



Original Article

Leopard distribution and abundance is unaffected by interference competition with lions

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Competition can have profound impacts on the structure and function of ecological communities. Despite this, the population-level effects of intraguild competition on large carnivores remain largely unknown, due to a paucity of long-term studies that focus simultaneously on competing species. Here, we comprehensively examine competitive interactions, including their demographic consequences, between 2 top predators, lions *Panthera leo* and leopards *P. pardus*. We tested the hypothesis that lions, as the dominant competitor, limit the distribution and abundance of leopards, using dietary, spatial, and life-history data collected concurrently on the 2 species. Dietary overlap between lions and leopards was limited, with lions targeting large- to very large-sized prey and leopards small- to medium-sized prey. Leopards did not actively avoid lions, either predictively or reactively, except in riparian woodland where the likelihood of encountering lions was highest. Lions accounted for more than 20% of leopard mortality, but this appeared to be compensatory. Observed and modeled population growth was similar between the 2 species, with both exhibiting net emigration. Our findings suggest that lions do not suppress leopard populations or limit their distribution, at least in our study area. Adequate availability of suitably-sized prey apparently enabled resource partitioning between lions and leopards, facilitating their coexistence. The potential for competition increases in areas devoid of large prey and should be considered in recovery efforts for the 2 species. Our study provides novel empirical evidence that intraguild competition does not always have population-level consequences for subordinates, even if they suffer from strong interference competition with dominant competitors.

Key words: carnivore demography, exploitative competition, interference competition, intraguild predation, *Panthera leo*, *Panthera pardus*, risk avoidance.

INTRODUCTION

Competition can have profound impacts on the structure and function of ecological communities, particularly for members of the large carnivore guild, due to their behavioral and morphological adaptations for predation (Creel et al. 2001; Donadio and Buskirk 2006). Competitive interactions manifest both directly and indirectly. Interference competition involves direct aggression between species (Schoener 1983); dominant carnivores can harass, steal food from or even kill subordinates, producing a range of demographic consequences from reduced individual fitness to population

suppression (Linnell and Strand 2000; Creel et al. 2001; Ritchie and Johnson 2009). Intraguild killing—the most extreme form of interference competition—is widespread among carnivores (Palomares and Caro 1999; Donadio and Buskirk 2006), with dominant carnivores sometimes responsible for more than 50% of subordinate carnivore mortality (e.g., gray wolves *Canis lupus* on coyotes *C. latrans*, Thurber et al. 1992; coyotes on swift foxes *Vulpes velox*, Kamler et al. 2003; dingoes *C. lupus dingo* on red foxes *V. vulpes*, Moseby et al. 2012).

To reduce the risk of potentially fatal encounters, subordinate carnivores may actively avoid dominant competitors. Such avoidance can be predictive or reactive (Broekhuis et al. 2013). African wild dogs *Lycan pictus* exhibit a pre-emptive response to lions

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Panthera leo, strongly avoiding areas with high lion densities (Vanak et al. 2013; Swanson et al. 2014). Cheetahs *Acinonyx jubatus*, in contrast, tend not to avoid areas with a high likelihood of encountering lions, but rather react to the immediate presence of lions (Broekhuis et al. 2013; Swanson et al. 2016). Long-term spatial segregation resulting from predictive avoidance is generally costlier than fine-scale reactive responses for subordinates, as it may restrict access to vital resources such as prey, water, or shelter (Cresswell 2008; Swanson et al. 2014).

In contrast to interference competition, exploitation competition occurs indirectly when species share a limiting resource (Schoener 1983). For large carnivores, this resource is usually food; a prey item consumed by one species cannot be consumed by another. Demonstrating the effects of exploitation competition is challenging in the absence of controlled experiments (Creel et al. 2001). Theoretical and correlative studies nevertheless suggest that it is particularly likely when food availability is low and dietary overlap extensive (Wiens 1993), as in many extant carnivore communities (Hayward and Kerley 2008).

Although intraguild competition among carnivores has received a great deal of attention, considerable debate still surrounds the population-level effects of competition. Here, we comprehensively examine competitive interactions, including their demographic consequences, between 2 top predators, lions and leopards *Panthera pardus*. Lions are sympatric with leopards in 91% of their extant range (Supplementary Figure S1), yet their interspecific relationships have rarely been studied concurrently (but see Vanak et al. 2013 and du Preez et al. 2015). Competition is likely asymmetrical due to their marked size difference: adult lions weigh 90–225 kg (West and Packer 2013) and adult leopards 18–72 kg (Hunter et al. 2013). Lions occasionally attack and kill leopards (Figure 1), and a telemetry study showed that proximity to lions induced leopards to move to denser habitats (du Preez et al. 2015). However, the strength and effects of exploitation and interference competition on lions and leopards otherwise remain largely unknown.

We used dietary, spatial, and demographic data collected in the Sabi Sand Game Reserve, South Africa, to test the hypothesis that

competition with lions limits the distribution and abundance of leopards. We assessed the potential for exploitation competition by estimating dietary overlap between lions and leopards. We also evaluated the extent of interference competition between lions and leopards by investigating rates of interspecific kleptoparasitism, spatial partitioning, and cause-specific mortality. Finally, we determined whether lions impact leopards at a population level by comparing rates of observed and modeled population growth between the 2 species. We made the following predictions in line with the hypothesis that lions suppress and/or displace leopards: 1) the 2 species will show extensive overlap in diet, or alternatively lions will force leopards to target suboptimal prey; 2) lions will kleptoparasitize a significant proportion of leopard kills; 3) leopards will avoid areas where the risk of encountering lions is high, losing access to key resources such as preferred prey; 4) rates of lion-inflicted leopard mortality will be high and additive to other mortality; and 5) population growth rates of lions and leopards will be inversely related.

