ORIGINAL ARTICLE

Persistence and local extinction of lion prides in the Ngorongoro Crater, Tanzania

Bernard M. Kissui · Anna Mosser · Craig Packer

Abstract African lions (*Panthera leo*) live in social groups (prides) that exhibit group territorial behavior. Pride persistence is expected to depend on its ability to compete against neighboring prides as well as on average rates of reproduction and survival, thus providing a meaningful measure of intergenerational reproductive success. We used Akaike's Information Criterion (AIC) to select the best approximating models explaining how demographic variables influenced pride persistence during a 30-year period in the Ngorongoro Crater, Tanzania, and identified landscape factors affecting those demographic variables. Pride persistence to 10 years depended on adult female density (pride size) and cub productivity (the ultimate source of new females). Average age of adult females had a weakly positive influence on pride persistence, while the effect of female mortality was weakly negative. Adult female mortality increased with disease epidemics and in territories with high human disturbance. Cub productivity was highest in territories closest to rivers and only slightly higher near swamps, and also high in areas of higher vegetative cover and high human use. No landscape variable significantly affected female density. The growth and population size of the Crater lions was closely linked to demographic performance of individual prides, while territorial behavior played a key role in mediating the interactive effects of landscape and demography.

B. M. Kissui (✉)
African Wildlife Foundation, P.O. Box 2658,
Arusha, Tanzania
e-mail: Kiss0043@umn.edu

A. Mosser · C. Packer
Department of Ecology, Evolution and Behavior,
University of Minnesota, 1987 Upper Buford Circle,
St. Paul, MN 55108, USA

Introduction

Population persistence is closely linked to landscape features and habitat quality through food supply (Miyashita et al. 2007), hunting success (Funston et al. 2001; Hopcraft et al. 2005; Packer et al. 2005), breeding success and individual survival (Stralberg and Williams 2002; Peak et al. 2004), carrying capacity (Hayward et al. 2007), parasitism, and predation risks (Budnik et al. 2002). Resource dispersion theory predicts that, in group-living species, the spatial distribution of key resources may influence group size and home range size, and could lead to inter-group competition over scarce resources (Bradbury and Vehrencamp 1976; Macdonald 1983), with larger groups out-competing smaller groups. Territorial species are predicted to follow an ideal despotic distribution in which some individuals or groups may select high quality areas in a landscape and exclude competing groups (Fretwell and Calver 1969; Zimmerman et al. 2003).

African lions (*Panthera leo*, Linnaeus 1758) live in social groups called prides and exhibit group territorial behavior (Schaller 1972; McComb et al. 1994). A pride territory is inherited by successive generations of the pride females, and 30% of female cohorts form new prides by dispersing from existing prides and settling nearby (Pusey and Packer 1987). Thus, pride home ranges persist for generations. Male lions are usually transient members of prides; they are replaced by new males who become resident for 2–4 years before being replaced by yet another coalition (Packer and Pusey 1987). Solitary females are

unable to maintain exclusive home ranges and experience low reproductive success (Pusey and Packer 1987; Packer and Pusey 1995) whereas large prides are more successful at defending their home ranges and out-compete small prides over high quality resources (Mosser and Packer 2009). High quality landscape patches for lions provide high hunting success, shelter for hiding cubs, water, and minimum disturbance from humans (Spong 2002; Hopcraft et al. 2005; Packer et al. 2005; Mosser 2008).

Ultimately, a female's survival and reproductive success depends on her pride: female lions are remarkably egalitarian, with no significant within-group variation in individual reproductive success (Packer et al. 2001). Given the importance of group size in maintaining successful reproduction (Pusey and Packer 1987; Packer et al. 1988, 2001), and the greater reproductive success of daughters that are recruited into their natal pride (Pusey and Packer 1987), pride persistence can be viewed as the single most important demographic outcome of lifetime and intergenerational reproductive success.

In this paper, we analyze long-term data for the Ngorongoro Crater lion population to determine demographic variables that influenced the persistence of lion prides over a 30-year period (1975–2005), and identified landscape factors affecting those demographic variables. We used an information-theoretic approach (Burnham and Anderson 2002), with Akaike's Information Criterion (AIC) to select the best statistical models. The demographic factors included in persistence analysis were female pride size (female density), size of the resident male coalition, frequency of male takeovers (incoming males kill or evict dependent offspring; Bygott et al. 1979; Packer et al. 1988), cub productivity, female age, and female mortality. We tested the effect of distance of pride territories to rivers, roads and swamps, pride territories' vegetative cover, exposure to anthropogenic factors (Maasai pastoralists kill lions for ritual purposes or in retaliation for cattle-killing; Ikanda and Packer 2008), and exposure to outbreaks of infectious disease (three severe epizootics have struck the Crater population over the past 15 years; Kissui and Packer 2004) on the demographic variables.

