LETTER

Serengeti real estate: density vs. fitness-based indicators of lion habitat quality

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Abstract

Habitat quality is typically inferred by assuming a direct relationship between consumer density and resource abundance, although it has been suggested that consumer fitness may be a more accurate measure of habitat quality. We examined density vs. fitness-based measures of habitat quality for lions in the Serengeti National Park, Tanzania. A 40-year average of female reproductive success (yearling cubs per female) was best explained by proximity to river confluences, whereas patterns of productivity (yearling cubs per km^2) and adult female density (individuals per km^2) were associated with more general measures of habitat quality and areas of shelter in poor habitat. This suggests that density may not accurately distinguish between high-quality 'source' areas and low-quality sites that merely provide refuges for effectively non-reproductive individuals. Our results indicate that density may be a misleading indicator of real estate value, particularly for populations that do not conform to an ideal free distribution.

Keywords

Habitat selection, ideal despotic distribution, ideal free distribution, landscape, lions, resource selection, scale, Serengeti National Park, source–sink dynamics.

INTRODUCTION

Common methods of estimating habitat quality, such as habitat suitability indices (U.S. Fish and Wildlife Service 1981) and resource selection functions (e.g. Boyce & McDonald 1999), use measurements of consumer distribution and abundance, assuming a direct relationship between consumer density and resource abundance or habitat quality. Although density-based assessment of habitat quality can be accurate (Bock & Jones 2004), the accuracy and predictive utility of this method has been questioned. Whether stated or not, such density-based methods assume a classic ideal free distribution (Fretwell & Lucas 1969) and habitat matching (Pulliam & Caraco 1984), but there are a number of reasons why such distributions are not reached (Van-Horne 1983; Tregenza 1995) and empirical evidence shows that undermatching is widespread (Kennedy & Gray 1993). Several authors have therefore recommended the use of demographic parameters rather than density (VanHorne 1983; Murphy & Noon 1991; Hall *et al.* 1997), because demographic measures should better identify causal factors necessary for the long-term persistence of a population.

Territorial animals are expected to fit an ideal despotic distribution (Fretwell & Lucas 1969), in which competitively superior individuals exclude conspecifics from high quality habitat. This distribution predicts that patterns of individual reproductive rates will reflect variation in resource abundance and habitat quality, but makes no precise predictions of how density will vary across the landscape. Source–sink dynamics (Pulliam & Danielson 1991) can result from a despotic distribution, and under such conditions only demographic parameters can reliably reveal the sources, while distribution patterns may correlate with a set of parameters that merely support short-term local persistence but not necessarily reproduction.

We compared density- and fitness-based measures of habitat quality and developed a method of analysis with a distinct landscape perspective. This method was also applied to individual reproductive success, rather than taking an individual-based approach typical of analyses considering fitness, and our analysis, therefore, does not consider fitness in a strict Darwinian sense. The unit of our analysis is a location in the landscape (a grid cell), rather than individuals

or their territories (cf. Breininger *et al.* 1985; Kerbiriou *et al.* 2006). This method shares similarities with spatial epidemiology (Elliott & Wartenberg 2004) and analysis of real estate values (e.g. Geoghegan *et al.* 1997). The grid-cell method facilitates comparison with density patterns, averages out individual variation and stochasticity, and allows for patterns to be mapped at any spatial or temporal scale within the limits of the available data. We determined 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 map of averaged reproductive real estate.

We applied this method of analysis to 40-years of continuous data on lions (*Panthera leo*) in the Serengeti National Park, Tanzania. The territorial patterns of Serengeti lions are consistent with a density-dependent despotic distribution; larger prides out-compete smaller prides for high quality habitat (they are the despots) and the degree of despotism decreases with increasing population density (greater territory overlap with increasing population density) (Mosser 2008). We therefore expected both fitness and population density to be higher in better quality habitat, based on landscape characteristics, but that density patterns would further reflect a pattern of overuse of poorer habitats. 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 density, fitness and habitat quality at the scale that individual lions use the landscape – the scale most relevant to testing the predictions of Fretwell & Lucas (1969) and Pulliam & Danielson (1991).

We mapped the fine-scale patterns of adult female density (individuals per km^2), cub productivity (yearling cubs per km^2) and female reproductive success (yearling cubs per female) over both short and long time-scales. Productivity was chosen as a measure akin to biomass in studies of vegetation, which can be estimated more easily than reproductive success for most populations. Each of these measures was examined separately for associations with six landscape variables that were expected to be important components of habitat quality. The long-term pattern of reproductive success confirmed a system of source–sink dynamics. Adult female density and cub productivity were also greater in higher quality habitat. For long time-scales, all three variables identified river confluences as an important landscape feature. Density and productivity, however, also identified additional influential landscape factors associated with sink refuges and failed to precisely isolate the characteristics of source areas. However, at shorter (from 2- to 10-year) time intervals, reproductive rates were sufficiently noisy that local productivity and density

provided a better measure of habitat quality if longer term estimates are not available or feasible.

