

# Context dependency of top-down, bottom-up and density-dependent influences on cheetah demography

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## Abstract

1. Research on drivers of demographic rates has mostly focused on top predators and their prey, and comparatively less research has considered the drivers of mesopredator demography. Of those limited studies, most focused on top-down effects of apex predators on mesopredator population dynamics, whereas studies investigating alternative mechanisms are less common.
2. In this study, we tested hypotheses related to top-down, bottom-up and density-dependent regulation of demographic rates in an imperilled mesopredator, the cheetah (*Acinonyx jubatus*).
3. We used a 25-year dataset of lion density, cheetah density and prey density from the Mun-Ya-Wana Conservancy in South Africa and assessed the effects of top-down, bottom-up and density-dependent drivers on cheetah survival and reproduction.
4. In contrast to the top-down and bottom-up predictions, both adult and juvenile cheetahs experienced the lowest survival during months with high prey densities and low lion densities. We observed support only for a density-dependent response in juvenile cheetahs, where they had a higher probability of reaching independence during times with low cheetah density and low prey density. We did not identify any strong drivers of litter size.
5. Collectively, our results indicate that high apex predator abundance might not always have negative effects on mesopredator populations, and suggest that context dependency in top-down, bottom-up and density-dependent factors may regulate demographic rates of cheetahs and other mesopredators. Our results highlight the complexities of population-level drivers of cheetah demographic rates and the importance of considering multiple hypotheses of mesopredator population regulation.

## KEYWORDS

*Acinonyx jubatus*, cheetah, demography, density dependence, mesopredator, reproduction, survival

## 1 | INTRODUCTION

Understanding drivers of population dynamics is a central theme of ecology and can help inform the conservation and management of imperilled species. Historically, research has attempted to identify top-down, bottom-up and density-dependent influences on survival, reproduction and overall population growth in a variety of systems (Hairston, Smith, & Slobodkin, 1960; Hanski, 1990; McNaughton, Oesterheld, Frank, & Williams, 1989). However, most previous research on population dynamics has focused on classic predator–prey systems, in which linkages exist between predators and their prey, and between prey and primary producers that they consume (Owen-Smith, Mason, & Ogutu, 2005; Sinclair & Krebs, 2002). In systems with higher-ranking apex predators and lower-ranking, subordinate predators (hereafter, ‘mesopredators’), the population dynamics of all trophic levels might differ from those in which there is only a single predator. Mesopredators often compete with apex predators for resources, and apex predators and mesopredators sometimes exhibit intraguild predation, in which the apex predator kills the mid-ranking predator (Palomares & Caro, 1999). As a result, the suite of factors influencing mesopredator population dynamics might be more complex than those in simple predator–prey systems.

Mesopredator population dynamics are frequently attributed to the processes of mesopredator suppression or mesopredator release, in which the density or abundance of an apex predator affects the population size, distribution, or behaviour of the mesopredator (Prugh et al., 2009; Ritchie & Johnson, 2009). However, the effects of apex predators on mesopredator populations remain equivocal in the literature (Crimmins et al., 2016; Gehrt & Prange, 2007). In addition, studies on mesopredator suppression or release often do not consider other mechanisms of population regulation for mesopredators, although research suggests that factors such as environmental productivity or prey availability can modulate mesopredator suppression (Elmhagen & Rushton, 2007; Greenville, Wardle, Tamayo, & Dickman, 2014; Pasanen-Mortensen et al., 2017). As a result, investigations into mesopredator demography should, ideally, compare the strength and interaction of top-down, bottom-up and density-dependent drivers simultaneously.

The cheetah (*Acinonyx jubatus*) is an ideal species with which to investigate ecological drivers of mesopredator population regulation. Although cheetahs are large in body size, they are mid-ranking predators in the African carnivore community (Swanson et al., 2014; Vanak et al., 2013) and thus might be influenced by both top-down and bottom-up factors. Cheetahs are subordinate to lions (*Panthera leo*) that predate on them (Laurenson, 1994; Mills & Mills, 2014). However, while predation by lions has been found to be the main cause of natural mortality in cheetahs in the Serengeti (Laurenson, 1994), a recent analysis of cheetah population sizes in relation to lion population sizes suggests that predation by, and competition with, lions might not scale up to population-level effects on cheetahs (Swanson et al., 2014). Therefore, other factors such as prey or conspecific densities could be at play in affecting specific demographic processes in cheetahs (Durant, Kelly, & Caro, 2004).

Additionally, cheetahs are a species of conservation concern (Durant et al., 2017; Weise et al., 2017) and future management activities could influence the sustained persistence of this species. Therefore, understanding the top-down, bottom-up and density-dependent factors associated with cheetah population regulation is critical. Previous work has examined demographic trends in cheetah populations in large unfenced protected areas (Durant et al., 2004; Kelly et al., 1998) and in agricultural-dominated areas (Marker, Dickman, Jeo, Mills, & Macdonald, 2003), but little research exists on the drivers of cheetah demography in fenced reserves, beyond purely descriptive statistics (Bissett & Bernard, 2011). Understanding drivers of cheetah demography in fenced reserves is particularly important because they represent an important component for the persistence of cheetahs (Buk, van der Merwe, Marnewick, & Funston, 2018; Durant et al., 2017). These fenced populations are also subjected to management-induced changes in apex predator, prey and conspecific densities (Balme, Slotow, & Hunter, 2009; Kettles & Slotow, 2009), which provides an ideal situation to test multiple hypotheses related to drivers of mesopredator demography.

We used a 25-year dataset of cheetah reproduction and survival to investigate support for three competing hypotheses of mesopredator population regulation: (a) cheetah reproduction and survival would be driven by lion densities (top-down regulation; Hairston et al., 1960), (b) cheetah reproduction and survival would be driven by prey densities (bottom-up regulation; McNaughton et al., 1989), and (c) cheetah reproduction and survival would be driven by cheetah densities (density-dependent regulation; Hanski, 1990). Under the top-down hypothesis, we predicted that cheetah litter sizes, survival and recruitment would be negatively related to lion density. Under the bottom-up hypothesis, we predicted that cheetah litter sizes, survival and recruitment would be positively related to prey density. Under the density-dependent hypothesis, we predicted that cheetah litter sizes, survival and recruitment would be negatively related to cheetah density. In addition, we predicted that drivers of demographic rates might be context-dependent, in that top-down, bottom-up, and density-dependent factors would interact. By understanding drivers of cheetah demography, we can better identify factors that might promote high rates of cheetah population growth, and develop a greater understanding of the complex factors that might regulate mesopredator populations.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

We studied cheetah demographics in Mun-Ya-Wana Conservancy (Phinda Private Game Reserve), in northern KwaZulu-Natal, South Africa, from 1992 to 2018. The elevation of Mun-Ya-Wana Conservancy ranges from 4 to 201 m above sea level, and the dominant vegetation type is broadleaf woodland, with open grasslands and semi-open wooded grasslands interspersed throughout the reserve. The climate is subtropical with warm, dry winters

(April–September) and hot, humid summers (October–March). The average annual rainfall is 550 mm, with the majority of rain falling in the summer (Janse van Rensburg, McMillan, Giżejewska, & Fattebert, 2018). The Mun-Ya-Wana Conservancy is surrounded by electrified game fencing and has grown in size as adjacent reserves have joined the Conservancy. From 1990 to 2004, the study area was 170 km<sup>2</sup> in area, after which time a fence was removed and the Conservancy expanded to 235 km<sup>2</sup> (Druce, Pretorius, & Slotow, 2008). Cheetahs and lions were reintroduced into the reserve in 1992 and have been monitored since (Hunter, 1998; Hunter et al., 2007; this study). The average cheetah density (0.10 cheetahs/km<sup>2</sup>) and the average lion density (0.11 lions/km<sup>2</sup>) in our study area were similar to those of other fenced reserves (0.001–0.29 cheetahs/km<sup>2</sup>, Buk et al., 2018; 0.02–0.17 lions/km<sup>2</sup>, Miller & Funston, 2014), but higher than the densities of cheetahs and lions in some unfenced protected areas such as Serengeti National Park (0.06 lions/km<sup>2</sup>, Bauer & Van Der Merwe, 2004; 0.005 cheetah/km<sup>2</sup>, Durant et al., 2017).