Materials and methods

Study area

The study was carried out in the Ngorongoro Crater, a 250-km^2 caldera with walls 400–610 m high located at the western edge of the Gregory Rift in northern Tanzania (Fig. 1). The dominant resident ungulate populations include blue wildebeest (*Connochaetes taurinus* Burchell, 1823), zebra (*Equus burchelli* Gray, 1824), buffalo

(*Syncerus caffer* Sparrman, 1779), and Grant's gazelle (*Gazella granti* Brooke, 1872), with smaller numbers of warthog (*Phachochoerus africanus* Gmelin, 1788), Coke's hartebeest (*Alcelaphus buselaphus* Pallas, 1776), common eland (*Taurotragus oryx* Pallas, 1766), waterbuck (*Kobus ellipsiprymnus* Ogilby, 1833), reedbuck (*Redunca redunca* Pallas,1767), and bushbuck (*Tragelaphus scriptus* Pallas, 1766) (Kissui and Packer 2004; Estes et al. 2006). Most of these ungulates spend the whole year in the Crater, although ∼20% of wildebeest and zebra migrate seasonally to the Serengeti plains (Estes and Small 1981; Estes et al. 2006). The most common prey species for the Crater lions are wildebeest and zebra. Buffaloes are an important prey species for lions in large prides while gazelle and other ungulates constitute only a small proportion of their overall diet (Kissui and Packer 2004). Additional predators in the Crater include spotted hyena (*Crocuta crocuta* Erxleben, 1777), golden jackal (*Canis aureus* Linnaeus, 1758), and black-backed jackal (*Canis mesomelas* Schreber, 1775). Cheetah (*Acinonyx jubatus* Schreber, 1775), African wild dog (*Lycaon pictus* Temminck, 1820), and leopard (*Panthera pardus* Linnaeus, 1758) are rarely seen in the Crater.

The Crater floor exhibits a range of landscape and vegetative characteristics (Fig. 1). The landscape is dominated by open grassland, but there are two *Acacia xanthophloea* forest patches and occasional patches of bush land dominated by *Euphorbia bussei* species (Estes et al. 2006). The Crater supports large numbers of resident ungulates owing to the permanent streams and rivers that originate from the northern highland catchment forests and the permanent springs that form persistent green belts of grass growth at the edges of marshes and swamps (Estes and Small 1981; Estes 2002; Estes et al. 2006).

With its high concentrations of wildlife, the Crater forms one of the most attractive tourist destinations in Tanzania. Maasai pastoralists resided on the Crater floor until 1974 when the wildlife authority relocated them, but they were subsequently permitted daytime access to the Crater for livestock grazing, watering, and salt licks (Fyumagwa et al. 2007). Thus, specific areas on the Crater floor continue to experience daily presence of humans. For example, the western quadrant is adjacent to the Maasai pastoralists' primary cattle trails and experiences 10–20 herders with large herds of livestock for most of the daytime. We classify such areas as "high human use" compared to the eastern section where pastoralists rarely visit which we term "low human use". The mere presence of livestock herders might not necessarily have a negative impact on wildlife, particularly ungulates, but Ngorongoro Maasai are known to kill lions with spears (Ikanda and Packer 2008), and our observations indicated that lions actively avoid encounters with Maasai.

Fig. 1 Hydrological/topographical map of the Ngorongoro Crater floor and the adjacent human settlement
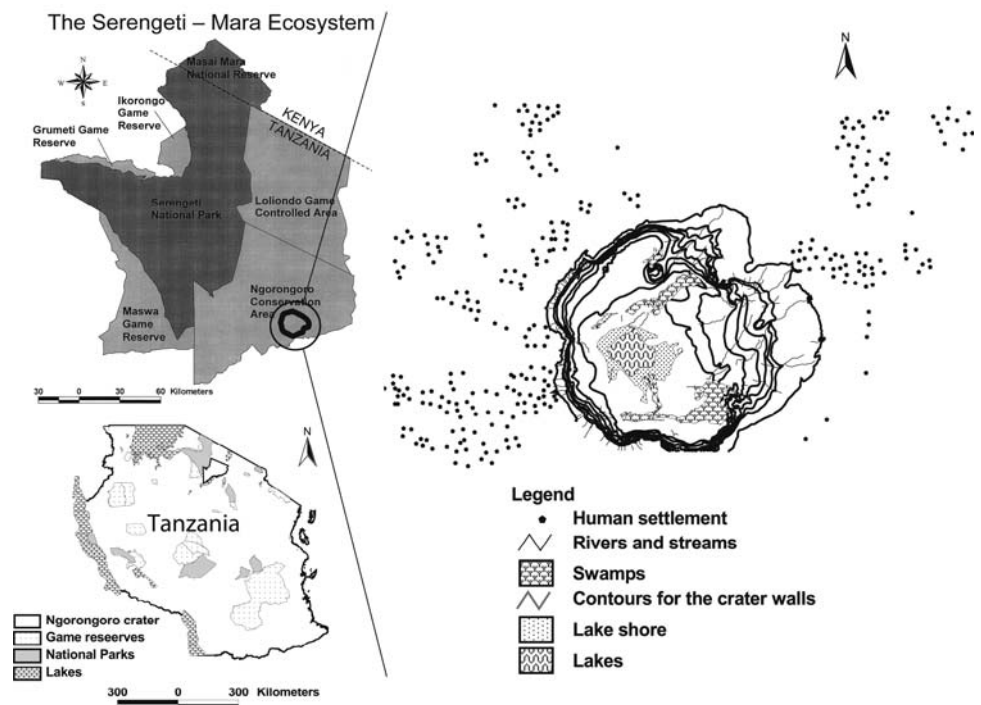
Study population

