

Demographic consequences of habitat loss and crowding in large carnivores: A natural experiment

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Funding information

Safari South (Pty) Ltd; Rann Safaris (Pty) Ltd; National Research Foundation, Grant/Award Number: 76584 and 109097

Abstract

Habitat loss is one of largest threats to the persistence of large carnivore populations. However, because most large carnivores are long-lived, cryptic and wide-ranging, few studies examine the demographic consequences of habitat loss, and the resultant crowding that ensues, on these species. We used long-term data to examine the demographic responses of an African lion (*Panthera leo*) population to flooding-induced habitat loss in a seasonal wetland, the Okavango Delta, during a transition from low to high annual flooding patterns. We found that intraspecific competition reduced cub survival and that this effect was exacerbated by habitat loss and consequent crowding. The proportion of cubs recorded in the population also declined as crowding increased, and both the survival of cubs and proportion of cubs recorded declined as prey abundance decreased. Apparent sub-adult survival declined with increasing pride size, but this likely reflects emigration rather than mortality. Adult survival remained relatively constant throughout the study period, a population response which is important in buffering populations against short-term fluctuations in ecological conditions. As many large carnivore populations face future habitat loss, it is important that we understand the demographic consequences of habitat loss in order to better mitigate its effects in the future.

Keywords: demographics, lion, Okavango Delta, *Panthera leo*, population, survival

1 INTRODUCTION

Habitat loss, or a reduction in patch size (Fahrig, 2003), is a major threat to long-term persistence of large carnivores (Cardillo et al., 2004; Ceballos & Ehrlich, 2002; Ripple et al., 2014). Because large carnivores are rare, require large spaces, are long-lived, and often come into conflict with humans, they are particularly vulnerable to loss of habitat precipitated by natural or anthropogenic forces (Cardillo et al., 2004; Woodroffe, 2000).

Currently, the leading causes of habitat loss are increasing human populations, land-use changes associated with human activities (Di Minin et al., 2016; Riggio et al., 2013; Woodroffe, 2000), natural disasters (Metcalf, Hampson, & Koons, 2007) or climate change (Mukul et al., 2019; Sahanatien & Derocher, 2012). For large carnivores, this can lead to lower genetic diversity (Flagstad et al., 2003; Frankham, 1996; Johnson et al., 2010), change in movement, dispersal and habitat selection patterns (Hornseth et al., 2014) and changes in social organisation (Kotze, Keith, Winterbach, Winterbach, & Marshal, 2018).

As habitat disappears, large carnivores are forced into remaining habitats or 'islands', resulting in 'crowding' or sudden increase in density (Metcalf et al., 2007). This crowding leads to an exacerbation of density-dependent population effects such as reduced survival or reproduction (Ordiz, Støen, Swenson, Kojola, & Bischof, 2008) and can ultimately result in population declines (Di Minin et al., 2016; Metcalf et al., 2007). In large carnivores, density-dependent effects can manifest through intraspecific competition, either via a reduction in per capita food availability or via behavioural or social responses (Cubaynes et al., 2014; Post, Peterson, Stenseth, & McLaren, 1999). In the former case, reduced food intake affects physiological condition of individuals which in turn may result in low survival, particularly for young offspring, delay oestrus or reduce frequency of mating activities in reproductively active individuals (Fuller & Sievert, 2001; Schaller, 1972). In the latter, crowding increases agonistic interactions which can lead to higher adult mortalities (Cubaynes et al., 2014; Mosser & Packer, 2009), change the age structure of a population (Rosenblatt et al., 2014) or suppress reproduction (Ordiz et al., 2008; Packer, Pusey, & Eberly, 2001).

While research on the demographic responses to crowding is more common on smaller species with shorter life histories, studying responses in long-lived, low-density and wide-ranging large carnivores is considerably more challenging (Martinez Cano, Tab oada, Naves, Fernández-Gil, & Wiegand, 2016; Rosenblatt et al., 2014). Furthermore, conducting research on large carnivores at the appropriate scale at which ecological processes occur, remains a challenge. For small species, habitat can be manipulated experimentally, and population responses are more easily monitored; for larger species, manipulations of habitat at the relevant scale, which may cover entire landscapes, are rarely possible, or at best expensive and time-consuming (Debinski & Holt, 2000). In seasonally flooded wetlands, however, space available to terrestrial animals declines with increasing flood level, and this provides an ideal landscape-scale, natural laboratory in which to investigate demographic responses of large carnivores to crowding.

As apex carnivores, lions lack natural predators, and as such, population demographics can be influenced in two main ways; extrinsically through abundance of prey (Schaller, 1972; Van Orsdol, Hanby, & Byogtt, 1985), or intrinsically through intraspecific competition for prey or territory (Mosser & Packer, 2009; Trinkel et al., 2010). Low prey availability, for example, reduces cub survival and reproductive rates (Hanby & Bygott, 1987; Ogotu & Dublin, 2002; Schaller, 1972; Van Orsdol et al., 1985), and intraspecific interactions via territorial disputes can result in adult mortality or infanticide of young (Mosser & Packer, 2009; Trinkel et al., 2010). These demographic responses are common across large carnivore populations (Fuller & Sievert, 2001).

We used long-term population data on African lions (*P. leo*) in a seasonally flooded wetland, the Okavango Delta, to investigate the demographic responses of a large carnivore to naturally induced crowding caused by a transition from low to high floods. We predicted that lower habitat availability, resulting in crowding, would directly lower survival of all age groups by increasing the effects of intraspecific competition. We also predicted a positive relationship between prey availability and survival of all age groups, and a negative relationship between pride size and sub-adult survival. Lastly, we predicted that declining land availability and declining prey availability would result in a lower proportion of young animals in the population.

2 MATERIALS AND METHODS

2.1 Study area

The Okavango Delta is the world's largest inland delta, situated in the north-west of Botswana (McCarthy & Ellery, 1998). Each year, November–February rains in the Angolan highlands cause a unimodal flood pulse that travels down the Okavango river and terminates in an alluvial fan covering an area of up to 14,000 km² (McCarthy & Ellery, 1998; Ramberg et al., 2006). This flood pulse reaches the Delta during the dry season (late February–March) and takes 3–4 months (April–August) to move through the entire system, resulting in a mosaic of seasonally inundated floodplains and dry islands (Gumbrecht, Wolski, & McCarthy, 2004). The study took place in wildlife management areas NG29 and NG30 (S 19° 33' to S 19° 53', E 22° 48' to E 23° 06') between 1997 and 2004. During this time, the Okavango Delta transitioned from a drying phase, containing one of the lowest floods on record in 1996, to a wetting phase from 1997 onwards in the multi-decadal cycle (Murray-Hudson, Wolski, Murray-Hudson, Brown, & Kashe, 2014). This resulted in a shift in vegetation from seasonally flooded grasslands to sedge-dominated floodplains over a large portion of the study area. This increases competition for available grazing, resulting in an accompanying decline in prey numbers (Burger, 2020).

2.2 Data collection

From 1997–2004, detailed data were collected on five resident lion prides. In 2003, flooding conditions resulted in insufficient data collection and this year was thus excluded from all analyses. One lioness in each pride was fitted with a VHF collar (AWT, Pretoria, South Africa) to facilitate regular tracking, and individuals identified using whisker spot patterns (Pennycuik & Rudnai, 1970). All collars were removed from the animals at the end of the study and approval gained from the Department of Wildlife and National Parks (permit reference numbers: OP 46/1 LXVIII (133) and EWT 3/3/8 XXIX [50]). When prides were located, either opportunistically or by telemetry, observers recorded the Global Positioning System (GPS) location, age, sex and identity of individuals. For cubs and sub-adults not followed from birth, age was determined by body size, or by mane development for sub-adult males, and adults were aged according to nose colour or tooth wear (see Smuts, 1982; Whitman & Packer, 2007).