## 2.2 | Carnivore monitoring

To ensure even monitoring, we subdivided the reserve into seven sections, and trained monitors typically drove the roads in each section at least once a week. In addition, monitors frequently followed up on sightings reported by game rangers conducting game drives within the reserve. Cheetahs and lions can be individually recognized using their spot patterns, whisker spots and scars, which allowed us to monitor the populations based on sightings alone (Caro, 1994). We included data from sightings only where the identity of the animals was known with complete certainty. We obtained an average of  $32 \pm 2$  cheetah sightings per month and an average of  $18 \pm 1$  lion pride sightings per month. We used data from 1992 to 2018 for general descriptive statistics (litter sizes, causes of death), but restricted our analyses of drivers of litter size, recruitment and survival to 2008–2018 (Figure S1).

When cheetahs or lions were observed, we recorded the location, behaviour and number of individuals present. We divided the total monthly cheetah or lion population size, including cubs, by the total area of the reserve to obtain monthly densities. However, we occasionally were not sure of the status of a cheetah or lion if we were unable to sight it or determine whether it was dead. Therefore, we removed individuals from the monthly population count if they had not been seen in 6 months, given that the probability of survival is  $<0.005$  if an animal is not seen for that long (this study). Cubs are rarely included in density estimates for large cats; however, we included them in our analyses because they comprised a large portion of the total felid biomass present and because older cubs are functional similar to adults in their food requirements. Our study area, along with most small fenced reserves, actively manages their lion populations through removals, introductions and female contraception (Ferreira & Hofmeyr, 2014; Miller et al., 2013). Therefore, fluctuations in the lion density within our study area were primarily the result of management actions, which allowed to us focus specifically

on drivers of cheetah demographics, without simultaneously assessing drivers of changes in lion density.

## 2.3 | Prey density

We estimated prey density in the reserve by collecting distance sampling data on impala (*Aepyceros melampus*) and nyala (*Tragelaphus angasii*) during the dry season (April–September) and the wet season (October–March) from 2010 to 2015 (Appendix S2). We limited our prey analyses to these species because they comprised 82% of cheetah kills in the study area (Hunter, 1998). We estimated prey abundance using hierarchical distance sampling models with spatial covariates on both the abundance and detection processes (Royle, Dawson, & Bates, 2004; Sillett, Chandler, Royle, Kéry, & Morrison, 2012), and used our top model to extrapolate prey abundance over our entire study period (Appendix S2). We divided the total seasonal prey abundances by the total area of the reserve to obtain seasonal densities.

## 2.4 | Cheetah reproductive output

We studied top-down, bottom-up and density-dependent effects on cheetah litter sizes. Reproduction in carnivores can be influenced by top-down, bottom-up and density-dependent drivers by the mechanisms of food limitation, female body condition or stress (Creel, Creel, Mills, & Monfort, 1997; Fuller & Sievert, 2001; Tannerfeldt & Angerbjörn, 1998). When a female cheetah was first seen with a new litter, we estimated the age of the cubs based on their size, following Caro (1994). Because cheetahs are hard to locate when they are denning, our litter sizes were typically counts of cubs after they had emerged from dens. Previous research suggests that some cub mortality occurs while still in the den (Laurenson, 1994; Mills & Mills, 2014) so we recognize that our counts might be biased low. However, post-emergence counts of litters have been used in similar studies of cheetah reproductive output (Bissett & Bernard, 2011; Kelly et al., 1998).

We analysed drivers of cheetah litter size using Generalized Linear Models with a generalized Poisson error distribution (Kendall & Wittmann, 2010) in Program R (Version 3.5.3; R Core Team, 2019). Litter sizes can be influenced by environmental conditions pre-conception and during gestation (Lack, 1948). Cheetahs can give birth at any time during the year, and cheetah gestation lasts approximately 3 months (Kelly et al., 1998); therefore, we calculated the average of our covariates of interest in the 6 months prior to a litter being born to incorporate effects during the pre-gestation and gestation time periods. We specified nine a priori models based on our hypotheses of interest related to litter size and considered covariates of monthly lion density, monthly prey density, monthly cheetah density and additive models, and models with interactions between pairs of covariates. Prior to this analysis, and all subsequent analyses, we assessed collinearity between continuous covariates using a Pearson correlation to determine whether any should be excluded from analysis ( $|r| > .75$ ).

For all analyses, we compared models using Akaike's information criterion corrected for sample size ( $AIC_c$ ; Burnham & Anderson, 2002), considered models within  $2 \Delta AIC_c$  of the top model to be competitive and evaluated whether covariates were informative by calculating 85% confidence intervals (Arnold, 2010).

## 2.5 | Cheetah recruitment

We analysed the probability of cubs reaching adulthood. Independence in cheetahs is typically marked by an abrupt and clear separation from the mother (Hunter, 1998), so we calculated age at independence to the nearest month after it was unequivocal that separation from the mother had occurred. Based on this criterion, we also calculated the percentage of litters with at least one cub reaching independence and the percentage of total cubs reaching independence. For each cub, we treated recruitment as a binary variable and used logistic regression to evaluate the relationship between recruitment and top-down, bottom-up and density-dependent drivers. We averaged lion density, prey density and cheetah density across the entire time period when a cheetah was a cub. Because cubs from the same litter might represent non-independent samples (Pettorelli & Durant, 2007), we included litter as a random effect. We specified nine a priori models and considered covariates of lion density, prey density, cheetah density and additive models, and models with interactions between pairs of covariates.

## 2.6 | Cheetah survival

We analysed drivers of cheetah monthly survival from February 2009 to March 2018. Because the cheetah population was intensively monitored and the reserve was surrounded by electric game fencing, we were able to determine the cause and time of death for most cheetahs. When a dead cheetah was recovered, we attempted to determine the cause of death by examining the carcass and the surrounding area for tracks and scat. For each month, we recorded if individual cheetahs were sighted or recovered dead as adults or cubs. If a cheetah was removed from the reserve for management purposes, we censored that individual animal from analyses. Because lion and cheetah density can vary greatly within a season, and because cubs can be born and become independent at any time during the year, we conducted our analysis on a monthly time-scale to best reflect the conditions that might be driving survival. We calculated the average prey density for each season, and the average lion density and cheetah density for every month, and used these values as covariates. In addition, we calculated the average prey density in the 6 months prior to every month to investigate a potential resource time-lag effect.

