territory quality

In chapter 1, we used spatial patterns of female reproductive success to determine the landscape characteristics of fitness value to Serengeti lions. This analysis showed that river confluences were the most valuable landscape feature. We therefore based landscape value on proximity to confluences (Fig. 2b). Distance to nearest confluence was mapped (as a grid map, 1km resolution) within the study area, and scaled from 1-100. Territory quality was calculated as the average of the landscape value grid cells within a 75% contour. We did not apply utilization values to this calculation, as small

Figure 2. a) Landscape features: major rivers (black lines), confluences (black circles), tributaries (white lines), and habitat type (light gray: plains, dark gray: woodlands). b) Landscape quality, based upon distance from nearest confluence.



sample sizes for some prides may have produced inaccurate estimates of intensity of activity within the territory.

Neighbor variables

Prides were defined as neighbors 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 assumption of interpride interaction and competition. For each pride time-step, neighbors were characterized in five ways: the number of neighboring prides, the total number of adult female neighbors, the total number of adult male neighbors, the total number of adult neighbors, and the total number of neighboring lions including cubs and sub-adults. We accounted for male coalition residency in multiple prides, thus a male was not counted as a neighbor if it was resident in both the focal and neighbor pride.

For each pair of neighboring prides, we determined, if applicable to the pride-pair, the time since a pride split (female dispersal). This was used as a proxy for relatedness. Prides that have split within 2 years are closely related and often include mother-daughter relationships. Neighbors that have split within 5 years generally do retain a high degree of genetic relatedness (Packer et al. 1991), but distinct territories and group autonomy have usually been well established. Prides that have split within 10 years share fewer genes, but are still more closely related to each other than to the general population (Packer et al. 1991). Neighbors were identified as recently split or not, using each time interval (2, 5, and 10 years). Note that all resident males were treated as unrelated, and were not associated with pride splits.

Prides at the edge of the study area were identified, as we may not have had an accurate estimate of neighbors for these prides. In all analyses of neighbor effects, ‘edge’ was included as an interaction variable and results are presented for *the non-edge interactions only*.

H1: Territorial behavior inflicts costs on neighbors

In this analysis, we modeled 2-year female per capita reproductive success and mortality against pride demography, territory quality, and neighbor variables. The distribution of reproductive success (RS) was heavily skewed towards zero (see Fig. 4a or 8b), so it was treated as a binomial (0: RS = 0, 1: RS > 0). We used binary logistic regression to analyze reproductive success and linear regression for mortality and belly size, with a repeated statement to account for multiple observations of the same pride (PROC GENMOD, SAS 9.1, SAS Institute Inc., Cary, NC). Prides were excluded from this analysis if they ranged unusually far from their usual territory (on average, 23 km from long-term core area), as these ranges overestimated the number of neighbors and did not accurately reflect the competitive environment experienced by a pride (46 out of 263 pride time-steps were dropped for this reason, giving a sample size of 217 pride 2-years for this analysis).

Pride variables were analyzed in a multivariate model, using backwards elimination, with a p-value exclusion criterion of 0.15 applied in all but the last step. Neighbor effects were then considered one at a time in a multivariate model including the significant pride variables and each of the neighbor variables independently.

H2: Risk influences sub-grouping patterns

Sightings of adult females, meeting the following conditions, were selected from the full data set of lion observations: no current dependent cubs, not with other pride mothers, not with resident males, not at a kill, and located using radio-tracking. The location of each sighting was characterized by its location relative to the pride's territory center (distance from center of activity) and the habitat type (plains or woodland). The size of these non-mother subgroups was then modeled against variables representing potential risk (distance from center of territory, habitat type, and number of neighbors), after controlling for maximum possible sub-group size (the total number of non-mothers in the pride). We applied linear regression (PROC GENMOD, SAS 9.1), with a repeated statement for multiple observations on the same pride. We plotted the data in a semi-variogram and did not find significant spatial autocorrelation (PROC VARIOGRAM, SAS 9.1), thus we did not account for this factor in the model.

H3: Group size determines outcome of territorial competition

For each 2-year time-step, we identified all occurrences of overlap between the territories (75% contours) of two prides. Prides that overlapped because of a pride split within the 2-year period or because they were sharing a coalition of males were not included in the analyses, as the underlying reasons for territory overlap in these cases was not expected to relate to territorial competition. Grid cells within an area of overlap were identified as *gained* if the only focal pride owned the cell (it fell within the 75% contour) in the next time-step, or as *lost* if only the competing pride owned the cell in the next time-step. Grid cells were identified as *shared* if both prides owned the cell or as *neither* if neither pride owned the cell in the next time-step. The proximity of the cell to the territory border was identified by using the kernel utilization values (1-75) of the grid cells, where lower values were cells near the territory center and values of 75 were cells on the territory boundary (the 75% kernel contour of the territory). There were 112 cases of overlap, with 1019 grid cells disputed in total.

The gain and loss of cells was modeled against the location of the disputed cell (proximity to the territory boundary) and relative pride sizes (natural log of focal pride size/neighbor pride size). For each case of overlap, grid cells within the area of overlap were randomly assigned, in equal proportions, to each of the two prides. We used binary logistic regression (PROC GENMOD, SAS 9.1), with a nested repeated statement to account for multiple cells for each case of overlap (which also accounts for spatial autocorrelation) and multiple observations on the same pride over time.

H4: Group size influences access to resources

Change in territory quality was calculated for each pride with a sufficient number of observations in consecutive 2-year time-steps. Prides that ranged far outside their usual territory were not included in the analysis (as above). Using linear regression (PROC GENMOD, SAS 9.1), we modeled change in territory quality against pride demography, changes in pride demography from one time-step to the next, and neighbor variables. A repeated statement was included in the model to account for multiple observations on the same pride. Variables were analyzed in a multivariate model, as described above.

RESULTS

H1: Territorial behavior inflicts costs on neighbors

Prides with more adult females, with fewer takeover events, and those in higher quality habitat had higher rates of reproductive success (Table 1a). After controlling for these pride variables, we found strong negative effects of neighbors on reproductive success, significant for all neighbor variables except the total number of neighbor prides (Table 1b). Z-values indicated that the total number of adult female neighbors had the strongest impact on reproductive success (Fig. 3). We also found that only prides not associated with a recent split (within 2 or 5 years), and thus less closely related to the focal pride, had a significant negative effect on reproductive success (Table 1c).

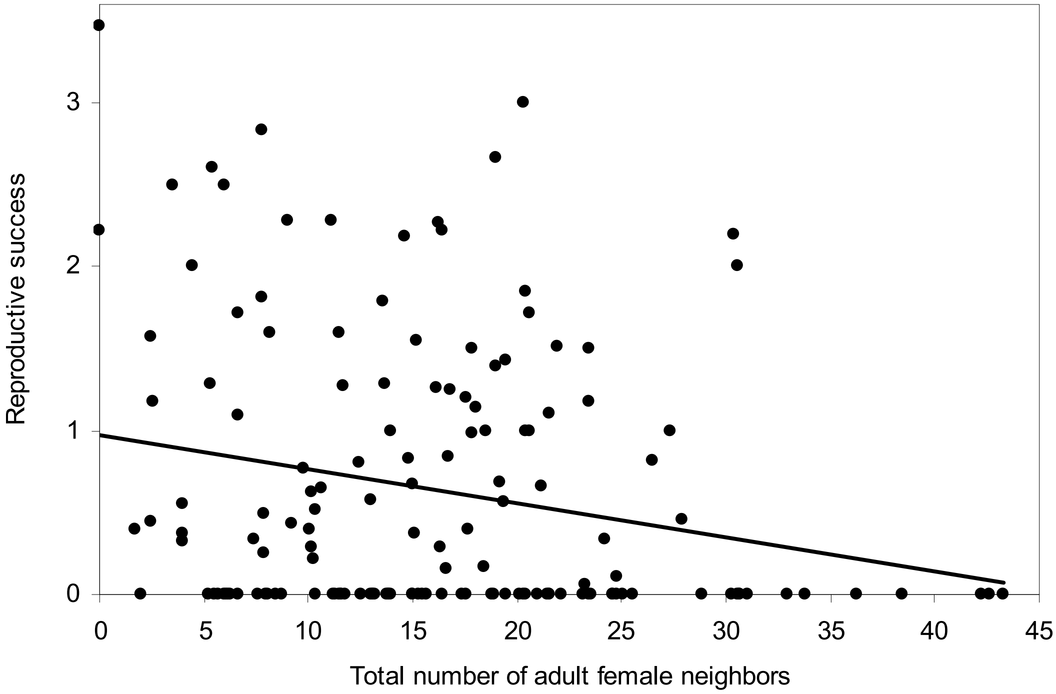
Larger prides (measured as number of adults) had lower rates of adult female mortality (Table 2). Higher rates of mortality were also significantly associated with prides that experienced multiple takeovers. Of the neighbor-pride effects, adult female mortality was significantly and most strongly associated with the number of adult male neighbors. We found no effects of time since pride splits in this analysis. We also found no effect of neighbors on adult female food intake, as estimated using average belly size.

Table 1. Hypothesis 1 – Per capita adult female reproductive success vs. pride and neighbor variables (n=217 pride 2-year time-steps). a) Pride variables were first analyzed in a multivariate logistic model. Significant variables are listed. Pride variables *not* significant: number of resident males, number of adults, average age of adult females, and adult female mortality rate. b) Each neighbor variable was independently added to the model containing the significant pride variables. c) Each pair of neighbor variables (split or no split, within 2, 5, and 10 years) was independently added to the model containing the significant pride variables.

Variable	Effect	Standard error	Z	P-value
a) *Significant pride variables:*				
Number of adult females	0.2948	0.078	3.78	<0.001
Number of takeovers	-0.5639	0.203	-2.78	0.006
Territory quality	0.0236	0.010	2.38	0.017
b) *Significant pride variables plus each neighbor variable:*				
Number of neighbor prides	-0.1647	0.089	-1.85	0.065
Adult female neighbors	-0.0570	0.016	-3.63	<0.001
Adult male neighbors	-0.1377	0.044	-3.11	0.002
Adult neighbors	-0.0452	0.013	-3.61	<0.001
Total neighbors	-0.0210	0.006	-3.52	<0.001
c) *Significant pride variables plus each neighbor variable, by time since pride split:*				
Split within 2 years:				
Number of neighbor prides (Yes)	-0.0595	0.343	-0.17	0.862
Number of neighbor prides (No)	-0.1872	0.115	-1.63	0.103
Adult female neighbors (Yes)	-0.0700	0.063	-1.12	0.265
Adult female neighbors (No)	-0.0543	0.018	-2.95	0.003
Adult neighbors (Yes)	-0.0674	0.063	-1.08	0.281
Adult neighbors (No)	-0.0435	0.014	-3.03	0.003
Total neighbors (Yes)	-0.0427	0.029	-1.49	0.136
Total neighbors (No)	-0.0184	0.007	-2.75	0.006
Split within 5 years:				
Number of neighbor prides (Yes)	0.1615	0.251	0.64	0.520
Number of neighbor prides (No)	-0.2179	0.127	-1.72	0.086
Adult female neighbors (Yes)	-0.0655	0.051	-1.30	0.194
Adult female neighbors (No)	-0.0564	0.021	-2.71	0.007
Adult neighbors (Yes)	-0.0561	0.052	-1.07	0.283
Adult neighbors (No)	-0.0447	0.016	-2.82	0.005
Total neighbors (Yes)	-0.0294	0.023	-1.29	0.196
Total neighbors (No)	-0.0200	0.008	-2.54	0.011
Split within 10 years:				
Number of neighbor prides (Yes)	-0.2756	0.219	-1.26	0.208
Number of neighbor prides (No)	-0.1556	0.122	-1.28	0.201
Adult female neighbors (Yes)	-0.1633	0.046	-3.58	<0.001
Adult female neighbors (No)	-0.0401	0.019	-2.07	0.039
Adult neighbors (Yes)	-0.1568	0.047	-3.35	0.001
Adult neighbors (No)	-0.0341	0.015	-2.28	0.023
Total neighbors (Yes)	-0.0646	0.021	-3.03	0.002
Total neighbors (No)	-0.0147	0.008	-1.93	0.053

Figure 3. a) Per capita adult female reproductive success (continuous) vs. total number of adult neighbors. b) Per capita adult female reproductive success (binomial) vs. total number of adult neighbors. Sample sizes are listed above each bar. Both plots include data for non-edge prides only (n = 152).

(a)



(b)

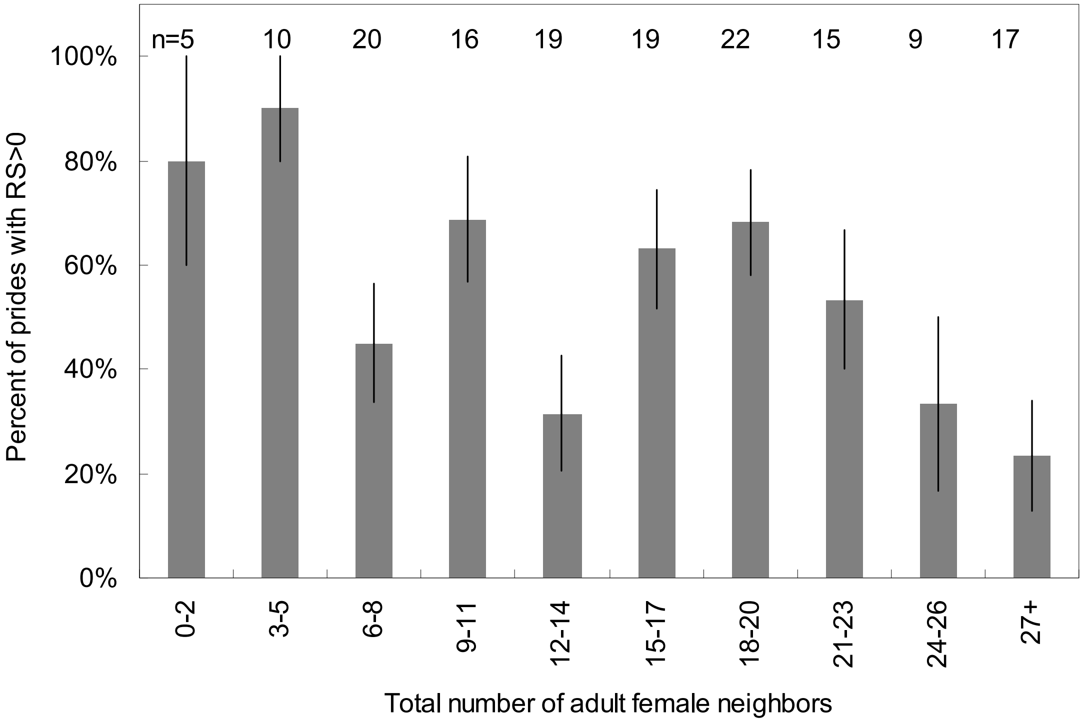


Table 2. Hypothesis 1 – Per capita monthly adult female mortality rate vs. pride and neighbor variables (n = 217 pride 2-year time-steps). a) Pride variables were first analyzed in a multivariate model. Significant variables are listed. Pride variables *not* significant: number of adult females, number of resident males, and average age of adult females. b) Each neighbor variable was independently added to the model containing the significant pride variables. c) Each pair of neighbor variables (split or not split, within 2, 5, and 10 years) was independently added to the model containing the significant pride variables.

Variable	Effect	Standard error	Z	P-value
a) *Significant pride variables:*				
Number of adults	-0.0006	0.0002	-2.70	0.007
Number of takeovers	0.0026	0.0010	2.73	0.006
b) *Significant pride variables plus each neighbor variable (with replacement) :*				
Number of neighbor prides	0.0003	0.0003	0.92	0.359
Adult female neighbors	0.0001	0.0001	1.01	0.314
Adult male neighbors	0.0004	0.0002	2.19	0.029
Adult neighbors	0.0001	0.0000	1.69	0.091
Total neighbors	0.0000	0.0000	0.95	0.340
c) *Significant pride variables plus each neighbor variable, by time since pride split:*				
Split within 2 years:				
Number of neighbor prides (Yes)	-0.0012	0.0022	-0.56	0.576
Number of neighbor prides (No)	0.0004	0.0004	1.02	0.306
Adult female neighbors (Yes)	0.0001	0.0005	0.14	0.888
Adult female neighbors (No)	0.0000	0.0001	0.62	0.535
Adult neighbors (Yes)	0.0000	0.0005	0.08	0.938
Adult neighbors (No)	0.0001	0.0001	1.27	0.203
Total neighbors (Yes)	-0.0001	0.0002	-0.27	0.791
Total neighbors (No)	0.0000	0.0000	0.93	0.352
Split within 5 years:				
Number of neighbor prides (Yes)	-0.0003	0.0013	-0.22	0.828
Number of neighbor prides (No)	0.0003	0.0004	0.84	0.398
Adult female neighbors (Yes)	0.0001	0.0004	0.18	0.860
Adult female neighbors (No)	0.0000	0.0001	0.61	0.541
Adult neighbors (Yes)	0.0000	0.0004	0.10	0.923
Adult neighbors (No)	0.0001	0.0001	1.20	0.229
Total neighbors (Yes)	-0.0001	0.0002	-0.44	0.660
Total neighbors (No)	0.0000	0.0000	1.07	0.282
Split within 10 years:				
Number of neighbor prides (Yes)	0.0007	0.0009	0.78	0.433
Number of neighbor prides (No)	0.0003	0.0004	0.71	0.479
Adult female neighbors (Yes)	0.0003	0.0004	0.78	0.437
Adult female neighbors (No)	0.0000	0.0001	0.46	0.645
Adult neighbors (Yes)	0.0003	0.0004	0.71	0.479
Adult neighbors (No)	0.0001	0.0001	1.04	0.298
Total neighbors (Yes)	0.0000	0.0002	0.24	0.810
Total neighbors (No)	0.0000	0.0000	0.87	0.383

H2: Risk influences sub-grouping patterns

For small prides (2-3 adult females), group sizes were smaller in risky locations, that is, in open plains habitat and when farther from their territory center (Table 3, Fig. 4). The effect of habitat was strong, though not significant for small prides. In contrast, in larger prides (4+ adult females) group sizes were larger in risky locations.