We derived covariate data for each pride based on pride home ranges, which were calculated using pooled GPS locations for each pride over the study period. Long-term

ranges were deemed more appropriate for the study as more robust representations of home range use (Hanby, Bygot, & Packer, 1995; Schaller, 1972). Home ranges were constructed using 90% kernel density isopleths (Börger et al., 2006; Mosser, 2008) and using an *href* smoothing factor (Kie, 2013; Worton, 1995). Home range analyses were conducted in ArcView GIS 3.2 (ESRI) using the Animal Movements extension (Hooge & Eichenlaub, 2000).

2.3 Covariates

2.3.1 Prey

Prey availability was estimated by driving transects along roads in the study area, in the dry season from August to November each year. Transects were driven at 10-20 km/h, in the mornings and afternoons, for 3 hr either side of sunrise and sunset. All sightings of herbivores within 200 m of either side of the road were recorded, including information on species, group size, GPS position and time. Lion pride home range boundaries were used as cut-off points to divide transects between home ranges. Each home range had an average of 164 km of transects covered each year (range 104–186 km).

Only preferred prey species for lions in the study area (see Kotze et al., 2018) was used for further analysis, and the availability of prey for each pride calculated by using a kilometric abundance index (KAI, total number of animals/total distance driven in kilometres; Vincent, Gaillard, & Bideau, 1991) for each species. Next, we converted the KAI for each prey species to kilometric biomass by multiplying the kilometric abundance of each species with the average female species weight (Loveridge et al., 2009). This total was then multiplied by 0.75 to account for individuals smaller than females (i.e. young; see Hayward, O'Brien, & Kerley, 2007). The total prey kilometric biomass was then calculated by adding the kilometric biomass of all prey species to determine the total biomass of prey encountered per kilometre in each pride home range (Loveridge et al., 2009). Lastly, to account for within-pride competition for food once prey has been killed (Packer, Scheel, & Pusey, 1990; Watts & Holekamp, 2009), the total kilometric biomass was divided by the total number of adult and sub-adult members of the pride (individuals over 2 years old) to produce a per capita prey index.

2.3.2 Flooding

The extent of flooding in the study area for 1997–2002 was calculated from processed satellite TM5 and satellite TM + imagery (obtained from the Global Land Cover Facility <https://www.sciencebase.gov/catalog/>) which distinguished between wet and dry pixels (see Wolski & Murray-Hudson, 2006). Images representing inundation at its maximum annual extent were used for analysis as an estimate when available dry land was most limited (Crawshaw & Quigley, 1991). The area of dry land available in each home range was calculated by multiplying the number of dry pixels by the pixel area (28 m × 28 m). We used MODIS imagery (MOD09Q1, 250 m resolution; https://lpdaac.usgs.gov/data_access) for the year 2004 where satellite imagery was not available (see Murray-Hudson, Wolski, Cassidy, et al., 2014). Analyses for all spatial covariates were done in ArcMap 10.2 (ESRI). All data were analysed in Universal Transverse Mercator (UTM) projection 34S.

2.3.3 Competition

Pride size was calculated annually by adding the total number of minimum known-alive adult females and sub-adults (male and female) present in the pride. The number of neighbouring adult females whose pride home ranges overlapped with the focal pride's home range was used as an index of intraspecific competition on the focal pride (Van der Waal, Mosser, & Packer, 2009). While competition might arise from other lions outside the study area, the extent of overlap between the study prides' home ranges was taken to represent direct competition for space and other resources. Only neighbouring adult females were considered, because these are the members of the pride most likely to engage in territorial conflict or take over kills (Heinsohn, Packer, & Pusey, 1996; Mosser & Packer, 2009). Adult males were excluded from the analysis because males often moved between prides and controlled more than one pride at a time. The population referred to in the rest of the text therefore excludes the adult pride males.

2.4 Data analysis

2.4.1 Baseline models for survival and recapture

We estimated survival using mark-recapture methods. Lions were considered 'captured' when they were observed in that year (Emmerson & Southwell, 2011) and their identity confirmed using whisker spots. Capture history information was constructed for each individual and then analysed in RMark (Laake, 2013) in R 3.2.2 (R Core Team, 2018), using the Cormack-Jolly-Seber (CJS; Lebreton, Burnham, Clobert, & Anderson, 1992). CJS models estimate two probabilities: recapture (p), representing the probability of re-encountering a lion, assuming it is alive and within the study area representing and apparent survival (ϕ), which is the probability of the animal surviving and remaining within or returning to the study area (Emmerson & Southwell, 2011). It is important that this is interpreted as apparent survival as it cannot distinguish between survival and emigration (Lebreton et al., 1992). To establish a baseline model, we first determined if the data met the assumptions of equal recapture probability and equal survival probability across the sampled population using the program RELEASE (Burnham, Anderson, White, Brownie, & Pollock, 1987). Heterogeneity in survival probability in the data indicated the need to divide the data into different age structures (Appendix 1). We therefore tested different potential age structures based on what was hypothesised to be biologically meaningful age divisions for lions. Using Akaike's Information Criterion for small sample sizes (Anderson & Burnham, 2002; Appendix 1), a three-group age structure for the survival sub-model and a time-varying recapture sub-model best fitted the data, and this model was selected as the baseline model for further analysis.

The next step in the modelling process was to determine which survival sub-model best described temporal variation in survival for each age group. Three additional models were therefore constructed, each constraining one age group at a time to constant survival probability. The model which best represented the age-specific temporal variation in survival was then selected as the final model for (a) calculation of survival probabilities for each age group each year and (b) the reference model (Ref_t) against which covariate models would be compared. The reference model was thus imported into MARK v 6.1 (White &

Burnham, 1999), and the goodness-of-fit was measured using the median \hat{c} approach, testing for a range of values for c with a lower bound of 1, upper bound of 5 and with 100 replicates (White & Burnham, 1999). To estimate apparent survival rates for each age group, averaged across the prides, we used the reference model's survival and recapture model structure but removed pride as an additive factor.

2.4.2 Covariate effects

To test for the effects of land availability, prey availability and intraspecific competition, for each age group, the covariates were averaged across prides for each year to represent the effects of each covariate across the population, and pride identity was included as an additional factor in models to account for inter-pride variation. The time effect (i.e. year of study) for each age group in the reference model was thus replaced with individual covariate effects, and where relevant, interactions between covariates (Grosbois et al., 2008). Covariate models were then compared to the reference model, which included the effect of time (Ref_t), as well as a baseline model for each age group where survival is held constant ($\varphi(.)$). Effectively, by substituting time with a covariate in the reference model Ref_t , QAICc can be used to determine whether covariate models perform better than constant and time-varying models, and thus best describe temporal variation in survival for each age group (Dybala, Eadie, Gardali, Seavy, & Herzog, 2013; Emmerson & Southwell, 2011; Grosbois et al., 2008; Kéry, Madsen, & Lebreton, 2006). Following Grosbois et al. (2008), covariates for each age group were considered to be statistically supported when covariate models (cov) performed better ($<AICc$) than constant models (cst, i.e. Ref_c or Ref_{SA}), but were as well or better supported than the time-variant models (t, i.e. Ref_t) (Anderson & Burnham, 2002; Guthery, Brennan, Peterson, & Lusk, 2005). Consequently, if $\Delta QAICc(cov) - QAICc(cst) < -2$ and $\Delta QAICc(cov) - QAICc(t) \leq 2$ the effect of the covariate is considered statistically significant (Grosbois et al., 2008). Covariates showed no collinearity, and all covariates were centred and divided by one standard deviation to make beta coefficients comparable when inferring relationships with predictor variables (Dybala et al., 2013; Schielzeth, 2010). To reduce model parameterisation and maintain model simplicity, each covariate was considered individually for each age group (Emmerson & Southwell, 2011).