### 2.6.1 | Model structure

We analysed cheetah survival using multi-state joint live-encounter dead-recovery models (Barker, White, & McDougall, 2005) using the *R*MARK *R* package (Laake, 2013). This model made use of our frequent

resightings and mortality data, and also allowed for survival estimation based on individuals that were never recorded as dead. In addition, because juvenile cheetahs stay with their mothers for variable amounts of time (Kelly et al., 1998), we could not incorporate a standard age structure into our models. Thus, we used a multi-state approach to estimate survival for both cubs and adults simultaneously. We specified the two model states as cub (juvenile cheetahs dependent on their mother) and adult (cheetahs that were independent from their mother). The study area is surrounded by electric game fencing that cheetahs very rarely penetrated. Accordingly, we did not incorporate immigration or emigration into our models.

### 2.6.2 | Hypothesis testing

We performed model selection in a multi-step approach to determine the appropriate model structure, before testing for covariate relationships (Cubaynes et al., 2014; Doherty, White, & Burnham, 2012). We first tested for seasonal or yearly effects on resighting rates ( $p$ ) while holding survival rates ( $S$ ) and reporting rates ( $r$ ) constant, and ranked models using  $AIC_c$ . Using our top resighting model, we next tested for effects of season and sex on survival rates, while holding reporting rate constant. It is hard to determine the sex of young cheetah cubs, so we only considered the effects of sex for adult cheetahs. Because of convergence issues, we were unable to test for yearly effects on survival. However, given pronounced differences in climatic conditions between wet and dry seasons at our study area, we felt that seasonal variation would be the more important temporal driver of survival. To aid in model convergence for our covariate models, we simplified our best structural model by grouping time periods or sexes that did not differ.

Finally, using our top simplified structural model, we tested for the effects of environmental covariates on cheetah survival. We developed 12 a priori models based on our hypotheses of interest that included covariates of monthly lion density, monthly prey density, monthly cheetah density, average prey density in the 6 months prior, and additive and multiplicative models with the same covariates. Because adults and cubs are known to have different survival rates (Kelly et al., 1998), we did not consider any models in which state was not included.

## 3 | RESULTS

### 3.1 | Reproductive parameters

We collected data on 61 cheetah litters from 1992 to 2018. The average litter size was  $3.26 \pm 0.17$ , and the average age at first reproduction for females was  $28.1 \pm 1.8$  months. Litters became independent at an average of  $16.7 \pm 1.0$  months, and mothers had an inter-birth interval of  $19.4 \pm 2.4$  months. Based on litters from 2008 to 2018, litter size variation was best described by the null model, but also by models including lion density and prey density (Table 1). However, the confidence intervals of the parameter estimates for lion density ( $\beta = 3.71$ ; 85% CI =  $-1.75$  to  $7.71$ ) and prey

**TABLE 1** Model selection results for cheetah litter size regression models, Mun-Ya-Wana Conservancy, KwaZulu-Natal, South Africa, 2008–2018

Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	$-2 \times \ln(L)^a$	$w^b$	$k^c$
Null	155.2	0	-76.55	0.33	1
Lion density	156.2	1.04	-75.97	0.19	2
Prey density	156.4	1.25	-76.07	0.18	2
Cheetah density	157.3	2.15	-76.52	0.11	2
Prey density + lion density	158.4	3.19	-75.89	0.07	3
Prey density + cheetah density	158.4	3.25	-75.92	0.06	3
Prey density + lion density + cheetah density	160.5	5.33	-75.74	0.02	4
Prey density $\times$ cheetah density	160.5	5.35	-75.75	0.02	4
Prey density $\times$ lion density	160.8	5.61	-75.89	0.02	4

<sup>a</sup>Log-likelihood.

<sup>b</sup>Akaike model weight.

<sup>c</sup>Number of model parameters.

density ( $\beta = -0.01$ ; 85% CI =  $-0.03$  to  $0.01$ ) overlapped 0, indicating that they were uninformative.

### 3.2 | Cheetah recruitment

We included 119 cubs from 40 litters from 2008 to 2018 in our analysis of recruitment. At least one cub reached independence in 56.7% of litters, and 41.5% of all cubs reached independence. Probability of recruitment was best described by a model with an interaction between cheetah density and prey density (Table 2). Based on this model, cheetahs had the highest probability of reaching independence if they were cubs during times of low prey density and low cheetah density (Figure 1).

### 3.3 | Survival

Of the 239 cheetahs monitored over the course of the study (1992–2018), 43.9% ( $n = 105$ ) died from unknown causes, 21.8% ( $n = 52$ ) had a known cause of death, and 9.2% ( $n = 22$ ) were still alive at the completion of this study. In addition, 52 cheetahs were translocated to other reserves and 8 cheetahs were known to have escaped the reserve in the months following reintroduction.

Predation accounted for 84.6% ( $n = 44$ ) of known deaths, accounting for 93.8% ( $n = 30$ ) of cub mortality and 70% ( $n = 14$ ) of adult mortality. Of the predation deaths, lions accounted for 63.3% ( $n = 19$ ) of cub predation and 35.7% ( $n = 5$ ) of adult predation, leopards accounted for 3.3% ( $n = 1$ ) of cub predation and 21.4% ( $n = 3$ ) of adult predation, hyaenas accounted for 7.1% ( $n = 1$ ) of adult predation, and unknown predators accounted for 20.0% ( $n = 6$ ) of cub predation and 7.1% ( $n = 1$ ) of adult predation. Adult cheetahs killed other cheetahs in 28.6% ( $n = 4$ ) of adult predation deaths and 13.3% ( $n = 4$ ) of cub predation deaths. Other sources of mortality included vehicle collisions ( $n = 2$ ), cub abandonment ( $n = 1$ ), injury ( $n = 2$ ) and snaring ( $n = 3$ ).

We included 138 cheetahs in our survival analysis from for a total of 110 months. Our best structural model included effects of year and season on resighting rates and effects of season and sex on survival (Table 3). Resighting rates were similar in most years

(Figure S3) with the exception of a lower average resighting rate in 2014 (0.48; 85% CI =  $0.42$ – $0.53$ ) and a higher average resighting rate in 2018 (0.95; 85% CI =  $0.87$ – $1.00$ ). However, resighting rates were similar between wet seasons (0.60; 85% CI =  $0.58$ – $0.62$ ) and dry seasons (0.63; 85% CI =  $0.61$ – $0.66$ ; Figure S4). Based on the top structural model, survival did not differ between males (0.98; 85% CI =  $0.969$ – $0.987$ ) and females (0.96; 85% CI =  $0.953$ – $0.974$ ; Figure S5). Across all cheetahs, survival was higher in wet seasons (0.96; 85% CI =  $0.954$ – $0.972$ ) compared to dry seasons (0.94; 95% CI =  $0.926$ – $0.948$ ; Figure S6). Based on these results, our final structural model for evaluating environmental covariates included effects of year on resighting rates and season on survival.

Survival was best described by a model with an interaction between monthly lion density and monthly prey density (Table 4). In contrast to predictions of top-down and bottom-up regulation, adults and cubs both experienced the lowest survival rates in months with high prey density and low lion density (Figure 2). At the lowest lion density (0.06 lions/km<sup>2</sup>), the odds of cub survival decreased by 27.6% for every 1-unit increase in prey density. At the highest prey density (46 prey/km<sup>2</sup>), the odds of cub survival increased 35.4% for every 1-unit increase in lion density (Figure S7). Similarly, at the lowest lion density, the odds of adult survival decreased by 21.4% for every 1-unit increase in prey density, and at the highest prey density, the odds of adult survival increased by 44.1% for every 1-unit increase in lion density (Figure S7). Based on the top model, adult cheetahs had an average monthly survival rate of 0.97 (85% CI =  $0.95$ – $0.98$ ), whereas cheetah cubs had an average monthly survival rate of 0.91 (85% CI =  $0.88$ – $0.94$ ).