The Crater lion population has been monitored continuously since the early 1960s; lions are identified individually, and records are maintained on reproductive history, maternity, and ranging patterns of each individual. A lion pride typically comprises 2–9 related females (range 1–21), their dependent cubs, sub-adults, and a resident coalition of 2–6 males (Schaller 1972; Bygott et al. 1979; Packer et al. 1990; Packer and Pusey 1993). Lions are observed on a regular basis by searching the entire study area and recording date and time of observation, pride composition and identification of individual lions, and the location of the pride is recorded using GPS (prior to 1995, pride locations were recorded on a UTM coordinate grid map). Although demographic data extend back to 1963 (Packer et al. 1991), ranging data were not recorded until 1975, so this analysis is restricted to the period from 1975 to 2005.

Demography and pride level variables

We measured 14 demographic and pride level variables calculated in 2-year time steps (which equals the average inter-birth interval for mothers of surviving cubs) (Table 1) from 1975. We used Pearson's correlation coefficients to check for redundancy in the demographic variables and selected only one for statistical analysis when two or more variables significantly correlated with each other ($r_s > 0.5$, with $P < 0.05$ as threshold). This procedure left six variables (Table 2) for subsequent analysis.

Most cub mortality occurs prior to the first birthday (Schaller 1972), so recruitment of yearlings is the best measure of cub productivity (Packer et al. 1988). We defined cub productivity as the number of cubs surviving to 1 year of age per km^2 of pride territory. Adult female mortality was defined as the number of females 3+ years that died/disappeared in each time step per km^2 of pride territory. Cub productivity, adult female mortality and number of adult females are scaled to pride territory area in order to link the influences of landscape features with these demographic parameters. Female density was the average number of females in the pride per km^2 of pride territory. Male takeovers were determined as the frequency of takeovers for each pride over a 2-year period. The number of adult males was calculated as the number of males in resident coalition(s) during a 2-year time step.

Landscape variables

We calculated landscape variables using GIS layers in Arc View 3.2, ESRI. Layers for roads, rivers and swamps were obtained from existing digital library and converted into 1,000-m grids. We calculated the distance from the centroid of each grid cell to the nearest road, river or swamp. For vegetation, a GIS layer was created by digitizing a vegetation map for the Crater published by Estes et al. (2006) and converted into 1,000-m grid cells. Vegetation types were categorized on the basis of height, cover and type of vegetation following Estes et al. (2006) classification: 0 = short grassland (grass height of <1 m), 1 = medium

Table 1 Demography and pride level variables for each pride calculated over 2-year intervals from 1975 to 2005. The 2-year period starting, for example, on November 1, 1974 ended on October 31, 1976 and was labeled as 1975 in the analysis

Variable description
1. Number of adult females age 3+ years old
2. Number of adult females age 3+ years old in each pride per km^2 of pride territory
3. Number of adult females age 3+ years old dying per km^2 of pride territory
4. Proportion of adult females 3+ years old dying each 2-year period
5. Number of females age 1–2 years old dispersed from a pride
6. Average number of adult females 3+ year old, averaged over 24 months
7. Average number of resident males, averaged over 24 months
8. Number of cubs surviving to year 1
9. Number of cubs surviving to year 1 per km^2 of pride territory
10. Total number of lions in a pride including females, cubs and males
11. Total number of lions in a pride including females, cubs and males per km^2 of pride territory
12. Average age of adult females 3+ years old
13. Number of male takeovers
14. Pride territory size

Table 2 Demographic variables selected for use in a priori model analysis

Description	Abbreviation
Average number of resident males, averaged over 24 months	Resmale
Average age of adult females 3+ years old	Fage
Number of male takeovers	Mto
Cub productivity: number of cubs surviving to year 1 per km^2 of pride territory	Cubsurv
Number of adult females 3+ years dying per km^2 of pride territory	Fmortality
Number of females 3+ years per km^2 of pride territory	Fdensity

grassland (grass height 1–1.5 m), 2 = bush land (dominated by bushy vegetation), 3 = woodland (vegetation dominated by woodland), 4 = reeds, and 5 = forest (Fig. 2). We did not have sufficient long-term data on prey distribution to include in this analysis; we instead relied on surrogate measures of prey availability (see below).

Anthropogenic factors

We used a combination of number of pastoralists, herd size and frequency of visits to categorize levels of human use for different areas of the Crater. We defined three categorical levels of human use: category 1 = low use areas (these are areas rarely accessed by pastoralists and livestock), category 2 = medium use areas (areas occasionally accessed by pastoralists and livestock), and category 3 = high use areas (areas accessed by pastoralists and livestock daily) (Fig. 3). The patterns of human use of the crater were inferred from long-term observations spanning the years 1975–2005.