To quantify the magnitude of the effect of each covariate, the analysis of deviance approach was applied to covariate and baseline constant and time-variant models (Grosbois et al., 2008; Skalski, 1996). This approach determines the fraction of annual variation in survival explained by the covariate for each age group ($R^2 dev$), similar to a 'coefficient of determination' (Dybala et al., 2013; Emmerson & Southwell, 2011). The $R^2 dev$ is therefore calculated as

$$\frac{Dev(cst) - Dev(cov)}{Dev(cst) - Dev(t)} \quad (1)$$

, where $Dev(cst)$ is the deviance for the constant model, $Dev(cov)$ the deviance for the covariate model, and $Dev(t)$ the deviance for the time-varying model (Emmerson & Southwell, 2011; Grosbois et al., 2008; Skalski, 1996). Covariates with an $R^2 dev$ value of

higher than 0.2 are considered potentially influential, as these covariates explain more than 20% of the annual variation in survival (Grosbois et al., 2008).

2.4.3 Population structure

The age structure of the population ($n = 5$ prides) was examined for each year of the study period. We divided the demographic groups into cubs (0–2 years), sub-adults (2–4 years) and adults (>4 years; Smuts, 1982) to make the study comparable to others (Ferreira, Beukes, Haas, & Radloff, 2020; Ogutu & Dublin, 2002; Schaller, 1972). We then determined which percentage of the population was represented by each age group on an annual basis. As an index of reproductive rates, we examined how the proportion of cubs in the population each year was influenced by area availability, prey availability, average pride size and average number of competing neighbours. These analyses were conducted using linear regression in R version 3.5.1 (R Core Team, 2018).

3 RESULTS

3.1 Baseline models for survival and recapture

The baseline model included a three-class age group structure with cubs (0–1 years), juveniles and sub-adults combined (1–4 years) and adults (>4 years) for survival probabilities and temporal variation in recapture probabilities (see Appendix 1). The model where cub and sub-adult survival varied temporally and adult survival remained constant, best explained the data (Akaike weight = 0.85; Table 1) and was thus used as the reference model (Ref_t) for further analysis. The median \hat{c} value for this reference model was 1.8, and all subsequent models derived from this model were thus adjusted for overdispersion.

TABLE 1. Model selection to select a reference model that best describes temporal variation in survival of lions (*P. leo*) in the south-western Okavango Delta for cubs (0–1 year), juveniles and sub-adults (1–4 years) and adults (>4 years)

Survival (ϕ)	Recapture (p)	k	AICc	Δ AICc	w
Adult constant (t/t/.) + Pride	Time (t)	24	512.36	0.00	0.8452
Sub-adult constant (t/.t) + Pride	Time (t)	24	515.93	3.57	0.1416
All time-varying (t/t/t) + Pride	Time (t)	29	521.85	9.49	0.0073
Cub constant (./t/t) + Pride	Time (t)	24	522.30	9.94	0.0059

Abbreviations: AICc, Akaike's Information Criterion for small sample sizes; k, number of parameters; w, model weight; Δ AICc, change in AICc.

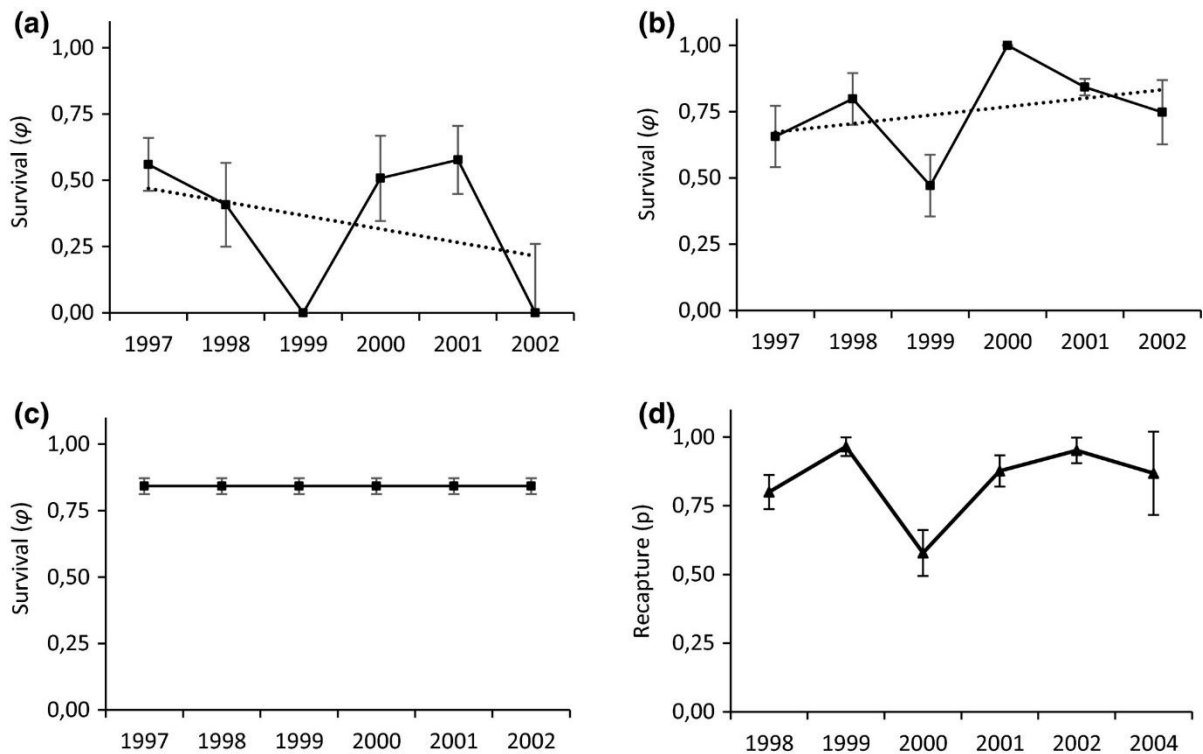


FIGURE 1. Apparent survival (a) for cubs (0–1 years old), (b) pooled juveniles and sub-adults (1–4 years old) and (c) adults over 4 years, plus (d) recapture rates for lion (*P. leo*) during the study period in the south-western Okavango Delta. Dotted lines indicate trend lines for survival of each age group over the study period. Error bars indicate standard errors as estimated in RMark. Standard errors for survival for the pooled sub-adult age class in 2000 and for survival of cubs in 1999 were estimated at boundaries

Apparent survival rates for the population indicated that cub and sub-adult survival decreased from 1997 to 1999, increased again towards 2000 and declined again in 2004 (Figure 1a,b). Overall trends showed that cub survival declined with time, while sub-adult survival increased (Figure 1a,b). Cub survival averaged across the study period was 34% ($SD = 25\%$), while sub-adult survival was substantially higher and averaged 75% ($SD = 18\%$). Apparent adult survival estimated over the study period remained constant at 84% ($SE = 3\%$; Figure 1c). Recapture probabilities were relatively high over the study period and were lowest in the year 2000, which also coincided with the highest flood levels (Figure 1d).

3.2 Covariate effects

Over the study period, the average available area of land in each home range at annual peak flood values steadily decreased from approximately 80% ($SD = 5\%$) in 1997, to 25% ($SD = 1\%$) in 2004 (Figure 2a, also see Appendix 2). Along with declining land availability, prey availability, measured as a kilometric index of abundance, also decreased considerably over the study period until 2000 and then appeared to stabilise towards 2004 (Figure 2b). Pride sizes remained relatively stable until a steep drop in 2004 (Figure 2c), and the average number of competing adult female neighbours remained relatively stable until a slight increase in 2002, followed by a drop in 2004 (Figure 2d).