## 4 | DISCUSSION

We found evidence suggesting that cheetah demographic rates, particularly survival and recruitment, varied in their sensitivity to top-down, bottom-up and density-dependent factors, although not always in the manner classically predicted in predator-prey systems. In particular, the recruitment, reproduction and survival rates of



	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	$-2 \times \ln(L)^a$	w <sup>b</sup>	k <sup>c</sup>
Cheetah density × prey density	115.96	0	-52.72	0.34	5
Cheetah density + prey density	116.00	0.04	-53.83	0.33	4
Cheetah density + lion density + prey density	117.93	1.96	-53.70	0.13	5
Cheetah density + lion density	119.04	3.08	-55.35	0.07	4
Cheetah density × lion density	119.78	3.81	-54.62	0.05	5
Cheetah density	120.92	4.95	-57.35	0.03	3
Lion density × prey density	121.15	5.19	-55.31	0.03	5
Prey density	121.96	5.99	-57.87	0.02	3
Lion density + prey density	122.40	6.44	-57.03	0.01	4
Lion density	124.09	8.12	-58.94	0.01	3
Null	131.37	15.41	-63.63	0.00	2

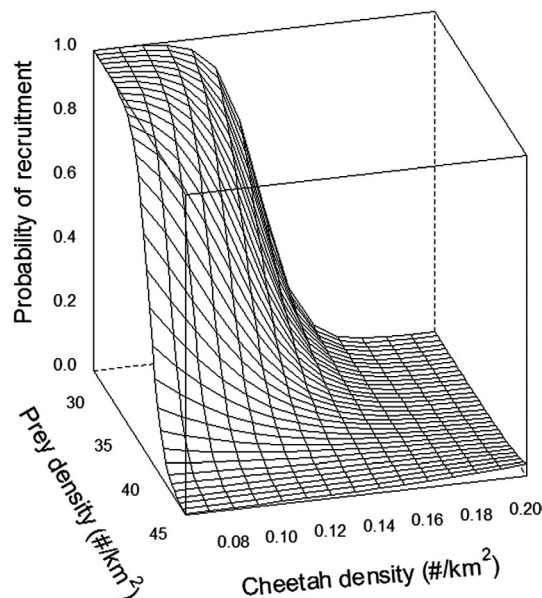
<sup>a</sup>Log-likelihood.

<sup>b</sup>Akaike model weight.

<sup>c</sup>Number of model parameters.

**TABLE 2** Model selection results for cheetah recruitment regression models, Mun-Ya-Wana Conservancy, KwaZulu-Natal, South Africa, 2008–2018

cheetahs did not appear to be negatively affected by high lion densities, which does not follow the predictions of mesopredator suppression (Prugh et al., 2009; Ritchie & Johnson, 2009). In contrast, survival was typically higher for both cubs and adults during periods of high lion density, but the strength of that effect depended on the density of prey. Further, a density-dependent effect on recruitment was observed, but only during periods of low prey availability. Collectively, our results highlight the context dependency in population-level top-down, bottom-up and density-dependent drivers of cheetah demographic rates, and the importance of simultaneously considering multiple mechanistic hypotheses of mesopredator regulation (Elmhagen & Rushton, 2007; Pasanen-Mortensen et al., 2017).



**FIGURE 1** Probability of cub recruitment in relation to cheetah density and prey density, Mun-Ya-Wana Conservancy, KwaZulu-Natal, South Africa, 2008–2018

## 4.1 | Reproduction

Our findings suggest that cheetah litter size was not as sensitive to top-down, bottom-up or density-dependent factors as other demographic parameters. There are likely several reasons for why we did not identify any strong drivers of cheetah litter size. First, we might not have seen density-dependent changes in litter size because density-dependent reproduction often occurs as a result of resource depletion or poor body condition of females (Fuller & Sievert, 2001). Although prey densities in our study area fluctuated, due to intensive management, there were no prolonged periods of low prey densities. As a result, even at times of high cheetah density there likely was not high competition for food resources. Second, similar to other carnivores, cheetahs might share a common optimal litter size, which maximizes fitness, but does not vary according to environmental conditions (Gaillard, Nilsen, Odden, Andrén, & Linnell, 2014). Finally, the management of lions in our study area could explain why we did not observe top-down drivers of cheetah litter sizes. Predators and predation risk have been found to reduce reproductive rates and litter sizes in some species (Karels, Byrom, Boonstra, & Krebs, 2000; Korpimäki, Norrdahl, & Valkama, 1994). However, in our study area the lion population was intensively managed within the reserve, and it might be managed at densities that are too low to affect cheetah reproductive rates.

## 4.2 | Recruitment

In contrast to litter size, we did see factors influencing the probability of cubs becoming independent and recruiting into the population. During times with the highest cheetah densities, cubs had a very low probability of reaching independence, regardless of the prey density (Figure 1). This relationship suggests that resource limitations likely were not driving the observed density-dependent recruitment at the highest cheetah densities. Instead, space

**TABLE 3** Model selection results for structural multi-state joint live-encounter dead-recovery survival models for cheetahs to incorporate variation by time and sex for resighting ( $p$ ) and survival ( $S$ ) rates, Mun-Ya-Wana Conservancy, KwaZulu-Natal, South Africa, 2008–2018

Parameter	Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	$-2 \times \ln(L)^a$	$w^b$	$k^c$
$p$	$p(\text{year} + \text{season})$	3,570.39	0	3,540.02	0.66	15
	$p(\text{year})$	3,571.70	1.31	3,543.38	0.34	14
	$p(\text{season})$	3,584.35	13.96	3,572.29	0.00	6
	$p(\text{null})$	3,584.37	13.98	3,574.33	0.00	5
$S$	$S(\text{sex} + \text{season})$	3,551.37	0	3,533.23	0.80	9
	$S(\text{sex})$	3,554.09	2.72	3,537.98	0.20	8
	$S(\text{season})$	3,578.76	27.39	3,564.67	0.00	7
	$S(\text{null})$	3,584.37	33.01	3,574.33	0.00	5

<sup>a</sup>Log-likelihood.

<sup>b</sup>Akaike model weight.

<sup>c</sup>Number of model parameters.

limitation might be affecting patterns that we observed. Density dependence resulting from space limitations rather than prey availability has been observed in other carnivore species such as wolves (Cubaynes et al., 2014), lions (Kissui & Packer, 2004) and leopards (Balme et al., 2013). Reduced recruitment because of density-dependent space use might be more pronounced when prey resources are limited because there is more competition for high-quality habitats. Indeed, we found that cheetah recruitment was most sensitive to density dependence when prey densities were low. By contrast, cheetahs experienced high recruitment during times of low prey density and low cheetah density. Not only is density dependence heightened when prey is low, but at low densities, prey were likely not distributed in dense aggregations. The lack of

large prey aggregations could have decreased the probability of cheetahs encountering lions (Hebblewhite & Pletscher, 2002), thus increasing the probability of cheetahs surviving long enough to become independent.