For all pride sizes, groups were generally larger when a pride had more neighbors, though the effects differ depending on pride size. Small prides were most strongly affected by the number of adult female neighbors (defined as 2 years old, rather than 3), while large prides were most strongly affected by the number of male neighbors. If all pride sizes were analyzed together, the total number of adult neighbors (with adult female neighbors defined as age 2 years or more) had the strongest correlation with sub-group size. We found strong effects of time since a pride split, and only neighbors that were not associated with a recent split had significant effects on average subgroup size.

H3: Group size determines outcome of territorial competition

For the analysis of gain of disputed territory (Table 4), we controlled for the location of the disputed grid cells within the each pride's territory. Grid cells nearer to the focal pride's territory border were less likely to be retained by the focal pride and grid cells near to neighbor pride's territory border were more likely to be gained by the focal pride; this illustrates that areas near territory edges are likely to change hands and that core areas are more consistent. Prides with more adult females were significantly more likely to gain a disputed area (Fig 5). Results were reversed for loss of disputed territory (i.e. larger prides were less likely to lose disputed grid cells). Adult females defined as 2 years or older provided a stronger fit to the data than did adult females defined as 3 years or older. We found an effect of the time since a pride split in only one case: relative pride size was not significant for prides that had split with 2 years, and were thus closely related.

Table 3. Hypothesis 2 – Subgroup size of adult females (with no dependent cubs) vs. risk factors. We first considered both location variables and then analyzed neighbor effects independently in a multivariate model that controlled for those two variables. Results are presented for a) small (n = 568 sightings) and b) larger prides (n = 1222 sightings). In all models we have controlled for the maximum possible group size (the number of non-mothers in the pride at the time of each sighting). Note that we did find an effect of time since pride split and all results presented in this table are for neighbors that had *not* split within 10 years. Results were qualitatively identical for splits within 2 or 5 years. Neighbors that had recently split had no significant effect in these analyses. *For small prides, neighboring adult females, defined as 2 years older, provided a stronger model fit.

Variable	Effect	Standard error	Z	P-value
a) *Prides of 2-3 adult females*				
Location variables:				
Habitat type (group size in plains vs. woodlands)	−0.1909	0.100	−1.91	0.056
Distance from territory center (km)	−0.0171	0.007	−2.46	0.014
Location variables plus each neighbor variable (no split within 10 years):				
Number of neighbor prides	0.0233	0.022	1.05	0.294
Adult female neighbors*	0.0089	0.003	2.90	0.004
Adult male neighbors	−0.0028	0.016	−0.18	0.861
Adult neighbors*	0.0055	0.003	2.00	0.046
Total neighbors	0.0040	0.002	2.46	0.014
b) *Prides of 4 or more adult females*				
Location variables:				
Habitat type (group size in plains vs. woodlands)	0.3653	0.108	3.39	0.001
Distance from territory center (km)	0.0165	0.007	2.48	0.013
Location variables plus each neighbor variable (no split within 10 years):				
Number of neighbor prides	0.0299	0.036	0.83	0.407
Adult female neighbors	0.0170	0.008	2.11	0.035
Adult male neighbors	0.0515	0.020	2.59	0.010
Adult neighbors	0.0148	0.006	2.41	0.016
Total neighbors	0.0071	0.003	2.18	0.029

Figure 4. Average adult female subgroup size (non-mothers) vs. distance from the territory center of activity. Sample sizes are indicated above or below error bars. The average territory radius is about 4 km, thus groups found in all but the smallest distance category listed here were outside their estimated territory boundary.

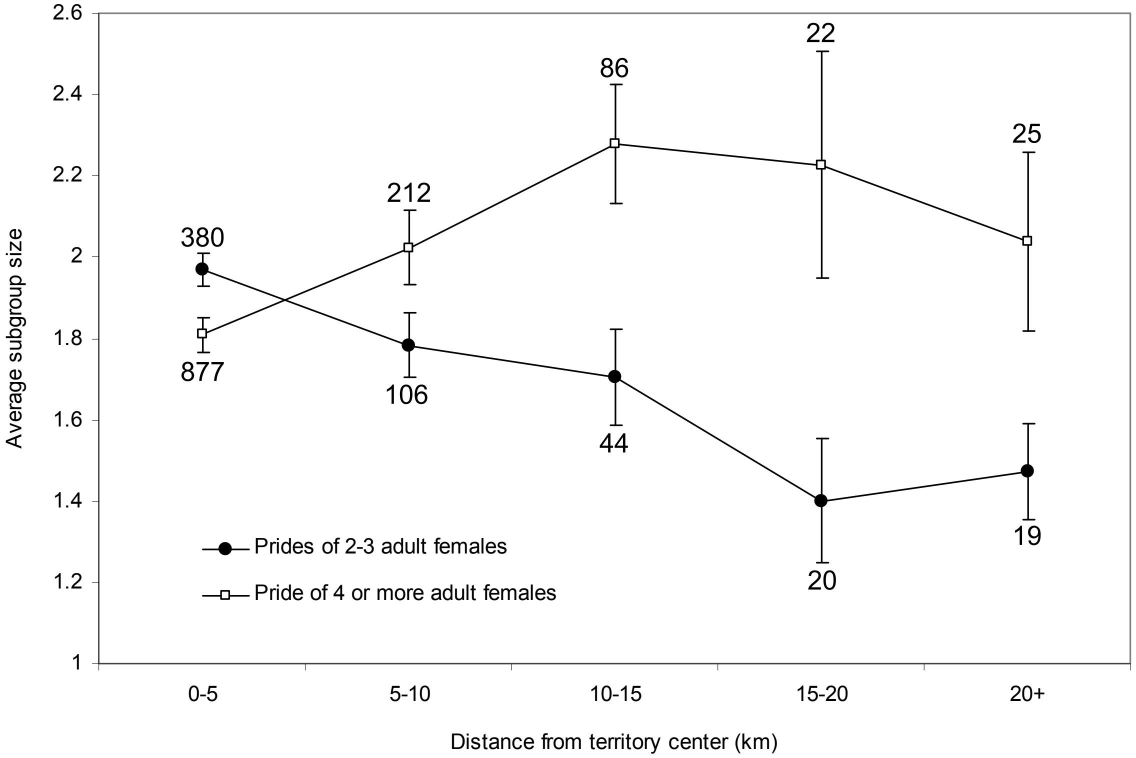
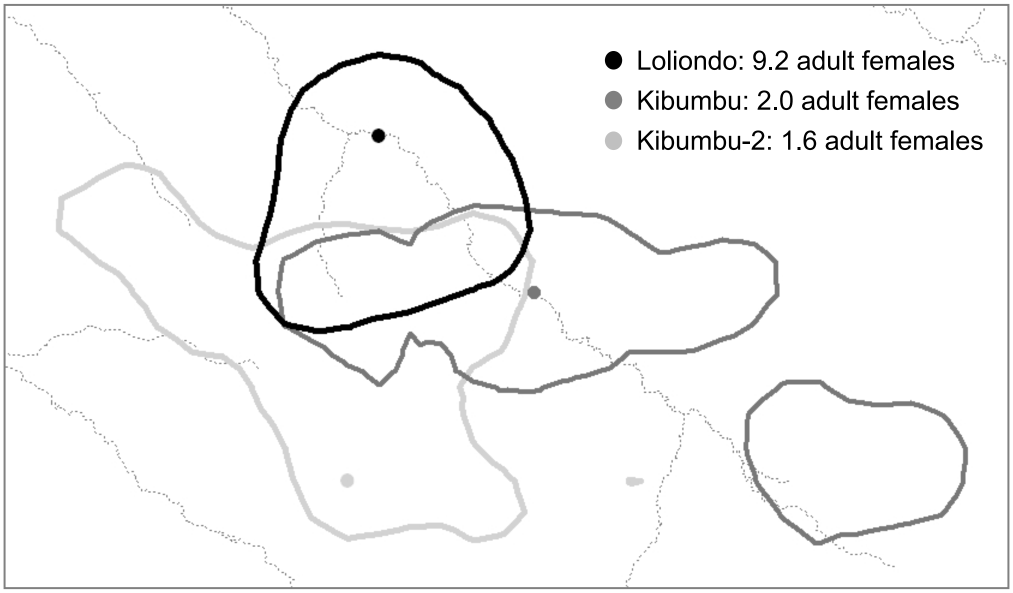


Table 4. Hypothesis 3 – Gain of disputed territory vs. location variables and relative pride size. a) All analyses controlled for the location of the disputed grid cell. b) Each neighbor variable was independently added to the model containing the location variables. c) Each pair of neighbor variables (split or no split, within 2, 5, and 10 years) was independently added to the model containing the location variables. *Neighboring adult females, defined as 2 years older, provided a stronger fit to the data.

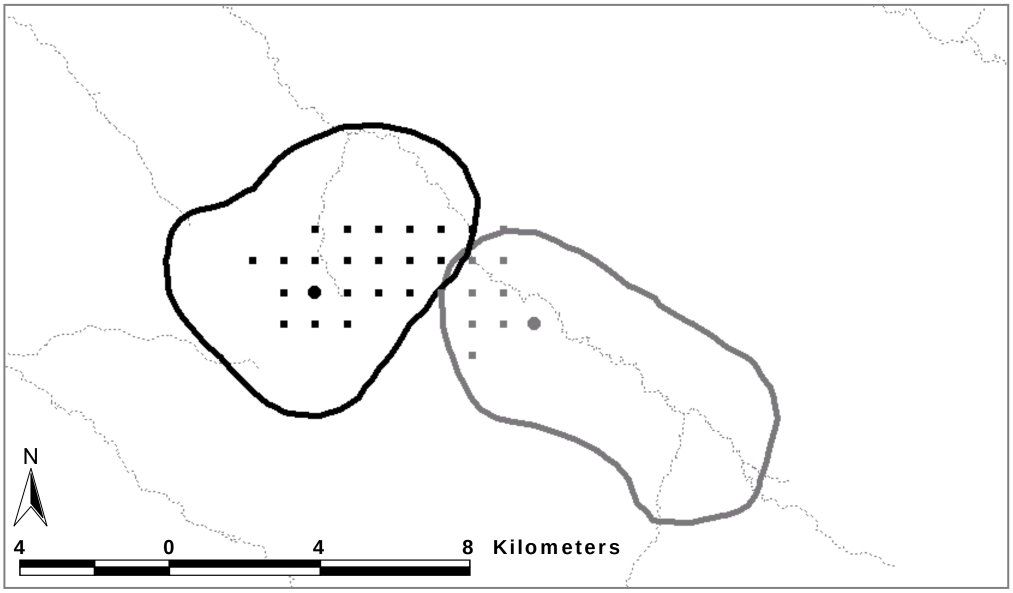
Variable	Effect	Standard error	Z	P-value
a) *Location variables:*				
Proximity to territory border: focal pride	-0.0140	0.005	-2.99	0.003
Proximity to territory border: neighbor pride	0.0147	0.005	2.80	0.005
b) *Location variables plus each neighbor variable :*				
Log relative pride size: females*	0.4359	0.133	3.29	0.001
Log relative pride size: males	0.0781	0.204	0.38	0.702
Log relative pride size: adults*	0.2021	0.182	1.26	0.209
Log relative pride size: total	0.2433	0.161	1.51	0.130
c) *Location variables plus each neighbor variable, by time since pride split:*				
Split within 2 years:				
Log relative pride size: females (Yes)*	0.4891	0.230	1.63	0.103
Log relative pride size: females (No)*	0.4297	0.144	2.98	0.003
Log relative pride size: adults (Yes)*	0.6168	0.646	0.95	0.340
Log relative pride size: adults (No)*	0.1913	0.180	1.06	0.287
Log relative pride size: total (Yes)	0.2604	0.487	0.53	0.593
Log relative pride size: total (No)	0.2414	0.171	1.42	0.157
Split within 5 years:				
Log relative pride size: females (Yes)*	0.7243	0.200	3.62	<0.001
Log relative pride size: females (No)*	0.3733	0.145	2.57	0.010
Log relative pride size: adults (Yes)*	0.4318	0.646	0.67	0.504
Log relative pride size: adults (No)*	0.2034	0.180	1.13	0.258
Log relative pride size: total (Yes)	0.1398	0.473	0.30	0.768
Log relative pride size: total (No)	0.2554	0.171	1.50	0.135
Split within 10 years:				
Log relative pride size: females (Yes)*	0.5744	0.249	2.31	0.021
Log relative pride size: females (No)*	0.4027	0.146	2.75	0.006
Log relative pride size: adults (Yes)*	-0.0650	0.662	-0.10	0.922
Log relative pride size: adults (No)*	0.2430	0.182	1.34	0.181
Log relative pride size: total (Yes)	-0.0610	0.453	-0.13	0.893
Log relative pride size: total (No)	0.2832	0.173	1.64	0.101

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 lost much of its territory and went extinct in the following time-step. a) Territory boundaries for the three prides in 1991-1992. Circles indicate the center of activity within the territory for each pride. Dotted gray lines show major rivers. b) Territory boundaries for the two surviving prides in 1993-1994. Circles indicate the centers of activity. Squares are the centers of the grid cells that were in dispute during the previous time-step and that were gained by one of the two prides.

(a) 1991-1992



(b) 1993-1994



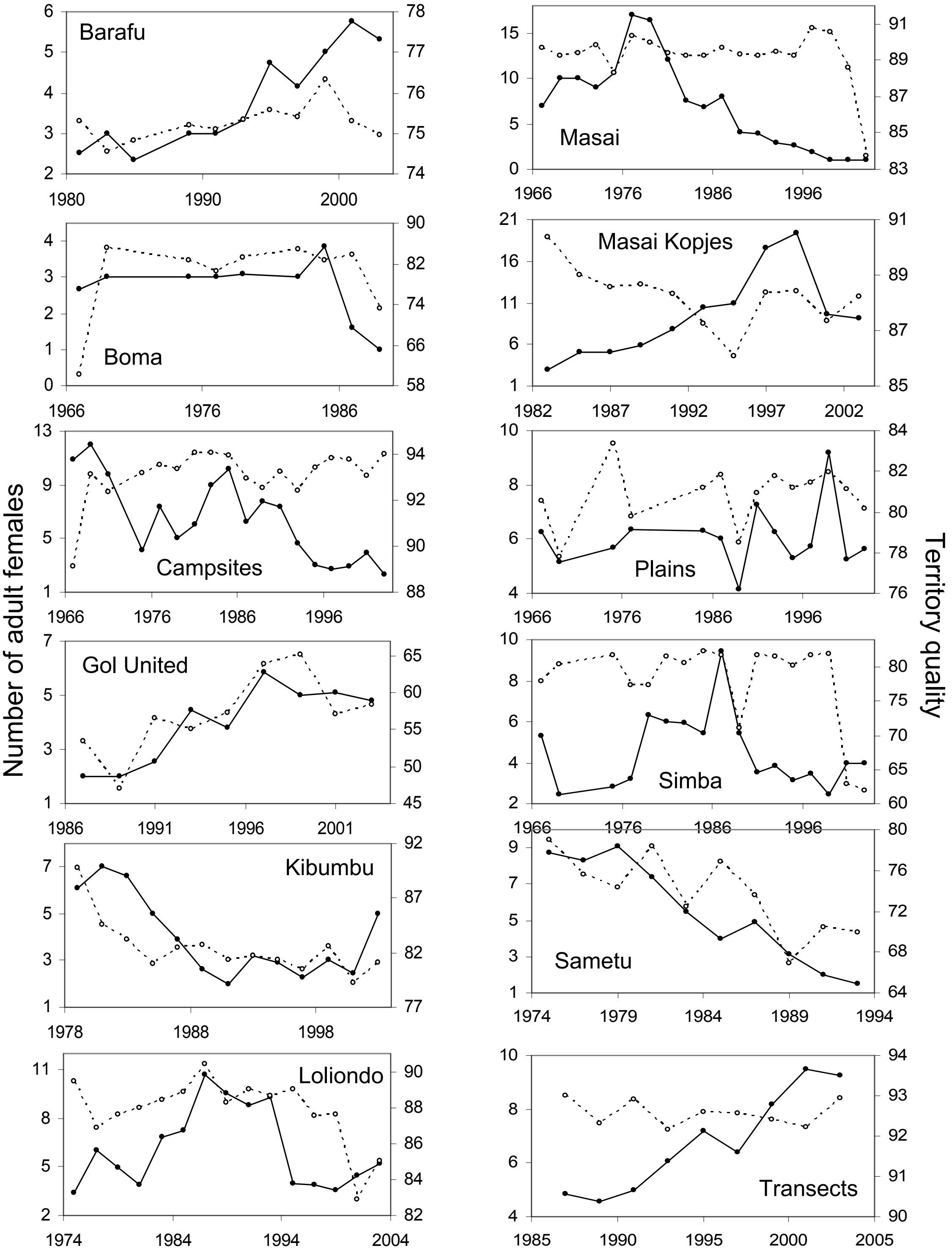
H4: Group size influences access to resources

Change in territory quality was significant and positively correlated with change in the number of adult females (Table 5, Fig. 6). We examined increases versus decreases in the number of adult females in a pride and found that an increase in the number of females was more strongly associated with improvement in territory quality, indicating that adult female recruitment is particularly important to gaining and maintaining access to high quality habitat. Also, adult female mortality was not significantly correlated with change in territory quality, suggesting that a loss of adult females does not immediately impact territory quality. The relative number of resident males in the pride also had a significant effect on change in territory quality. No strong effects of time since a pride split were found in these analyses.