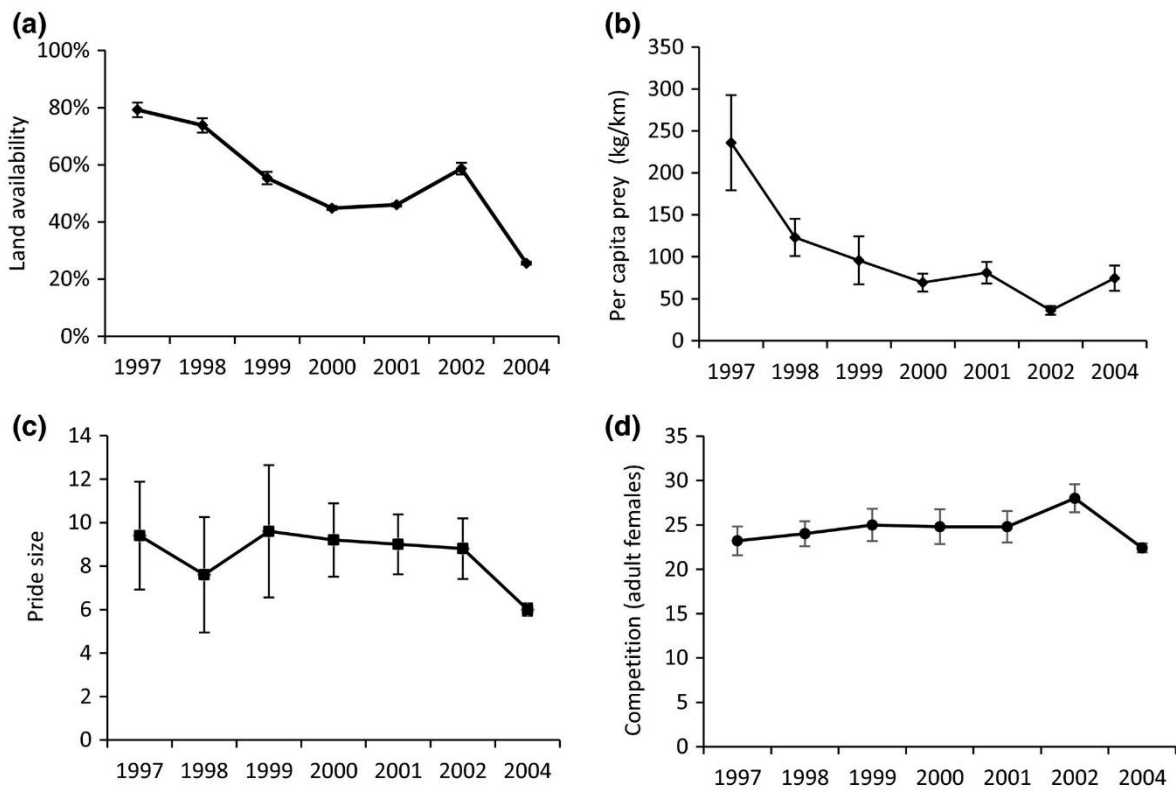


FIGURE 2. Temporal trends in covariates, namely (a) per cent of dry land in home ranges, (b) average kilometric prey availability, (c) average pride size, including adult females and sub-adults and (d) average number of extra-pride females competing with each focal pride of lions (*P. leo*) in the population between 1997 and 2004 in the south-western Okavango Delta, Botswana

Cub survival was positively related to per capita prey availability ($\beta = 0.58$, 95% CI: 0.07, 1.08), but had a negative relationship with competition ($\beta = -1.11$, 95% CI: -2.23 , 0.02; Table 2). Although land availability was positively related to cub survival ($\beta = 0.25$, 95% CI: -0.37 , 0.87), it only proved significant by enhancing the negative effect of competition on cub survival (slope = -0.98 , 95% CI: -1.92 , 0.03). These were the only three models which significantly influenced cub survival according to model deviance analysis; per capita prey availability and intraspecific competition as covariates explained 41.85% and 41.31% of the variation in annual cub survival respectively, and the interaction effect between land availability and competition explained 34.02% of the temporal variation in cub survival (Table 2). For sub-adult survival, only one covariate model, which included pride size, performed better than the constant model (Table 2). Pride size negatively affected sub-adult survival ($\beta = -1.04$, 95% CI: -2.12 , 0.05) and described a significant proportion in sub-adult survival at 58.33% (Table 2). Adult survival did not vary temporally in the baseline model, and the temporal effects of covariates on this survival probability could therefore not be measured.

TABLE 2. Reference models and covariate models examining temporal variation in survival for cub and sub-adult lions (*P. leo*) in the south-western Okavango Delta

Cub and sub-adult survival	k	QAICc	Δ QAICc	Dev	chat	Δ (cov-t)	Δ (cov-cst)	%Dev
Baseline models								
Constant sub-adult ($\varphi(t/. /.)p(t)$)	19	299.92	0.00	466.60	1.8			
Constant cub ($\varphi(.t/.)p(t)$)	19	303.23	3.30	472.54	1.8			
Reference ($\varphi(t/t/.)p(t)$)	24	307.91	7.98	460.01	1.8			
Covariates for cub age group								
Prey availability	19	300.31	0.00	467.30	1.8	-7.59	-2.91	0.42
Competition	19	300.35	0.04	467.36	1.8	-7.56	-2.88	0.41
Flood:Competition	19	300.86	0.55	468.28	1.8	-7.05	-2.37	0.34
Flood	19	302.88	2.56	471.91	1.8	-5.03	-0.35	0.05
Pride size	19	303.00	2.69	472.13	1.8	-4.91	-0.23	0.03
Covariates for sub-adult age group								
Pride size	19	297.79	0.00	462.75	1.8	-10.12	-2.13	0.58
Pride size:Flood	19	299.58	1.79	465.97	1.8	-8.33	-0.35	0.09
Flood	19	299.83	2.04	466.43	1.8	-8.07	-0.09	0.02
Pride size	19	303.00	2.69	472.13	1.8	-4.91	-0.23	0.03
Covariates for sub-adult age group								
Pride size	19	297.79	0.00	462.75	1.8	-10.12	-2.13	0.58
Pride size:Flood	19	299.58	1.79	465.97	1.8	-8.33	-0.35	0.09
Flood	19	299.83	2.04	466.43	1.8	-8.07	-0.09	0.02
Prey availability	19	299.87	2.08	466.50	1.8	-8.03	-0.05	0.01
Competition	19	299.89	2.10	466.54	1.8	-8.01	-0.03	0.01

Note

All models include pride as an additive factor. Covariate models which performed better than constant models and better or equally well as time-varying models are considered important, and those with a percentage deviance greater than 20% (in bold) are considered significant.

Abbreviations: %Dev, percentage of deviance in time-dependent models explained by the covariates; chat, value by which all models were adjusted for overdispersion; Dev, model deviance; k, number of model parameters; QAICc, quasi-likelihood model ranking using Akaike's Information Criterion (AICc) for small sample size; $\Delta(\text{cov-cst})$, difference in QAICc between constant and covariate models; $\Delta(\text{cov-t})$, difference in QAICc between covariate and time-varying reference model; ΔQAICc , difference in QAICc scores for different models.

3.3 Population structure

The average pride size was 8.5 ± 4.3 individuals (range 4–18), including adult females and sub-adults (Figure 2c). Average overall home range size per pride was $217 \pm 47 \text{ km}^2$ (range 166–287 km^2 ; see Appendix 2). The number of adults in the population, based on minimum known-alive individuals, remained relatively stable throughout the study period (average 42.6 ± 6.4 ; Figure 3) but showed a slight increase in 2002 as previous cohorts were recruited and reached maturity, before declining again. Sub-adults increased in the population following the recruitment of cubs from 1997 and 1998 cohorts, but then also declined towards the end of the study period as fewer cubs were born (Figure 3).