#### 4.3 | Survival

Although resources and apex predators affected cheetah survival under certain conditions, the overall direction of response was typically opposite of what is predicted for classic predator-prey systems. In particular, we did not observe negative effects of apex predators on mesopredators, as predicted by the mesopredator suppression hypothesis (Prugh et al., 2009; Ritchie & Johnson, 2009). Our

**TABLE 4** Model selection results for multi-state joint live-encounter dead-recovery survival models for cheetahs, Mun-Ya-Wana Conservancy, KwaZulu-Natal, South Africa, 2008–2018

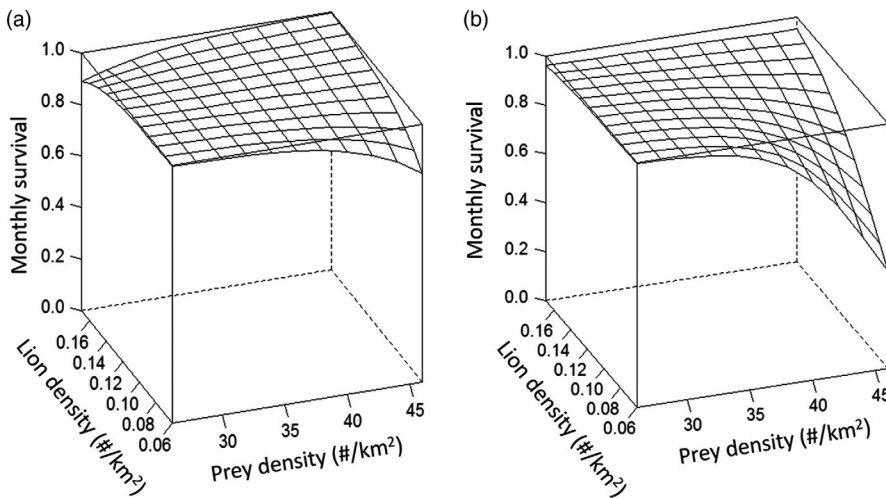
Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	$-2 \times \ln(L)^a$	$w^b$	$k^c$
$S(\text{state:lion density} \times \text{state:prey density})$	3,538.66	0.00	3,518.49	0.94	10
$S(\text{state:cheetah density} + \text{state:lion density} + \text{state:prey density})$	3,545.57	10.23	3,525.41	0.03	10
$S(\text{state:prey density} + \text{state:lion density})$	3,546.69	10.54	3,530.58	0.02	8
$S(\text{state:prey density})$	3,549.04	13.76	3,536.98	0.01	6
$S(\text{state:prey density} + \text{state:cheetah density})$	3,549.68	16.06	3,533.57	0.00	8
$S(\text{state:prey density} \times \text{state:cheetah density})$	3,550.12	16.35	3,529.95	0.00	10
$S(\text{state:average prey density 6 months prior} + \text{state:cheetah density})$	3,567.74	29.52	3,551.63	0.00	8
$S(\text{state:average prey density 6 months prior} + \text{state:lion density})$	3,569.32	33.48	3,553.21	0.00	8
$S(\text{state:average prey density 6 months prior})$	3,573.93	35.45	3,561.86	0.00	6
$S(\text{state:lion density})$	3,577.17	36.19	3,565.11	0.00	6
$S(\text{state:cheetah density})$	3,580.14	43.16	3,568.08	0.00	6
$S(\text{state})$	3,584.37	45.42	3,574.33	0.00	5

Note: States in the model include cubs (juveniles dependent on their mothers) and adults (non-juveniles). All models include effects of year on recovery rates and season on survival rates.

<sup>a</sup>Log-likelihood.

<sup>b</sup>Akaike model weight.

<sup>c</sup>Number of model parameters.



**FIGURE 2** Monthly survival for (a) adult and (b) cub cheetahs in relation to prey density and lion density during dry seasons of years with average resighting rates, Mun-Ya-Wana Conservancy, KwaZulu-Natal, South Africa, 2008–2018

findings contrast with previous work, suggesting that lions suppress cheetah populations (Chauvenet, Durant, Hilborn, & Pettorelli, 2011; Laurenson, 1994), and rather provide support to recent work, which indicates that lions might not have substantial effects on the persistence of cheetahs (Swanson et al., 2014). Much of the research that found significant top-down effects on cheetah dynamics was conducted in large, unfenced protected areas with open habitats (Durant et al., 2004; Kelly et al., 1998; Laurenson, 1994), which highlights the need to understand variation in drivers of cheetah demography, especially in fenced populations. Whereas cheetahs in the Serengeti sometimes move great distances to follow migratory prey (Durant, Caro, Collins, Alawi, & Fitzgibbon, 1988), and are able to immigrate and emigrate, the fenced boundaries of our study area resulted in little seasonal home range shifts and a lack of long-distance dispersal. Contrary to leopards (Fattebert, Balme, Dickerson, Slotow, & Hunter, 2015), the inability of cheetahs to disperse out of the fenced reserve, along with high local concentrations of predators and prey, may result in the changing community-level spatial relationships and behaviour that we hypothesize were the mechanisms behind our observed survival trends. Additionally, our study area contains areas of dense vegetation, which could reduce cheetah mortality from lions by acting as a predation refuge (Mills & Mills, 2014), whereas the open plains of the Serengeti do not offer substantial cover for hiding cheetahs. Research in other systems has also found a lack of strong evidence for top-down regulation of mesopredator populations. For example, recovering wolf (*Canis lupus*) populations in Wisconsin did not limit the abundance of coyotes (*Canis latrans*), potentially because of prey availability or habitat arrangements that benefited coyotes (Crimmins & Van Deelen, 2019). Similarly, research in Australia suggests that dingos (*Canis lupus dingo*) do not exclude feral cats (*Felis catus*) from areas, although top-down effects might be context-dependent (Allen, Allen, & Leung, 2015).

Our results add to the growing literature, suggesting that top-down regulation of mesopredators might not be ubiquitous and that bottom-up or density-dependent factors can modulate the strength of top-down effects (Elmhagen & Rushton, 2007; Pasanen-Mortensen et al., 2017). Under classical predator–prey

theory, top-down influences should be greatest when predators are abundant and bottom-up conditions are limited (Leibold, 1989). By contrast, our results suggest that when lions were at their lowest densities and prey was most readily available, cheetahs exhibited their lowest survival. While seemingly counterintuitive, we believe there are several behavioural trade-offs that potentially explain this pattern. First, cheetahs and lions have been found to use the same general areas on a landscape scale, particularly during times of high prey densities when prey form into large aggregations (Durant, 1998; Vanak et al., 2013). This shared space use could have increased intraguild predation rates. However, cheetahs use fine-scale temporal partitioning to avoid interactions with lions (Broekhuis, Cozzi, Valeix, Mcnutt, & Macdonald, 2013; Rostro-García, Kamler, & Hunter, 2015; Swanson, Arnold, Kosmala, Forester, & Packer, 2016; Vanak et al., 2013). During periods of low lion density, cheetahs might reduce their fine-scale partitioning with lions and thus have higher encounter rates. Similarly, our observed pattern of cheetah survival could be related to changes in cheetah vigilance behaviour. Mesopredators can adjust their anti-predator behaviours under varying levels of predation risk from apex predators. For example, coyotes spend more time vigilant while feeding in areas of high wolf activity (Switalski, 2003). Thus, lower cheetah survival during periods of low lion density might be related to decreased temporal avoidance and vigilance behaviour, which could have increased their risk of attack by lions. A second explanation might be that the behaviour of lions influenced cheetah survival patterns. During times of high prey densities, lions might not have needed to invest as much time and energy on finding and killing prey. Therefore, they could have afforded to spend more time on territorial behaviours and actively pursuing cheetahs, which in turn could reduce cheetah survival rates.