MATERIAL AND METHODS

Study area

The Serengeti study area (Fig. 1), located at the centre 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 most heavily concentrated along rivers (Herlocker 1975) and kopjes (rocky inselbergs) are dispersed throughout the study area. The study area does not directly border areas of dense human settlement.

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 during the transition between seasons. 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 & Bygott 1979; Packer *et al.* 2005). The woodland lions have been monitored continuously over this entire period, but the plains lions were not studied from November 1969 until October 1974. The size of the study population has ranged between roughly 50 and 300 known individuals living in 5–30 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 2 weeks. All observations include date, time, spatial coordinates based on GPS readings, pride membership, group composition, individual identification, prey consumed and reproductive status and behaviour. Demographic records for the population (individual birth, death and pride
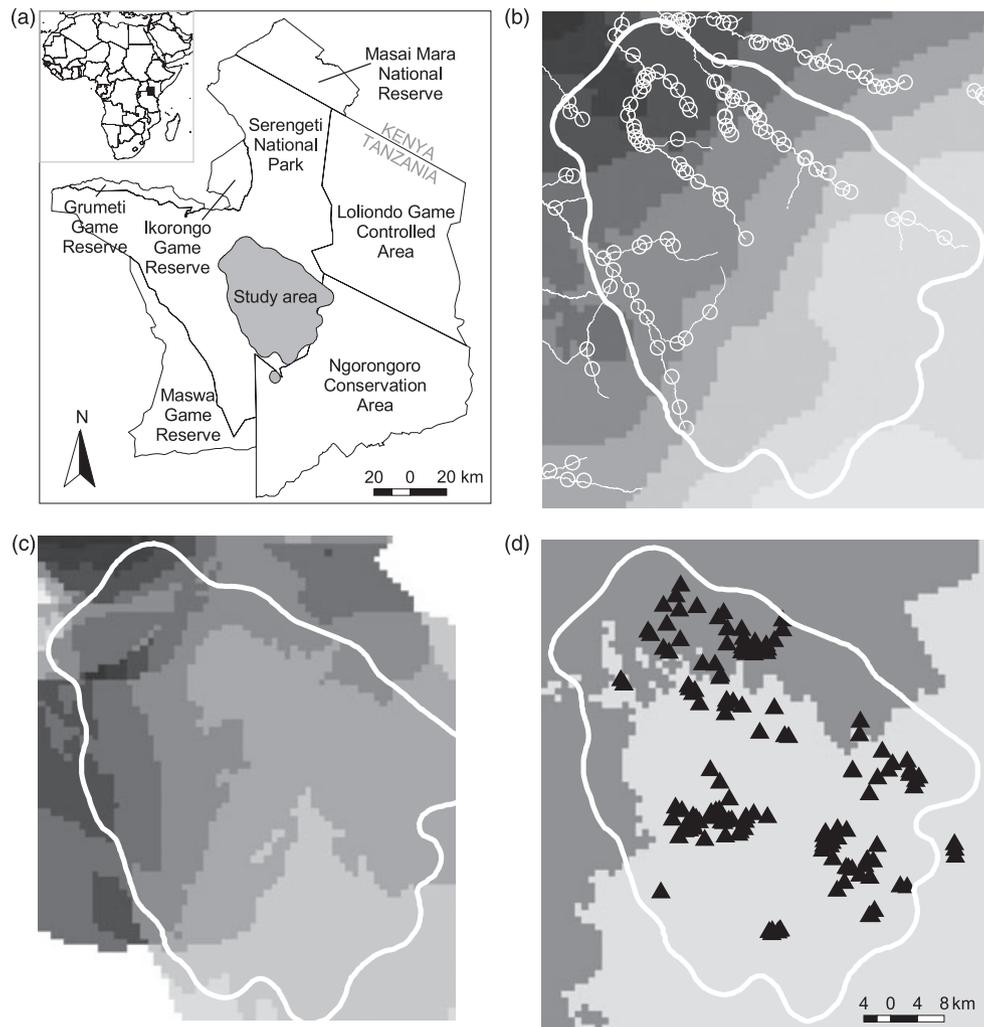
Figure 1 (a) Serengeti–Mara ecosystem, located in east Africa (inset), spans the border between Tanzania and Kenya. The lion study area (grey) is determined by the ranges of the current 26 study prides. The study area is outlined in white in B, C and D. (b) Average dry season rainfall ranging from 94 to 232 mm (light to dark shading), main rivers (white lines) and confluences (white circles). (c) Prey herd density, ranging from 0.4 to 2.4 herds per km^2 (light to dark shading). (d) Woodlands (dark grey), plains (light grey) and kopjes (black triangles).

immigration/emigration dates) were maintained on an ongoing basis.