Table 5. Hypothesis 4 – Change in territory quality vs. pride and neighbor variables. a) Pride variables were first analyzed in a multivariate model. Significant variables are listed. Pride variables *not* significant: number of adult females, number of resident males, number of adults, total pride size, average age of adult females, changes in other demographic variables, adult female mortality rate, number of takeovers, and territory size. b) Each neighbor variable was independently added to the model containing the significant pride variable. c) Each pair of neighbor variables (split or no split within 2, 5, and 10 years) was independently added to the model containing the significant pride variable.

Variable	Effect	Standard error	Z	P-value
a) *Significant pride variables:*				
Change in pride size: adult females	0.1765	0.086	2.06	0.039
b) *Significant pride variables plus each neighbor variable:*				
Log relative pride size: females	0.7552	0.528	1.43	0.153
Log relative pride size: males	2.7781	0.980	2.83	0.005
Log relative pride size: adults	1.4663	0.672	2.18	0.029
Log relative pride size: total	0.7314	0.434	1.69	0.092
c) *Location variables plus each neighbor variable, by time since pride split:*				
Split within 2 years:				
Log relative pride size: females (Yes)	0.9281	1.457	0.64	0.524
Log relative pride size: females (No)	0.1835	0.840	0.22	0.827
Log relative pride size: adults (Yes)	1.2811	-2.519	-0.01	0.995
Log relative pride size: adults (No)	1.8798	-0.045	1.94	0.053
Log relative pride size: total (Yes)	0.6584	-1.048	0.37	0.712
Log relative pride size: total (No)	1.0572	-1.433	0.60	0.546
Split within 5 years:				
Log relative pride size: females (Yes)	1.8945	1.260	1.50	0.133
Log relative pride size: females (No)	-0.6420	0.712	-0.90	0.367
Log relative pride size: adults (Yes)	1.1540	-0.647	1.40	0.162
Log relative pride size: adults (No)	0.7901	-1.988	-0.56	0.578
Log relative pride size: total (Yes)	1.2260	0.761	1.61	0.107
Log relative pride size: total (No)	-0.8192	0.586	-1.40	0.162
Split within 10 years:				
Log relative pride size: females (Yes)	1.5505	1.180	1.31	0.189
Log relative pride size: females (No)	-0.5230	0.522	-1.00	0.316
Log relative pride size: adults (Yes)	1.0840	-0.774	1.25	0.213
Log relative pride size: adults (No)	0.5997	-1.732	-0.93	0.353
Log relative pride size: total (Yes)	0.7229	-0.435	1.36	0.174
Log relative pride size: total (No)	0.5322	-1.845	-1.51	0.132

Figure 6. Pride size (number of adult females, solid lines) and territory quality (dashed lines) over time, for 12 Serengeti prides. Circles indicate time-steps with a sufficient number of observations (10 or more). In some cases prides were rarely seen during a given time-step and values were linearly interpolated over periods with insufficient data. Note that the axis scales differ for each pride.



DISCUSSION

Our results confirmed that larger prides, defined as the number of adult females, have a broad competitive advantage in intergroup competition: larger prides gained control of disputed areas (*H3*) and prides that recruited adult females improved the quality of their territories (*H4*). Larger prides also had higher rates of reproductive success (*H1*) and lower rates of mortality (*H1*), and were able to form larger subgroups when in potentially risky locations (*H2*). Most analyses also supported the expectation that territorial competition would be most intense between unrelated adult females: effects on reproductive success (*H1*), sub-grouping patterns (*H2*), and gain of disputed territory (*H3*) were associated only with neighbors that had not recently split. Unexpected was the impact of male neighbors on female mortality and the role of males in improvement in territory quality; these results are discussed in more detail below.

For most analyses, pride size and female neighbors were best defined as 3 years or older. An exception to this, where adult females were defined as 2 years or older, was the effect of neighbor females on subgroups sizes in smaller prides. This suggests that small prides are highly vulnerable and are potentially threatened by even young female competitors. Females defined as age 2 or older also provides a stronger result in the analysis of disputed territory. This indicates that young females, who have begun to express territorial behavior, do indeed have an impact on the outcome of territorial competition.

Mortality and aggression

Neighbors may impact one another through direct aggression. We found that larger groups had lower monthly rates of mortality, reflecting the quality of their territories and the potential to form larger safer groups. We also examined monthly wounding rates for adult females (Table 6) and found that larger prides also had fewer wounds per female. Prides that suffered more resident male takeovers had higher rates of mortality, potentially resulting from efforts to defend cubs from infanticide. Observers in the

Table 6. Per capita adult female wounding rate vs. pride and neighbor variables (n=217 pride 2-year time-steps). a) Pride variables were first analyzed in a multivariate model. Significant pride variables are listed. Pride variables *not* significant: number of resident males, number of adults, total pride size, average age of adult females, number of takeover events, and coalition sharing. b) Each neighbor variable was independently added to the model containing the significant pride variable. c) Each pair of neighbor variables (split or no split, within 2, 5, and 10 years) was independently added to the model containing the significant pride variable. In all analyses, we controlled for the number of observations of the pride during each 2-year time-step.

Variable	Effect	Standard error	Z	P-value
a) *Significant pride variables:*				
Number of adult females	-0.0252	0.010	-2.45	0.014
b) *Pride variables plus each neighbor variable (with replacement) :*				
Number of neighbor prides	0.0537	0.020	2.66	0.008
Adult female neighbors	0.0111	0.005	2.39	0.017
Adult male neighbors	0.0362	0.010	3.59	<0.001
Adult neighbors	0.0097	0.003	2.81	0.005
Total neighbors	0.0039	0.002	2.09	0.037
c) *Significant pride variables plus each neighbor variable, by time since pride split:*				
Split within 2 years:				
Number of neighbor prides (Yes)	0.1181	0.058	2.02	0.043
Number of neighbor prides (No)	0.0471	0.018	2.56	0.011
Adult female neighbors (Yes)	0.0018	0.011	0.16	0.871
Adult female neighbors (No)	0.0110	0.005	2.15	0.032
Adult neighbors (Yes)	0.0005	0.011	0.04	0.965
Adult neighbors (No)	0.0098	0.004	2.70	0.007
Total neighbors (Yes)	0.0024	0.005	0.53	0.598
Total neighbors (No)	0.0036	0.002	1.77	0.076
Split within 5 years:				
Number of neighbor prides (Yes)	0.0233	0.048	0.49	0.622
Number of neighbor prides (No)	0.0572	0.023	2.50	0.013
Adult female neighbors (Yes)	-0.0007	0.010	-0.07	0.947
Adult female neighbors (No)	0.0128	0.006	2.24	0.025
Adult neighbors (Yes)	-0.0029	0.010	-0.30	0.763
Adult neighbors (No)	0.0108	0.004	2.75	0.006
Total neighbors (Yes)	-0.0002	0.004	-0.04	0.971
Total neighbors (No)	0.0044	0.002	1.85	0.064
Split within 10 years:				
Number of neighbor prides (Yes)	0.0766	0.060	1.28	0.201
Number of neighbor prides (No)	0.0506	0.022	2.30	0.022
Adult female neighbors (Yes)	0.0062	0.013	0.50	0.620
Adult female neighbors (No)	0.0126	0.006	2.06	0.039
Adult neighbors (Yes)	0.0038	0.012	0.31	0.754
Adult neighbors (No)	0.0107	0.004	2.60	0.009
Total neighbors (Yes)	0.0023	0.005	0.46	0.643
Total neighbors (No)	0.0043	0.003	1.70	0.089

Serengeti have witnessed females being killed while defending cubs from males (K. Skinner, personal communication).

Notably, neighbor effects on mortality were only associated with the number of neighboring males. Wounding rates were also most strongly associated with the number of neighbor males (Table 6), though female neighbors did also have a significant effect.

What is the basis for this link between neighbor males and female mortality and wounding? Female mortality was not exclusively associated with females that had cubs and thus mother defense against infanticide. Females had dependent offspring (cubs age 2 or younger) during 53% of months, on average, from the age of 3 to 10 years; of the females that died within this age range (180 total), 45% had cubs, and 59% had cubs within 3 months of their death. Neither of these values is significantly lower or higher than expected, given the percent of time that females had cubs. Also, the probability of an adult female death occurring in a pride was significantly lower if there were more mothers present (Table 7). These statistics suggest that both mothers and non-mothers were wounded and killed by neighboring males.

Why might a male attack and potentially kill a neighboring female, given that the alternative is to mate with her? Our results demonstrate that there are a number of distinct advantages to reducing the number of neighbors, and altering the balance of power in territorial competition (Manson and Wrangham 1991). Although the link between female

Table 7. Logistic regression of occurrence of female death within a month (yes or no) vs. number of females, number of takeovers, and proportion of females that were mothers. The number of females was entered into the model as a polynomial; the probability of a death in a pride initially increases with group size, due naturally to a higher probability of a death if there are more females present, and then decreases due to a pride size advantage, as seen before.

Variable	Effect	Standard error	Z	P-value
Number of adult females	0.3151	0.049	6.50	<0.001
Number of adult females^2	-0.0115	0.003	-3.84	<0.001
Number of takeovers	0.1620	0.075	2.16	0.031
Proportion mothers	-0.5614	0.210	-2.68	0.008

mortality and male neighbors may relate to sexual dimorphism, the evidence suggests that it may be an example of adaptive lethal aggression. A handful of accounts describe lethal attacks on females, by one or more males, that were not associated with infanticide (Schenkel 1966 p.20, Schaller 1972 p.159). Male chimpanzees sometimes attack and kill adult females in neighboring communities if the females are not sexually receptive (Wilson and Wrangham 2003, Willimas et al. 2004), indicating the females pose a competitive threat to the males' own community. A neighboring lioness, if not receptive to mating, may also be viewed by male lions as a competitor for scarce resources and as potentially infanticidal, threatening their success during their short residency in a pride. Lethal attacks are associated with fission-fusion social groups (Wrangham and Peterson 1996), in which small subgroups may form that are vulnerable to an attack by neighbors. Our results show that subgrouping patterns are sensitive to the number of neighbors, suggesting that the risk of attack is very real. Male lions may actively seek opportunities to attack, wound, and kill neighboring females in order to secure the success of their current pride and improve their own long-term fitness, but currently, we have only circumstantial statistical evidence and few direct accounts of such behavior.

Fission-fusion grouping patterns

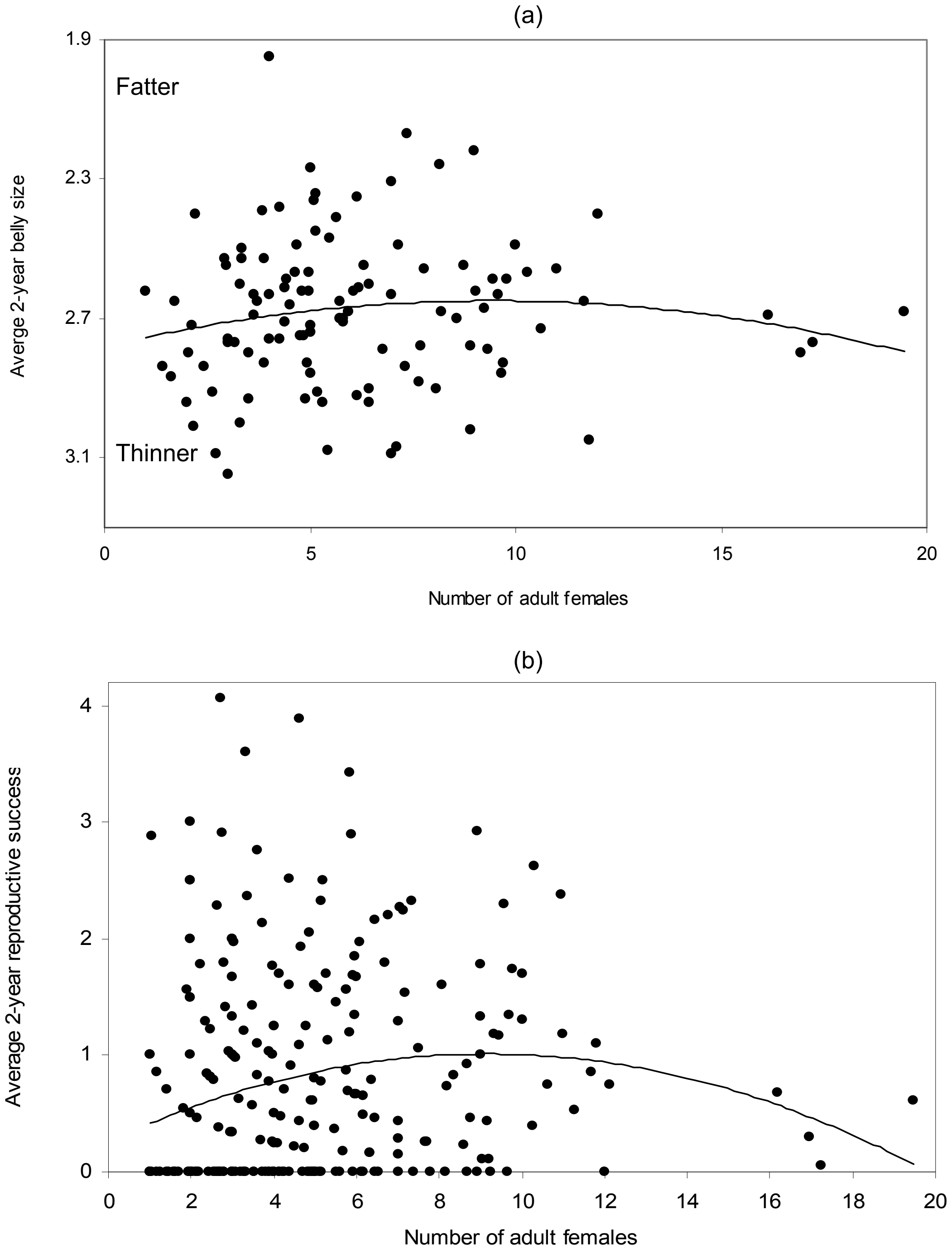
Packer at al (1990) showed that female grouping patterns within small prides (2-4 adult females) could not be fully explained by foraging success or the need to protect dependent young. Our analysis of subgroups of non-mothers shows that grouping patterns are affected by the number of neighbors for all pride sizes and that grouping patterns probably serve a territorial function. Prides with many neighbors 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 (farther from the territory center or in open habitat) non-mothers in small prides were found in smaller subgroups. These patterns suggest that lionesses in smaller prides may try to evade detection in risky environments. Alternatively, larger prides formed larger groups in risky locations, especially in open plains vs. woodland habitat. In these prides, the lionesses 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 and Pletscher 2002).

Inter-group and intra-group resource competition

The results of hypotheses 3 and 4 suggest that the impact of neighbors on reproductive success is due to the loss of territory to larger and successful neighboring prides, hampering access to resources and reducing the survival of cubs. Changes in territory size are also associated with the number of neighbors (controlling for current territory size and habitat type, change in territory size vs. total number of neighboring lions: effect = -0.0625, SE = 0.0195, Z = -3.20, p = 0.001). Thus, smaller prides and prides with more neighbors are forced in to smaller territories in lower quality habitat, which should result in reduced foraging success, but analysis of average adult female belly sizes revealed no significant relationship between food intake and any measure of the number of neighbors. We did find, however, a polynomial relationship between average belly size and pride size; small and large prides had the smallest belly sizes and presumably lower rates of food intake (Fig. 8a). For small prides, this likely reflects the impact of territorial competition (and not reduced hunting success, Packer et al. 1990).

Larger prides are successful competitors and enjoy higher quality larger territories, but there appears to be an upper limit to the benefits of increasing pride size in Serengeti lions. Medium sized prides have the highest rates of food intake, but the largest prides seem to experience increased within-pride food competition (Fig. 8a). A quadratic relationship was also found for reproductive success (as a continuous variable) vs. pride size (Fig. 8b), which again reflects the effects of intergroup competition for small prides and the effects of intragroup competition for very large prides.