MATERIALS AND METHODS

Study area

The Sabi Sand Game Reserve (hereafter SSGR; midpoint: 31°29' E, 24°49' S), South Africa, is a 625 km² privately-owned conservancy. The western boundary of the SSGR is fenced, but the northern boundary is open to Manyeleti Game Reserve and the southern and the eastern boundaries to Kruger National Park, allowing animals to range freely across a protected landscape of more than 22,000 km². The prevailing vegetation is open to wooded savanna, structurally classified into 6 habitat types (in order of increasing cover): 1) grassland; 2) open woodland; 3) semiopen woodland; 4) sodic areas; 5) riparian woodland; and 6) koppies (Supplementary Figure S2). Mean monthly temperatures range from 28 °C in January to 17 °C in July. The area receives an average of 620 mm of rain each year, which falls mainly during the wet season from October to March. Most extant indigenous mammal



Figure 1

An adult lioness attacks and kills a 3-year-old male leopard in the Sabi Sand Game Reserve, South Africa (photo credit: Liam Rainier).

species are present on the reserve, including the entire large carnivore guild, as well as their primary prey base (Radloff et al. 2004). Estimated lion and leopard densities (excluding dependent cubs) within the SSGR were 10.8 ± 0.2 lions/100 km² and 12.2 ± 0.1 leopards/100 km² respectively (G. A. Balme, unpublished data).

Field observations

The SSGR hosts several ecotourism lodges that operate high-end photographic safaris. Clients are taken on 2 “game drives” daily (ca. 06:00–09:30 and 15:30–19:00, including after dark with a spotlight), which are led by an experienced guide and coincide with activity peaks exhibited by lions and leopards (Hayward et al. 2009). On average, 98 ± 2 vehicles are active throughout the SSGR per game drive, resulting in a mean density of 1 vehicle per 6 km² (the number of vehicles per drive does not vary seasonally; $\chi^2 = 0.003$, $P = 0.953$). The high number of vehicles, together with an extensive road network (a total length of 3159 km and mean density of 5 roads per km²), ensures that most of the reserve is covered daily. Game drives are also not limited to roads; a skilled tracker on the front of each vehicle scans for signs of charismatic species such as lions and leopards. Once tracks are detected, the guide and tracker follow the tracks by vehicle or on foot until the animal is located or the tracks lost. Guides also maintain radio contact with each other to maximize the probability of sighting animals. Due to this intensive search effort, sightings are frequent; on average, 6355 ± 113 unique lion sightings and 6428 ± 914 unique leopard sightings are recorded annually. Lions and leopards in the SSGR are extremely habituated to the presence of game-drives and guides are familiar with the resident individuals using their traversing area (individual lions and leopards can be distinguished by the unique patterns of their vibrissa spots; Pennycuik and Rudnai 1970; Miththapala et al. 1989). Guides are required to record sightings of lions and leopards after each game drive. Records date back to the mid-1970s, but levels of reporting across the reserve varied between years. Accordingly, we used different time periods for different analyses. From 1 January 2013, data collection protocols were standardized across lodges through the implementation of sightings capture software (Peak Performance International, Cape Town, South Africa). Data included the identity of the individual(s) present (if known), the location of the sighting (recorded on a geo-referenced map), the presence and number of offspring, whether the animal(s) had a kill, the species, sex, and age class (juvenile, subadult, and adult) of prey, whether the kill was kleptoparasitized, and other notable behaviors (e.g., intra- and interspecific interactions, life-history events). Although multiple guides sometimes submitted data from the same sighting, we retrospectively filtered the data to ensure that each unique sighting was captured only once, that is, an individual lion or leopard was included in only a single sighting per game drive. To assess the accuracy of the guides’ ability to distinguish individuals, we asked them to submit photographs with the putative identity of the animal from a random subset of sightings; they correctly identified the individual lion ($n = 45$) and leopard ($n = 112$) in all photos. We also cross-referenced data submitted by guides from different lodges to assess the consistency of the information captured and we found no significant discrepancies (Balme et al. 2013).

Dietary overlap

We limited our assessment of dietary overlap to 2013–2015. Diet composition was based on the numbers of unique lion and leopard kills recorded by guides. We included only prey items deemed

by guides to have been killed by the predator; that is, obvious (e.g., the presence of an agitated subordinate predator near the kill) or observed cases of scavenging were excluded. Kills were assigned to 1 of 4 size classes: small (<25 kg); medium (25–99 kg); large (100–349 kg); and very large (≥ 350 kg). Estimates of adult male and female prey body mass were taken from Radloff et al. (2004) and Owen-Smith and Mills (2008). In the absence of growth curves for all prey species, we approximated subadult mass by multiplying adult male or female mass by 0.7, and approximated juvenile mass by multiplying mean adult mass by 0.3 (Radloff et al. 2004). Due to the opportunistic nature of data collection, it was possible that larger kills were over-represented, particularly for lions (Owen-Smith and Mills 2008). Accordingly, for each species, we used a Pearson chi-squared test to compare the sizes of kills located once the predator(s) had already begun feeding to kills that were observed directly (i.e., from the start to the finish of the hunt; hereafter “observed kills”). We estimated the biomass consumed by each species based on the edible proportion of carcasses (from Owen-Smith and Mills 2008). We used Levin’s index (Smith 1982) to define dietary niche breadth for lions and leopards. Dietary overlap was calculated using Pianka’s index (Pianka 1973) for each species individually, as well as for the 2 species combined (using Pianka’s “multiplicative measure of overlap”). Dietary overlap was assessed both seasonally and annually.

Kleptoparasitism

We estimated rates of interspecific kleptoparasitism between lions and leopards based on kill records from 2013 to 2015. We determined the proportion of leopard kills kleptoparasitized by lions (and other large carnivores), and the proportion of lion kills from which leopards scavenged (leopards never displaced lions from kills). Kleptoparasitism was either observed directly or inferred from tracks and/or the presence of a dominant competitor found feeding on the remains of a kill (kills were rarely abandoned voluntarily prior to completion; Balme et al. 2017).