Mapping measures of habitat quality

Adult female density, cub productivity and reproductive success were calculated for each pride at 2-year intervals. Two years is the average interbirth interval as well as the average tenure length for resident males (Packer *et al.* 1988), and 2-year periods increased the sample size per time-step. Time-steps begin in November (the start of wet season) and are labelled for the years that comprise the majority of the time-step (e.g. from November 1966 to October 1968 was labelled as '1967–1968'). Time-steps do not overlap. 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. The number of cubs reaching 1 year of age within each time-step was totalled for each pride. 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. Cub productivity was calculated in the same manner (total cubs km^{-2}) and thus was a measure the density of cubs supported by each pride's territory. Per capita reproductive success was defined as the total number of cubs divided by the average number of adult females in the pride over the same 2-year period. There is little within-pride variation in female reproductive success (Packer *et al.* 2001) and individual ranging patterns, so this variable was analysed at the level of the pride rather than for specific individuals.

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). Adult mortality primarily results from density independent disease (Packer *et al.* 1999; Kissui & Packer 2004) and intraspecific aggression (Packer *et al.* 1988; Mosser & Packer 2009). Cub productivity was chosen as a potential measure of landscape value from a population level perspective. Reproductive success was chosen as the best proxy for individual female fitness.

The lion ranging data included records on 44 prides and 1190 adult female lions collected from November 1966 to October 2006. 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 2003–2004 overlapped by an average of 75%). Territory boundaries were determined from utilization–distribution curves calculated from the lion sightings (ArcView GIS 3.2, Environmental Systems Research Institute, Redlands, CA, USA), using a fixed kernel with a smoothing parameter (*h*) of 3000 m, roughly the mean distance moved by a lion each day plus 1 SD. Due to the potential sensitivity of kernel density estimates to sample size (Harris *et al.* 1990), 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 (by incorporating short forays from a territory) while smaller 50% kernels are more sensitive to sampling bias and can incorrectly identify the location used. The average 75% kernel territory size was 62 km^2 (62 grid cells), ranging from 15 to 219 km^2, with the larger territories located in open grassland habitat. Territory maps were converted to grid maps with a cell size of 1 × 1 km.

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 (six 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 territory estimates.

Each pride's 2-year density, cub productivity or 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 single overall map for each time-step. In areas of territory overlap values were averaged. For reproductive success, the average was weighted by the number of adult females in the respective prides. The merged short-term maps contained 69–1239 grid cells. We controlled for interannual sources of variation in cub productivity and reproductive success by scaling the values from 0 to 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 lion density, resource density, or other ecological features over time were minimized. Absolute measures, however, were used in the initial analysis of source–sink dynamics.

To construct a single 40-year long-term picture of lion real estate values, all twenty 2-year time step maps were overlaid, and average values were calculated for each grid square (again weighting by the number of females for reproductive success). Grid cells were excluded from the final map if fewer than three 2-year maps contributed to the overall average, to remove the effect of extreme values in a single year producing outliers in the final map. The long-term map contained 1443 grid cells. Note that all maps are left-truncated, because we did not quantify the value of grid cells that fell outside estimated pride home ranges and are probably of the lowest value.

Source–sink dynamics

To determine source and sink areas, average 2-year reproductive success and exponential population growth rates [ln(N_{t+1}/N_t)] were used to determined the reproductive success value above which the growth rate would be expected to be positive. Data were from 1975 to 2004, as the full population was not consistently monitored until 1975. The regression of population growth vs. reproductive success ($y = -0.1907 + 0.2589x$, $F_{1,14} = 6.48$, $P = 0.026$, $R^2 = 0.35$; Fig. S1) suggests that population growth would be positive above a reproductive success rate of 0.74 yearling cubs per female. Areas with average long-term reproductive success > 0.74 were thus designated as 'sources'.

Landscape variables

Distance to river, confluences, kopjes and tree cover
For these discrete landscape features, grid cell values equalled the distance (km) of that cell's centroid to the nearest landscape feature of a particular type. The tree cover map was a simplified version of a map created by Herlocker (1975), and designated two vegetation types: areas with greater than or <2% canopy cover (i.e. woodland and plains). 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 environment experienced by lions over the full time-span.

Herd density

Prey distribution was estimated from monthly herbivore counts collected in the dry seasons of (July–October) of 2004–2008. Observers drove a predetermined 404 km track every month and counted all large mammals < 100 m from the vehicle. Only the most common lion prey species (as listed above) were included here. We used herd density (herds km^{-2}), rather than total prey density (animals km^{-2}), as this more accurately reflects the availability of prey for lions (Fryxell *et al.* 2007). Monthly maps of herd density were created via Kriging interpolation based on counts totalled within hexagonal regions of roughly 100 km^2 (interpolation parameters were based on a Gaussian semivariogram of the data). These distributions were then averaged over all dry season months across all 5 years. This prey distribution only represents five seasons, thus we have also included dry season rainfall (described below) as a additional (surrogate) measure of prey abundance because of the impact of dry season precipitation on herbivore migratory patterns (Hanby & Bygott 1979).