Figure 8. a) Average 2-year belly size vs. pride size (number of adult females). A quadratic curve provided the best model fit, although the first term was marginally significant (number of females: effect = -0.0278, p = 0.068; number of females^2: effect = 0.0015, p = 0.038, n=111 pride 2-year time-steps). Note that smaller numbers indicate larger bellies, and thus the axis is reversed, as is the direction of the parameter effects. b) Average 2-year reproductive success vs. pride size. Again, a quadratic curve provided the best fit to the data (number of females: effect = 0.1635, p = <0.001; number of females^2: effect = -0.0089, p = <0.001; n=263 pride 2-year time-steps).



Conclusions

We have demonstrated that there is a strong long-term individual advantage to group territoriality in lions. With these analyses, we reveal the mechanisms underlying the shape of the left-hand portion of the curve in Figure 8b, that is, why individuals in larger groups have higher rates of reproductive success (and presumably higher fitness) than 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 inter-group competition are direct and immediate, so much so that male coalitions, usually resident in a pride for only a single reproductive cycle, also play a prominent role in the dynamics of territorial competition. Group-territorial competition therefore provides strong selection for cooperative territorial defense and a solid basis for sociality in lions.

Intra-group resource competition also plays an important role in lion society. Very large groups (12+ adult females) suffer in terms of food intake, thus food competition reduces the benefits of group territoriality and places an upper limit on group size. Intra-group competition also provides the basis for a fission-fusion society, in which foraging costs force individuals into smaller subgroups (Janson and Goldsmith 1995). This may relate to the evolution of lethal aggression and the patterns we observed in adult female mortality, as food competition forces individuals to leave the safety of the group.

The benefit of cooperative territorial defense is the primary driver in the evolution lion sociality. Past work has shown that it plays an important role in the social life of lions and has led to the evolution of complex traits, such as numerical assessment (McComb et al. 1994) and cooperation (Heinsohn and Packer 1995). But a full picture of lion sociality must also include the daily need to find food, which appears to be a constant challenge and ultimately places a limit on the advantages of forming a territorial group. The fission-fusion sociality of African lions is a result of a balance between inter-group competition for prime real estate and intra-group competition for food.

CHAPTER 3

The evolution of group territoriality: balance of power in a heterogeneous landscape

(with Margaret Kosmala[1] and Craig Packer)

INTRODUCTION

Group territoriality is widespread among animal taxa; it occurs in insects (e.g. ants: Adams 1990), fish (e.g. parrotfish: Clifton 1990), birds (e.g. Florida scrub jays: Woolfenden and Fitzpatrick 1984), carnivores (e.g. wolves: Mech 1973, lions: Heinsohn 1997, hyenas: Boydston et al. 2001), and primates (e.g. humans: Tinbergen 1968, chimpanzees: Nishida et al. 1985, vervet monkeys: Cheney 1986). Territoriality can generally be defined as the exclusive use of space, resulting from the economic defendability of limiting resources (Pitelka 1959, Brown 1964, Mitani and Rodman 1979). It is strongly associated with conspecific aggression and is inextricably linked to the structure of the landscape, but an understanding of the role of these factors in the evolution of group territoriality has not been well developed. Moreover, the potential advantage of cooperative territorial defense is not broadly recognized as an independent mechanism for the evolution of sociality.

Balance of power (i.e. relative group size) is a strong force in group-territorial species. The aggressive nature of territorial behavior (Howard 1948, Lorenz 1966) leads to, in its gregarious form, the potential for escalated intergroup competition that directly impacts individual survival and fitness. The resulting pressure to build or assess relative group strength is often invoked in explanations of many complex traits, including numerical

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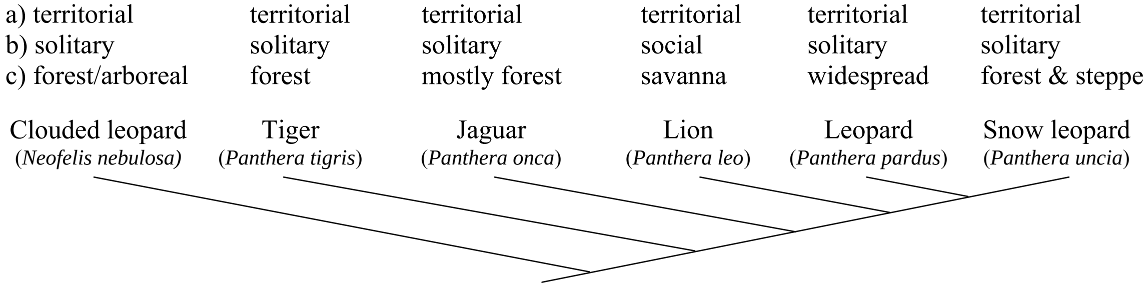
assessment (McComb et al. 1994), adaptive lethal aggression (Manson and Wrangham 1991), and altruism (Olendorf et al. 2004, Choi and Bowles 2007), as well as human warfare (Durham 1976, Wrangham and Peterson 1996) and ethnic identification (Toft 2006). Empirical work confirms that larger groups enjoy many benfits: they win intergroup contests (Carlson 1986, Cheney 1987, Adams 1990, Wilson and Wrangham 2003), have higher quality territories (Chapter 2, Woolfenden and Fitzpatrick 1984, Kauffman et al. 2007), and reduce costs due to shared territory defense (Davies and Houston 1981, Clifton 1990). Willingness to engage in intergroup interactions is also highly dependent upon relative group size (Harrington and Mech 1979, McComb et al. 1994, Heinsohn 1997, Wilson et al. 2001). Despite the evidence that the benefits of cooperative territorial defense may often outweigh the costs of sociality, little theoretical work has been developed to explore the degree to which the defensive advantages of group size may have contributed the evolution of sociality in territorial animals.

The resource dispersion hypothesis (RDH), proposed by Macdonald (1983), formalized the long standing recognition of the relationship between resource distribution and patterns of sociality (Crook 1964, Wilson 1975, Bradbury and Vehrencamp 1976, Kruuk 1978, von Schantz 1984). It is among the few hypotheses for the evolution of social behavior that explicitly address the role of landscape structure. Although empirical verification of this hypothesis has proven difficult (Johnson et al. 2002), the theoretical foundations of RDH have been valuable to an understanding of group-territorial behavior. The RDH states that landscape heterogeneity facilitates the formation of social groups, because the economics of territory defense in a variable landscape may lead to territories that not only support an individual or breeding pair, but that also sometimes supports additional individuals at low cost to the territory owner. Macdonald (1983) termed these passive aggregations ‘spatial groups’. Criticism of RDH (Revilla 2003a, b) has prompted the clarification that landscape heterogeneity alone is an unlikely causal mechanism for the evolution of sociality, but, paired with an advantage to grouping (such as cooperative territorial defense), ‘spatial groups’ pave the way to consistent sociality (Johnson and Macdonald 2003).

We developed a spatially explicit agent-based simulation model that explores the evolution of group territoriality within landscapes of differing structure. The model is patterned after the biology of African lions (*Panthera leo*), well known for their pronounced sociality. Lions live in matrilineal prides of 2-18 adult females, with dependent young and a temporary coalition of 1-9 unrelated adult males (Packer et al. 1990). All other felids, though groupings are occasionally observed, lead successful lives as solitaries, while lions are highly dependent upon their pride or coalition mates for their survival and reproduction. This has intrigued researchers, since it presents an isolated case of an evolutionary transition to sociality that can be associated with a specific difference in ecological context (Fig. 1). Accordingly, lion sociality is viewed as an adaptation to savanna habitat (Kleiman and Eisenberg 1973, Packer 1986, Mattern and McLennan 2000), a landscape characterized by heterogeneity (Sinclair 1979). Detailed study of lions points to cooperative territorial defense as the foundation of the lion social group (Packer et al. 1990, Chapter 2). In the Serengeti National Park, Tanzania, analysis of spatial patterns of reproductive success revealed that individual fitness is dependent upon access to river confluences, which provide food, water, and shelter in a single location (Chapter 1), very much like the high quality patches envisioned in the resource dispersion hypothesis (Macdonald 1983). The impetus for this model was therefore to understand the evolution of lion group territoriality in a savanna-like landscape.

Figure 1. Phylogeny of the *Panthera* lineage. Adapted from Yu & Zhang (2005) and Mattern & McLennan (2000). Listed characteristics: a) resource defense strategy, b) typical grouping pattern, and c) habitat.



Using the model, we explore four hypotheses related to the evolution of group territoriality. First, we test whether group territoriality is more likely to evolve in a heterogeneous landscape. Next, we test whether heterogeneity must be paired with one or more positive advantages of grouping: cooperative territorial defense, larger territories, and territorial inheritance.

We then consider the role of population density in the evolution of group territoriality. Studies of cooperative breeders, which are usually group-territorial, often stress the role of density and habitat saturation, as saturated environments are associated with high dispersal costs and low rates of new territory establishment (reviewed by Koenig et al. 1992). In addition, the advantages of grouping may not be realized in a low density environment because, for example, a defensive advantage depends upon high rates of contact with neighbors. We therefore test whether group territoriality is less likely to evolve in a low density environment (Packer 1986).

Finally, we integrate the concepts of landscape structure and territorial competition and consider the impact of heterogeneity on rates on intergroup conflict. An uneven distribution of resources imposes a pattern of inequality across the landscape, in which groups occupying low quality territories are compelled to fight for access to high quality habitat. Also, continuous variation in the landscape and the drive for more 'efficient' territories will lead to larger groups vying for higher quality patches within their neighbor's territory, and thus heterogeneity alone may lead to higher levels of conflict even if the resource needs of a group are met. The role of heterogeneity has been relatively well established in the literature on human conflict; for example, scarcity, unequal resource distributions, and monopolizable resources are often associated with war and violence (Blau 1977, Homer-Dixon 1994, Billon 2001, Murshed and Gates 2005, Zaidise et al. 2007). Largely due to feasibility, however, this question has not been well explored in other animals (but see Dearborn 1998, Jensen et al. 2005, Harris 2006). Here, we test the hypothesis that conflict between territorial groups will be greater in more heterogeneous landscapes.

METHODS

The simulation model has five major components: landscapes, individuals, groups, territories, and intergroup competition. We varied landscape structure to capture different patterns of heterogeneity. Individuals in the model resemble female African lions in terms of demography (age at maturity, mortality rates and reproductive rates). Each individual is associated with a "group" that contains one or more individuals. For solitary individuals, this is the mother's group until it disperses to form its own new group, and for those with the social gene, this is the mother's group throughout the lifespan, unless the individual is forced to disperse. Groups may or may not have a territory. Territories are exclusive and are owned by a group, they are composed of a variable number of grid cells and their sizes and shapes depend upon the landscape and the resource requirements of the group. Neighboring groups compete with one another for ownership of grid cells on the landscape.

Model landscape

The model runs on a 60x40 grid cell lattice, for which we vary minimum and maximum resource values and patterns of heterogeneity. We consider three landscape patterns: homogeneous (all grid cells are equal), a confluence hotspot landscape, and a random hotspot landscape (Fig. 2). The confluence landscape is the map of confluences on the major rivers in the Serengeti lion project study area (71 confluences total). The distribution of confluences conforms to a power law relationship (Fig. 3), which is not unexpected for a fractal drainage network (Turcotte 2007). For the random configuration, 71 hotspots were fixed at random locations on the landscape.

Figure 2. a) Confluence hotspot landscape, based upon the locations of river confluences in the Serengeti study area. b) 71 randomly located hotspots.

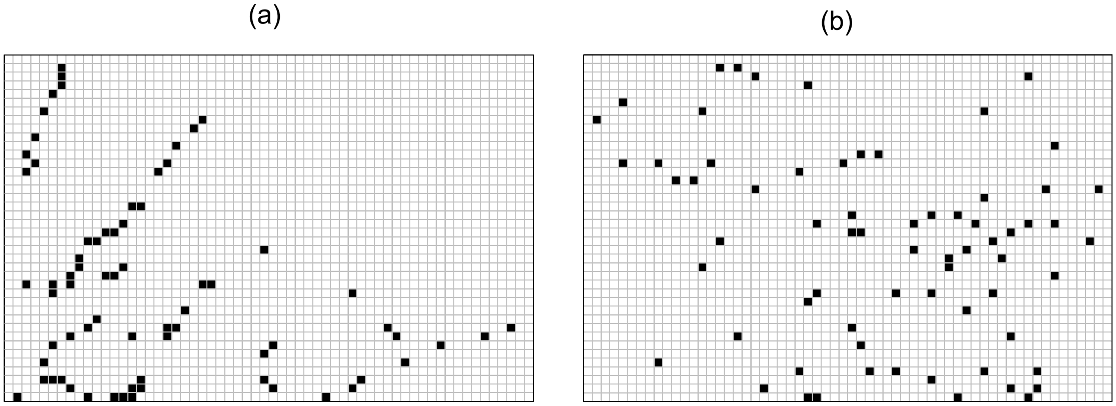
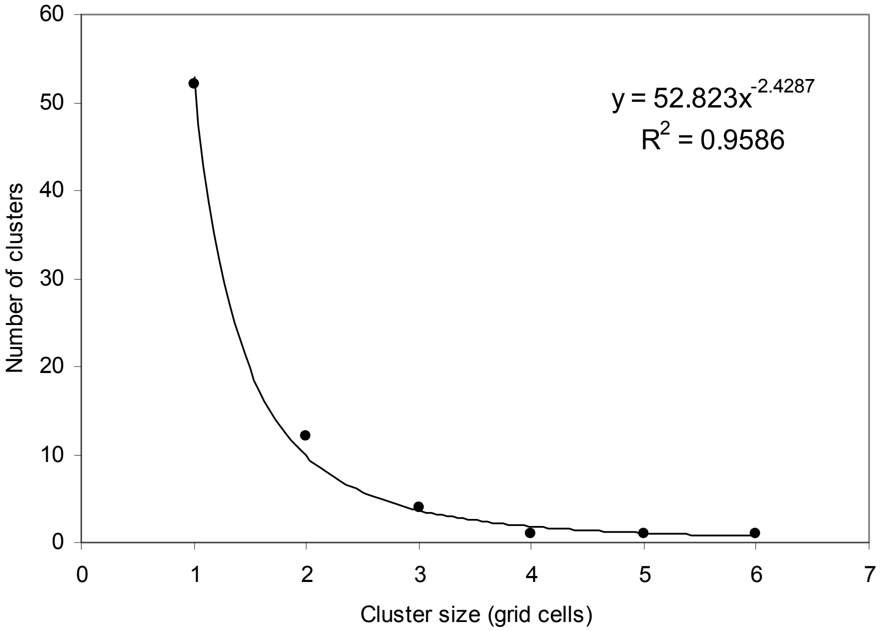


Figure 3. Power-law clustering of confluence hotspots (see Fig. 2a). We plotted the inverse cumulative distribution for clusters of 1 to 6 hotspots. We considered only adjacent (non-diagonal) grid cells in identification of each cluster.



In the heterogeneous landscapes, maximum resource values are assigned to each hotspot. Equation 1 determines how cell values decline with distance from a hotspot,

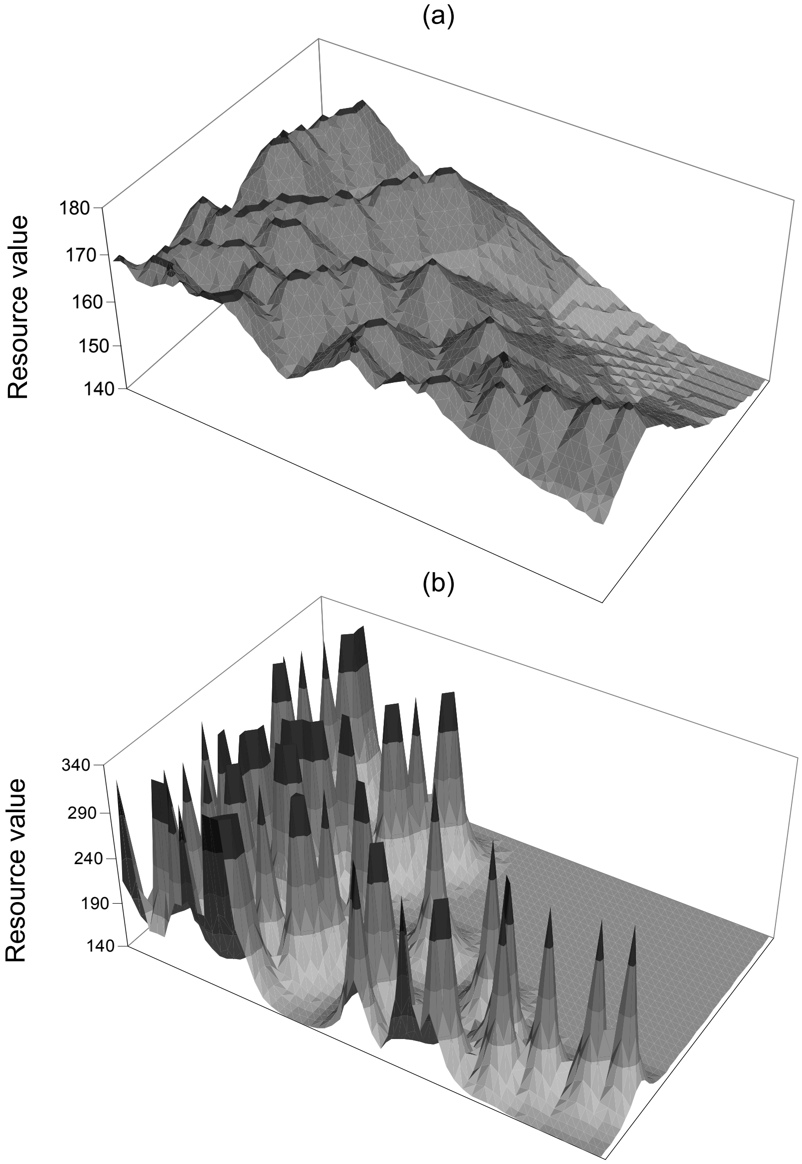
$$V = \left(\frac{V_{\max}}{D_{\max}{}^{P}} \right) \left(D_{\max} - D_{Hotspot} \right)^{P} \qquad \text{(Eq. 1)}$$

where V is the cell resource value, V_{max} the maximum resource value, $D_{Hotspot}$ the distance from nearest hotspot, and D_{max} is the length of the diagonal across landscape, which is the maximum possible distance from a hotspot. The slope of decline with distance from a hotspot, or "peaked-ness" of a hotspot, is varied by changing the power exponent (P). Finally, landscape values are rescaled to fit between the maximum and minimum values as set in the model.