Lion pride home ranges

We considered new prides to have appeared in the population when at least two females of 2+ years old split from an existing pride and established an independent territory. No

new pride originated from lions immigrating into the population from outside the Crater. A pride was deemed locally "extinct" when the number of females fell to one (since solitaries never succeeded in raising surviving offspring).

We constructed pride home ranges for each 2-year period over the period 1975–2005 for sightings from 15 prides. Home ranges were determined from utilization contours using a 75% fixed kernel in Arcview GIS 3.2. We used a smoothing parameter (h) of 2,700 m, representing the mean daily distance traveled by adult female lions in the Crater. The 75% kernel was considered an optimum compromise between large and small kernels: large kernels such as 95% typically tend to overestimate the home range, while kernels of 50% are too small (Worton 1989; Mosser 2008). Home ranges were based on observations containing one or more females that were 2+ years old. The analysis only included prides that were observed at least 3 times per year during the life span of a pride. About 17% of the pride–range estimates contained <20 observations, ranging from 8 to 501 sightings per 2-year time step. Lions show high territorial site-fidelity, and an earlier study of lion home-ranges found no systematic error in estimates based on comparable sample sizes (Mosser 2008). Home ranges were converted to 1,000-m grids; the average territory size was 30 km^2 (range 14–69 km^2).
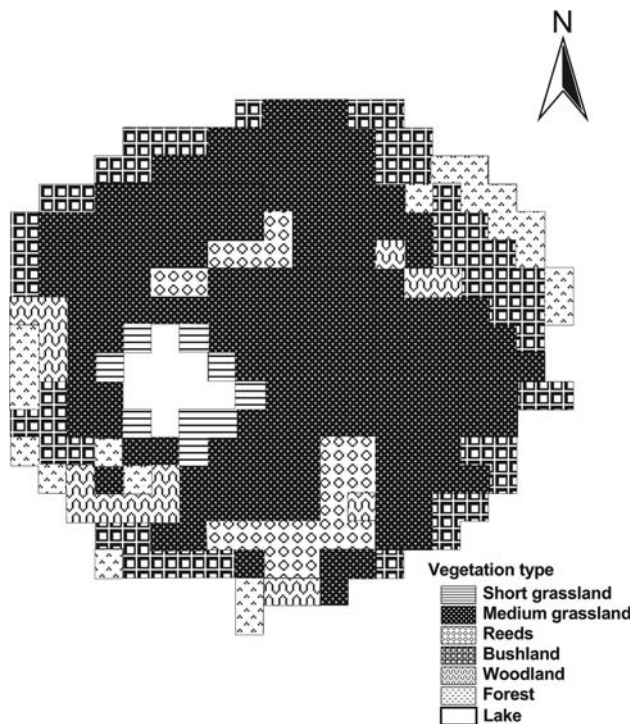
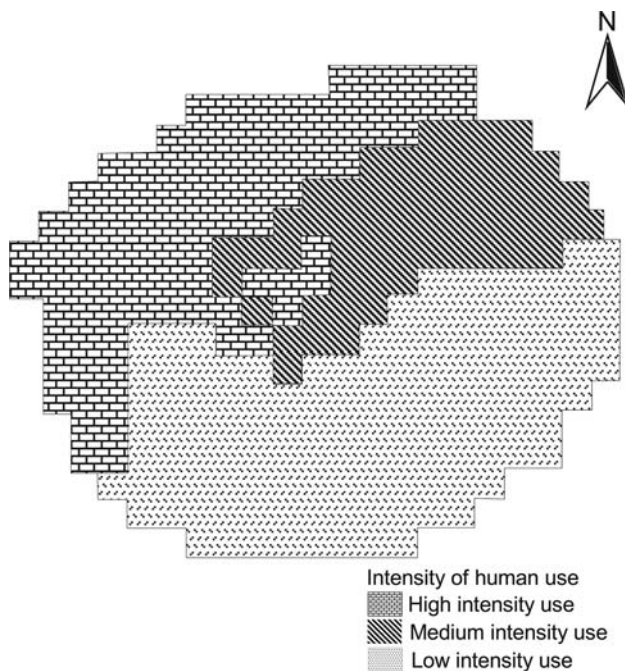**Fig. 2** 1,000 m grid vegetation map for the Crater floor

Fig. 3 1,000 m grid map of the intensity of human use across the Crater floor based on the amount of daytime that people and livestock are present in each section of the crater

Data analyses

For continuous landscape variables such as distance to rivers and swamps, we averaged grid outputs from the GIS overlay analysis to obtain a mean value for each pride territory for each 2-year period. For variables such as level of human-use and vegetation types, for which grids had categorical values (i.e., 1, 2, 3), we used the most frequent value to characterize pride territory, for example a pride territory with 2/3 of its grids having vegetation category 1 (medium grassland) and 1/3 having category 3 (low woodland) was characterized as category 1, the dominant category. Landscape variables for each pride territory were merged with the corresponding demographic variables to produce the final dataset over each 2-year period from 1975 to 2005. Disease epidemics were designated as dichotomous variable with 1 for years with an outbreak and 0 for years with no outbreaks.