Rainfall

Dry season rainfall maps (total mm rainfall, June–October) were generated through spatial interpolation of data collected from rain gauges located across the ecosystem, using regression interpolation based upon elevation (Coughenour 1992). Maps were then averaged within each 2-year period and over a 38-year time span. Data were not available for the last time-step, thus 2-year analyses involving this variable included only the first nineteen maps (1966–2004).

All landscape maps were projected into UTM (Universal Transverse Mercator) coordinates (zone 36S, datum Clarke 1880) and the scale of analysis was limited by the data set with the coarsest resolution (rainfall maps at 1 × 1 km).

Statistical analysis

Statistical relationships between habitat quality variables and landscape variables were analysed using linear mixed models (PROC MIXED, SAS 9.1; SAS Institute Inc., Cary, NC, USA; Littell *et al.* 2002). Spatial structure was built into each 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 the underlying biological process (i.e. pride territories covering 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 each habitat

quality measure were modelled as a function of 24 *a priori* candidate models: a null model (intercept only), six univariate models and 17 multivariate models of all variables combinations excluding combinations of highly correlated variables (Table S1; distance to rivers, confluences and tree cover; prey density and rainfall). Akaike Information Criterion (AIC) values were used to evaluate the fit of the alternative models (Burnham & Anderson 2002). For a set of candidate models, information-theoretic weights (ω) were calculated from the ΔAIC values, comparing each model to the model with the lowest (worst) AIC value. The model with the highest weight was interpreted as providing the best fit to the data, although models with very similar weights (ΔAIC values of < 2) were also considered as plausible models. We expected each dependent variable to be negatively correlated with distance to rivers, confluences,

Table 1 Analysis of short-term (2-year) adult female density, cub productivity and reproductive success with respect to each landscape variable

Model	Min. ω	Max. ω	Mean ω	SD ω	+/−
Female density					
Null	0.000	0.288	0.041	0.073	
Distriv	0.000	0.677	0.127	0.194	1/19
Distcon	0.000	0.901	0.221	0.288	0/20
Disttree	0.000	0.723	0.096	0.166	3/17
Distkpj	0.000	0.958	0.107	0.242	7/13
Prey	0.000	0.367	0.026	0.082	14/6
Rain	0.000	1.000	0.402	0.408	17/3
Cub productivity					
Null	0.000	0.222	0.043	0.069	
Distriv	0.000	0.968	0.133	0.238	3/17
Distcon	0.000	0.821	0.216	0.279	2/18
Disttree	0.000	1.000	0.249	0.348	2/18
Distkpj	0.000	0.761	0.070	0.170	4/16
Prey	0.000	0.245	0.034	0.071	14/6
Rain	0.000	1.000	0.269	0.377	14/5
Female reproductive success					
Null	0.000	0.196	0.056	0.067	
Distriv	0.000	0.931	0.128	0.213	5/15
Distcon	0.000	0.689	0.136	0.189	4/16
Disttree	0.000	1.000	0.233	0.349	8/12
Distkpj	0.000	0.840	0.109	0.202	9/11
Prey	0.000	0.542	0.052	0.126	15/5
Rain	0.000	0.989	0.302	0.370	14/5

Minimum, maximum, mean and standard deviation of Akaike weights (ω) across all 20 time-steps are listed for each alternative univariate model. The number of models with positive or negative ($\pm$) associations with the dependent variable are also listed. Note that no rainfall map was available for the 2005–2006 time-step.
Variables: distriv, distance to river (km); distcon, distance to confluence; disttree, distance to tree cover; distkpj, distance to kopje; prey, herd density (per km^2); rain, dry season rainfall (mm).

Table 2 Analysis of long-term (40-year) average adult female density, cub productivity and reproductive success with respect to each candidate model