We use landscapes with the same average resource value but five different values for peaked-ness (P = 1, 4, 16, 32, and 64). We hold constant the minimum value of the landscape and maintain the same average by increasing the maximum (hotspot) resource value. Resources are therefore more concentrated at highly peaked hotspots, with higher values of P (Fig. 4). Variance in resource value also increases with peaked-ness (see standard deviations in Fig. 7). Note that landscapes with the greatest peaked-ness are slightly more homogeneous, as these landscapes have larger areas of uniformly low values (see Moran's index (I) values (Griffith 1987) in Table 7).

For the analyses, we use low and high average value landscapes. The low value landscapes have an average resource value of 100, which supports only solitary territories in a homogeneous landscape, and a minimum value of 40, which is too low to support the survival of any individuals. The high value landscapes have an average resource value of 160 and a minimum value of 140, both of which are high enough to support solitary and social strategies in a homogeneous landscape. These patterns of resource value are applied to both the confluence and random hotspot heterogeneous landscape maps.

Figure 4. Two examples of heterogeneous landscape maps with confluence hotspots. a) Peaked-ness value (*P*) of 4. Average resource value of 160, minimum of 140 and maximum of 171. b) Peaked-ness value (*P*) of 64. Average resource value of 160, minimum of 140 and maximum of 330.



Territories

Territories incorporate several grid cells and are anchored at a central point. Cell resource values are discounted, at a linear rate, with increasing distance from the center point, up to a maximum radius as set in the model (Fig. 5a). We therefore assume that activity is centralized within the territory and that the realized value for a given cell is discounted by the cost of traveling from the territory center to that location (Getty 1981, Mitchell and Powell 2004). This distance-discounting formula is the basis for all territory calculations,

$$V_{terr} = V(1 - \frac{D}{R_{\max}}) \qquad \text{(Eq. 2)}$$

where V_{terr} is the value of a cell to the territory owner, V the absolute cell value, D the distance from territory center, and R_{max} the maximum radius for the territory.

The maximum radius for solitary groups is set to 4 cells (4 km is the average territory radius for prides in the Serengeti study area), yielding a maximum territory size of about 50 grid cells. If larger groups defend a larger territory, then the maximum radius increases with group size. Larger groups may defend a larger territory in order to overcome the costs of intra-group competition or because they share the costs of defending a larger territory. In the Serengeti woodlands, lion territory sizes increase linearly with the number of adult females in a pride (Chapter 2), so we set the maximum radius (R_{max} in Eq. 2) to increase additively by the square root of the number of adults in a group, to give an approximately linear increase in territory area with an increase in group size,

$$R_{\max} = R_{soliary} + \sqrt{N - 1} \qquad \text{(Eq. 3)}$$

where R_{max} is maximum radius, $R_{solitary}$ the territory radius for a solitary adult (4km), and N is the group size, as number of adults).

Territories are associated with a minimum and goal value (Fig 5b). The minimum value is sufficient for adult survival and the goal is sufficient for adult survival and reproduction. Minimum values are set to 1000 for a solitary adult, and increase by 1000 for each additional adult in the group.

We examine the model dynamics for goal values 500 or 1000 points higher than the minimum, thus either smaller or equal to the minimum for the next larger group size (N+1). For homogeneous landscapes, individuals with the social gene are increasingly more likely to be successful as landscape value increases, but the degree of success for social individuals depends upon the territory goal value. A high goal value (1000 points greater than the minimum for a group of N, and equal to the minimum for a group of N+1) facilitates the formation of social groups, because the mother's territory can already support the recruitment of offspring. Sociality therefore evolves, in part, by virtue of the structure of the modeled territories. At a low goal value (500 points greater than the minimum for a group of N, but less than the minimum for a group of N+1), groups must be able to increase the value of their territory in order to survive. This requires some form of inter-group competition our simulations are based on these restrictive circumstances.

Groups adjust their territory size and location to maximize the resource density within the territory and territories will be of the smallest size necessary to meet the resource requirements. As a result, territories are smaller in high value landscapes. This efficiency maximizing strategy (Stephens and Krebs 1986) is similar to the territorial contractors described by Kruuk and Macdonald (1985).

The maximum territory radius limits the maximum possible value of a territory within a landscape of a given value, and because larger groups require more resources, group size is limited by the value of the landscape (Fig. 5c). We considered landscapes with average resource values between 80 and 240, which supported from about 40 to 200 territories and group sizes of 1 to 14 adults, respectively.

Figure 5. a) Territories will increase in size, accumulating the benefits of resource gain, until the costs of travel outweigh the benefits and the territory value is maximized (where benefits minus costs is maximized). The maximum territory size and value is determined by the maximum radius (R_{max}), as set in the model. b) Territories (six are pictured here) are associated with a minimum (inner white lines) and goal values (outer red lines). Territories are abandoned if the minimum cannot be reached and will not grow beyond the goal value. c) An illustration of how landscape resource values set a limit on group size. In this example all cell values are set to 140, and groups of size 2 (black) can reach both the minimum and goal, groups of size 5 (green) can reach the minimum territory value but not the goal, and groups of size 8 (orange) cannot reach the minimum and are not support by this landscape.

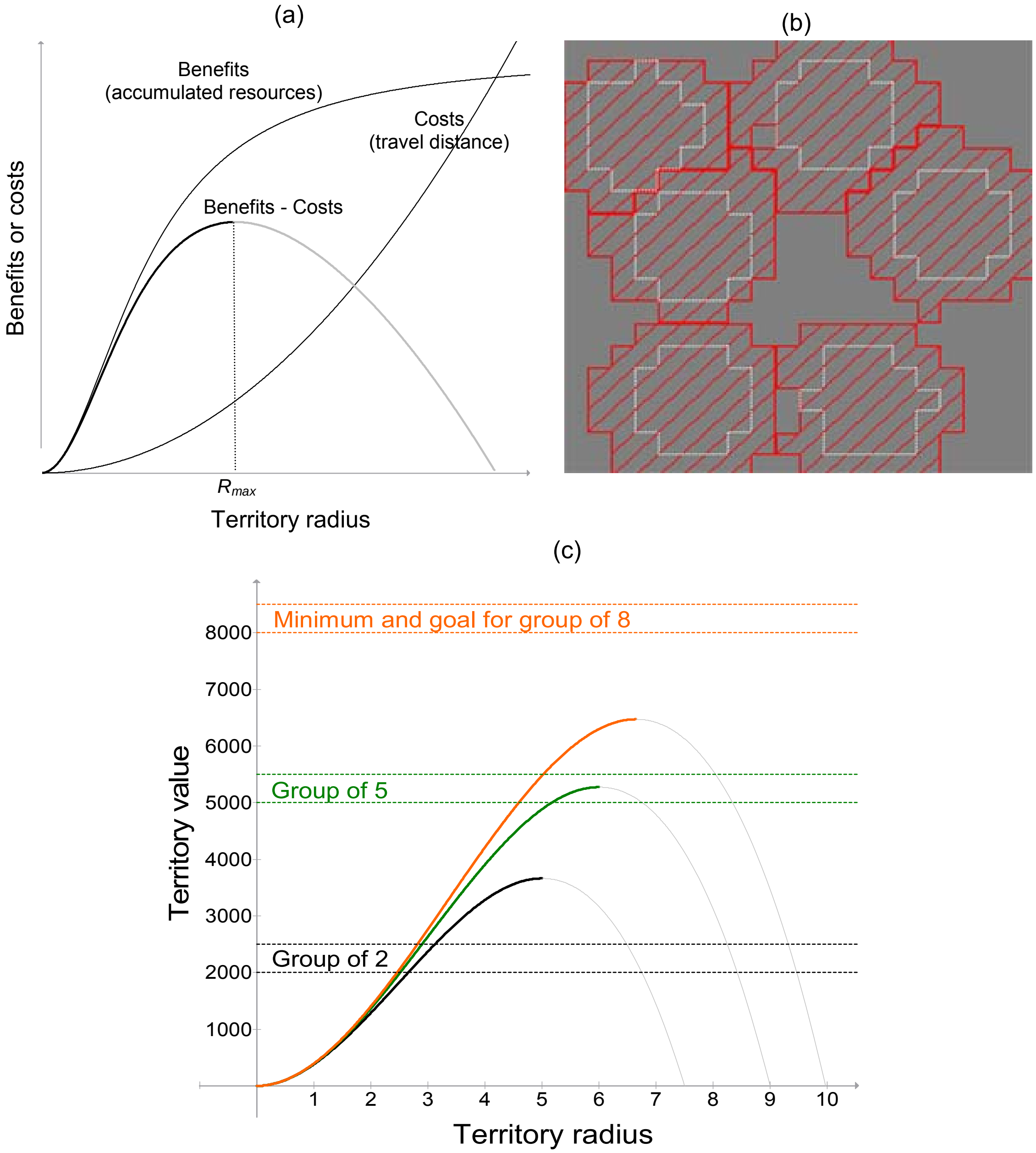
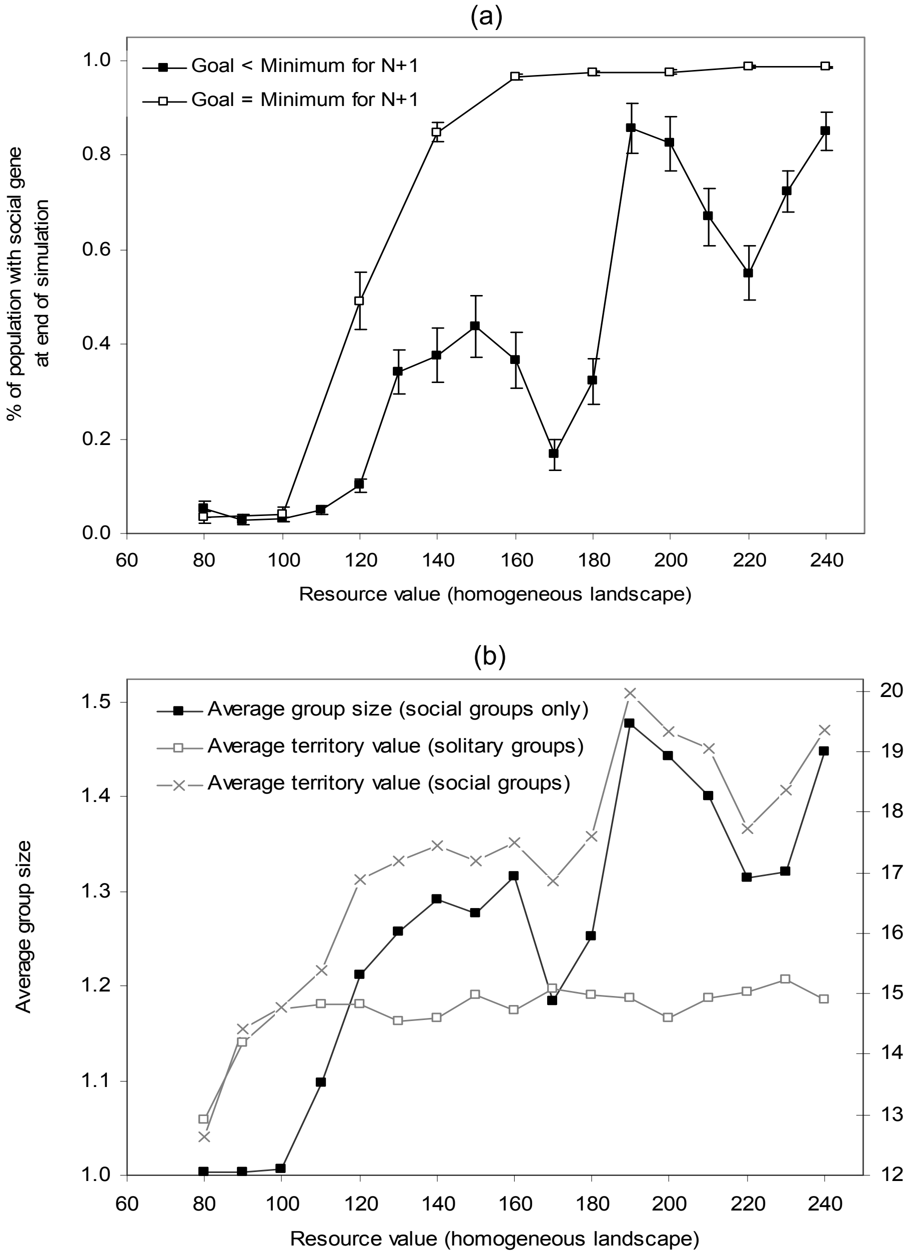


Figure 6. a) Proportion of population with social gene for last time-step vs. resource value in homogeneous landscapes, for different goal values. Social individuals are very successful and transition easily to larger group sizes when the territory goal value is set to equal the minimum territory value for the next larger group size (N+1). When the goal is less than the minimum for the next larger group size, transitions to larger groups and thus the success of social individuals depends upon substantial immediate gain in territory value. A growing group must compete and win territory from neighbors in order to support the recently matured offspring. b) For “Goal < Minimum for N+1”, average group size of social groups (left y-axis) and territory value (right y-axis) vs. resource value. Average group sizes and territory values for social groups reflect the pattern observed in the upper graph. For resource values of 170 and 220, for example, average group sizes and territory values drop because the resource values support high reproductive rates but social groups cannot transition successfully to the next larger group size when offspring mature, so maturing social individuals are forced out of the group alone or in small cohorts. Note that group sizes in homogeneous landscape remain quite small.



Social mutation and group advantages

A change in individual dispersal pattern is the key component in the evolution of group territoriality (Cahan et al. 2002). In our model, individuals with the social "gene" simply remain in, rather than disperse from, their natal territory. Maturing *solitaries* (reaching the age of 3 years/time-steps) always disperse on their own and attempt to establish a new territory, while maturing *social* individuals refuse to leave and are usually tolerated by their mother. If resources are very low, however, maturing individuals with a social gene are not tolerated and are forced out of their natal territory, though they may leave with a cohort of same-aged individuals.

We model three advantages to group formation. 1) Groups may benefit from a cooperative territorial defensive advantage, which gives larger groups a higher probability of winning an intergroup encounter, and consequently gaining disputed grid cells (see below for details). 2) Groups might defend larger territories, as described above, and thus benefit from access to more resources and higher territory values. 3) Individuals in groups may benefit from territorial inheritance (Lindstrom 1986). Social individuals stay in their natal territory and thus passively gain the established territory from their older relatives. To remove this advantage, we force social individuals to disperse, though they may still benefit from the other two advantages if they disperse with a cohort.

Intergroup competition

We modeled competition between groups as a series of decisions. The group first considers the value of adjacent grid cells in a neighbor's territory (groups may contest up to 25% of a neighbor's territory, which is the average amount of overlap between pride territories in the Serengeti study area) and if the gain of those cells will improve the value of the group's territory, then they may initiate an attack. The decision to attack depends upon the odds of winning a fight, based on relative group size, modified by the current territory value relative to the goal (Table 1). A group is more likely to fight if it has a low territory value, at which point it has more to lose if additional territory is surrendered to a neighbor (i.e. a 'desperado' effect,Grafen 1987). The modified odds are determined by the following equation,

$$Odds_{modified} = (\frac{N_a}{N_a + N_d}) + 0.5(\frac{G - T}{G - M}) \qquad \text{(Eq. 4)}$$

were N_a is the number of adults in attacking group, N_d the number of adults in defending group, G the goal territory value, M the minimum territory value, and T the current territory value). To calculate the modified odds of defending a territory against an attack, N_a is replaced by N_d in the numerator of the first term.

A group will attack its neighbor if the $Odds_{modified} \geq 0.55$ and will defend if $Odds_{modified} \geq 0.45$. Thus, groups play a "bourgeois" strategy (respect for ownership, Maynard Smith and Parker 1976) under a limited set of conditions. Note that groups do not know the status of the neighbor's territory and thus how willing the neighbor might be to defend the territory, and this does not factor into the decision to attack a territory. When an attack is initiated, if the neighbor retreats, the disputed cells are gained by the attacking group. If the neighbor defends, a fight occurs, and the odds of winning are based only upon the relative group sizes. The winner gains the disputed grid cells. Fights are associated with a 10% adult mortality rate per group.