Finally, our observed patterns of survival might also reflect changes in the overall predator community. Although we were only able to include lion density in our models, leopard abundance increased and spotted hyaenas (*Crocuta crocuta*) persisted at low densities within the study area during our study period (Balme et al., 2009). During times of high prey density, multiple top predator species might have used areas of highly aggregated prey and thus increased encounter rates



with cheetahs. In addition, lions occasionally kill and compete with leopards and hyaenas (Balme, Miller, Pitman, & Hunter, 2017; Trinkel & Kastberger, 2005), and leopards, similar to cheetahs, have been found to use fine-scale spatial partitioning to avoid interactions with lions (du Preez, Hart, Loveridge, & Macdonald, 2015; Vanak et al., 2013). Therefore, when lion densities were low and prey densities were high, leopard and hyaenas might have used areas typically used by lions and imposed top-down effects on cheetahs, either through direct interactions or through exploitative competition. Similarly, in many systems worldwide subordinate large carnivores have been found to fill the functional role of extirpated or declining apex predator populations and to induce top-down effects on mesopredator populations (Gompper, 2002; Letnic, Ritchie, & Dickman, 2012; Oakwood, 2000; Ralls & White, 1995).

## 5 | CONCLUSIONS

We highlight the complexities in understanding the ecological drivers of mesopredator population dynamics and the importance of investigating support for multiple, often interacting hypotheses on multiple demographic rates. We found support for hypotheses related to top-down, bottom-up and density-dependent drivers of cheetah survival and recruitment. However, density-dependent recruitment was the only finding that corresponded with classical predictions. Conversely, we found that apex predators and prey affected cheetah survival in the opposite direction to classical linear interpretations based on top-down and bottom-up hypotheses. In addition, we found that different demographic rates differed in their sensitivity to top-down, bottom-up and density-dependent drivers. We showed that high apex predator abundance did not always have negative effects on mesopredator populations, and demonstrated that the processes of mesopredator suppression and release were not be universal across all species and systems.

## ACKNOWLEDGEMENTS

We thank Mun-Ya-Wana Conservancy and Phinda Private Game Reserve for allowing us to conduct research on their land, the numerous employees and volunteers who assisted in the data collection for this research, and J. Janse van Rensburg for providing some of the prey data.

## AUTHORS' CONTRIBUTIONS

L.C.G., D.S.J. and R.S. conceived the ideas; L.T.B.H., J.F. and C.S.-D. collected the data; L.C.G. analysed the data; L.C.G. and D.S.J. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## DATA AVAILABILITY STATEMENT

Data used in this study are archived in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.3d88cs0> (Gigliotti et al., 2019).

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## REFERENCES

- Allen, B. L., Allen, L. R., & Leung, L. K. P. (2015). Interactions between two naturalised invasive predators in Australia: Are feral cats suppressed by dingoes? *Biological Invasions*, 17, 761–776. <https://doi.org/10.1007/s10530-014-0767-1>
- Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management*, 74, 1175–1178. <https://doi.org/10.2193/2009-367>
- Balme, G. A., Batchelor, A., De Woronin Britz, N., Seymour, G., Grover, M., Hes, L., ... Hunter, L. T. B. (2013). Reproductive success of female leopards *Panthera pardus*: The importance of top-down processes. *Mammal Review*, 43, 221–237. <https://doi.org/10.1111/j.1365-2907.2012.00219.x>
- Balme, G. A., Miller, J. R. B., Pitman, R. T., & Hunter, L. T. B. (2017). Caching reduces kleptoparasitism in a solitary, large felid. *Journal of Animal Ecology*, 86, 634–644. <https://doi.org/10.1111/1365-2656.12654>
- Balme, G. A., Slotow, R., & Hunter, L. T. B. (2009). Impact of conservation interventions on the dynamics and persistence of a persecuted leopard (*Panthera pardus*) population. *Biological Conservation*, 142, 2681–2690. <https://doi.org/10.1016/j.biocon.2009.06.020>
- Barker, R. J., White, G. C., & McDougall, M. (2005). Movement of Paradise Shelduck between molt sites: A joint multistate-dead recovery mark-recapture model. *Journal of Wildlife Management*, 69, 1194–1201. [https://doi.org/10.2193/0022-541X\(2005\)069\[1194:MOPSBM\]2.0.CO;2](https://doi.org/10.2193/0022-541X(2005)069[1194:MOPSBM]2.0.CO;2)
- Bauer, H., & Van Der Merwe, S. (2004). Inventory of free-ranging lions *Panthera leo* in Africa. *Oryx*, 38(1), 26–31. <https://doi.org/10.1017/S0030605304000055>
- Bissett, C., & Bernard, R. T. F. (2011). Demography of cheetahs in fenced reserves in South Africa: Implications for conservation. *South African Journal of Wildlife Research*, 41, 181–191. <https://doi.org/10.3957/056.041.0205>
- Broekhuis, F., Cozzi, G., Valeix, M., McNutt, J. W., & Macdonald, D. W. (2013). Risk avoidance in sympatric large carnivores: Reactive or predictive? *Journal of Animal Ecology*, 82, 1098–1105. <https://doi.org/10.1111/1365-2656.12077>
- Buk, K. G., van der Merwe, V. C., Marnewick, K., & Funston, P. J. (2018). Conservation of severely fragmented populations: Lessons from the transformation of uncoordinated reintroductions of cheetahs (*Acinonyx jubatus*) into a managed metapopulation with self-sustained growth. *Biodiversity and Conservation*, 27, 3393–3423. <https://doi.org/10.1007/s10531-018-1606-y>
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. New York, NY: Springer Science & Business Media.
- Caro, T. M. (1994). *Cheetahs of the serengeti plains*. Chicago, IL: The University of Chicago Press.
- Chauvenet, A. L. M., Durant, S. M., Hilborn, R., & Pettorelli, N. (2011). Unintended consequences of conservation actions: Managing disease in complex ecosystems. *PLoS ONE*, 6, e28671. <https://doi.org/10.1371/journal.pone.0028671>
- Creel, S., Creel, N. M., Mills, M. G. L., & Monfort, S. L. (1997). Rank and reproduction in cooperatively breeding African wild dogs: Behavioral and endocrine correlates. *Behavioral Ecology*, 8, 298–306. <https://doi.org/10.1093/beheco/8.3.298>