We determined the dichotomous response variable, pride persistence, by scoring 1 for each year a pride was present after its appearance in the population and 0 otherwise. The demographic variables were used in a logistic regression as predictors of pride persistence to year 10. We used generalized linear models to identify landscape factors affecting demographic variables that were important to pride persistence. We considered both disease and anthropogenic factors as landscape variables.

We constructed a priori candidate models representing hypotheses concerning the effects of demography on pride persistence to 10 years (Table 3). Given the available data and knowledge of the study population, we constructed each candidate model based on the plausibility of a priori hypothesis (Burnham and Anderson 2002). We performed model selection using Kullback–Leibler information-theoretic approach with Akaike's Information Criterion corrected for small sample size (AICc) (Anderson and Burnham 2002; Burnham and Anderson 2002). We determined the maximized log-likelihood for each candidate model and calculated the values for AICc, $\Delta AICc = (AIC_i - \min AIC)$: min AIC is the minimum AIC value of all models, and ω_i = Akaike weight (the weight of evidence that model i is the best approximating model given the data and the set of candidate models considered) using equations by Burnham and Anderson (2002).

We analyzed pride persistence to 10 years using GENMOD in SAS system 9.1 with binomial distribution and logit link function (logistic regression). To check the effect of landscape on demographic variables, we used a generalized linear model (GENMOD) with Poisson distribution and a log-link function. Log of pride territory was used as an offset in GENMOD to model cub productivity and adult female mortality as rates (Flynn 2007). In GENMOD, we used pride as a random effect with years as repeated measures. We used Pearson's chi-square to check the goodness of fit of the models.

Results

Over the period 1975–2005, 22 prides were observed in the Crater, but 7 prides were dropped from the analysis because they were observed too infrequently to estimate home-range utilization kernels. At the time of this analysis, 12 (80%) of the 15 prides had gone extinct; average persistence was 18 years ± 12 years (range 2–39 years).

Pride persistence

We selected the best model among a set of 34 a priori candidate models constructed to predict pride persistence to year 10. The model with the lowest AIC and highest Akaike weight (ω_i) values is regarded as the best approximating model in the set of candidate models considered. Models with $\Delta AICc < 2$ are said to have strong support and represent a confidence set of the best model, $\Delta AICc$ values of 2–4 have weak support, $\Delta AICc$ values of 4–7 little support, and values >7 have no support (Burnham and Anderson 2002). Table 3 shows only models with $\Delta AICc$ rank of <5 and the null model (i.e., the model with only the intercept).

Logistic regression analysis indicated that the model containing adult female density and cub productivity to be the best for predicting pride persistence to year 10 (Tables 3 and 4). However, $\Delta AICc$ revealed that models 2

and 3 had values <2, thus constituting the confidence set of the best model. The Akaike weights (ω_i) showed that the best model was only 2.7 times as likely as models 2 and 3. The confidence set suggested that age of females and female mortality influenced pride persistence. Table 4 shows model averaged parameter estimates for the best model and models in the confidence set. Although both adult female mortality and female age influenced pride persistence, their effects appear to be weak (Table 4), but cub productivity and adult female density are the most important factors to pride persistence.

Effects of landscape on cub productivity, adult female density and female mortality

We used AIC and generalized linear models to identify landscape factors affecting adult female mortality, cub productivity, and female density. There is no plausible a priori hypothesis for how the landscape might affect female age.

Effects on adult female mortality

We constructed a priori candidate models for hypotheses explaining the effect of landscape factors on adult female mortality. Table 5 shows models with $\Delta AICc$ values of <5. Results suggest a model containing disease epidemic and level of human use to be the best approximating model for the effect on adult female mortality. The best model is about 2.7 times as likely to be better than the next model, but no model fell within the confidence set. Parameter estimates for the best model are presented in Table 6.

Effects on cub productivity

Among the 23 a priori candidate models for the effect of landscape on cub productivity, only three models had $\Delta AICc < 5$ (Table 7). The best fitting model contained five variables including distance to rivers, distance to swamps, amount of vegetative cover, disease epidemics, and the impact of human use (Table 7). The next model had $\Delta AICc > 2$ suggesting no support for any alternative

Table 3 A priori logistic regression models for repeated measures data predicting the effect of demographic factors on pride persistence to 10 years

Model no.	Model set[a]	K	AICc	ΔAICc	ω_i
1	Fdensity, cubsurv	3	95.40	0.00	0.35
2	Fdensity, cubsurv, fage	4	97.33	1.93	0.13
3	Fdensity, cubsurv, fmortality	4	97.39	1.99	0.13
4	Cubsurv	2	98.45	3.05	0.08
5	Cubsurv, fmortality	3	99.14	3.74	0.05
6	Fdensity, cubsurv, fmortality, fage	5	99.30	3.90	0.05
7	Cubsurv, mto	3	99.41	4.01	0.05
8	Cubsurv, resmale	3	99.56	4.17	0.04
9	Cubsurv, fage	3	100.18	4.78	0.03
10	Null model	1	112.69	17.29	0.00

AIC values were corrected for small sample size ($n = 80$)