Table 1. Intergroup competition: calculation of the modified odds and decisions to attack or defend territory. a) Territory values for both the attacking and defending group are equal to the goal value, and decisions to attack and defend are based only upon the odds of winning (the modified odd are the same). A group will attack if the modified odds are greater than 0.55 and will defend if the modified odds are greater than 0.45. Note that for these high territory values actual fights do not occur, because in no cases do we get an attack paired with a defend. b) Territory values do not meet the goal value and the odds are modified (in this case 0.15 is added to the odds), such that groups are more likely to attack and defend. Here fights will occur between groups of 2 vs. 2, 3 vs. 2, and 4 vs. 2 (attackers vs. defenders). For 1 vs. 2, an attack would not be initiated, and in all other pairings an attack would not be met with a defense by the territory owners.

	Attacking group:						Defending group:					
	# attackers	# defenders	Odds of winning	Relative territory value (% of goal)	Modified odds	Attack?	# defenders	# attackers	Odds of winning	Relative territory value (% of goal)	Modified odds	Defend?
a)	1	2	0.33	100	0.33	No	2	1	0.67	100	0.67	Yes
	2	2	0.50	100	0.50	No	2	2	0.50	100	0.50	Yes
	3	2	0.60	100	0.60	Yes	2	3	0.40	100	0.40	No
	4	2	0.67	100	0.67	Yes	2	4	0.33	100	0.33	No
	5	2	0.71	100	0.71	Yes	2	5	0.29	100	0.29	No
	6	2	0.75	100	0.75	Yes	2	6	0.25	100	0.25	No
	7	2	0.78	100	0.78	Yes	2	7	0.22	100	0.22	No
	8	2	0.80	100	0.80	Yes	2	8	0.20	100	0.20	No
	9	2	0.82	100	0.82	Yes	2	9	0.18	100	0.18	No
	10	2	0.83	100	0.83	Yes	2	10	0.17	100	0.17	No
b)	1	2	0.33	70	0.48	No	2	1	0.67	70	0.82	Yes
	2	2	0.50	70	0.65	Yes	2	2	0.50	70	0.65	Yes
	3	2	0.60	70	0.75	Yes	2	3	0.40	70	0.55	Yes
	4	2	0.67	70	0.82	Yes	2	4	0.33	70	0.48	Yes
	5	2	0.71	70	0.86	Yes	2	5	0.29	70	0.44	No
	6	2	0.75	70	0.90	Yes	2	6	0.25	70	0.40	No
	7	2	0.78	70	0.93	Yes	2	7	0.22	70	0.37	No
	8	2	0.80	70	0.95	Yes	2	8	0.20	70	0.35	No
	9	2	0.82	70	0.97	Yes	2	9	0.18	70	0.33	No
	10	2	0.83	70	0.98	Yes	2	10	0.17	70	0.32	No

Reproduction and mortality

Individuals reproduce asexually and they can only reproduce if they have a territory. Reproductive rates depend upon the current territory value relative to the goal and minimum values, and decline linearly as the territory value approaches the minimum. At goal, there is a 100% probability of reproduction. Litter sizes range from 1-3 and are drawn from a set distribution (Table 2).

Table 2. Litter size distribution

Litter size	Probability
1	0.50
2	0.35
3	0.15

The model incorporates three types of adult mortality: background mortality (Table 3), non-territory holder mortality (for individuals without a territory, set to 50%), and fighting mortality (10%). Two additional types of mortality apply to cubs only: low resource mortality (cubs die if the territory is at or below the minimum value) and orphan mortality (for cubs that lose their mother, set to 75%).

Table 3. Age specific mortality rates

Age	Mortality rate
1	0.3
2	0.2
3	0.1
4	0.05
5	0.05
6	0.05
7	0.05
8	0.05
9	0.05
10	0.05
11	0.05
12	0.05
13	0.05
14	0.10
15	0.20
16	0.50
17+	0.90

Model assumption: incomplete knowledge

We assume that individuals do not have complete knowledge of the landscape. During territory adjustment and competition, a group can only asses the value of adjacent cells, and when an individual disperses, it chooses the nearest open location, without regard to its relative resource value. Many of the landscapes, however, do contain resource value gradients. On such a landscape, territories will move (if unconstrained by neighbors) to the best locations, as long as cells adjacent to their territory are higher in value. The outcome is therefore similar to a model that assumes complete knowledge of the landscape.

Model flow

For each year, the simulation runs as follows (For steps 1-4, groups are run in a random order, and for steps 1-3, individuals are run from oldest to youngest within the group. Before step 5, groups are randomly reordered.):

1) Ageing and mortality (by individual)

Individual ages one year or dies according to the age specific, non-territory holder, or orphan mortality rates.

2) Dispersal and territory establishment (by individual)

If the individual is weaned (reaches 3 years of age) and has the solitary gene, it disperses. If it has the social gene, it stays in mom's territory or disperses if forced out. If the individual (or cohort) disperses, it attempts to establish a territory in the nearest open area, and will 'float' without a territory if no sufficient area can be found. If a territory is established, the group can then compete with neighbors within the same time-step.

3) Reproduction (by individual)

If an individual is of reproductive age (4+ years), has no unweaned offspring, and has a territory, it may reproduce.

4) Territory assessment (by group)

Groups with no territory attempt to establish one, in the manner described for dispersers in step 2. For groups with a territory, minimum and goal territory values are recalculated based upon current group membership. Territories move, grow, or shrink in attempt to meet the minimum and goal values. The territory center is also adjusted in order to maximize the territory value. If the territory value is below the minimum, cohorts of newly weaned individuals are forced out (applies to social groups only). If the territory value is still below the minimum, unweaned offspring die. Finally, if the territory value is still below the minimum, the group abandons the territory. Cohorts forced out and groups with abandoned territories will attempt to establish a new one in an open area.

5) Territorial competition (by group)

For each group, neighbors are considered in a random order, and disputable cells are identified within the neighbor's territory. Potential fights proceed as described above. Mortality is calculated after each fight, and unweaned offspring die, with a given probability, if the mother is killed due to a fight. Territory values are reassessed (repeat of step 4) after each neighbor encounter. If a group loses a territory due to a fight, it will attempt to establish one in an open area.

Simulations and hypothesis testing

For each set of simulations with a given set of parameter values, we first populated the landscape with solitary individuals. The simulations were then started from this point, with the potential for mutation. The mutation rate was set to 0.01, and each individual born might mutate to the social state that differs from its mother (solitary to social, and vice versa). We ran each simulation for 500 time-steps, with 20 replicates for each set of parameter values.

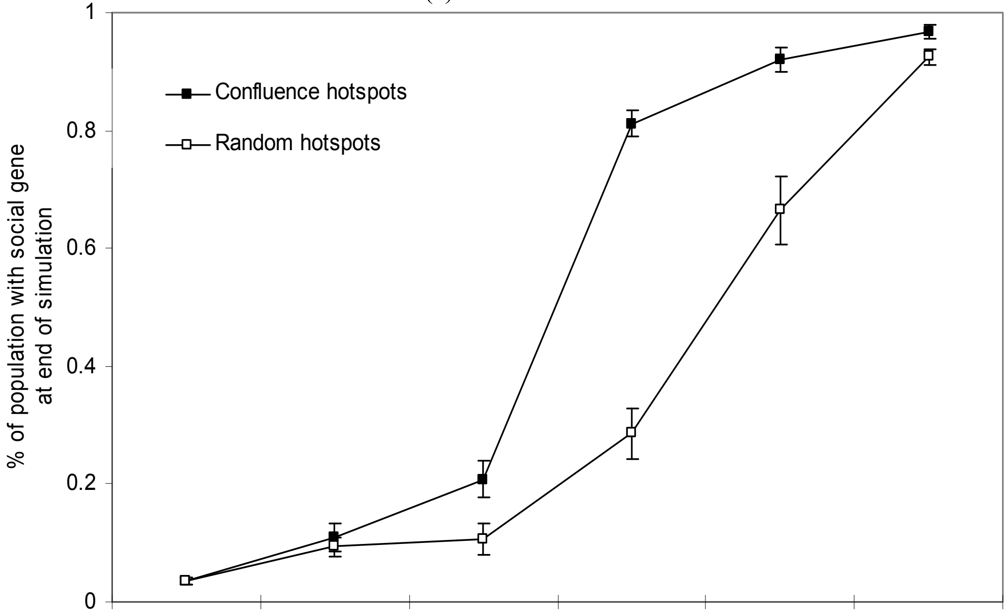
To assess the success of the solitary and social strategies, we calculated the proportion of the social individuals in the population for the last time-step of each simulation, and averaged over the 20 replicates. We tested the effect of landscape heterogeneity on the evolution of group territoriality by comparing this statistic for simulations run in the homogeneous versus heterogeneous landscapes. We also compared outcomes for the different types of heterogeneous landscapes (low and high resource value for confluence and random hotspot distributions). To examine the role of group advantages, we ran eight types of simulations, for each possible combination of the three group advantages (no advantage to full advantage). To hold the population at a low density, we increased the adult mortality by threefold and decreased the maximum reproductive rate to 0.75. Again, the proportion of social individuals in the final population was used to assess the effect of low population density on the evolution of group territoriality. We examined patterns of conflict by calculating the number of fights per group for the last 50 time-steps of each simulation and averaged this value for the 20 replicates. Rates of intergroup conflict were compared for the homogeneous versus heterogeneous landscapes.

RESULTS AND DISCUSSION

Social groups are more successful in heterogeneous landscapes (Fig. 7). This provides clear corroboration of the resource dispersion hypothesis. This is especially evident in the low value landscapes, where sociality develops solely in the context of heterogeneity (Fig. 7a), as only heterogeneous landscapes contain patches of high enough value to support the formation of groups. In these landscapes, survival depends upon access to the hotspots and the proportion of social individuals in the population is largely driven by the value of these locations (note the maximum values listed for each landscape). Social individuals represent a larger percentage of the final population in the confluence landscapes, where the hotspot values are higher in order to balance the larger areas of low resource value in these landscapes. In addition, given the power law clustering of confluences, territories can encompass several hotspots to yield higher territory values that support larger groups, which again emphasizes the role of resource dispersion. In the high value landscapes (Fig. 7b), we find a similar pattern, although group territoriality is not exclusively associated with heterogeneity. Also, survival is not dependent upon access to hotspots and solitaries thrive in the low value areas, so the social strategy is slightly less successful in the landscapes with the most peaked and concentrated hotspots (*P*=64).

Figure 7. Percent of individuals in the population carrying the social gene at the end of simulation vs. peaked-ness (*P*), for landscape with confluence and random distributions of hotspots, and a) low average resource values or b) high average resource values. *P*=0 denotes a homogeneous landscape. 20 replicates were run for each value of *P*, and bars indicate the standard error for each mean. Statistics for each landscape (Moran's *I*, mean resource value, minimum, maximum, and standard deviation) are listed. Values of *I* nearer to 1 indicate a more heterogeneous landscape.

(a)

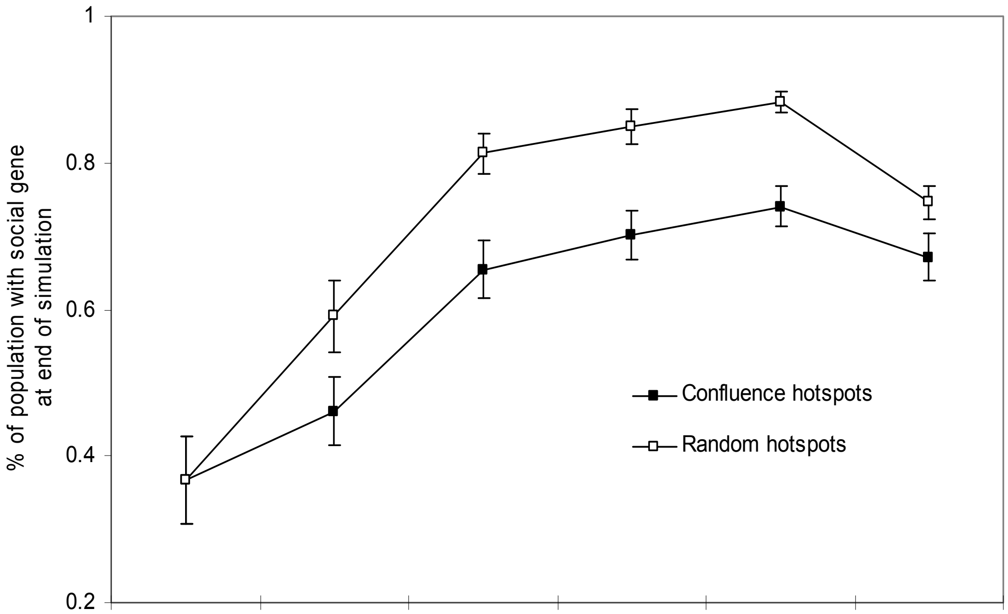


	P	0	1	4	16	32	64
Confluence hotspots:	Moran's *I*	0.00	0.98	0.98	0.96	0.90	0.72
	Mean value	100	100	100	100	100	100
	Minimum	100	40	40	40	40	40
	Maximum	100	118	130	199	313	595
	SD	0.00	17.16	23.08	44.41	66.68	109.88

	P	0	1	4	16	32	64
Random hotspots:	Moran's *I*	0.00	0.91	0.91	0.89	0.83	0.66
	Mean value	100	100	100	100	100	100
	Minimum	100	40	40	40	40	40
	Maximum	100	122	127	162	235	458
	SD	0.00	13.59	15.65	26.41	43.20	81.30

Figure 7 continued.

(b)



	P	0	1	4	16	32	64
Confluence hotspots:	Moran's *I*	0.00	0.98	0.98	0.96	0.90	0.67
	Mean value	160	160	160	160	160	160
	Minimum	160	140	140	140	140	140
	Maximum	160	166	171	193	231	330
	SD	0.00	5.76	7.96	14.79	22.27	37.56

	P	0	1	4	16	32	64
Random hotspots:	Moran's *I*	0.00	0.91	0.91	0.89	0.83	0.65
	Mean value	160	160	160	160	160	160
	Minimum	160	140	140	140	140	140
	Maximum	160	168	170	181	205	280
	SD	0.00	4.60	5.32	8.97	14.41	27.27

Cases of coexistence between the two territorial strategies are found in all the types of modeled landscapes: homogeneous and heterogeneous, low and high average resource value, as well as confluence and random distributions of hotspots. Figures 8-11 illustrate the observed patterns of coexistence for homogeneous, low value confluence, and high value confluence landscapes. Coexistence is often associated with resource or habitat partitioning (Schoener 1976, Rosenzweig 1981, Ritchie 2002), yet here we find that coexistence is largely driven by the trade-offs of the alternative territorial strategies and it is not dependent upon heterogeneity. Social groups succeed by gaining control of the high value areas, while solitary individuals are successful in the low value homogeneous areas and benefit from higher dispersal rates by quickly filling any openings in landscape.

Figure 8. Visual output for homogeneous landscape of value 160, in which solitary and social strategies coexist. Territories held by solitaries are shown in blue with horizontal hatching. Territories held by social groups are shown in red with diagonal hatching.

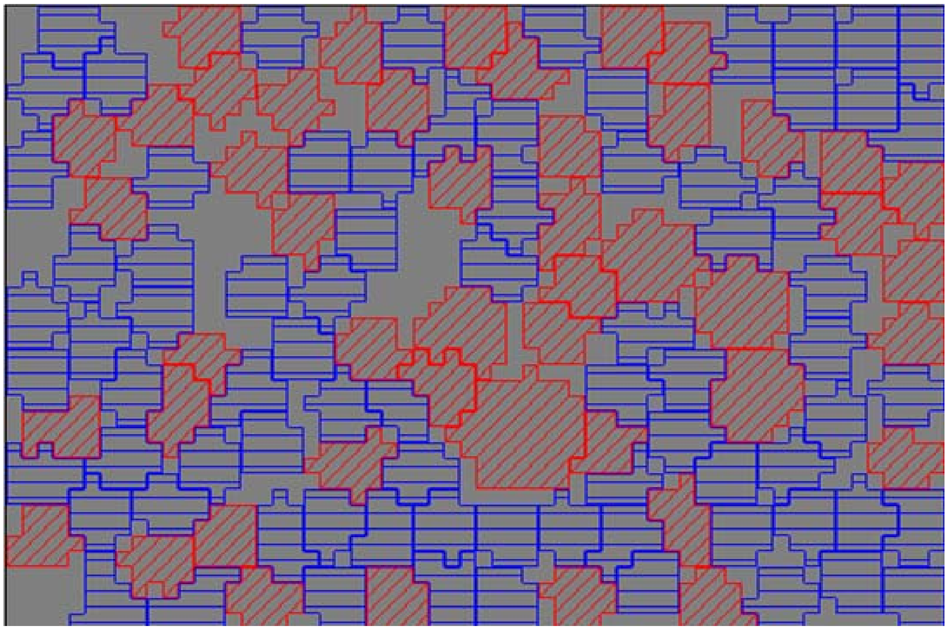


Figure 9. Visual output for heterogeneous confluence landscape with a low average resource value and moderately peaked hotspots (mean=100 and *P*=4), in which solitary and social strategies coexist. Territories held by solitaries are shown in blue with horizontal hatching. Territories held by social groups are shown in red with diagonal hatching.