- Crimmins, S. M., & Van Deelen, T. R. (2019). Limited evidence for meso-carnivore release following wolf recovery in Wisconsin, USA. *Wildlife Biology*, 1, 1–7. <https://doi.org/10.2981/wlb.00511>
- Crimmins, S. M., Walleaser, L. R., Hertel, D. R., Mckann, P. C., Rohweder, J. J., & Thogmartin, W. E. (2016). Relating mesocarnivore relative abundance to anthropogenic land-use with a hierarchical spatial count model. *Ecography*, 39, 524–532. <https://doi.org/10.1111/ecog.01179>
- 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. <https://doi.org/10.1111/1365-2656.12238>
- Doherty, P. F., White, G. C., & Burnham, K. P. (2012). Comparison of model building and selection strategies. *Journal of Ornithology*, 152(Suppl. 2), 317–323. <https://doi.org/10.1007/s10336-010-0598-5>
- Druce, H. C., Pretorius, K., & Slotow, R. (2008). The response of an elephant population to conservation area expansion: Phinda Private Game Reserve, South Africa. *Biological Conservation*, 141, 3127–3138. <https://doi.org/10.1016/j.biocon.2008.09.024>
- du Preez, B., Hart, T., Loveridge, A. J., & Macdonald, D. W. (2015). Impact of risk on animal behaviour and habitat transition probabilities. *Animal Behaviour*, 100, 22–37. <https://doi.org/10.1016/j.anbehav.2014.10.025>
- Durant, S. M. (1998). Competition refuges and coexistence: An example from Serengeti carnivores. *Journal of Animal Ecology*, 67, 370–386. <https://doi.org/10.1046/j.1365-2656.1998.00202.x>
- Durant, S. M., Caro, T. M., Collins, D. A., Alawi, R. M., & Fitzgibbon, C. D. (1988). Migration patterns of Thomson's gazelles and cheetahs on the Serengeti Plains. *African Journal of Ecology*, 26, 257–268. <https://doi.org/10.1111/j.1365-2028.1988.tb00978.x>
- Durant, S. M., Kelly, M., & Caro, T. M. (2004). Factors affecting life and death in Serengeti cheetahs: Environment, age, and sociality. *Behavioral Ecology*, 15(1), 11–22. <https://doi.org/10.1093/beheco/arg098>
- Durant, S. M., Mitchell, N., Groom, R., Pettorelli, N., Ipavec, A., Jacobson, A. P., ... Young-Overton, K. (2017). The global decline of cheetah *Acinonyx jubatus* and what it means for conservation. *Proceedings of the National Academy of Sciences of the United States of America*, 114, 528–533. <https://doi.org/10.1073/pnas.1611122114>
- Elmhagen, B., & Rushton, S. P. (2007). Trophic control of mesopredators in terrestrial ecosystems: Top-down or bottom-up? *Ecology Letters*, 10, 197–206. <https://doi.org/10.1111/j.1461-0248.2006.01010.x>
- Fattebert, J., Balme, G., Dickerson, T., Slotow, R., & Hunter, L. (2015). Density-dependent natal dispersal patterns in a leopard population recovering from over-harvest. *PLoS ONE*, 10, e0122355. <https://doi.org/10.1371/journal.pone.0122355>
- Ferreira, S. M., & Hofmeyr, M. (2014). Managing charismatic carnivores in small areas: Large felids in South Africa. *South African Journal of Wildlife Research*, 44, 32–42. <https://doi.org/10.3957/056.044.0102>
- Fuller, T., & Sievert, P. (2001). Carnivore demography and the consequences of changes in prey availability. In J. L. Gittleman, S. M. Funk, D. Macdonald, & R. K. Wayne (Eds.), *Carnivore conservation* (pp. 163–179). Cambridge, UK: Cambridge University Press.
- Gaillard, J. M., Nilsen, E. B., Odden, J., Andrén, H., & Linnell, J. D. C. (2014). One size fits all: Eurasian lynx females share a common optimal litter size. *Journal of Animal Ecology*, 83, 107–115. <https://doi.org/10.1111/1365-2656.12110>
- Gehrt, S. D., & Prange, S. (2007). Interference competition between coyotes and raccoons: A test of the mesopredator release hypothesis. *Behavioral Ecology*, 18, 204–214. <https://doi.org/10.1093/beheco/arl075>
- Gigliotti, L. C., Slotow, R., Hunter, L. T. B., Fattebert, J., Sholto-Douglas, C., & Jachowski, D. S. (2019). Data from: Context-dependency of top-down, bottom-up, and density-dependent influences on cheetah demography. Dryad Digital Repository, <https://doi.org/10.5061/dryad.3d88cs0>
- Gompper, M. (2002). Top carnivores in the suburbs? Ecological and conservation issues raised by colonization of northeastern North America by coyotes. *BioScience*, 52, 185–190. [https://doi.org/10.1641/0006-3568\(2002\)052\[0185:TCITSE\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2002)052[0185:TCITSE]2.0.CO;2)
- Greenville, A. C., Wardle, G. M., Tamayo, B., & Dickman, C. R. (2014). Bottom-up and top-down processes interact to modify intraguild interactions in resource-pulse environments. *Oecologia*, 175, 1349–1358. <https://doi.org/10.1007/s00442-014-2977-8>
- Hairton, N. G., Smith, F. E., & Slobodkin, L. B. (1960). Community structure, population control, and competition. *The American Naturalist*, 94, 421–425. <https://doi.org/10.1086/282146>
- Hanski, I. (1990). Density dependence, regulation and variability in animal populations. *Philosophical Transactions of the Royal Society B*, 330, 141–150. <https://doi.org/10.1098/rstb.2010.0098>
- Hebblewhite, M., & Pletscher, D. H. (2002). Effects of elk group size on predation by wolves. *Canadian Journal of Zoology*, 80, 800–809. <https://doi.org/10.1139/z02-059>
- Hunter, L. T. B. (1998). *The behavioural ecology of reintroduced lions and cheetahs in the Phinda Resource Reserve, Kwazulu-Natal, South Africa*. Phd Thesis (September), 1–206.
- Hunter, L. T. B., Pretorius, K., Carlisle, L. C., Rickelton, M., Walker, C., Slotow, R., & Skinner, J. D. (2007). Restoring lions *Panthera leo* to northern KwaZulu-Natal, South Africa: Short-term biological and technical success but equivocal long-term conservation. *Oryx*, 41, 196–204. <https://doi.org/10.1017/S003060530700172X>
- Janse van Rensburg, J., McMillan, M., Giżejewska, A., & Fattebert, J. (2018). Rainfall predicts seasonal home range size variation in nyala. *African Journal of Ecology*, 56, 418–423. <https://doi.org/10.1111/aje.12455>
- Karels, T. J., Byrom, A. E., Boonstra, R., & Krebs, C. J. (2000). The interactive effects of food and predators on reproduction and overwinter survival of arctic ground squirrels. *Journal of Animal Ecology*, 69, 235–247. <https://doi.org/10.1046/j.1365-2656.2000.00387.x>
- Kelly, M. J., Laurenson, M. K., FitzGibbon, C. D., Collins, D. A., Durant, S. M., Frame, G. W., ... Caro, T. M. (1998). Demography of the Serengeti cheetah (*Acinonyx jubatus*) population: The first 25 years. *Journal of Zoology*, 224, 473–488. <https://doi.org/10.1111/j.1469-7998.1998.tb00053.x>
- Kendall, B. E., & Wittmann, M. E. (2010). A stochastic model for annual reproductive success. *The American Naturalist*, 175, 461–468. <https://doi.org/10.1086/650724>
- Kettles, R., & Slotow, R. (2009). Management of free-ranging lions on an enclosed game reserve. *South African Journal of Wildlife Research*, 39(1), 23–33. <https://doi.org/10.3957/056.039.0103>
- Kissui, B. M., & Packer, C. (2004). Top-down population regulation of a top predator: Lions in the Ngorongoro Crater. *Proceedings of the Royal Society B: Biological Sciences*, 271, 1867–1874. <https://doi.org/10.1098/rspb.2004.2797>
- Korpimäki, E., Norrdahl, K., & Valkama, J. (1994). Reproductive investment under fluctuating predation risk: Microtine rodents and small mustelids. *Evolutionary Ecology*, 8, 357–368. <https://doi.org/10.1007/BF01238188>
- Laake, J. L. (2013). *RMark: An R interface for analysis of capture-recapture data with MARK. Version 2.2.4*. AFSC Processed Rep 2013-01, 25 p. Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., Seattle, WA.
- Lack, D. (1948). The significance of litter-size. *The Journal of Animal Ecology*, 17, 45–50. <https://doi.org/10.1111/j.1474-919X.1947.tb04155.x>
- Laurenson, M. K. (1994). High juvenile mortality in cheetahs (*Acinonyx jubatus*) and its consequences for maternal care. *Journal of the Zoological Society of London*, 234, 387–408. <https://doi.org/10.1111/j.1469-7998.1994.tb04855.x>