Model	Female density Coefficient estimate(s)			Δ AIC	ω	Cub productivity Coefficient estimate(s)			Δ AIC	ω	Reproductive success Coefficient estimate(s)			Δ AIC	ω
Null				56.7	0.000				34.8	0.000				10.8	0.001
Distriv	−0.0032			21.5	0.000	−0.0101			11.6	0.001	−0.0097			2.1	0.104
Distcon	−0.0031			20.9	0.000	−0.0108			5.8	0.022	−0.0095			1.7	**0.127**
Disttree	−0.0016			42.7	0.000	−0.0053			24.8	0.000	−0.0035			10.4	0.002
Distkpj	−0.0028			41.0	0.000	−0.0063			30.5	0.000	0.0021			12.5	0.001
Prey	0.0037			58.3	0.000	−0.0073			36.7	0.000	−0.0357			11.8	0.001
Rain	0.0006			31.4	0.000	0.0018			20.6	0.000	0.0003			12.6	0.001
Distriv distkpj	−0.0032	−0.0028		5.4	0.033	−0.0101	−0.0063		7.2	0.011	−0.0097	0.0021		3.8	0.044
Distcon distkpj	−0.0031	−0.0028		4.7	0.047	−0.0108	−0.0063		1.3	**0.208**	−0.0095	0.0021		3.4	0.054
Disttree distkpj	−0.0016	−0.0027		28.3	0.000	−0.0052	−0.0059		21.2	0.000	−0.0036	0.0024		12.0	0.001
Distriv prey	−0.0033	−0.0054		22.8	0.000	−0.0108	−0.0370		11.2	0.001	−0.0110	−0.0658		0.7	**0.209**
Distriv rain	−0.0025	0.0004		14.8	0.000	−0.0081	0.0010		9.1	0.004	−0.0111	−0.0008		3.0	0.066
Distcon prey	−0.0032	−0.0060		22.0	0.000	−0.0116	−0.0420		4.8	0.036	−0.0108	−0.0681		0.0	**0.296**
Distcon rain	−0.0024	0.0004		15.6	0.000	−0.0091	0.0008		5.0	0.033	−0.0113	−0.0009		2.1	0.104
Disttree prey	−0.0018	−0.0056		44.0	0.000	−0.0063	−0.0404		24.2	0.000	−0.0049	−0.0615		9.7	0.002
disttree rain	−0.0007	0.0005		31.6	0.000	−0.0028	0.0014		20.3	0.000	−0.0043	−0.0004		12.2	0.001
Distkpj prey	−0.0028	0.0028		42.8	0.000	−0.0064	−0.0094		32.4	0.000	0.0020	−0.0351		13.5	0.000
distkpj rain	−0.0026	0.0006		17.6	0.000	−0.0058	0.0018		17.2	0.000	0.0022	0.0003		14.3	0.000
Distriv distkpj prey	−0.0033	−0.0028	−0.0064	6.4	0.020	−0.0109	−0.0065	−0.0392	6.6	0.015	−0.0109	0.0019	−0.0651	2.4	0.089
Distriv distkpj rain	−0.0026	−0.0027	0.0004	0.0	**0.498**	−0.0082	−0.0060	0.0010	5.3	0.028	−0.0111	0.0019	−0.0007	4.7	0.028
Distcon distkpj prey	−0.0033	−0.0028	−0.0070	5.5	0.032	−0.0116	−0.0065	−0.0443	0.0	**0.399**	−0.0108	0.0019	−0.0675	1.8	**0.120**
Distcon distkpj rain	−0.0025	−0.0027	0.0003	0.6	**0.369**	−0.0092	−0.0061	0.0008	1.0	**0.242**	−0.0113	0.0018	−0.0009	3.8	0.044
Disttree distkpj prey	−0.0017	−0.0027	−0.0061	29.4	0.000	0.0061	−0.0060	−0.0416	20.5	0.000	−0.0049	0.0023	−0.0610	11.3	0.001
Disttree distkpj rain	−0.0006	−0.0026	0.0005	18.0	0.000	−0.0027	−0.0058	0.0013	17.1	0.000	−0.0043	0.0023	−0.0004	13.8	0.000

Coefficients are listed for each parameter, respectively, and ΔAIC (Akaike Information Criterion) values (relative to the minimum AIC value for each set of candidate models) and Akaike weights (ω) are listed for each model. Models with the strongest weight and those within two AIC points of that model are indicated in bold.

Variables: distriv, distance to river (km); distcon, distance to confluence; disttree, distance to tree cover; distkpj, distance to kopje; prey, herd density (per km^2); rain, dry season rainfall (mm).

tree cover and kopjes, but positively correlated with prey herd density and dry season rainfall.

RESULTS

Despotism and source–sink dynamics

The short-term (2-year) and long-term (40-year) spatial patterns of adult female density, productivity and reproductive success were consistent with a despotic distribution (Fretwell & Lucas 1969; Fretwell 1972). Under an ideal free distribution, fitness-based measures should be equal across the study area, but all three measures showed significant heterogeneity and were higher in better habitats (Tables 1 and 2; Figs 2 and 3). For example, reproductive success decreased with increasing distance from rivers. Accordingly, reproductive success was strongly correlated with female density in both the short-term maps (70% of the 2-year reproductive success maps were positively and significantly correlated with 2-year density, at $P \leq$ Bonferroni corrected threshold of 0.003) and the long-term map (relative reproductive success vs. adult female density: effect = 1.56, SE = 0.14, $P < 0.001$).