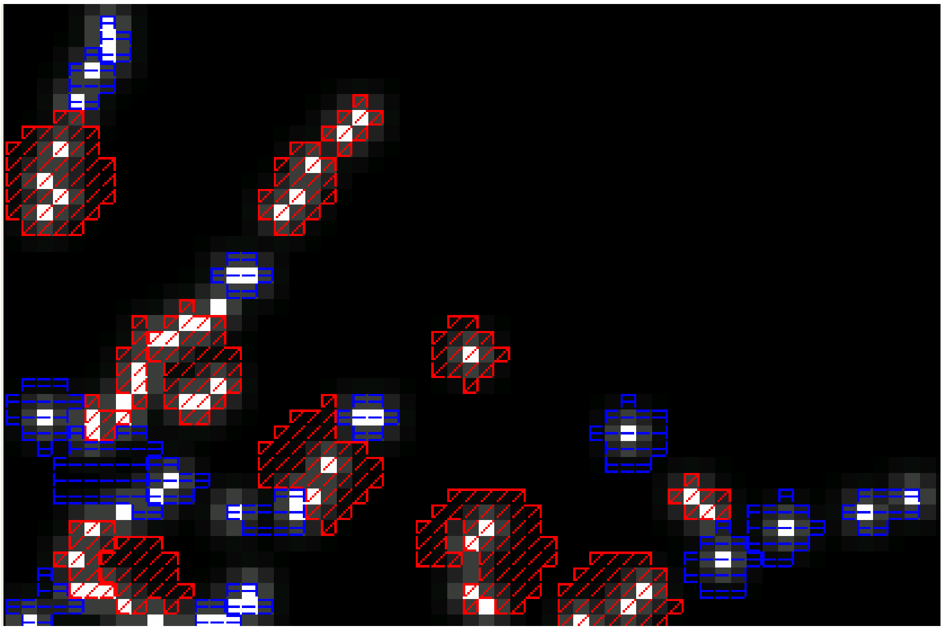


Figure 10. Visual output for heterogeneous confluence landscape with a high average resource value and highly peaked hotspots (mean=160 and *P*=64), in which solitary and social strategies coexist. Territories held by solitaries are shown in blue with horizontal hatching. Territories held by social groups are shown in red with diagonal hatching.

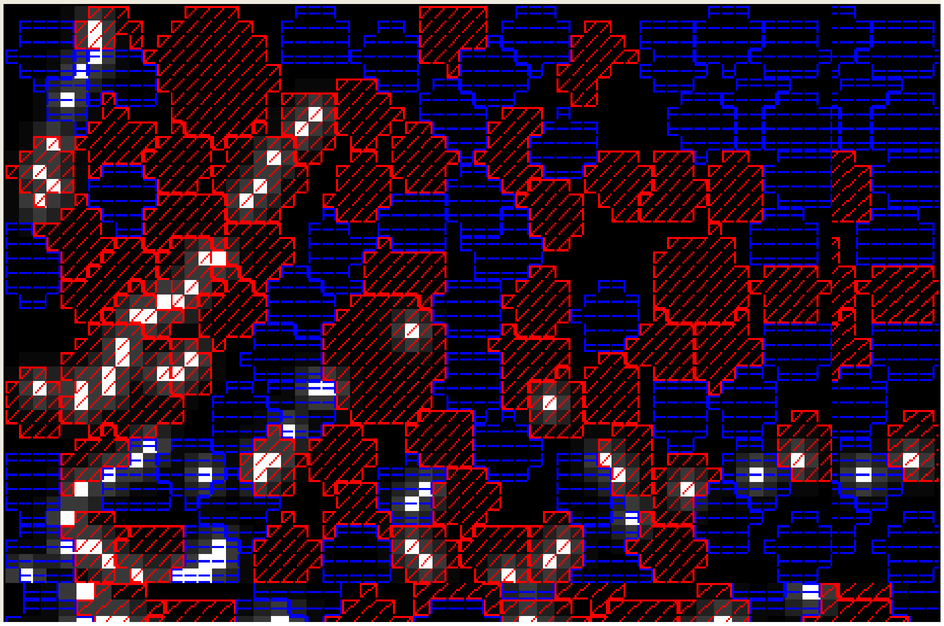
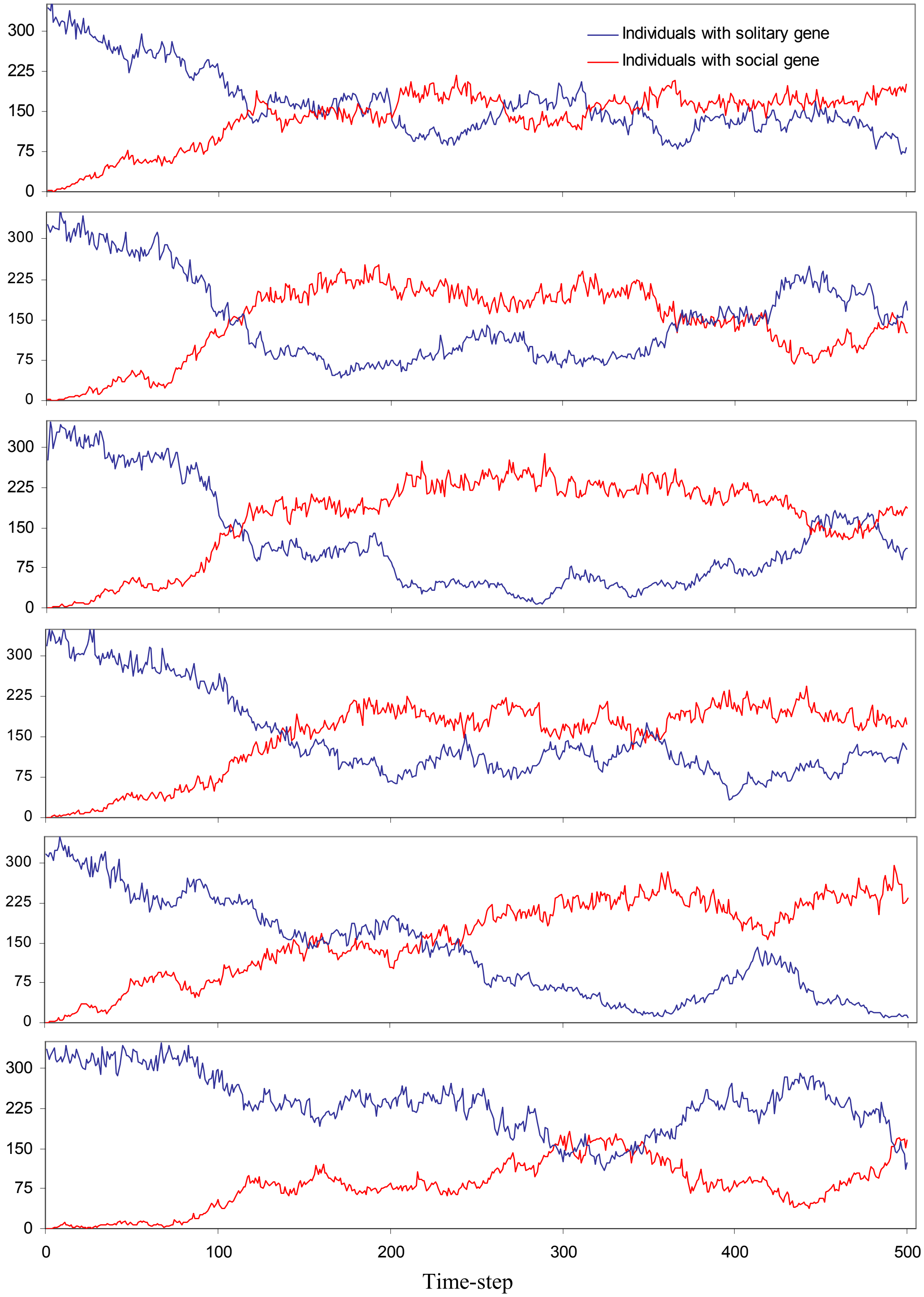


Figure 11. Six representative simulations illustrating the coexistence of solitary and social strategies in a heterogeneous confluence landscape of high average resource value and highly peaked hotspots (mean=160 and *P*=64). The number of solitary individuals is indicated by the blue line and the number of social individuals by the red line.



The model supports the theoretical prediction that heterogeneity per se is inadequate to account for the evolution of sociality. Group territoriality requires a distinct group advantage, and, although heterogeneity facilitates the formation of groups, obligate sociality is unlikely to evolve by virtue of landscape structure alone. Without an advantage to grouping, individuals with the social gene do poorly and can not invade a population of solitary territory holders. This is true in both the low and high value landscapes (Fig. 12).

The results highlight cooperative territorial defense as the most important group advantage. In the low value heterogeneous landscapes (Fig. 12a) with highly peaked hotspots, a defensive advantage alone confers a significant benefit to social groups, while the other advantages confer little to no competitive edge. When two group advantages are included, social groups do best if one is the defensive advantage. These patterns are also found for the high average value landscapes (Fig. 12b), though the boost a defensive advantage affords to social groups is not nearly as pronounced. With this result, we meet the empirical evidence (e.g. regarding group-territoriality in humans, chimpanzees, and lions) with a theoretical confirmation; balance of power and a need for cooperative defense of shared territory is the central element in the evolution of group territoriality.

We find strong patterns of synergy (Corning 2002) when we include two or more group advantages in the model. For example, in the high value landscapes (Fig. 12b), the inclusion of both cooperative defense and territorial inheritance results in social individuals representing a larger proportion of the population than would be predicted based upon the effects of these advantages considered in isolation. In retrospect, these combined effects are understandable: a defensive advantage allows social groups to gain access to the best locations and territorial inheritance ensures that these hard-won gains are enjoyed by the future generations. Synergy is also evident in nearly all the simulations that include all three group advantages. This pattern is particularly strong for the high value landscapes, where sociality emerges as the predominant strategy in the population only when we model the full group advantage.

Figure 12. Percent of individuals in the population carrying the social gene at the end of simulation vs. group-territorial advantages, for a) low average value landscapes and b) high average value landscapes. We consider all eight configurations for presence or absence of each potential group advantage, as indicated below the graph. Simulations were run for five types of landscapes: homogeneous, confluence heterogeneous with *P*=4, confluence heterogeneous with *P*=64, random heterogeneous with *P*=4, and random heterogeneous with *P*=64. We ran 20 replicates for each and bars indicate standard errors for each mean. We examine the effects of including group advantages by comparing the outcome of the simulation that incorporates the advantage(s) to the outcome of the simulation with no advantages (those on the far left). Simulations with a significant positive effect on the % of social individuals in the population are indicated with stars (one tailed t-test; $*$: $p<0.05$, $**$: $p<0.01$, $***$: $p<0.001$). We also consider synergistic effects for combinations of two or more group advantages: S = additive and multiplicative synergy, where the outcome can not be predicted based upon either the additive or multiplicative combinations of the isolated effects of the each advantage; S_a = additive synergy, where the outcome can be predicted based upon the multiplicative effect of the each isolated advantage, but can not be predicted based upon the additive combination of the effects of each isolated advantage.

(a)

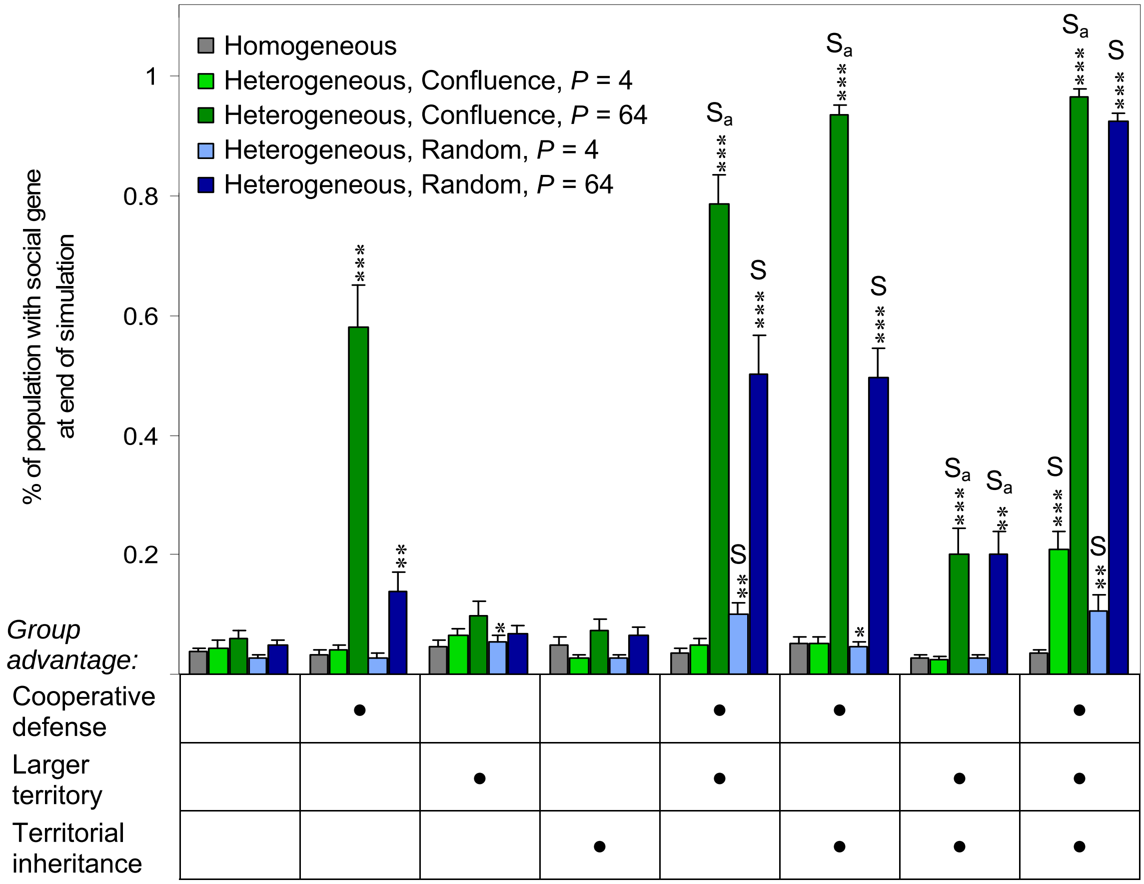
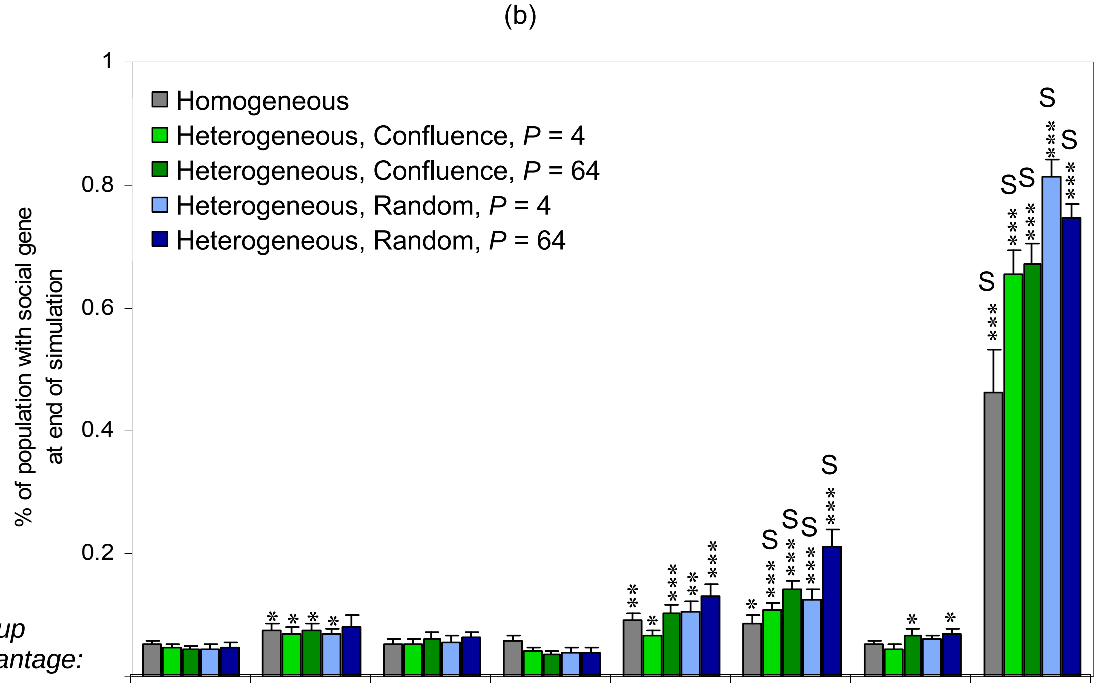


Figure 12 continued.



Group advantage:								
Cooperative defense		●			●	●		●
Larger territory			●		●		●	●
Territorial inheritance				●		●	●	●

The low value landscapes provide one example of low population density (see Fig. 9), but usable portions of these landscapes are saturated and individuals still experience a high degree of competition. As a result, social groups are successful in these low density competitive environments. We also examine the effects of holding population density at a low level in high value landscapes, resulting in an unsaturated habitat, and find that social individuals are less successful in these environments (Fig. 13a). Increasing the mutation rate does have an effect, but the success of the social strategy is still significantly lower in the low density heterogeneous landscapes. In an unsaturated landscape, social groups do not benefit from the potential group advantages. For example, groups have fewer neighbors and fights are much less frequent (Fig. 13b), thus any defensive advantage is not realized. Evidence from humans (Ember 1982) and lions (Heinsohn 1997) confirms that conflict between territorial groups is less intense at lower population densities. Also, there is no hindrance to growing a larger territory and little relative benefit to territorial inheritance when open space in plentiful. Based upon these results, we expect that group-territoriality would be more likely to evolve when animals live at high densities, and lions, within the broader context of felid species, provide one example that supports this prediction (Packer 1986).