Spatial partitioning

We limited our assessment of spatial partitioning to 2015, the only year for which we had complete data on the distribution of lions and leopards throughout the SSGR. Following Broekhuis et al. (2013), we first assessed general habitat selection by each species, and then investigated whether leopards exhibited predictive and/or reactive avoidance of lions. To determine whether lions and leopards selected specific habitat types, we ran a compositional analysis using the package *adehabitatHS* (Calenge 2006) in the R statistical environment (R Core Team 2015). We restricted our analyses to lion prides ($n = 9$) and leopards ($n = 45$) with entire home ranges in the SSGR, and for which we recorded a minimum of 50 unique sightings (lion: mean number of sightings per pride = 288 ± 26 ; leopard: mean number of sightings per individual = 150 ± 12). To ensure sampling effort was consistent between individuals, we randomly extracted 200 locations for each lion pride and 50 locations for each leopard. We detected no seasonal bias in the number of locations randomly extracted for lions ($\chi^2 = 0.435$, $P = 0.510$) or leopards ($\chi^2 = 0.300$, $P = 0.584$). We examined habitat selection at 2 scales by calculating: 1) the proportion of lion and leopard locations within each habitat type compared to the proportion of each habitat type available within the study area and 2) the proportion of each individual’s locations within each habitat type compared to the proportion of each habitat type available within that individual’s home range. Home ranges were based on a 90% isopleth

from fixed kernel utilization distributions (UDs) created using the R package *adehabitatHR* (Calenge 2006) using the reference bandwidth. The study area was defined as the area intersected by the sum of home ranges of both species. We used Ivlev's electivity index (Krebs 1999) to investigate whether lions and leopards used habitat types in accordance to their availability at both the study area and home range scale. Values ranged from +1 (maximum preference) to -1 (maximum avoidance; Krebs 1999). We also used annual aerial count data (Sabi Sand Wildtuin, unpublished data) to assess habitat selection by African buffalo *Syncerus caffer* and impala *Aepyceros melampus*, the principal prey species of lions and leopards respectively (see Results for details).

To determine whether leopards exhibited predictive avoidance of lions, we modeled leopard occurrence as a function of habitat and lion risk. We created a population-level UD for lions using a grid cell size of 100 × 100 m and the same randomly extracted lion locations ($n = 1800$) used in the compositional analysis. The value of each pixel in the resulting raster (Supplementary Figure S3) represented the probability of the pixel being used by a lion pride, and therefore the long-term risk of leopards encountering lions across the study area (sensu Broekhuis et al. 2013). We did not weight pixels based on the number of individuals in a pride, as encounter rates were unlikely to vary with group size (Fryxell et al. 2007). No unknown lion prides and few transients (2% of 6241 sightings) were seen in the study area during 2015. We used generalized linear mixed models (GLMMs) with a binomial error structure to determine whether the risk of encountering lions affected leopard presence. Within each individual leopard's home range, we generated the same number of random points as sightings recorded for that individual. To increase the sample size, we included all leopards ($n = 65$) that were seen on ≥ 20 occasions during 2015 (mean number of sightings per individual = 114 ± 10). The binomial response variable was 0 or 1, where 1 represented a leopard sighting and 0 a randomly generated point. The predictor variables included in models were the pixel value of lion risk at each point, habitat type, and the interaction between lion risk and habitat type. The identity of the leopard was included as a random factor.

We also used GLMMs to test whether leopards exhibited reactive avoidance of lions (Broekhuis et al. 2013). For each unique leopard sighting ($n = 7418$), we determined whether a lion(s) was seen in that individual leopard's home range during the same game drive. In such cases ($n = 3045$), we calculated the distance from the leopard to the nearest lion, as well as the distance from the leopard to a randomly generated point in the home range. We included the same response and predictor variables in models as in the GLMMs assessing leopards' predictive avoidance, except that lion risk was replaced by distance to the nearest lion or random point.

We examined GLMMs consisting of all combinations of variables and used Akaike's Information Criterion corrected for small sample sizes (AICc) to select the most parsimonious models (Burnham and Anderson 2002). Continuous variables were scaled around a mean of 0 and variance of 1 to facilitate comparison. When candidate models were within $\Delta\text{AICc} < 2$, we performed model averaging using the R package *glmulti* (Calcagno and Mazancourt 2010).

Intraguild killing

To examine the extent of intraguild killing between lions and leopards, we extracted evidence of known-cause mortality for both species from the historical sightings records. For lions, the demographic data ranged from 1998 to 2015 and for leopards from 1975

to 2015. We only included records in which the actual mortality event was observed or could be unambiguously determined by postmortem and evidence collected at the site. We assessed cause-specific mortality based on 2 age classes, juveniles (< 2 years old) and subadults and adults (≥ 2 years old), for both lions and leopards.

To establish whether lion-inflicted leopard mortality was additive or compensatory, we regressed annual leopard survival against lion-inflicted mortality. If lion-inflicted mortality was additive, we would expect a negative monotonic relationship between leopard survival and lion mortality. Conversely, if lion-inflicted mortality was compensatory, we would expect no (or a positive) relationship between leopard survival and lion mortality (Murray et al. 2010). Estimates of annual survival were based on the Kaplan–Meier method calculated using the R package *survival* (Therneau 2015). Individuals that disappeared or were still alive at the end of each year were right censored. Estimates of lion-inflicted mortality were based on cumulative incidence functions (CIFs) generated using the R package *etm-CIF* (Alignol 2014). We restricted our estimates of annual leopard survival and CIFs to 2005–2015, when rates of reporting were consistent across the study area and most leopards were known (Balme et al. 2013).

Population growth

We restricted our estimates of population growth to 2010–2015, when we had complete demographic data for lions throughout the study area. We estimated population growth rates 2 ways, first through vital rate estimation and matrix modeling, and second by direct observation. We estimated sex- and age-specific survival rates for 254 lions and 355 leopards monitored over the 6 years. We used the same 3 age classes for both species: juveniles (< 2 years); subadults (2–3 years); and adults (≥ 4 years). On average, lion litters were first detected at 1.1 ± 0.2 months and leopard litters at 1.2 ± 0.1 months. Our estimates of juvenile survival were therefore likely conservative as some may have died before discovery, though this source of bias was similar for both species. We assigned the median litter size of 2 to litters that disappeared before cubs could be counted (lions: $n = 4$; leopards: $n = 28$; parturition was obvious due to lactation stains) and assumed an equal sex ratio at birth (Packer et al. 1988; Balme et al. 2013).