Analysis of the average (absolute) female reproductive success and dispersal patterns revealed source–sink dynamics (Fig. 2). Based upon our best estimate of the reproductive success required to yield a positive growth rate, 44% of the mapped study area was identified as source habitat. Analysis of female dispersal (*c*. 30% of females disperse in cohorts from their natal pride to establish new prides, Pusey & Packer 1987) confirms that the sink areas are largely fed via immigration from the sources. Of the sink–area prides of known origin, 69% (nine of 13) were the result of dispersal from a source–area pride. The rate of source-to-sink dispersal was roughly once every 3 years. In contrast, no source–area prides of known origin descended from a pride located in a sink. Reverse dispersal is predicted for stable source–sink systems (e.g. Morris 1991), but this lack of sink to source dispersal may reflect the overall growth of this population during the study period (Packer *et al.* 2005).

Short-term patterns in the 2-year maps

Overall, the short-term patterns of density, productivity and reproductive success (Figs S2–S4) had the expected directional relationships with the landscape variables (Table 1). These directional relationships were significant across many of the sets of 2-year analyses. If there were no association between the landscape variable and the habitat quality measure, half the maps would be expected to show a positive effect and half to show a negative effect. When 15 or more maps of 20 trend in one direction, the trend is significant ($P \leq 0.05$) using a chi-square test ($n = 20$, expected proba-
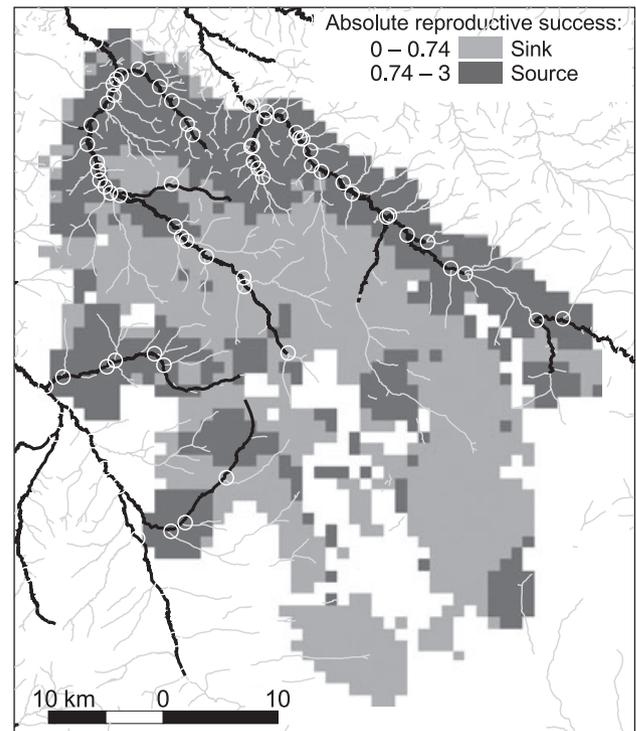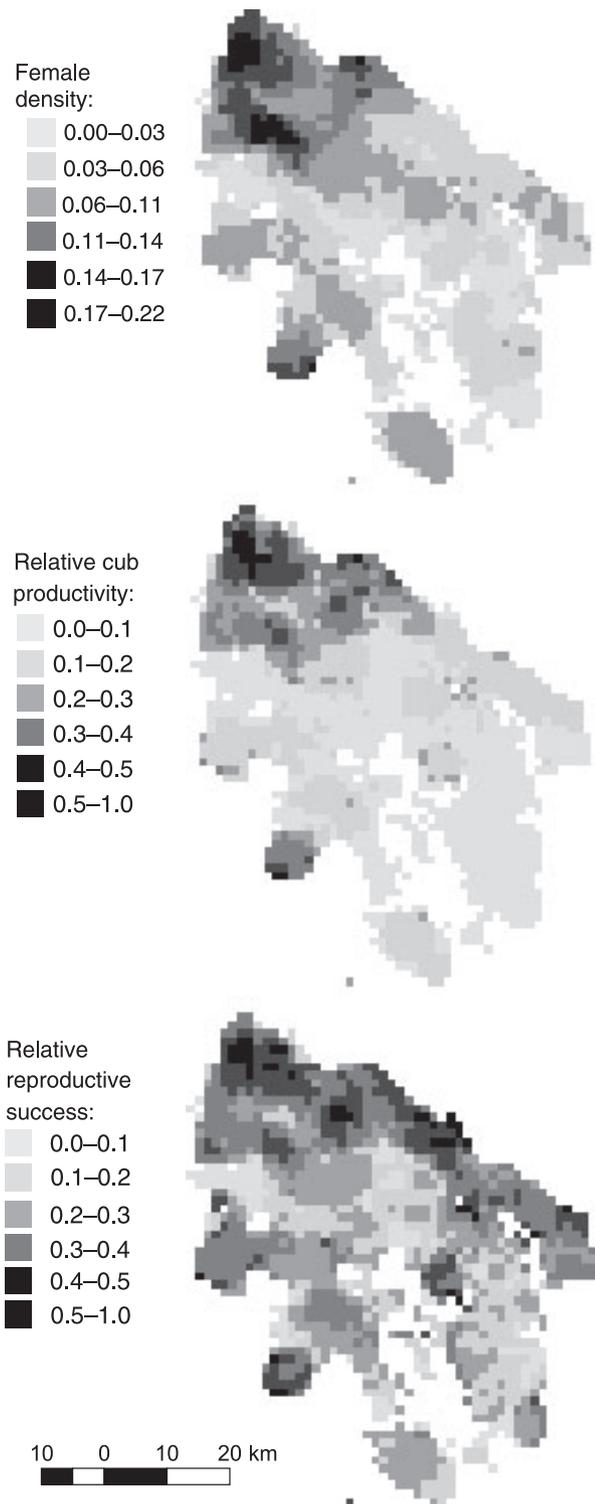