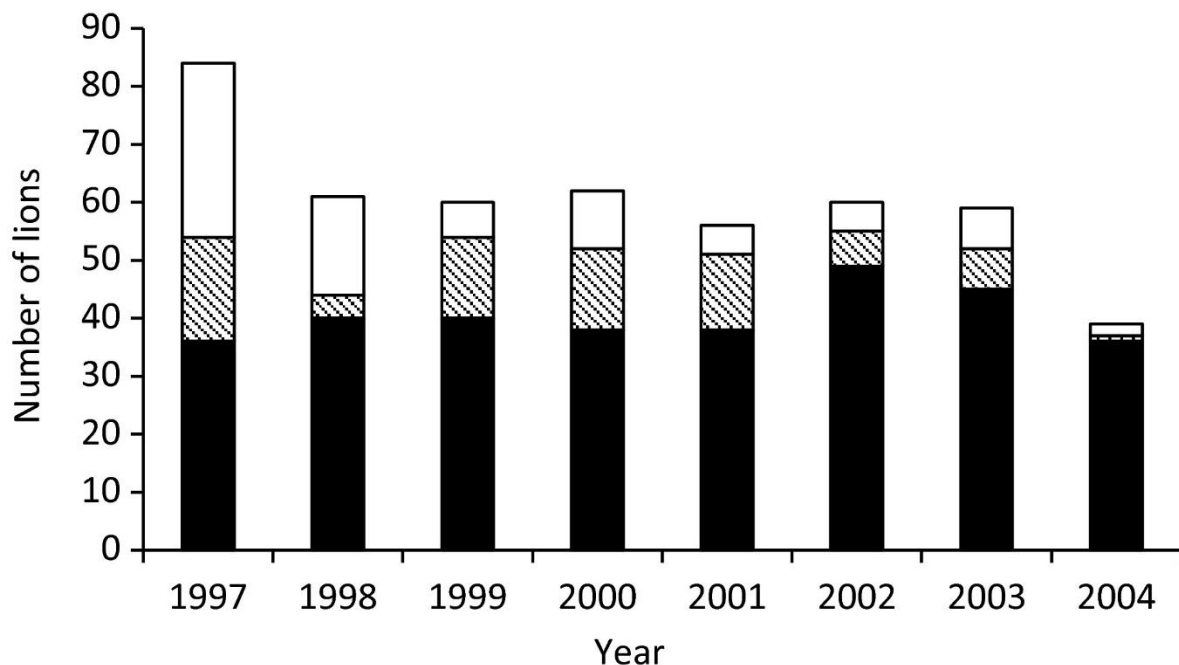


FIGURE 3. Age structure of the lion (*P. leo*) population ($n = 5$ prides) in the south-western Okavango Delta between 1997 and 2004. The graph represents the number of adults (solid), sub-adults (pattern) and cubs (clear) in the population in each year. Adults \Rightarrow 4 years, sub-adults = 2–4 years and cubs = 0–2 years

The proportion of cubs in the population showed the greatest variation, declining from 35.7% in 1997 to 5.1% in 2004 (Figure 3). Results from linear regression analyses indicated that at the population level, land availability within annual home ranges had a significant positive relationship with the proportion of cubs in the population ($\beta = 0.53$, $F = 11.5$, $p < 0.05$, $r^2 = 0.70$), as did prey availability ($\beta = 0.16$, $F = 15.58$, $p < 0.05$, $r^2 = 0.76$). For intraspecific competition, the proportion of cubs did not appear to be significantly related to pride size ($\beta = 0.02$, $F = 0.324$, $p = 0.59$, $r^2 = 0.06$) or to average number of competing neighbours ($\beta = 0.02$, $F = 0.619$, $p = 0.47$, $r^2 = 0.11$).

4 DISCUSSION

In the Okavango Delta, a seasonally flooded wetland, declining space and resultant crowding influenced lion population demographics by exacerbating the negative effect of intraspecific competition on cub survival, in accordance with our predictions. As lions are forced to share smaller areas, the risk of agonistic interactions increases; this may result in injured mothers or cubs, or result in cubs being scattered, increasing the risk of infanticide by neighbouring adults (Mosser & Packer, 2009; Schaller, 1972). During the study period, adult females were recorded to be wounded with significant bite marks and scratches on hind quarters or paw wounds on 15 separate occasions, and agonistic interactions with neighbours were regularly recorded. Cubs may be killed and/or separated from the pride during these interactions; on one such occasion where an unfamiliar adult male usurped a kill, a cub was found dead at the site, and in a separate incident, another cub had to be killed due to severe injuries. In addition to crowding, declines in prey availability during the study period also negatively influenced cub survival, in accordance with our initial predictions and other studies on lion demographics (Mosser & Packer, 2009; Ogotu & Dublin, 2002; Schaller, 1972). Due to their small size and fast growth rates, cubs have higher energetic demands and are therefore more vulnerable to mortality from nutritional stress as a result of poor milk production from nursing females or from feeding competition at carcasses, when prey is scarce (Bertram, 1975; Van Orsdol et al., 1985). Other wetland environments, such as the Busanga floodplains in Kafue National Park, Zambia, experience similarly poor cub survival over periods characterised by high floods (Midlane, 2013), and we suggest that declining prey as well as increased competitive interactions as a result of declining land availability may be responsible for this change in lion populations during years of high floods.

Lions may be limited not only by inter-pride competition, but by within group density-dependence (Van der Waal et al., 2009). In this study, pride size proved to be the most important factor in influencing apparent survival of sub-adults (2–4 years) and juveniles (1–2 years). However, it is important to note that the mark-recapture analysis does not distinguish between survival and emigration and that the results could reflect a mixture of both demographic processes (Lebreton et al., 1992). Young male lions disperse between the age of 2–4 years (Bygott, Bertram, & Hanby, 1979; Pusey & Packer, 1987), and as such may never be recaptured, resulting in lower apparent survival rates. For example, in 1999, sub-adult survival was shown to be low at only 50%, but much of the apparent low survival can be attributed to emigration by a large cohort of sub-adult males who were born in 1997. While we initially predicted that crowding caused by lower land availability would have negative impacts on sub-adult survival, it appears not to be the case here. While we would expect dispersal of sub-adult females to increase (and apparent survival to therefore decrease) as crowding increases, other studies have shown that where densities of neighbours are high and there is a lack of vacant territories, sub-adult lionesses instead remain philopatric, particularly when habitat quality is higher (Van der Waal et al., 2009). In this study, for example, all sub-adult females were recruited into prides and no deaths of sub-adult females were recorded. This may further explain why the number of adult females in the population remained relatively stable and slightly increased towards the end of the study period.

Despite the fluctuations in social and ecological factors, and contrary to our expectations, survival in the adult age group remained constant throughout the study period. Across numerous species, adult survival rates are most resistant to environmental stochasticity or density-dependence (Forcada, Trathan, & Murphy, 2008; Gaillard, Festa-Bianchet, & Yoccoz, 1998; Portier, Festa-Bianchet, Gaillard, Jorgenson, & Yoccoz, 1998). For lion populations, female adult survival is the most important factor in ensuring the viability of a population (Van Vuuren, Hermann, & Funston, 2005). Adults would therefore only be vulnerable to extreme ecological events such as disease outbreaks (Roelke-Parker et al., 1996), or other stochastic ecological changes (Packer et al., 2005).