We calculated annual maternity rates as the number of offspring born to adult females in a year divided by the total number of adult females monitored that year. We assumed only adult females reproduced with age at first reproduction of 4 years for both species (Packer et al. 1988; Balme et al. 2013). We then calculated annual fecundity rates as mean adult female survival multiplied by the mean annual maternity (Williams et al. 2002).

We used our survival and fecundity estimates to construct stage-based dual-sex Leslie matrix models for both lions and leopards in the program RAMAS (Akçakaya and Root 2007). Such closed-population models assume that immigration and emigration are balanced and do not affect growth (Williams et al. 2002). We calculated the deterministic population growth rate (λ_p) for each species over the 6-year period as the dominant eigen value of the matrix under a stable age distribution.

Observed population growth was based on monthly counts of individual lions and leopards known to be alive in the study area from 2010 to 2015. Sampling effort remained constant over this period and detection rates for resident individuals were high for both species; resident lions were seen every 1.5 ± 0.1 days and resident leopards every 3.9 ± 0.4 days. Unknown transient individuals were occasionally seen, but very rarely in comparison to sightings

of known lions and leopards (2% of lion sightings; 4% of leopard sightings). Home range analyses further showed that there were few vacant territories available to unknown residents (Supplementary Figure S4). Cubs were considered to enter the population on their estimated birth date whereas immigrants entered the population upon first detection. We calculated the observed population growth rate (λ_o) for lions and leopards separately as $\lambda_o = (n_t / n_0)^{1/t}$, where n_0 is the starting population, n_t is the final population, and t is the number of transitions between the start and end of the population projection (Williams et al. 2002). We ran generalized least-square models in the R package *nlme* (Pinheiro et al. 2016) to compare lion and leopard population sizes over time, applying autoregressive correlation structures in the first order to control for temporal autocorrelation. We estimated the emigration rate (e) for each species as $e = \lambda_D - \lambda_o$, and assumed a population was at its ecological carrying capacity if it experienced net emigration ($e > 1$) over the study period (Peery et al. 2006).

RESULTS

Dietary overlap

From 2013 to 2015, lions were recorded feeding on 939 kills, comprising 24 species. Over the same period, leopards were recorded feeding on 2032 kills, comprising 40 species (Supplementary Table S1). There was no difference in the size of observed kills (lion: $n = 171$; leopard: $n = 264$) from those located after the predator had begun feeding (lion: $n = 768$; leopard: $n = 1768$) for either lions ($\chi^2_3 = 0.726$, $P = 0.867$) or leopards ($\chi^2_2 = 2.470$, $P = 0.291$). As such, we included all documented kills in our dietary analyses. Buffalo was the most common prey of lions (41% of kills and 63% of biomass consumed) and impala the most frequent prey of leopards (51% of kills and 52% of biomass consumed). There was no seasonal difference in the size of prey killed by lions, but leopards killed more small prey and fewer medium-sized prey in the wet season (and vice versa in the dry season; Supplementary Table S2). In general, lions killed larger prey (mean prey body mass = 292 ± 8 kg, range = 4–1540 kg) than leopards (37 ± 1 kg, range = 0–303 kg; $z = -36.805$, $P < 0.001$; Figure 2) and exhibited a broader

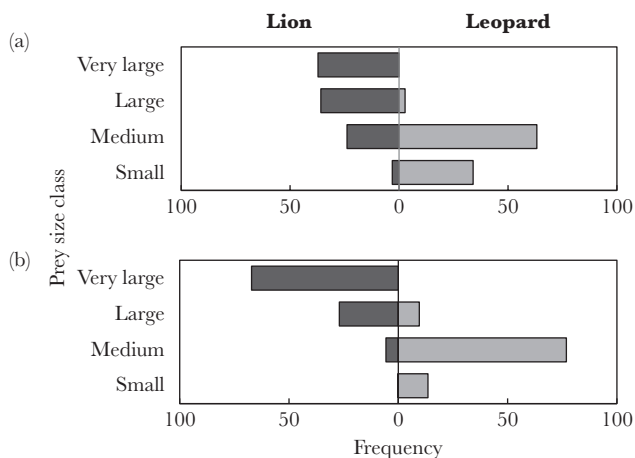


Figure 2 Relative contribution of prey size classes to the (a) number and (b) edible biomass of kills made by lions ($n = 939$ kills) and leopards ($n = 2032$ kills) in the Sabi Sand Game Reserve, South Africa, from 2013 to 2015.

dietary niche breadth (Table 1). The 2 species showed little overlap in diet across seasons (Table 1).

Kleptoparasitism

At least 21% of leopard kills were kleptoparasitized (Table 2). Spotted hyaenas *Crocuta crocuta* were the most common perpetrators (responsible for 50% of kleptoparasitized leopard kills), followed by other leopards (39%). Lions accounted for 9% of kleptoparasitized kills, or 2% of all leopard kills. Lions displaced leopards in all cases where they kleptoparasitized kills.

Leopards were observed scavenging from lion kills on 6 occasions (<1% of lion kills). Leopards fed from 4 old kills that lions had abandoned, and fed briefly from 2 fresh kills while remaining undetected by lions.

Spatial partitioning

Lions and leopards showed significant habitat preferences, in the study area (lions: $\lambda = 0.156$, $P = 0.011$; leopards: $\lambda = 0.205$, $P \leq 0.001$) and within their home ranges (lions: $\lambda = 0.051$, $P = 0.028$; leopards: $\lambda = 0.150$, $P = 0.002$). At both scales of selection, lions and leopards preferred koppiess and riparian woodland and avoided grassland (Figure 3). Leopards showed greater preference for sodic areas than lions, and lions avoided semiopen woodland more than leopards. Buffalo and impala exhibited similar habitat selection to their respective predators, both preferring riparian woodland (and sodic areas in the case of impalas) and avoiding grassland (Supplementary Figure S5). However, unlike lions and leopards, both prey species strongly avoided koppiess.