Figure 2 Source and sink areas based upon the 40-year average of absolute (not relative) reproductive success. White areas indicate grid squares with insufficient ranging data. Major rivers are shown in black, tributaries are light grey, and confluences on major rivers are white open circles.

bility of 50%). There was, however, great variation in the AIC weights of these models from one time step to another, indicating that no one landscape variable provided the best explanation of density, productivity, or reproductive success consistently across the 20 time steps. Across all univariate models (Table 1), dry season rainfall had the strongest weight for each of the three dependent variables (especially for female density), but the effect of rainfall (on its own) largely disappeared when considering all candidate models in a multivariate analysis (Tables S2–S4), where no one model emerged as being consistently strongest.

Long-term patterns in the 40-year maps

The best model for long-term average density (Table 2) included a negative effect of distance to rivers, a negative effect of distance to kopjes and a positive influence due to dry season rainfall. The best model for cub productivity included a negative effect of distance to nearest river confluence, a negative effect of distance to kopje and an unexplainable negative effect of prey herd density. A univariate model based solely on prey density had an AIC weight less than the null model. Excluding models with

Figure 3 Long-term (40-year) average adult female density, relative cub productivity and relative reproductive success. White areas indicate grid squares with insufficient ranging data. Note that the legend scales for cub productivity and reproductive success are not evenly distributed and are extended for lower values to better illustrate the observed patterns.

prey density, the best model for cub productivity included distance to confluence, distance to kopje and rainfall. The best model for average reproductive success included a negative effect of distance to confluence and an unexplainable negative effect of prey herd density. A univariate model based on prey density was again weaker than the null model. Excluding all models including prey herd density as a covariate, the best model for reproductive success includes only proximity to river confluences. To further examine the potential importance of prey distribution, we analysed the single time-step in which we had both lion and prey data (2005–2006), and the fit of the univariate model based on prey herd density was weaker than the null model for all three response variables.

DISCUSSION

Areas near river confluences were identified as population sources, owing to their strong correlation with long-term average reproductive success (Fig. 2). This finding stresses the importance of landscape pattern, rather than resource abundance, reinforcing the findings of Hopcraft *et al.* (2005), which showed that hunting success is associated with landscape characteristics that enhance prey capture, rather than prey abundance itself. Confluences are associated with open water and high probabilities of prey capture due to increased cover (Hopcraft *et al.* 2005), which has consistently been shown to improve hunting success throughout Africa (e.g. VanOrsdol 1984; Funston *et al.* 2001). Additional analysis of kill locations (Fig. 4) also suggests that herbivores may get funnelled into and trapped at confluence locations, perhaps because they are wary of crossing rivers or moving in to the thick riverbank vegetation (Hopcraft 2002; A.R.E Sinclair, personal communication).

As expected, in the long-term maps, the pattern of 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 breadth of the lions' realized niche is consistent with source–sink dynamics (Pulliam 1988). More importantly, though, the patterns of long-term density and productivity resulted in a different set of habitat correlates than did reproductive success. By solely using density or productivity, we would have concluded that habitat quality is associated with proximity to rivers or confluences, proximity to kopjes and dry season rainfall. The correlations with rivers and rainfall are fairly consistent with the results for the reproductive success (rainfall is a summary variable that correlates with all the landscape variables, except kopjes). The association with kopjes, however, is misleading; kopjes are one of the few refuges in the sink areas of open plains
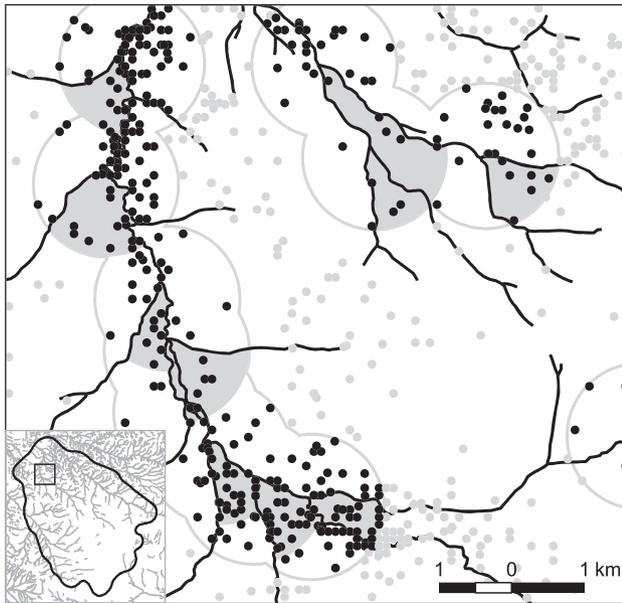
Figure 4 We analysed the position of lion kills < 1 km from a confluence (black circles within grey outlines). Of these kills, more prey were captured between the converging tributaries (i.e. upstream of a confluence; grey shaded areas) than expected by chance, based on area ($\chi^2 = 96.8$, $n = 1141$, $P < 0.001$). Each kill location was only considered once in the analysis. The map shown here is just a portion of the full study area (inset).