When we related the proportion of cubs in this population to environmental and social covariates, we found that lower land availability and lower prey availability both contributed to the observed decline in the proportion of cubs in the population over the study period. For this same population, reproductive rates were shown to be negatively influenced by lower land availability and lower prey availability (see Kotze et al., 2018). These observations are concurrent with other studies on lions (Bertram, 1975; Ogutu & Dublin, 2002; Schaller, 1972) and other large carnivores (see Fuller & Sivert, 2001) where lower reproductive rates and poor cub survival often follow declines in availability of resources.

5 CONCLUSION

In the Okavango Delta, inundation patterns are characterised by multi-decadal hydrological patterns, which alternate between periods of high and low flood (Murray-Hudson, Wolski, Cassidy, et al., 2014). These landscape-scale changes will likely result in the establishment of new population equilibria for the lions related to long-term inundation patterns (Packer et al., 2005). During years of high inundation, when conditions mimic habitat loss, lions experience increased intraspecific competition caused by crowding, which together with reduced prey availability, appears to reduce the survival probability of cubs under 12 months. This negative demographic response and skewing of the population towards older individuals can lead to population declines (Packer et al., 2005). Habitat loss is thus a significant threat to large carnivores, and the ensuing demographic responses may reinforce natural population oscillations, driving populations towards extinction rather than a level at which they would otherwise recover (Metcalf et al., 2007). These responses will likely be further amplified in the face of climate change or additive anthropogenic mortalities such as the introduction of disease (Roelke-Parker et al., 1996) or edge effects caused by human-wildlife conflict (Darkoh & Mbaiwa, 2009; Van Vuuren et al., 2005; Woodroffe & Ginsberg, 1998). This is particularly true for social carnivores where population oscillations can be extreme (see Packer et al., 2005). As many extant large carnivore populations exist in isolated protected areas that face future habitat loss (Henschel et al., 2014; Wikramanayake et al., 2004), knowing how population demographics may be affected can inform population modelling to predict the efficacy of strategies, such as the creation of corridors to allow for emigration, in mitigating further declines (Hansen, 2011; Rabinowitz & Zeller, 2010; Wikramanayake et al., 2004).

ACKNOWLEDGEMENTS

We thank the President of Botswana, the Ministry of Environment, Natural Resources, Conservation and Tourism and the Botswana Department of Wildlife and National Parks for granting permission to conduct this research. We also thank Safari South (Pty) Ltd, Rann Safaris (Pty) Ltd and andBeyond for funding and logistical support and the volunteers who assisted in data collection. Finally, we thank Mike Murray-Hudson, Piotr Wolski and Kgalalelo Thito from the Okavango Research Institute for granting us access to processed satellite data on flooding patterns. JPM and RK acknowledge support from the National Research Foundation (grants 76584 and 109097).

CONFLICT OF INTEREST

The authors agree there is no conflict of interest to be reported in this study.

REFERENCES

- Anderson, D. R., & Burnham, K. P. (2002). Avoiding pitfalls when using information-theoretic methods. *Journal of Wildlife Management*, *66*, 912– 918. <https://doi.org/10.2307/3803155>
- Bertram, B. C. B. (1975). Social factors influencing reproduction in wild lions. *Journal of Zoology*, *177*, 463– 482. <https://doi.org/10.1111/j.1469-7998.1975.tb02246.x>
- Börger, L., Franconi, N., De Michele, G., Gantz, A., Meschi, F., Manica, A., ... Colson, T. (2006). Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology*, *75*, 1393– 1405. <https://doi.org/10.1111/j.1365-2656.2006.01164.x>
- Burger, K. G. (2020). The relationship between flooding parameters and grazing herbivores in the south-western Okavango Delta. PhD Thesis. Johannesburg: University of the Witwatersrand.
- Burnham, K. P., Anderson, D. R., White, G. C., Brownie, C., & Pollock, K. H. (1987). Design and analysis methods for fish survival experiments based on release-recapture. *American Fisheries Society Monographs*, *5*, 1– 437.
- Bygott, J. D., Bertram, B. C. R., & Hanby, J. P. (1979). Male lions in large coalitions gain reproductive advantages. *Nature*, *26*, 839– 841. <https://doi.org/10.1038/282839a0>
- Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J. L., Bielby, J., & Mace, G. M. (2004). Human population density and extinction risk in the world's carnivores. *PLoS Biology*, *2*, e197. <https://doi.org/10.1371/journal.pbio.0020197>
- Ceballos, G., & Ehrlich, P. R. (2002). Mammal population losses and the extinction crisis. *Science*, *296*, 904– 907. <https://doi.org/10.1126/science.1069349>

Crawshaw, P. G. J., & Quigley, H. B. (1991). Jaguar spacing, activity and habitat use in a seasonally flooded environment in Brazil. *Journal of Zoology*, 223, 357– 370. <https://doi.org/10.1111/j.1469-7998.1991.tb04770.x>

Cubaynes, S., MacNulty, D. R., Stahler, D. R., Quimby, K. A., Smith, D. W., & Coulson, T. (2014). Density-dependent intraspecific aggression regulates survival in northern Yellowstone wolves (*Canis lupus*). *Journal of Animal Ecology*, 83, 1344– 1356.

Darkoh, M. B., & Mbaiwa, J. E. (2009). Land-use and resource conflicts in the Okavango Delta, Botswana. *African Journal of Ecology*, 47, 161– 165. <https://doi.org/10.1111/j.1365-2028.2008.01064.x>

Debinski, D. M., & Holt, R. D. (2000). A survey and overview of habitat fragmentation experiments. *Conservation Biology*, 14, 342– 355. <https://doi.org/10.1046/j.1523-1739.2000.98081.x>

Di Minin, E., Slotow, R., Hunter, L. T. B., Pouzols, F. M., Toivonen, T., Verburg, P. H., ... Moilanen, A. (2016). Global priorities for national carnivore conservation under land use change. *Scientific Reports*, 6, 23814. <https://doi.org/10.1038/srep23814>

Dybala, K. E., Eadie, J. M., Gardali, T., Seavy, N. E., & Herzog, M. P. (2013). Projecting demographic responses to climate change: Adult and juvenile survival respond differently to direct and indirect effects of weather in a passerine population. *Global Change Biology*, 19, 2688– 2697. <https://doi.org/10.1111/gcb.12228>

Emmerson, L., & Southwell, C. (2011). Adélie penguin survival: Age structure, temporal variability and environmental influences. *Oecologia*, 167, 951– 965. <https://doi.org/10.1007/s00442-011-2044-7>

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution and Systematics*, 34, 487– 515. <https://doi.org/10.1146/annurev.ecolsys.34.011802.132419>

Ferreira, S. M., Beukes, B. O., Haas, T. C., & Radloff, F. G. (2020). Lion (*Panthera leo*) demographics in the south-western Kgalagadi Transfrontier Park. *African Journal of Ecology*, 58, 348– 360. <https://doi.org/10.1111/aje.12728>

Flagstad, Ø., Walker, C. W., Vila, C., Sundqvist, A.-K., Fernholm, B., Hufthammer, A. K., ... Ellegren, H. (2003). Two centuries of the Scandinavian wolf population: Patterns of genetic variability and migration during an era of dramatic decline. *Molecular Ecology*, 12, 869– 880. <https://doi.org/10.1046/j.1365-294X.2003.01784.x>

Forcada, J., Trathan, P. N., & Murphy, E. J. (2008). Life history buffering in Antarctic mammals and birds against changing patterns of climate and environmental variation. *Global Change Biology*, 14, 2473– 2488. <https://doi.org/10.1111/j.1365-2486.2008.01678.x>