The global model, included all the predictor variables, was the most supported model among the GLMMs assessing predictive avoidance of lions (Table 3). Consistent with our compositional analysis, leopards were found in koppiess ($\beta = 0.812 \pm 0.241$, $z = 3.370$, $P < 0.001$), riparian woodland ($\beta = 0.768 \pm 0.068$, $z = 11.232$, $P < 0.001$), and sodic areas ($\beta = 0.305 \pm 0.072$, $z = 4.210$, $P < 0.001$) more often than expected. Leopards were also more likely to be found in areas where the long-term risk of encountering lions was greater ($\beta = 0.117 \pm 0.049$, $z = 2.412$, $P = 0.016$). However, within habitats, leopard occurrence was negatively related to lion risk in riparian woodland ($\beta = -0.151 \pm 0.062$, $z = -2.419$, $P = 0.016$).

The top ranked model among the GLMMs assessing leopards' reactive avoidance of lions included habitat type and distance to the nearest lion, but not their interaction (Table 4). Again, leopard occurrence was positively related to riparian woodland ($\beta = 0.847 \pm 0.104$, $z = 8.138$, $P < 0.001$) and sodic areas ($\beta = 0.309 \pm 0.111$, $z = 2.773$, $P = 0.006$). Leopards were also found at significantly shorter distances from lions than expected ($\beta = -0.327 \pm 0.031$, $z = -10.501$, $P < 0.001$). The mean distance from leopards to the nearest lion in their home range was 2.3 ± 0.1 km, while the mean distance from the leopards to any random point in their home range was 2.8 ± 0.1 km (mean home range circumference = 5.8 ± 0.2 km).

Intraguild killing

We ascertained cause of death for 52% of lion mortalities ($n = 333$) and 45% of leopard mortalities ($n = 433$) (Figure 4). Conspecifics were responsible for the greatest percentage (lion: 69%; leopard: 40%) of known-cause mortality for both species. Leopards accounted for 3% of known-cause juvenile lion deaths ($n = 121$); leopards were not recorded killing lions older

Table 1

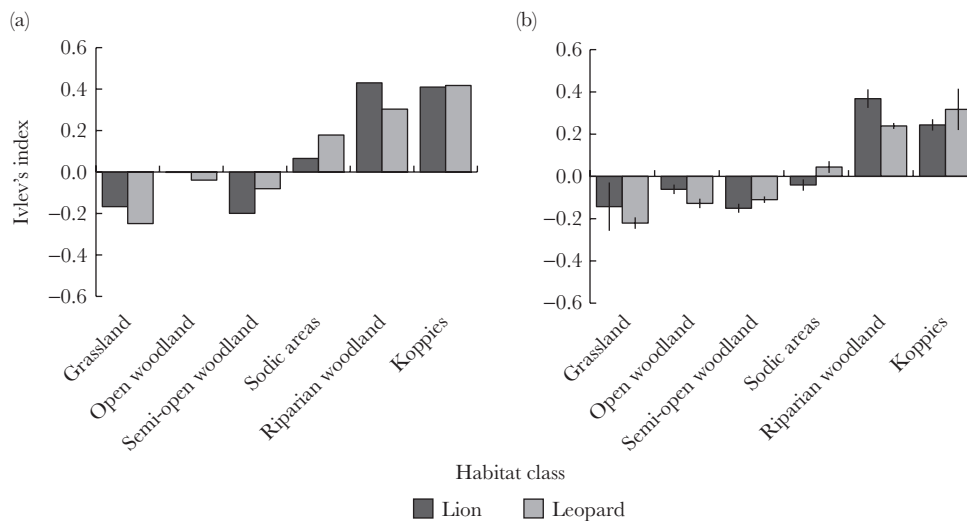
Seasonal and annual estimates of dietary breadth and overlap for lions ($n = 939$ kills) and leopards ($n = 2032$ kills) in the Sabi Sand Game Reserve, South Africa, from 2013 to 2015

Species	Dry season		Wet season		Total	
	Levin's index	Pianka's index	Levin's index	Pianka's index	Levin's index	Pianka's index
Lion	5.165	0.221	4.027	0.158	4.621	0.190
Leopard	3.475	0.181	3.299	0.143	3.398	0.163
Combined		0.412		0.287		0.351

Table 2

Frequency of leopard kills kleptoparasitized by competitors in the Sabi Sand Game Reserve, South Africa, from 2013 to 2015

Competitor	Number of kills kleptoparasitized	Percentage of total kills ($n = 2032$)	Percentage of kleptoparasitized kills ($n = 423$)
Baboon, chacma <i>Papio ursinus</i>	2	<1	<1
Crocodile, Nile <i>Crocodylus niloticus</i>	2	<1	<1
Hyena, spotted	215	11	51
Leopard	162	8	38
Lion	37	2	9
Wild dog, African	5	<1	1

**Figure 3**

Habitat selection by lions and leopards within (a) the study area and (b) their individual home ranges in the Sabi Sand Game Reserve, South Africa, during 2015 based on Ivlev's index. Values >0 indicate a habitat was used more than available (preference) and values <0 indicate a habitat was used less than available (avoidance). Vertical lines show standard error.