K Number of estimable parameters (each covariate + intercept) in approximating model, *AICc* Akaike's Information Criteria adjusted for small sample size, *ΔAICc* (AICi − min AIC), min AIC is the minimum AIC value of all models, ω_i Akaike weight, is the weight of evidence that model *i* is the best approximating model given the data and set of candidate models considered (also represent the probability that model *i* is the best among candidate models considered)

[a] Abbreviations explained in Table 2

Table 4 Model averaged parameter estimates and the 95% confidence intervals (CI) for the best model for pride persistence to 10 years

Parameter	Estimate	SE	95% CI	
			Upper	Lower
Adult female density	3.8634	1.7981	7.3697	0.3572
Cub productivity	5.2570	2.7980	10.7132	−0.1991
Adult female mortality	−1.7657	5.0899	8.2104	−11.7419
Adult female age	0.0653	0.1210	0.3024	−0.1718

Table 5 A priori candidate models explaining the effect of landscape factors on adult female mortality for Crater prides during 1975–2005

Model no.	Model set	K	AICc	ΔAICc	ω_i
1	Epidemic, humuse	3	152.96	0.00	0.390
2	Epidemic, riverdis, humuse	4	155.04	2.08	0.137
3	Epidemic	2	156.10	3.14	0.081
4	Epidemic, riverdis	3	156.80	3.84	0.057
5	Epidemic, humuse, riverdis, roaddis, vegtype	6	157.10	4.14	0.049
6	Epidemic vegtype	3	157.40	4.44	0.042
7	Epidemic, swampdis	3	157.91	4.95	0.033
15	Null model	1	160.71	7.75	0.008

Models were analyzed using a Poisson generalized linear model for repeated data, corrected for small sample size ($n = 95$), and ranked according to ΔAICc

Epidemic Disease epidemic, *riverdis* distance to rivers, *humuse* human use, *vegtype* vegetative cover, *swampdis* distance to swamps, *roaddis* distance to roads

Table 6 Parameter estimates and 95% confidence intervals (CI) for parameters in the best model for adult female mortality, 1975–2005

Parameter	Estimate	SE	95% CI	
			Upper	Lower
Human use	0.2163	0.1285	0.4682	−0.0357
Disease epidemic	0.5471	0.2503	0.0565	1.0377

Table 7 A priori candidate models for the effect of landscape on cub productivity in Crater prides for 1975–2005

Model no.	Model set	K	AICc	ΔAICc	ω_i
1	Riverdis, vegtype, epidemic, humuse, swampdis	6	−243.66	0.00	0.644
2	Humuse, riverdis	3	−241.38	2.28	0.206
3	Riverdis, vegtype, epidemic, humuse	5	−240.73	2.93	0.149
4	Null model	1	−202.53	41.13	0.000

Models were analyzed using Poisson generalized linear model for repeated data. Models are ranked based on (ΔAICc). AIC values were corrected for small sample size ($n = 95$)

All terms and abbreviations as in Table 5

Table 8 Parameter estimates and the 95% confidence intervals (CI) for the best model for effects of landscape variables on cub productivity, 1975–2005

Parameter	Estimate	SE	95% CI	
			Upper	Lower
Distance to swamps	−0.0002	0.0002	0.0002	−0.0007
Disease epidemic	−0.2434	0.4420	0.6228	−1.1097
Anthropogenic factors	0.3168	0.1744	0.6586	−0.0249
Amount of vegetative cover	0.1723	0.1962	0.5569	−0.2122
Distance to rivers	−0.0013	0.0005	−0.0003	−0.0024

in the models predicting cub productivity. It is possible that human presence enhanced cub productivity by repelling Cape buffalo and spotted hyenas from these areas; buffalo have been seen to trample cubs on several occasions in the Crater (B. Kissui, personal observation), and hyenas are known to kill lion cubs elsewhere (Schaller 1972).

Effects on adult female density

Among 21 a priori models tested for the effect of landscape factors on adult female density, no model performed better than the null model. Table 9 shows the null model and models with ΔAICc < 5. Adult female density may not be directly influenced by landscape factors.

Discussion

This analysis suggests that female density, cub productivity, adult female mortality, and the average age of adult females determine the long-term persistence of a lion pride. "Adult female density" is a measure of pride size, and

model in the candidate list. Analysis of parameter estimates for the best model indicated the effects of distance to swamps, amount of vegetative cover, disease epidemics, and the impact of human use on cub productivity to be weak (Table 8), but distance to rivers influences cub productivity most significantly. Cub productivity is also influenced by adult female density; we therefore introduced this variable in models to check whether positive anthropogenic effect disappears. However, cub productivity was still higher in areas with higher human activities after introducing adult female density as a covariate

Table 9 A priori candidate models for the effects of landscape factors on adult female density for Crater pride during 1975–2005