(providing shelter and occasionally pools of water) but they correlate with a localized density pattern of effectively non-reproductive adults.

Two-year snapshots of population density, cub productivity and reproductive success were poor indicators of lion habitat quality. Short-term reproductive success is more strongly correlated with pride size, infanticide and territorial competition (Mosser & Packer 2009). It is also more responsive than long-term measures to environmental stochasticity, such as variation in rainfall or severe disease outbreaks. If we consider the statistical significance of the univariate models only, density was marginally better at gauging habitat quality in the short-term, given that a higher proportion of models were significant (for density, productivity and reproductive success, 34%, 24% and 19% of univariate models, respectively, were significant, at $P \leq 0.003$ with a Bonferroni correction). Nonetheless, short-term analyses should be interpreted with caution.

All three response variables became more robust measures of habitat quality once patterns were averaged over longer time periods (Table S5). For example, when reproductive success was averaged over 12-year periods, 87% of the maps showed a significant ($P \leq 0.05$) negative correlation with distance to river confluence, compared with only 35% for the 2-year maps. The temporal variability in reproductive success was dampened when localized patterns

were averaged over at least 12 years, at which point reproductive success becomes a reliable measure of habitat quality. Density and productivity are more reliable indicators of habitat quality at shorter time intervals, but perform little better or worse than reproductive success for intervals of longer than 12 years.

The short-term spatial patterns of reproductive success and productivity showed consistent positive associations with dry season rainfall, but rainfall was not significantly correlated with long-term reproductive success across the study area. Analysis of temporal patterns revealed that average 2-year productivity and reproductive success were significantly correlated with average dry season rainfall (Fig. S5). Migratory herds tend to remain in the study area during wetter dry seasons (Hanby & Bygott 1979), which reduces the risk of starvation and boosts cub survival for the population as a whole. Long-term average spatial variation in rainfall did not contribute significantly to long-term spatial variation in lion reproductive success and thus was not a strong indicator of habitat quality. Nonetheless, interannual variation in rainfall strongly affects growth rates at the population level and has an important effect on the dynamics of the Serengeti lion population (Packer et al. 2005).

Our results highlight the importance of forming an animal's-eye view (Altmann & 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 spatial 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 (where differential access to resources influences differential fitness). 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 population (Howe & Davis 1991). A long-term fitness-related measure was required to identify the ecological characteristics of source habitats. Density patterns revealed resources within the realized niche that allow adults to survive, but not necessarily to replace themselves. Long-term studies are indispensable in clarifying the linkages between landscape and population dynamics and in informing effective management decisions.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 2-year exponential population growth rate ($\ln(N_{t+1}/N_t)$) vs. average 2-year female reproductive success, 1975–2004 ($y = -0.1907 + 0.2589x$, $F_{1,14} = 6.48$, $P = 0.026$, $R^2 = 0.35$).

Figure S2 Short-term (2-year) adult female density (females km^{-2}).

Figure S3 Short-term (2-year) relative cub productivity.

Figure S4 Short-term (2-year) relative reproductive success.

Figure S5 Linear regression of cub productivity and reproductive success vs. dry season rainfall, averaged across the study area within each 2-year period (cub productivity: $n = 19$ biennial time-steps, $R^2 = 0.41$, $P = 0.003$; reproductive success: $n = 19$ biennial time-steps, $R^2 = 0.28$, $P = 0.02$).

Table S1 Correlation table of landscape variables.

Table S2 Short-term (2-year) adult female density: Akaike weights (ω), plus mean and variance, for each alternative model for each time-step.

Table S3 Short-term (2-year) cub productivity: Akaike weights (ω), plus mean and variance, for each alternative model for each time-step.

Table S4 Short-term (2-year) reproductive success: Akaike weights (ω), plus mean and variance, for each alternative model for each time-step.

Table S5 Adult female density, cub productivity and reproductive success averaged over increasing time-scales vs. distance to river confluence.

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