Table 3

Generalized linear mixed models assessing the probability of leopard occurrence (presence/absence) in relation to habitat type and the long-term risk of encountering lions in the Sabi Sand Game Reserve, South Africa, in 2015

Model set	K	Log likelihood	$AICc$	Δ_i	w_i
Lion risk, habitat, lion risk \times habitat	13	-9820.41	19,666.85	0	0.77
Lion risk, habitat	8	-9826.73	19,669.47	2.62	0.21
Habitat	7	-9830.19	19,674.39	7.54	0.02
Lion risk, lion risk \times habitat	8	-9984.19	19,984.38	317.53	0
Lion risk	3	-9992.11	19,990.22	323.37	0

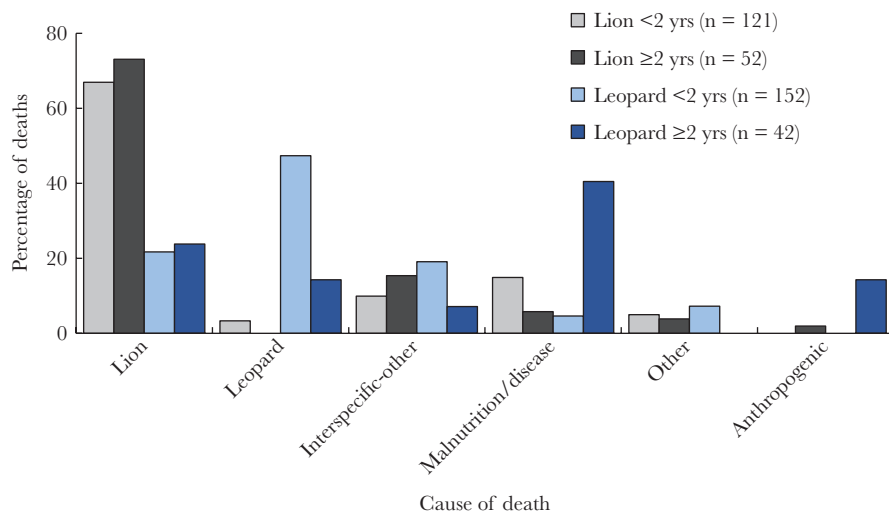
The identity of the leopard ($n = 65$) was included as a random factor in all models. Models were ranked according to their Akaike weights (w_i) based on the Akaike Information Criterion for small samples ($AICc$). The 5 best supported models are presented. Included are the number of estimable parameters (K), the log likelihood, and the $AICc$ differences (Δ_i).

Table 4

Generalized linear mixed models assessing the probability of leopard occurrence (presence/absence) in relation to habitat type and distance to the nearest lion in the Sabi Sand Game Reserve, South Africa, in 2015

Model set	K	Log likelihood	AIC_c	Δ_i	w_i
Habitat, distance	8	-4066.46	8148.95	0	0.98
Habitat, distance, habitat \times distance	13	-4065.26	8156.58	7.63	0.02
Distance	3	-4143.36	8292.73	143.78	0
Habitat	7	-4140.83	8295.67	146.72	0
Distance, habitat \times distance	8	-4142.02	8300.06	151.12	0

The identity of the leopard ($n = 65$) was included as a random factor in all models. Models were ranked according to their Akaike weights (w_i) based on the Akaike Information Criterion for small samples (AIC_c). The 5 best supported models are presented. Included are the number of estimable parameters (K), the log likelihood, and the AIC_c differences (Δ_i).

**Figure 4**

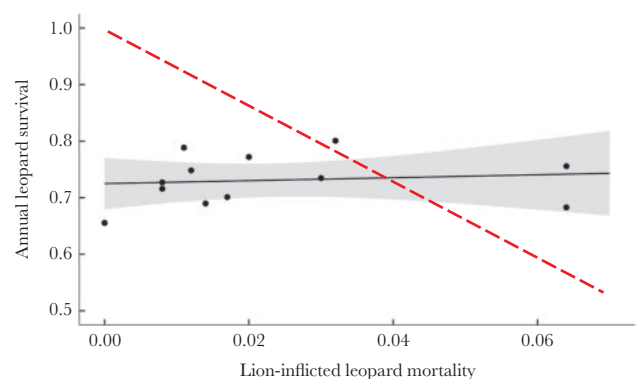
Known causes of mortality for juvenile (<2 years) and independent (\geq 2 years) lions and leopards in the Sabi Sand Game Reserve, South Africa, from 1975 to 2015. Sample sizes are presented in parentheses. “Interspecific—other” includes animals killed by species other than lions or leopards, usually by other predators (e.g., spotted hyaenas, Nile crocodiles) or prey (e.g., buffalos, chacma baboons). “Malnutrition/disease” includes lions and leopards that were malnourished and disappeared soon after (normally old individuals (i.e., \geq 16 years) or juveniles that were orphaned), as well as individuals that were known to die from disease (e.g., sarcoptic mange). “Other” includes natural causes of mortality such as drowning and fire. “Anthropogenic” includes lions and leopards killed by people, typically when they ranged beyond the reserve into surrounding communities.

than 7 months. Lions accounted for 22% of known-cause leopard cub deaths ($n = 152$) and 23% of independent (\geq 2 years old) leopard deaths ($n = 44$). The mean age of lions killed by leopards was 0.22 ± 0.12 years (range = 0.08–0.58 years), while the mean age of leopards killed by lions was 2.71 ± 0.75 years (range = 0.08–16.59 years).

We estimated survival and CIFs for 123 ± 5 leopards annually from 2005 to 2015. Annual survival rates ranged from 0.66 to 0.80 (mean = 0.73 ± 0.01) and rates of lion-inflicted mortality from 0 to 0.06 (mean = 0.02 ± 0.01). There was no relationship between annual leopard survival and lion mortality ($R^2 = 0.093$, $F_{1,10} = 0.920$, $P = 0.363$; Figure 5), suggesting that lion-caused leopard mortality in the SSGR was compensatory.