Model no.	Model set	K	AICc	ΔAICc	ω_i
1	Null model	1	102.43	0.00	0.196
2	Humuse	2	103.66	1.23	0.106
3	Epidemic	2	104.11	1.68	0.084
5	Riverdis	2	104.23	1.80	0.080
7	Swamps	2	104.46	2.03	0.071
6	Vegtype	2	104.46	2.03	0.071
4	Humuse, riverdis	3	104.58	2.15	0.067
8	Epidemic, humuse	3	105.41	2.98	0.044
9	Humuse, vegtype	3	105.70	3.27	0.038
10	Epidemic, riverdis	3	105.96	3.53	0.034
14	Epidemic, swampdis	3	106.16	3.73	0.030
15	Vegtype, riverdis	3	106.29	3.86	0.028
11	Epidemic, humuse, swampdis, riverdis	4	106.33	3.90	0.028
13	Epidemic, riverdis, humuse	4	106.44	4.01	0.026
16	Vegtype, swampdis	3	106.50	4.08	0.026
12	Humuse, riverdis, vegtype	4	106.59	4.16	0.024

Models were analyzed using Poisson generalized linear model for repeated data. Models are ranked based on (ΔAICc). AIC values were corrected for small sample size ($n = 95$)

All terms and abbreviations as in Table 5

larger prides would certainly be expected to persist longer because of the competitive advantage of large groups over smaller groups. Territorial behavior plays a crucial role by enabling large prides to occupy high quality areas in terms of food supply and shelter (Mosser and Packer 2009). Cub productivity is the ultimate source of recruitment of all future females within the pride. Rivers have a positive effect on cub productivity and are associated with lower female mortality.

According to our best-fitting landscape model, exposure to disease epidemics and higher levels of human activity increased the mortality of adult females. Age-specific mortality typically follows a U-shaped curve, with high mortality prior to the first birthday and accelerating mortality from 11 years onward (Packer et al. 1998). However, during documented disease outbreaks, lions in the middle age classes experience unusually high mortality (Packer et al. 1999; Kissui and Packer 2004), and two of three disease epidemics in the Crater were deduced from abnormally high adult mortality over a short period of time (Kissui and Packer 2004). The effect of human activities is likely to result from the type of human–lion conflicts that have been identified as an important cause of population decline in many ecosystems (e.g., Kissui 2008).

Although we failed to find a direct link of landscape factors to adult female density, pride territories closest to

rivers and swamps and higher vegetative cover experienced the highest cub productivity. However, our analysis showed high cub productivity to occur in areas with high human presence in the crater. One possible explanation for this counterintuitive result is that humans repel Cape buffalo and spotted hyenas from the immediate area, thus reducing cub mortality. Buffalo and hyenas are both known to kill lion cubs, although the extent of this impact is difficult to determine. High recruitment of young into the adult population ameliorates the effect of adult mortality and promotes pride persistence. Proximity to rivers and swamps and high vegetative cover increase lions' hunting and reproductive success (Hopcraft et al. 2005; Mosser 2008) through greater prey availability/accessibility (Spong 2002; Funston et al. 2003; Hopcraft et al. 2005), and more effective shelter for cubs (Mosser 2008).

Our analysis illustrates the value of using pride persistence to assess the combined role of pride level complexities such as territorial behavior, landscape quality, and individual demography on the temporal dynamics of a lion population. Because of high space fidelity by lion prides, focusing on pride persistence has the advantage of allowing meaningful comparisons to be made between prides in heterogeneous landscapes. Prides can potentially persist far longer than the average lifespan of an adult female, thus pride persistence is the best measure of intergenerational reproductive success. In terms of management concerns, the results presented here suggest that while increased human activities may not negatively affect cub productivity, it has negative effects on the adult segment of the lion population: adult female lion mortality increases in areas with high human interference. The human population in the Ngorongoro Conservation Area has nearly quadrupled over the past four decades (Ikanda and Packer 2008), raising concerns over the future of the lion population in the crater floor.

References

Anderson DR, Burnham KP (2002) Avoiding pitfalls when using information-theoretic methods. J Wildl Manage 66:912–918

Bradbury JW, Vehrencamp SL (1976) Social organization and foraging in Emballonurid bats. Behav Ecol Sociobiol 1:337–381

Budnik JM, Thompson FR III, Ryan MR (2002) Effect of habitat characteristics on the probability of parasitism and predation of bell's vireo nests. J Wildl Manage 66:232–239

Burnham KP, Anderson DR (2002) Model selection and multimodal inference: a practical information-theoretic approach, 2nd edn. Springer, New York

Bygott JD, Bertram BCR, Hanby JP (1979) Male lions in large coalitions gains reproductive advantages. Nature 282:839–841

Estes RD (2002) Ngorongoro Crater ungulate study (1996–1999) final report, Part 1. Unpublished report

Estes RD, Small R (1981) The large herbivore population of Ngorongoro Crater. Proceedings of the fourth annual African wildlife symposium. Afr J Ecol 19:175–185

Estes RD, Atwood JL, Estes AB (2006) Downward trends in Ngorongoro Crater ungulate populations 1986–2005: Conservation concerns and the need for ecological research. Biol Conserv 131:106–120

Flynn M (2007) Modeling event count data with PROC GENMOD and the SAS system. Statistics, Data Analysis, and Modeling. Paper 265 (www.sas.com/proceedings/sugi24/stats/p265-24)

Fretwell SD, Calver JS (1969) On territorial behavior and other factors influencing habitat distribution in birds. 2. Sex ratio variation in dickcissel. Acta Biotheor 19:37–44