Overall, the rates of intergroup fighting are low, less than one fight per group per time-step, but we do find a significant effect of landscape structure, as intergroup conflict is higher in the most heterogeneous landscapes (Fig. 14). Accordingly, the proportion of adult deaths due to fights also follows this pattern. As expected, an uneven distribution of resources and variation in the landscape, where the patch in your neighbor's territory may be better than your own, leads to an increase in conflict. Rates of intergroup fighting, however, decline in landscapes with the most peaked hotspots ($P \geq 32$), to levels at or below that in homogeneous landscapes. These landscapes have larger homogeneous patches, fewer groups, and the high value hotspots leads to groups defending small territories that are isolated from contact with other groups.

Figure 13. The effect of population density on the evolution of group territoriality. At high density a population includes about 300 individuals, and at low density about 100 individuals. Landscapes have a high average resource value of 160 and, in the heterogeneous landscapes, moderate peaked-ness (*P*=4). For low population densities we used four rates of mutation, as listed below the graph. a) Percent of individuals in population carrying the social gene at end of simulation vs. population density and mutation rate. b) Fights per group vs. population density and mutation rate.

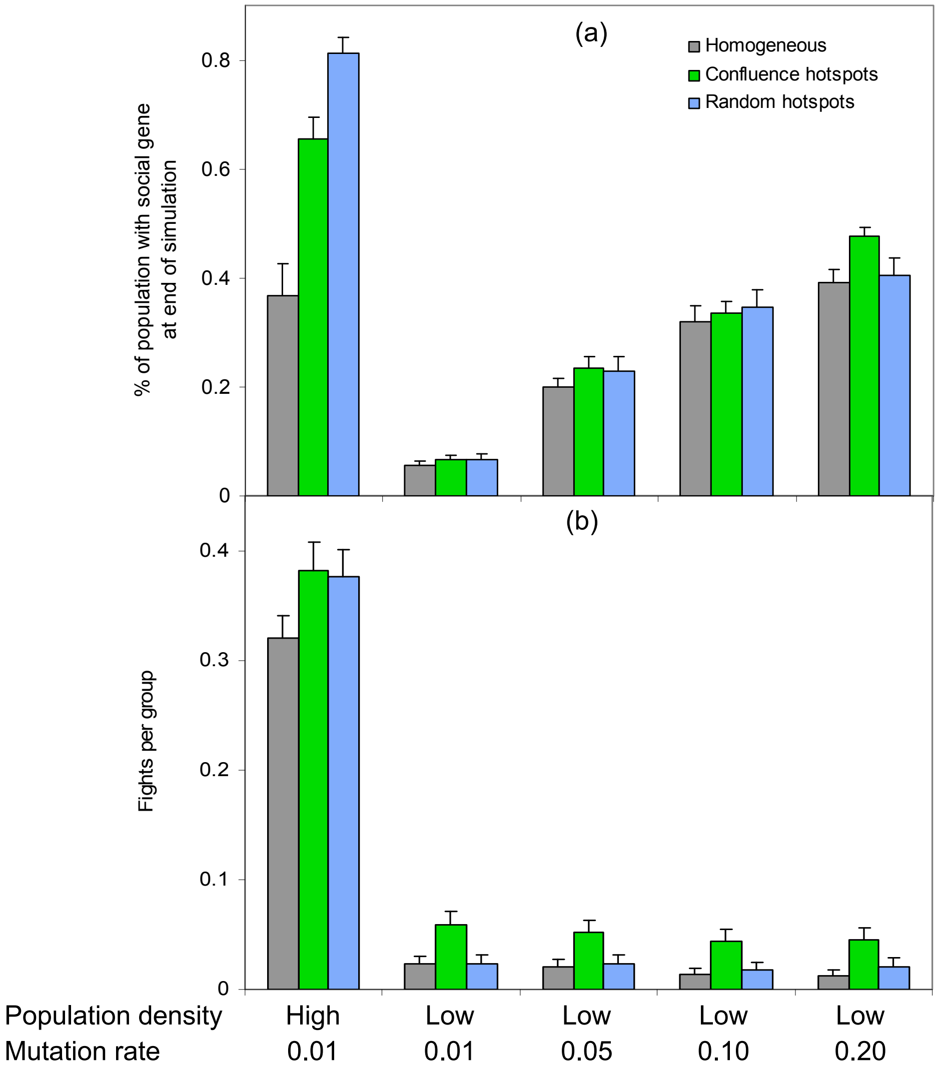
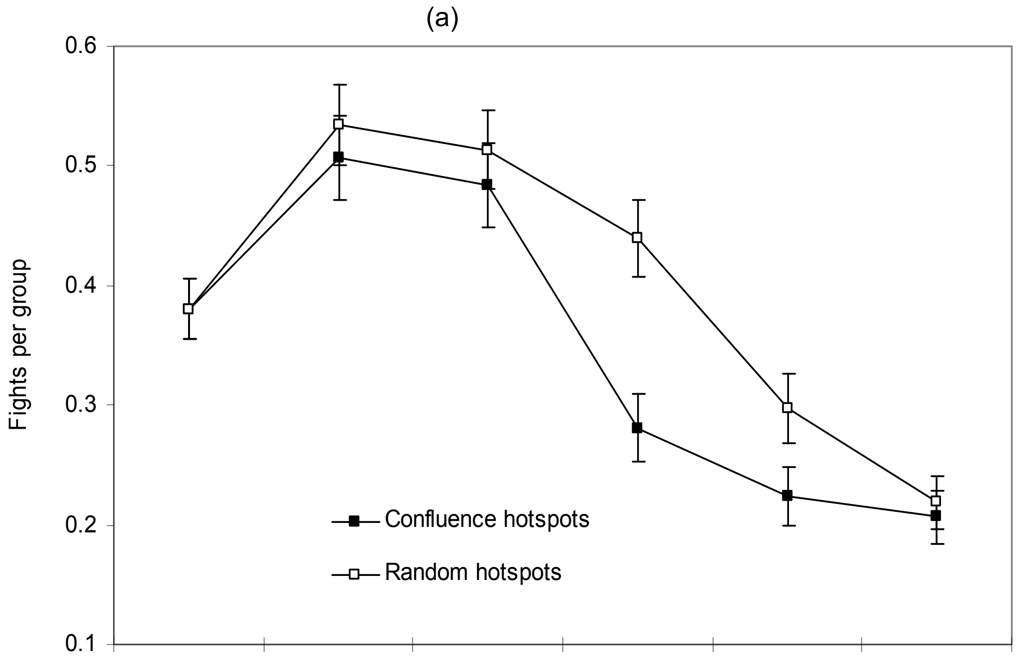


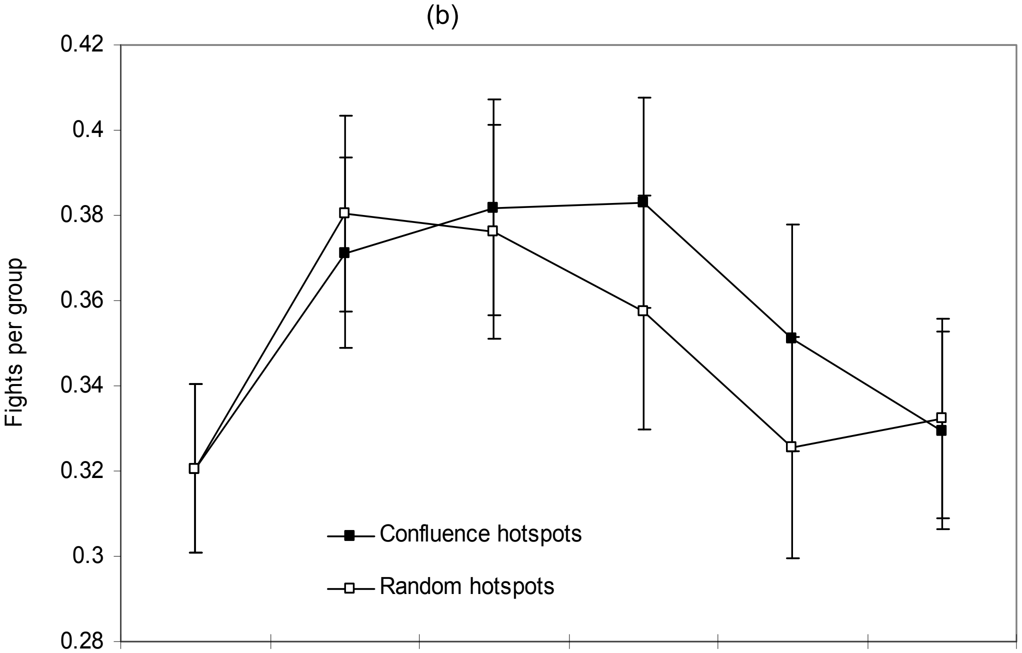
Figure 14. Number of territorial fights per groups vs. peaked-ness (*P*), for landscapes with confluence and random distributions of hotspots, and a) low average resource values or b) high average resource values. 20 replicates were run for each simulation and bars indicate standard error for each mean. Statistics for each landscape are listed (Moran's I, average percent of individuals with social gene at end of simulation, and average population size).



	P	0	1	4	16	32	64
Confluence hotspots:	Moran's *I*	0.00	0.98	0.98	0.96	0.90	0.72
	% social	3%	11%	21%	81%	92%	97%
	Pop. size	139	128	126	113	119	131
	# groups	65	61	57	42	41	40

	P	0	1	4	16	32	64
Random hotspots:	Moran's *I*	0.00	0.91	0.91	0.89	0.83	0.66
	% social	3%	9%	11%	29%	67%	93%
	Pop. size	139	124	124	125	118	138
	# groups	65	58	56	56	49	50

Figure 14 continued.



	P	0	1	4	16	32	64
Confluence hotspots:	Moran's *I*	0.00	0.98	0.98	0.96	0.90	0.67
	% social	37%	46%	65%	70%	74%	67%
	Pop. size	318	316	300	297	281	284
	# groups	138	133	121	110	103	104

	P	0	1	4	16	32	64
Random hotspots:	Moran's *I*	0.00	0.91	0.91	0.89	0.83	0.65
	% social	37%	59%	81%	85%	88%	75%
	Pop. size	318	312	299	282	277	281
	# groups	138	125	110	101	96	100

Territorial behavior is influenced by landscape structure and is associated with conspecifics aggression; both these elements have a strong impact on the evolution of group-territoriality. Social territorial groups are more likely to evolve in saturated heterogeneous landscapes, which create an environment of intense competition for sparse resources, and numerical advantage in aggressive territorial interactions is the most important group advantage. Social individuals were very successful in the low value landscapes with highly peaked, high value hotspots contrasting with areas unusable due to their low value (Figs. 7&9), a landscape that closely resembles that of the Serengeti savanna.

The evolution of social behavior is idiosyncratic, resulting from the interaction between phylogenetic inertia and ecological pressures (Wilson 1975). An animal's phylogenetic legacy has a strong impact on its future path of evolution, and whether or not a species evolves towards group-territorial behavior depends upon several preexisting conditions. Phylogenetic analysis suggests that, within the order Carnivora, the evolutionary pathway to group territoriality has been via a solitary territorial species (Kruuk 1989). There must also be a behavioral predisposition for tolerance of some conspecifics (most likely kin) and intolerance of others, a flexible dispersal pattern, and certainly the potential for cooperative territorial defense. Group-territoriality occurs in animals without complex cognitive abilities (e.g. ants and fish), thus intelligence does not appear to a prerequisite for this form of sociality. Group-territorial competition, however, is often related to the evolution of human intelligence (Flinna et al. 2005). Finally, group territoriality can only evolve in species in which resource requirements do not constrain the formation of social groups, and some animals may rely upon a limited resource, such as a nesting hole or den, which cannot be shared so do not permit the formation of social groups.

Group territoriality evolves in a relatively narrow range of ecological conditions that, as we saw in chapter 2, balance the pressures of intra-group versus inter-group competition. The benefits of group-territoriality are only reaped in a highly a competitive environment where inter-group competition is intense, yet the pattern of resource distribution must provide areas of high enough value that intra-group competition does not curtail the formation of social groups. Thus low value homogenous landscapes, though competitive, do not lead to the evolution of sociality. Group-territorial animals benefit from territorial inheritance, but this can only be achieved if the environment is spatially predictable, so the evolution of group territoriality likely depends on a distribution of resources that is relatively fixed in space over time. Group-territorial animals also benefit from the ability to form a larger territory, which allows a social group to overcome the costs of intra-group competition. But, again, this benefit can depend upon the distribution of resources, and a larger territory is beneficial if high value patches are clustered. Thus group territoriality may be more likely to evolve in landscapes that exhibit power-law cluster patterns, such as the drainage network of confluences used in this model, or the vegetation patterns observed in southern Africa (Scanlon et al. 2007).

Although group territoriality does occur in a broad range of animal taxa, it is also relatively rare, owing to the many conditions that must be present to allow for its evolution. Yet when these conditions do converge, each quite simple in their own respect, the result is a remarkable and powerful emergent behavior. Group territoriality has emerged in many species of high conservation value (e.g. wolves, lions, and chimpanzees), as well as in ourselves. Understanding the basis of group territoriality, and especially its tie to the landscape, allows us to make informed management decisions, as changes in landscape structure directly influence population dynamics (Packer et al. 2005), and are likely to affect patterns of inter-group conflict and mortality. An inquiry into the evolution of group-territorial behavior also provides us with, at the very least, a view into our own nature and motivations, and, at the very best, tools for reducing human conflict. We are far from the first to urge the same:

> *On the one hand he is a social primate; on the other, he has developed similarities to wolves, lions and hyenas. In our present context one thing seems to stand out clearly, a conclusion that seems to me of paramount importance to all of us, and yet has not been fully accepted as such. As a social, hunting primate, man must originally have been organized on the principle of group territories.(Tinbergen 1968)*

> *[Territorial behavior is] a force shaping our lives in countless unexpected ways, threatening our existence only to the degree that we fail to understand it. (Ardrey 1966)*

CONCLUSION

This thesis research has determined the primary landscape feature that defines real estate value for Serengeti lions (river confluences), has confirmed that the advantages of group-territorial defense provided the basis for the evolution of lion sociality. Simulation modeling also suggested that group territoriality is most likely to evolve in heterogeneous landscapes and that it requires cooperative territorial defense. This research also leaves several questions unanswered and opens new lines of potential inquiry.

The conclusions drawn from the first chapter, in particular, ought to be tested for their external validity. Are the parameters of lion habitat quality similar in other locations? Similar analyses, to date, are on a much larger scale and unfortunately there are few datasets that can provide the same level of detail. But as a part of my research I have laid the foundation for such comparative work, through collaboration with researchers working in the Kruger National Park and other small reserves in South Africa.

An area of research not well developed, due largely to feasibility, relates to the mechanics of territorial defense, scent marking in particular. How are territorial borders established and how do they shift with time? Are territory borders influenced by both natural and anthropogenic influences? Detailed analyses of such questions likely await the development of new research tools.

An additional potential advantage to grouping in lions relates to the renewal rates of prey. The short-term temporal patterns of prey moving in response to predators may place constraints on the grouping patterns of lions. Slow renewal rates may add a benefit to grouping, as scattered individual lions could scatter prey out of their territory. High prey renewal rates, however, may remove this cost to sub-group formation. It is not known if prey movement patterns affect the fission-fusion grouping patterns of lions. As a part of my thesis research, I did begin to collect data on this topic, but after six months of data collect it became clear that addressing this question properly could be a thesis project in and on itself. I was able to preliminarily conclude that prey movement in open grasslands was only minimally related to the location of predators, as the prey can easily see the predators in that habitat, but it is certainly possible that prey renewal rates may influence grouping patterns in more closed woodland or mosaic habitat.

The role of males in territorial competition, as stated, was unexpected. The analyses in this thesis are from the point of view of female lions (e.g. female reproductive success and female mortality). Although a similar analysis from the point of view of males would be of value in its own right, in light of these new results relating to males, there are several additional interesting questions. One in particular: What determines whether a male mates with or attacks a neighboring female? More general questions include: How do male lions view the savanna landscape, and does this incorporate the distribution of females as well as landscape features? Could this question be untangled? What determines the patterns of coalition residency in multiple prides and how does this impact female inter-group territorial competition?

And finally, what might be the impact of disease on group territorial competition? In 1994, there was an outbreak of canine distemper virus (see Fig. 2a in the introduction), which resulted in the death of a third of the population. This outbreak impacted some prides more than others, and may have led to the extinction of some prides (the Masai pride, for example). Through spatial variation in mortality patterns, disease outbreaks may severely alter the territorial status quo, and may essentially precipitate a regime change in pride dominance status. Group-territorial competition may also exacerbate the effects of a disease die-off. Thus an analysis of the role of disease in a group-territorial population is not only of intellectual interest in terms of further understanding the dynamics of group territoriality, but it may be of importance in predicting a population’s response to the threat of disease.

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