Population growth

One hundred and seventy-three lions and 222 leopards died between 2010 and 2015. A further 81 lions and 133 leopards were censored either because they disappeared (lion: $n = 16$; leopard: $n = 41$) or were still alive at the end of the study (lion: $n = 65$; leopard: $n = 92$). Age-specific survival rates over the 6-year period ranged from 0.52 to 0.93 for lions and from 0.39 to 0.98 for leopards (Supplementary Table S3). The average annual maternity rate for lions was 1.08 ± 0.26 cubs per year (range = 0.48–1.96; based

**Figure 5**

Relationship between lion-inflicted leopard mortality and annual leopard survival in the Sabi Sand Game Reserve, South Africa, from 2005 to 2015. Each black circle represents 1 year, the solid black line shows the fitted relationship, and the shaded area indicates the 95% confidence interval. The dashed red line denotes the expected relationship if mortality was completely additive.

on 34 females that gave birth to 158 cubs in 61 litters) and for leopards 1.27 ± 0.06 cubs per year (range = 1.04–1.41; based on 48 females that gave birth to 251 cubs in 139 litters). Deterministic

growth for lions was 1.04 and for leopards 1.07. Monthly counts of lions in the overlapping study area ranged from 67 to 101 (mean = 82 ± 1) and observed annual growth from 0.75 to 1.38 (mean = 1.00 ± 0.02). For leopards, monthly counts ranged from 80 to 100 (mean = 89 ± 1) and observed growth from 0.88 to 1.14 (mean = 1.00 ± 0.01) (Figure 6). Lion and leopard populations accordingly exhibited estimated net annual emigration rates of 4% and 7%, respectively. Time-series analysis showed that lion population size had no effect on leopard population size ($P = 0.50$; Figure 7).

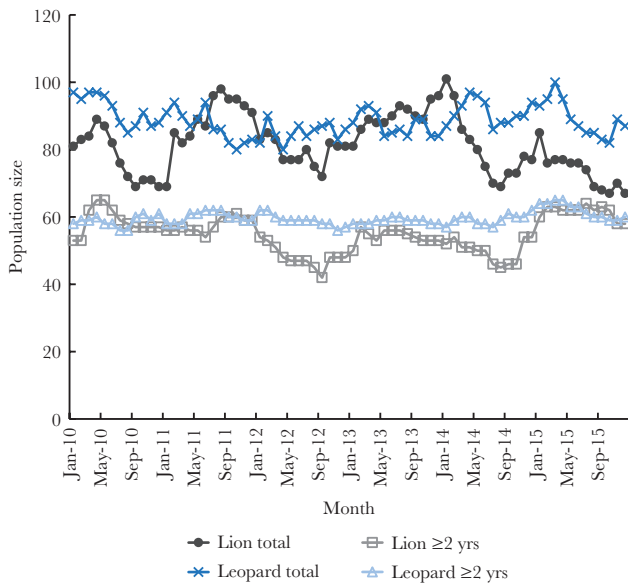


Figure 6

Estimated population sizes (total and individuals ≥ 2 years) of lions and leopards in the Sabi Sand Game Reserve, South Africa, from 2010 to 2015 based on monthly counts of individuals known to be alive in the overlapping study area.

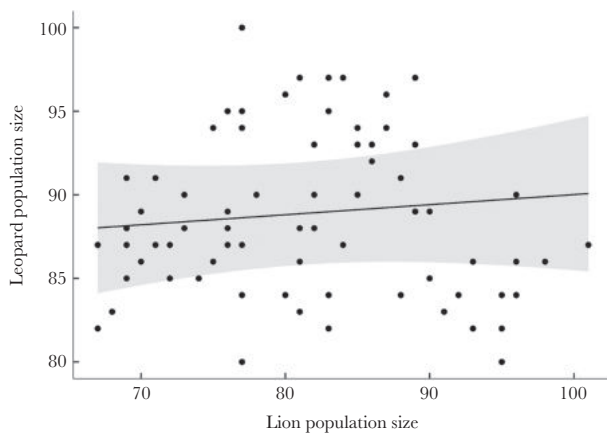


Figure 7

Relationship between lion and leopard population size in the Sabi Sand Game Reserve, South Africa, from 2010 to 2015 based on generalized least-square models accounting for temporal autocorrelation. Each black circle represents one monthly count, the solid black line shows the fitted relationship, and the shaded area indicates the 95% confidence interval. The wet season spanned from October to March and the dry season from April to September.

DISCUSSION

In contrast to our predictions, leopards apparently suffered few costs from coexisting with lions despite strong unidirectional interference competition. Leopards did not appear to alter their diet in response to lions, nor were they displaced by lions. Lions accounted for more than 20% of leopard mortality, but we found no relationship between lion-inflicted leopard mortality and annual leopard survival, suggesting that lion-inflicted mortality was compensatory (Murray et al. 2010). If lions suppressed leopards, we may have expected leopard numbers to decline by 3- to 4-fold; the scale of decline typically observed for mesopredator populations limited by dominant predators (Ritchie and Johnson 2009). In contrast, lion and leopard populations both remained stable over the study period. Alternatively, if leopard populations were already depressed due to historical competition with lions (“the ghost of competition past”; Connell 1980), we would have expected leopard numbers to be well below their ecological threshold. However, our estimates of population growth suggested that leopard and lion populations were at capacity, with both species exhibiting net emigration. Leopard densities in the SSGR are also among the highest recorded for the species (see Hunter et al. 2013 for review). Lion-inflicted leopard mortality may therefore be compensated through density-dependent processes that reduce other causes of mortality (Boyce et al. 1999), increase reproduction (Crooks et al. 1998), and/or decrease rates of emigration (e.g., Karki et al. 2007).

We found no evidence of exploitative competition between lions and leopards, with little overlap in diet and each targeting different-sized prey. Lions mainly killed large- to very large-sized prey, while leopards primarily killed small- to medium-sized prey. It seems unlikely that lions excluded leopards from killing larger prey. Throughout their range, leopards preferentially select prey weighing 10–40 kg, regardless of the presence of lions or other dominant competitors (Hayward et al. 2006). Although leopards can kill prey many times their size, they rarely do so, probably due to the risks inherent in attacking large prey as a solitary predator (and of losing large prey to spotted hyenas; see Balme et al. 2017). In contrast, group hunting by lions allows them to kill prey larger than themselves safely and consistently; across their range, lions preferentially select prey weighing 190–550 kg (Hayward et al. 2005). Accordingly, the realized and fundamental dietary niche of lions and leopards in the SSGR appear to coincide (Hutchinson 1957). This may be mediated by the adequate availability of prey in different size classes in our study area (Karanth and Sunquist 1995). Intraguild competition between tigers *P. tigris* and leopards appears strong in parts of Asia, but mainly where prey abundance is low or at least where large prey is scarce (Odden et al. 2010; Harihar et al. 2011; Mondal et al. 2012). At such sites, leopard populations have been shown to decline alongside tiger population recoveries (Harihar et al. 2011; Mondal et al. 2012). The potential for exploitation competition between lions and leopards similarly increases in areas devoid of large ungulate prey (Holt and Huxel 2007). This was reflected to some extent in our study by an increase in dietary overlap between lions and leopards during the dry season when buffalos were less common (Funston et al. 1994). Increased exploitative competition could manifest either in leopards being forced to switch to smaller, suboptimal prey (e.g., Harihar et al. 2011), or otherwise leopards outcompeting lions by more efficiently exploiting shared prey (e.g., Steinmetz et al. 2013). However, evidence from other parts of leopard range (Odden et al. 2010), as well as from other carnivore species (Vanak et al. 2013; Witczuk et al. 2015;