- Frankham, R. (1996). Relationship of genetic variation to population size in wildlife. *Conservation Biology*, 10, 1500– 1508. <https://doi.org/10.1046/j.1523-1739.1996.10061500.x>
- Fuller, T. K., & Sievert, P. R. (2001). Carnivore demography and the consequences of changes in prey availability. In J. L. Gittleman, S. M. Funk, D. W. Macdonald, & R. K. Wayne (Eds.), *Carnivore Conservation* (pp. 163– 178). Cambridge, UK: Cambridge University Press and the Zoological Society of London.
- Gaillard, J. M., Festa-Bianchet, M., & Yoccoz, N. G. (1998). Population dynamics of large herbivores: Variable recruitment with constant adult survival. *Trends in Ecology and Evolution*, 13, 58– 63. [https://doi.org/10.1016/S0169-5347\(97\)01237-8](https://doi.org/10.1016/S0169-5347(97)01237-8)
- Grosbois, V., Gimenez, O., Gaillard, G. M., Pradel, R., Barbraud, C., Clobert, J., ... Weimerskirch, H. (2008). Assessing the impact of climatic variation on survival in vertebrate populations. *Biological Reviews*, 83, 357– 399.
- Gumbrecht, T., Wolski, P., Frost, P., & McCarthy, T. S. (2004). Forecasting the spatial extent of the annual flood in the Okavango Delta, Botswana. *Journal of Hydrology*, 290, 178– 191. <https://doi.org/10.1016/j.jhydrol.2003.11.010>
- Guthery, F. S., Brennan, L. A., Peterson, M. J., & Lusk, J. J. (2005). Information theory in wildlife science: Critique and viewpoint. *Journal of Wildlife Management*, 69, 457– 465.
- Hanby, J. P., Byggtot, J. D., & Packer, C. (1995). Ecology, demography, and behaviour of lions in two contrasting habitats: Ngorongoro Crater and the Serengeti plains. In A. R. E. Sinclair, & P. Arcese (Eds.), *Serengeti II: Dynamics, management, and conservation of an ecosystem* (pp. 315– 331). Chicago, IL: Chicago University Press.
- Hanby, J. P., & Bygott, J. D. (1987). Emigration of sub-adult lions. *Animal Behaviour*, 35, 161– 169. [https://doi.org/10.1016/S0003-3472\(87\)80221-X](https://doi.org/10.1016/S0003-3472(87)80221-X)
- Hansen, A. J. (2011). Contribution of source-sink theory to protected area science. In J. Liu, V. Hull, A. Morzillo, & J. Wiens (Eds.), *Sources, Sinks, and Sustainability across Landscapes* (pp. 339– 360). Cambridge, UK: Cambridge University Press.
- Hayward, M. W., O'Brien, J., & Kerley, G. I. H. (2007). Carrying capacity of large African predators: Predictions and tests. *Biological Conservation*, 139, 219– 229. <https://doi.org/10.1016/j.biocon.2007.06.018>
- Heinsohn, R., Packer, C., & Pusey, A. E. (1996). Development of co-operative territoriality in juvenile lions. *Proceedings of the Royal Society, London, Series B*, 263, 475– 479.
- Henschel, P., Coad, L., Burton, C., Chataigner, B., Dunn, A., MacDonald, D., ... Hunter, L. T. (2014). The lion in West Africa is critically endangered. *PLoS One*, 9, e83500. <https://doi.org/10.1371/journal.pone.0083500>

Hooge, P. M., & Eichenlaub, B. (2000). Animal movement extension to ArcView. Ver, 2.

Hornseth, M. L., Walpole, A. A., Walton, L. R., Bowman, J., Ray, J. C., Fortin, M. J., & Murray, D. L. (2014). Habitat loss, not fragmentation, drives occurrence patterns of Canada lynx at the southern range periphery. *PLoS One*, 9, e113511. <https://doi.org/10.1371/journal.pone.0113511>

Johnson, W. E., Onorato, D. P., Roelke, M. E., Land, E. D., Cunningham, M., Belden, R. C., ... O'Brien, S. J. (2010). Genetic restoration of the Florida panther. *Science*, 329, 1641– 1645. <https://doi.org/10.1126/science.1192891>

Kéry, M., Masden, J., & Lebreton, J.-D. (2006). Survival of Svalbard pink-footed geese *Anser brachyrhynchus* in relation to winter climate, density and land-use. *Journal of Animal Ecology*, 75, 1172– 1181. <https://doi.org/10.1111/j.1365-2656.2006.01140.x>

Kie, J. G. (2013). A rule-based ad hoc method for selecting a bandwidth in kernel home-range analyses. *Animal Biotelemetry*, 1, 13. <https://doi.org/10.1186/2050-3385-1-13>

Kotze, R., Keith, M., Winterbach, C. W., Winterbach, H. E., & Marshal, J. P. (2018). The influence of social and environmental factors on organization of African lion (*Panthera leo*) prides in the Okavango Delta. *Journal of Mammalogy*, 99, 845– 858. <https://doi.org/10.1093/jmammal/gyy076>

Laake, J. L. (2013). RMark: An R Interface for analysis of capture-recapture data with MARK. Seattle, WA: ASFC Processed Report 2013–01. Alaska Fisheries Science Centre, NOAA, National Marine Fisheries Service.

Lebreton, J. D., Burnham, K. P., Clobert, J., & Anderson, D. R. (1992). Modelling survival and testing biological hypothesis using marked animals: A unified approach with case studies. *Ecological Monographs*, 62, 67– 118.

Loveridge, A. J., Valeix, M., Davidson, Z., Murindagomo, F., Fritz, H., & Macdonald, D. (2009). Changes in home range size of African lions in relation to pride size and prey biomass in a semi-arid savannah. *Ecography*, 32, 953– 962. <https://doi.org/10.1111/j.1600-0587.2009.05745.x>

Martinez Cano, I., Taboada, F. G., Naves, J., Fernández-Gil, A., & Wiegand, T. (2016). Decline and recovery of a large carnivore: Environmental change and long-term trends in an endangered brown bear population. *Proceedings of the Royal Society, London, Series B*, 283, 20161832.

McCarthy, T. S., & Ellery, W. N. (1998). The Okavango Delta. *Transactions of the Royal Society of South Africa*, 53, 157– 182. <https://doi.org/10.1080/00359199809520384>

Metcalf, C. J. E., Hampson, K., & Koons, D. N. (2007). What happens if density increases? Conservation implications of population influx into refuges. *Animal Conservation*, 10, 478– 486. <https://doi.org/10.1111/j.1469-1795.2007.00138.x>

- Midlane, N. (2013). The conservation status and dynamics of a protected African lion *Panthera leo* population in Kafue National Park, Zambia. University of Cape Town. PhD Thesis.
- Mosser, A. (2008). Group territoriality of the African lion: Behavioural adaptation in a heterogeneous landscape. University of Minnesota. PhD Thesis.
- Mosser, A., & Packer, C. (2009). Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. *Animal Behaviour*, 78, 359– 370. <https://doi.org/10.1016/j.anbehav.2009.04.024>
- Mukul, S. A., Alamgir, M., Sohel, M. S. I., Pert, P. L., Herbohn, J., Turton, S. M., ... Laurance, W. F. (2019). Combined effects of climate change and sea-level rise project dramatic habitat loss of the globally endangered Bengal tiger in the Bangladesh Sundarbans. *Science of the Total Environment*, 663, 830– 884. <https://doi.org/10.1016/j.scitotenv.2019.01.383>
- Murray-Hudson, M. M., Wolski, P., Cassidy, L., Brown, M. T., Thito, K., Kashe, K., & Mosimanyana, E. (2014). Remote sensing-derived hydroperiod as a predictor of floodplain vegetation composition. *Wetland Ecology and Management*, 23, 603– 616.
- Murray-Hudson, M. M., Wolski, P., Murray-Hudson, F., Brown, M. T., & Kashe, K. (2014). Disaggregating hydroperiod: Components of the seasonal flood pulse as drivers of plant species distribution in floodplains of a tropical wetland. *Wetlands*, 34, 927– 942. <https://doi.org/10.1007/s13157-014-0554-x>
- Ogutu, J. O., & Dublin, H. T. (2002). Demography of lions in relation to prey and habitat in the Masai Mara National Reserve, Kenya. *African Journal of Ecology*, 40, 120– 129.
- Ordiz, A., Støen, O. G., Swenson, J. E., Kojola, I., & Bischof, R. (2008). Distance-dependent effect of the nearest neighbour: Spatiotemporal patterns in brown bear reproduction. *Ecology*, 38, 3327– 3335.
- Packer, C., Hilborn, R., Mosser, A., Kissui, B., Borner, M., Hopcraft, G., ... Sinclair, A. R. E. (2005). Ecological change, group territoriality, and population dynamics in Serengeti lions. *Science*, 436, 927– 928. <https://doi.org/10.1126/science.1105122>
- Packer, C., Pusey, A. E., & Eberly, L. E. (2001). Egalitarianism in female African lions. *Science*, 293, 690– 693. <https://doi.org/10.1126/science.1062320>
- Packer, C., Scheel, D., & Pusey, A. E. (1990). Why lions form groups: Food is not enough. *American Naturalist*, 136, 1– 19. <https://doi.org/10.1086/285079>
- Pennycuik, C. J., & Rudnai, J. (1970). A method of identifying individual lions *Panthera leo* with an analysis of the reliability of identification. *Journal of Zoology*, 160, 497– 508. <https://doi.org/10.1111/j.1469-7998.1970.tb03093.x>