- Leibold, M. A. (1989). Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *The American Naturalist*, 134, 922–949. <https://doi.org/10.1086/285022>
- Letnic, M., Ritchie, E. G., & Dickman, C. R. (2012). Top predators as biodiversity regulators: The dingo *Canis lupus dingo* as a case study. *Biological Reviews*, 87, 390–413. <https://doi.org/10.1111/j.1469-185X.2011.00203.x>
- Marker, L. L., Dickman, A. J., Jeo, R. M., Mills, M. G. L., & Macdonald, D. W. (2003). Demography of the Namibian cheetah, *Acinonyx jubatus jubatus*. *Biological Conservation*, 114, 413–425. [https://doi.org/10.1016/S0006-3207\(03\)00069-7](https://doi.org/10.1016/S0006-3207(03)00069-7)
- McNaughton, S. J., Oesterheld, M., Frank, D. A., & Williams, K. J. (1989). Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature*, 341, 189–192. <https://doi.org/10.1038/340301a0>
- Miller, S. M., Bissett, C., Burger, A., Courtenay, B., Dickerson, T., Druce, D. J., ... Zimmermann, D. (2013). Management of reintroduced lions in small, fenced reserves in South Africa: An assessment and guidelines. *South African Journal of Wildlife Research*, 43, 138–154. <https://doi.org/10.3957/056.043.0202>
- Miller, S. M., & Funston, P. J. (2014). Rapid growth rates of lion (*Panthera leo*) populations in small, fenced reserves in South Africa: A management dilemma. *South African Journal of Wildlife Research*, 44(1), 43–55. <https://doi.org/10.3957/056.044.0107>
- Mills, M. G. L., & Mills, M. E. J. (2014). Cheetah cub survival revisited: A re-evaluation of the role of predation, especially by lions, and implications for conservation. *Journal of Zoology*, 292, 136–141. <https://doi.org/10.1111/jzo.12087>
- Oakwood, M. (2000). Reproduction and demography of the northern quoll, *Dasyurus hallucatus*, in the lowland savanna of northern Australia. *Australian Journal of Zoology*, 48, 519–539. <https://doi.org/10.1071/ZO00028>
- Owen-Smith, N., Mason, D. R., & Ogutu, J. O. (2005). Correlates of survival rates for 10 African ungulate populations: Density, rainfall and predation. *Journal of Animal Ecology*, 74, 774–788. <https://doi.org/10.1111/j.1365-2656.2005.00974.x>
- Palomares, F., & Caro, T. M. (1999). Interspecific killing among mammalian carnivores. *The American Naturalist*, 153, 492–508. <https://doi.org/10.1086/303189>
- Pasanen-Mortensen, M., Elmhagen, B., Lindén, H., Bergström, R., Wallgren, M., van der Velde, Y., & Cousins, S. A. O. (2017). The changing contribution of top-down and bottom-up limitation of mesopredators during 220 years of land use and climate change. *Journal of Animal Ecology*, 86, 566–576. <https://doi.org/10.1111/1365-2656.12633>
- Pettorelli, N., & Durant, S. M. (2007). Family effects on early survival and variance in long-term reproductive success of female cheetahs. *Journal of Animal Ecology*, 76, 908–914. <https://doi.org/10.1111/j.1365-2656.2007.01266.x>
- Prugh, L. R., Stoner, C. J., Epps, C. W., Bean, W. T., Ripple, W. J., Laliberte, A. S., & Brashares, J. S. (2009). The rise of the mesopredator. *BioScience*, 59, 779–791. <https://doi.org/10.1525/bio.2009.59.9.9>
- R Core Team. (2019). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Ralls, K., & White, P. J. (1995). Predation on San Joaquin kit foxes by larger canids. *Journal of Mammalogy*, 76, 723–729. <https://doi.org/10.2307/1382743>
- Ritchie, E. G., & Johnson, C. N. (2009). Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, 12, 982–998. <https://doi.org/10.1111/j.1461-0248.2009.01347.x>
- Rostro-García, S., Kamler, J. F., & Hunter, L. T. B. (2015). To kill, stay or flee: The effects of lions and landscape factors on habitat and kill site selection of cheetahs in South Africa. *PLoS ONE*, 10, e0117743. <https://doi.org/10.1371/journal.pone.0117743>
- Royle, J. A., Dawson, D. K., & Bates, S. (2004). Modelling abundance effects in distance sampling. *Ecology*, 85, 1591–1597. <https://doi.org/10.1890/03-3127>
- Sillett, T. S., Chandler, R. B., Royle, J. A., Kéry, M., & Morrison, S. A. (2012). Hierarchical distance sampling models to estimate population size and habitat-specific abundance of an island endemic. *Ecological Applications*, 22, 1997–2006. <https://doi.org/10.1890/11-1400.1>
- Sinclair, A. R. E., & Krebs, C. J. (2002). Complex numerical responses to top-down and bottom-up processes in vertebrate populations. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 357, 1221–1231. <https://doi.org/10.1098/rstb.2002.1123>
- Swanson, A., Arnold, T., Kosmala, M., Forester, J., & Packer, C. (2016). In the absence of a 'landscape of fear': How lions, hyenas, and cheetahs coexist. *Ecology and Evolution*, 6(23), 8534–8545. <https://doi.org/10.1002/ece3.2569>
- Swanson, A., Caro, T., Davies-Mostert, H., Mills, M. G. L., Macdonald, D. W., Borner, M., ... Packer, C. (2014). Cheetahs and wild dogs show contrasting patterns of suppression by lions. *Journal of Animal Ecology*, 83, 1418–1427. <https://doi.org/10.1111/1365-2656.12231>
- Switalski, T. A. (2003). Coyote foraging ecology and vigilance in response to gray wolf reintroduction in Yellowstone National Park. *Canadian Journal of Zoology*, 81, 985–993. <https://doi.org/10.1139/z03-080>
- Tannerfeldt, M., Angerbjörn, A., & Angerbjörn, A. (1998). Fluctuating resources and the evolution of litter size in the arctic fox. *Oikos*, 83, 545–559. <https://doi.org/10.2307/3546681>
- Trinkel, M., & Kastberger, G. (2005). Competitive interactions between spotted hyenas and lions in the Etosha National Park, Namibia. *African Journal of Ecology*, 43, 220–224. <https://doi.org/10.1111/j.1365-2028.2005.00574.x>
- Vanak, A. T., Fortin, D., Thaker, M., Ogden, M., Owen, C., Greatwood, S., & Slotow, R. (2013). Moving to stay in place: Behavioral mechanisms for coexistence of African large carnivores. *Ecology*, 94, 2619–2631. <https://doi.org/10.1890/13-0217.1>
- Weise, F. J., Vijay, V., Jacobson, A. P., Schoonover, R. F., Groom, R. J., Horgan, J., ... Pimm, S. L. (2017). The distribution and numbers of cheetah (*Acinonyx jubatus*) in southern Africa. *PeerJ*, 5, e4096. <https://doi.org/10.7717/peerj.4096>

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**How to cite this article:** Gigliotti LC, Slotow R, Hunter LTB, Fattebert J, Sholto-Douglas C, Jachowski DS. Context dependency of top-down, bottom-up and density-dependent influences on cheetah demography. *J Anim Ecol*. 2020;89: 449–459. <https://doi.org/10.1111/1365-2656.13099>