Palomares et al. 2016), suggest that subordinates are more likely to exhibit niche differentiation along the spatial rather than dietary axis in response to increased competition with dominant intraguild competitors for shared resources.

Leopards did not actively avoid lions at a population level. Lions and leopards generally selected the same habitats; as has been shown in other parts of their range (e.g., Schaller 1972; Spong et al. 2002, Bailey 2005), lions and leopards both preferred riparian woodland and koppies and avoided grassland. Preferential selection for riparian woodland was likely driven by prey distribution; buffalos and impalas—the principal prey of lions and leopards respectively—also favored riparian woodland. Impalas, like leopards, additionally preferred sodic areas. The dense cover characteristic of riparian woodland and sodic areas would also likely improve the hunting success of lions and leopards, both of which are stalk-and-pounce predators (Hopcraft et al. 2005; Balme et al. 2007). Koppies, in contrast, were likely selected by lions and leopards as den sites for young cubs and/or vantage points to locate prey (Schaller 1972; Bailey 2005). The similar habitat preferences exhibited by the 2 predators likely explained why leopards were typically found in areas where the likelihood of encountering lions was high, as well as at shorter distances to lions than expected under a random distribution.

Even though riparian woodland was a preferred habitat of leopards, they avoided those areas within riparian woodland where the likelihood of encountering lions was greatest. The risks posed by lions in such areas likely outweighed the benefits that leopards gained from increased access to prey and cover. Lion occurrence was highest in riparian woodland in our study area (Supplementary Figure S3). Accordingly, at a broader scale, this finding suggests that there may be a maximum lion density above which leopards choose to avoid an area, regardless of the resources available (e.g., Swanson et al. 2016).

The scale of our analysis may have been too coarse to detect leopards' reactive avoidance of lions. Vanak et al. (2013) showed that radio-collared leopards moved away from lions, but only within 50 m. In our study, leopards also typically fled when encountering lions, but usually only a short distance (50–100 m). If lions gave chase, the leopard would attempt to climb a nearby tree for safety (G. A. Balme, personal observations). Thus, leopards do react to lions, but not at a spatial scale that would result in any broad-scale displacement or prevent leopards from accessing key resources. The ability of leopards to climb trees may be a particularly important adaptation in terms of allowing them to coexist with lions without segregating spatially. Lions can climb trees; however, they generally only do so when motivated by the presence of a free meal (Balme et al. 2017). Other sympatric carnivores that cannot climb trees (or at least rarely do so) typically avoid lions, either predictively (e.g., African wild dogs; Vanak et al. 2013; Swanson et al. 2014) or reactively (e.g., cheetah; Broekhuis et al. 2013; Swanson et al. 2016). Prevailing vegetation is thus likely to mediate coexistence between lions and leopards (Janssen et al. 2007). It is possible that leopards would show greater avoidance of lions in more open environments. This may partly explain the strong avoidance that leopards in our study area showed for grassland.

We demonstrated previously that the high rates of kleptoparasitism observed for leopards in our study area (at least 21% of kills were kleptoparasitized) impacted individual fitness; female leopards that lost more kills to competitors generally had lower reproductive success (Balme et al. 2017). Lions contributed to such losses, but only marginally. Although both species benefited occasionally by scavenging from each other's kills (lions more so than leopards),

this likely occurred too infrequently to contribute significantly to their diets.

Research that examines the competitive effects of dominant carnivores on subordinates typically focuses on localized aspects of behavior (e.g., harassment, kleptoparasitism, spatial avoidance; see Creel et al. 2001 and Ritchie and Johnson 2009 for reviews). We explored a diverse range of competitive interactions between lions and leopards, but most importantly the population-level effects of each species on the other. Few empirical studies have quantified the demographic consequences of intraguild competition among carnivore species, or other taxa (but see Eccard and Ylönen 2002; Hoogland and Brown 2016; Wittwer et al. 2015); however, it is often inferred that behavioral responses reflect population impacts. While dietary, spatial, and temporal niche displacement are pathways through which dominant competitors can affect subordinates (Ritchie and Johnson 2009), they do not always lead to population suppression. Our results corroborate others (Broekhuis et al. 2013; Vanak et al. 2013; Swanson et al. 2014) in demonstrating that fine-scale partitioning along any of these axes may facilitate coexistence. However, the outcomes of intraguild competition are likely to vary with resource availability and habitat structure (Holt and Huxel 2007; Janssen et al. 2007). Competition between lions and leopards therefore needs to be examined over a wider selection of landscapes to better gauge its effects. In the absence of controlled experiments, a comparison of lion and leopard densities (e.g., Swanson et al. 2014) and spacing patterns (e.g., Palomares et al. 2016) across a range of habitats will add insight. We also assessed competition only between a pair of species, but most terrestrial ecosystems include multiple competing species, all of which may influence community dynamics (Vanak et al. 2013). Ideally, the scope of intraguild competition studies should broaden to account for all interacting species; a rich, but formidably challenging, research opportunity.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data deposited in the Dryad Digital Repository by Balme et al. (2017).

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