- Portier, C., Festa-Bianchet, M., Gaillard, J.-M., Jorgenson, J. T., & Yoccoz, N. G. (1998). Effects of density and weather on survival of bighorn sheep lambs (*Ovis canadensis*). *Journal of Zoology*, 245, 271– 278. <https://doi.org/10.1111/j.1469-7998.1998.tb00101.x>
- Post, E., Peterson, R. O., Stenseth, N. C., & McLaren, B. E. (1999). Ecosystem consequences of wolf behavioural response to climate. *Nature*, 401, 905– 907. <https://doi.org/10.1038/44814>
- Pusey, A. E., & Packer, C. (1987). The evolution of sex-biased dispersal in lions. *Behaviour*, 101, 275– 310. <https://doi.org/10.1163/156853987X00026>
- R Core Team (2018). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Rabinowitz, A., & Zeller, K. A. (2010). A range-wide model of landscape connectivity and conservation for the jaguar, *Panthera onca*. *Biological Conservation*, 143, 939– 945. <https://doi.org/10.1016/j.biocon.2010.01.002>
- Ramberg, L., Hancock, P., Lindholm, M., Meyer, T., Ringrose, S., Silva, J., ... Vanderpost, C. (2006). Species diversity in the Okavango Delta, Botswana. *Aquatic Sciences*, 68, 310– 337.
- Riggio, J., Jacobson, A., Dollar, L., Bauer, H., Becker, M., Dickman, A., ... Pimm, S. (2013). The size of savannah Africa: A lion's (*Panthera leo*) point of view. *Biodiversity Conservation*, 22, 17– 35.
- Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., ... Wirsing, A. J. (2014). Status and Ecological Effects of the World's Largest Carnivores. *Science*, 343, 1241484. <https://doi.org/10.1126/science.1241484>
- Roelke-Parker, M. E., Munson, L., Packer, C., Kock, R., Cleveland, S., Carpenter, M., ... Appel, M. J. G. (1996). A canine distemper virus epidemic in Serengeti lions (*Panthera leo*). *Nature*, 379, 441– 445. <https://doi.org/10.1038/379441a0>
- Rosenblatt, E., Becker, M. S., Creel, S., Droge, E., Mweetwa, T., Schuette, P. A., ... Mwape, H. (2014). Detecting declines of apex carnivores and evaluating their causes: An example with Zambian lions. *Biological Conservation*, 180, 176– 186. <https://doi.org/10.1016/j.biocon.2014.10.006>
- Sahanatien, V., & Derocher, A. E. (2012). Monitoring sea ice habitat fragmentation for polar bear conservation. *Animal Conservation*, 15, 397– 406.
- Schaller, G. B. (1972). The Serengeti lion: A study of predator prey relations. Chicago, IL: Chicago University Press.
- Schielzeth, H. (2010). Simple means to improve interpretability of regression coefficients. *Methods in Ecology and Evolution*, 1, 103– 113.

- Skalski, J. R. (1996). Regression of abundance estimates from mark-recapture surveys against environmental covariates. *Canadian Journal of Fisheries and Aquatic Sciences*, 53, 196– 204.
- Smuts, G. L. (1982). *Lion*. Johannesburg, South Africa: Macmillan.
- Trinkel, M., Funston, P., Hofmeyr, M., Hofmeyr, D., Dell, S., Packer, C., & Slotow, R. (2010). Inbreeding and density-dependent population growth in a small, isolated lion population. *Animal Conservation*, 13, 374– 382. <https://doi.org/10.1111/j.1469-1795.2009.00344.x>
- Van Der Waal, K. L., Mosser, A., & Packer, C. (2009). Optimal group size, dispersal decisions and post-dispersal relationships in female African lions. *Animal Behaviour*, 77, 949– 954. <https://doi.org/10.1016/j.anbehav.2008.12.028>
- Van Orsdol, K. G., Hanby, J. P., & Bygott, J. D. (1985). Ecological correlates of lion social organisation (*Panthera leo*). *Journal of Zoology*, 206, 97– 112.
- Van Vuuren, J. H., Hermann, E., & Funston, P. J. (2005). Lions in the Kgalagadi Transfrontier Park: Modelling the effects of human-caused mortality. *International Transactions in Operational Research*, 12, 145– 171.
- Vincent, J. P., Gaillard, J. M., & Bideau, E. (1991). Kilometric index as biological indicator for monitoring forest roe deer populations. *Acta Theorologica*, 36, 315– 328. <https://doi.org/10.4098/AT.arch.91-33>
- Watts, H. E., & Holekamp, K. E. (2009). Ecological determinants of survival and reproduction in the spotted hyena. *Journal of Mammalogy*, 90, 461– 471. <https://doi.org/10.1644/08-MAMM-A-136.1>
- White, G. C., & Burnham, K. P. (1999). Program MARK: survival estimation from populations of marked animals. Retrieved from <http://www.cnr.colostate.edu/gwhite/software/ht-ml>
- Whitman, K. L., & Packer, C. (2007). *A hunter's guide to aging lions in eastern and southern Africa*. Huntington Beach, CA: Long Beach Press.
- Wikramanayake, E., McKnight, M., Dinerstein, E., Joshi, A., Gurung, B., & Smith, D. (2004). Designing a conservation landscape for tigers in human-dominated environments. *Conservation Biology*, 18, 839– 844. <https://doi.org/10.1111/j.1523-1739.2004.00145.x>
- Wolski, P., & Murray-Hudson, M. M. (2006). Reconstruction of 1989–2005 inundation history in the Okavango Delta, Botswana, from archival Landsat imagery. In *Globwetland Symposium*, Frascati, Italy: ESA-ESRIN.
- Woodroffe, R. (2000). Predators and people: Using human densities to interpret declines of large carnivores. *Animal Conservation*, 3, 165– 173. <https://doi.org/10.1111/j.1469-1795.2000.tb00241.x>

Woodroffe, R., & Ginsberg, J. R. (1998). Edge effects and the extinction of populations inside protected areas. *Science*, 280, 2126– 2128. <https://doi.org/10.1126/science.280.5372.2126>

Worton, B. J. (1995). Using Monte-Carlo simulation to evaluate kernel-based home range estimators. *Journal of Wildlife Management*, 59, 794– 800. <https://doi.org/10.2307/3801959>