Funston PJ, Mills MGL, Biggs HC (2001) Factors affecting the hunting success of male and female lions in the Kruger national park. J Zool (Lond) 253:419–431

Funston PJ, Mills MGL, Richardson PRK, Van Jaarsveld AS (2003) Reduced dispersal and opportunistic territory acquisition in male lions (Panthera leo). J Zool (Lond) 259:131–142

Fyumagwa RD, Runyoro V, Horak IG, Hoare R (2007) Ecology and control of ticks as disease vectors in wildlife of the Ngorongoro Crater, Tanzania. S Afr J Wildl Res 37:79–90

Hayward MW, O' Brien J, Kerley GIH (2007) Carrying capacity of large African predators: predictions and tests. Biol Conserv 139:219–229

Hopcraft JGC, Sinclair ARE, Packer C (2005) Planning for success: Serengeti lions seek prey accessibility rather than abundance. J Anim Ecol 74:559–566

Ikanda DK, Packer C (2008) Ritual vs. retaliatory killing of African lions in the Ngorongoro Conservation Area, Tanzania. Endang Species Res 6:67–74

Kissui BM (2008) Livestock predation by lions, leopards, sported hyenas, and their vulnerability to retaliatory killing in the Maasai steppe, Tanzania. Anim Conserv 11:422–432

Kissui BM, Packer C (2004) Top-down population regulation of a top predator: lions in the Ngorongoro Crater. Proc R Soc Lond B 271:1867–1874

Macdonald D (1983) The ecology of carnivore social behavior. Nature 301:379–384

McComb K, Packer C, Pusey A (1994) Roaring and numerical assessment in contests between groups of female lions (Panthera leo). Anim Behav 47:379–387

Miyashita T, Suzuki M, Takada M, Fujita G, Ochiai K, Asada M (2007) Landscape structure affects food quality of sika deer (Cervus nippon) evidenced by fecal nitrogen levels. Popul Ecol 49:185–190

Mosser A (2008) Group territoriality of the African lion: behavioral adaptation in a heterogeneous landscape. PhD thesis, University of Minnesota, Minneapolis

Mosser A, Packer C (2009) Group territoriality and the benefits of sociality in the African lion, Panthera leo. Anim Behav. doi: 10.1016/j.anbehav.2009.04.024

Packer C, Pusey AE (1987) Intrasexual cooperation and the sex ratio in African lions. Am Nat 130:636–642

Packer C, Pusey AE (1993) Dispersal, kinship, and inbreeding in African lions. In: Thornhill NW (ed) The natural history of in breeding and out breeding. University of Chicago Press, Chicago, pp 375–391

Packer C, Pusey AE (1995) The lack clutch in a communal breeder: lion litter size is a mixed evolutionary stable strategy. Am Nat 145:833–841

Packer C, Herbst L, Pusey AE, Bygott JD, Hanby JP, Cairns SJ, Borgerhoff Mulder M (1988) Reproductive success in lions. In: Clutton-Brock TH (ed) Reproductive success. University of Chicago Press, Chicago, pp 363–383

Packer C, Scheel D, Pusey AE (1990) Why lions form groups: food is not enough. Am Nat 136:1–19

Packer C, Pusey AE, Rowley H, Gilbert DA, Martenson J, O'Brien SJ (1991) Case study of a population bottleneck: lions of Ngorongoro Crater. Conserv Biol 5:219–230

Packer C, Tatar M, Collins A (1998) Reproductive cessation in female mammals. Nature 392:807–811

Packer C, Altizer S, Appel M, Brown E, Martenson J, O'brien SJ, Roelke-Parker M, Hofmann-Lehmann R, Lutz H (1999) Viruses of the Serengeti: pattern of infection and mortality in African lions. J Anim Ecol 68:1161–1178

Packer C, Pusey AE, Eberly LE (2001) Egalitarianism in female African lions. Science 293:690–693

Packer C, Hilborn R, Mosser A, Kissui B, Borner M, Hopcraft G, Wilmshurst J, Mduma S, Sinclair ARE (2005) Ecological change, group territoriality, and population dynamics in Serengeti lions. Science 307:390–393

Peak RG, Thompson FR III, Shaffer TL (2004) Factors affecting songbird nest survival in riparian forests in a Midwestern agricultural landscape. Auk 121:726–737

Pusey AE, Packer C (1987) The evolution of sex-biased dispersal in lions. Behavior 101:275–310

Schaller GB (1972) Serengeti lion; a study of predator–prey relations. University of Chicago Press, Chicago

Spong G (2002) Space use in lions, Panthera leo, in the Selous Game Reserve: social and ecological factors. Behav Ecol Sociobiol 52:303–307

Stralberg D, Williams B (2002) Effect of residential development and landscape composition on the breeding birds of Placer County's foothill oak woodlands: USDA Forest Service. USDA Forest Service Gen Tech Report, pp 341–366

Worton BJ (1989) Kernel methods for estimating the utilization distribution in home range studies. Ecology 70:164–168

Zimmerman GS, La-Haye WS, Gutiérrez RJ (2003) Empirical support for a despotic distribution in a California spotted owl population. Behav Ecol 14:433–437