Received: 3 January 2018 | Accepted: 13 June 2018

DOI: 10.1111/1365-2656.12883

RESEARCH ARTICLE

Journal of Animal Ecology | BRITISH ECOLOGICAL SOCIETY

Lions and leopards coexist without spatial, temporal or demographic effects of interspecific competition

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Funding information
Directorate for Biological Sciences, Grant/Award Number: 115057

Handling Editor: Laura Prugh

Abstract

1. Although interspecific competition plays a principal role in shaping species behaviour and demography, little is known about the population-level outcomes of competition between large carnivores, and the mechanisms that facilitate coexistence.
2. We conducted a multilandscape analysis of two widely distributed, threatened large carnivore competitors to offer insight into coexistence strategies and assist with species-level conservation.
3. We evaluated how interference competition affects occupancy, temporal activity and population density of a dominant competitor, the lion (*Panthera leo*), and its subordinate competitor, the leopard (*Panthera pardus*). We collected camera-trap data over 3 years in 10 study sites covering 5,070 km^2. We used multispecies occupancy modelling to assess spatial responses in varying environmental and prey conditions and competitor presence, and examined temporal overlap and the relationship between lion and leopard densities across sites and years.
4. Results showed that both lion and leopard occupancy was independent of—rather than conditional on—their competitor's presence across all environmental covariates. Marginal occupancy probability for leopard was higher in areas with more bushy, "hideable" habitat, human (tourist) activity and topographic ruggedness, whereas lion occupancy decreased with increasing hideable habitat and increased with higher abundance of very large prey. Temporal overlap was high between carnivores, and there was no detectable relationship between species densities.
5. Lions pose a threat to the survival of individual leopards, but they exerted no tractable influence on leopard spatial or temporal dynamics. Furthermore, lions did not appear to suppress leopard populations, suggesting that intraguild competitors can coexist in the same areas without population decline. Aligned conservation strategies that promote functioning ecosystems, rather than target individual species, are therefore advised to achieve cost- and space-effective conservation.

KEYWORDS

carnivore, demography, interspecific competition, multispecies occupancy model, *Panthera leo*, *Panthera pardus*, species density, temporal overlap

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1 | INTRODUCTION

Interspecific competition plays a principal role in shaping ecological communities and species temporal and spatial distributions, and can have important implications for management and conservation (Connell, 1983). Competition can affect species at both the individual and population levels by influencing ecological processes which ultimately determine fitness, such as energetics, habitat use, foraging strategies and mortality (Caro & Stoner, 2003; Creel, 2001; Macarthur, 1972). Competitive interactions between carnivores may have especially strong influences on ecosystem function and community structure because many serve as keystone species in driving trophic cascades (Ripple et al., 2014; Schmitz, Krivan, & Ovadia, 2004; Terborgh, Holt, & Estes, 2010). Given that 59% of large carnivores worldwide are threatened with extinction, understanding the dynamics and consequences of interactions between carnivores across their broad geographical distributions is of paramount importance for preserving healthy ecosystems and for developing management strategies that effectively conserve competing species (Cardillo et al., 2004; Di Minin et al., 2016; Ferreira & Hofmeyr, 2014; Marshall, Stier, Samhouri, Kelly, & Ward, 2015).

Numerous studies have explored intraguild competition among carnivores, yet several important questions remain unanswered. Interspecific competition between carnivores often manifests as interference competition, whereby dominant species prevent subordinates from accessing resources, either directly through aggressive interactions like intraguild killing and kleptoparasitism (Balme, Miller, Pitman, & Hunter, 2017; Palomares & Caro, 1999), or indirectly by encouraging spatial and temporal shifts to safer but potentially less optimal resources (Swanson et al., 2014; Vanak et al., 2013). The demographic consequences of these behaviours are unknown for many species (Balme, Pitman et al., 2017; Linnell & Strand, 2000). Because the responses of subordinate carnivores may vary with environmental conditions, including resource gradients (Karanth et al., 2017), habitat structure (Michel, Jiménez-franco, Naef-daenzer, & Grüebler, 2016) and human development (Lewis, Bailey, Vandewoude, & Crooks, 2015), quantifying interspecific interactions across a wide selection of landscapes is necessary to inform management, particularly for large carnivores with extensive ranges (Balme, Pitman et al., 2017; Di Minin et al., 2016). Yet ecological studies are commonly conducted at small spatial scales, typically as case studies at single sites, and rarely encompass multiple landscapes and populations (Schmitz, 2005).

To address these gaps, we assessed behavioural interactions, and any resulting population effects, between lions (*Panthera leo*) and leopards (*Panthera pardus)* across a broad geographic region. Both species are high-conservation priority carnivores listed as "Vulnerable" on the IUCN Red List of Threatened Species (IUCN, 2016). Lions are sympatric with leopards in 91% of their extant range (Balme, Pitman et al., 2017), where they interact as intraguild competitors by exerting dominance over leopards (Hayward & Slotow, 2009; Owen-Smith & Mills, 2008; Vanak et al., 2013). These carnivores engage in reciprocal intraguild killing (Balme, Pitman et al., 2017; Palomares & Caro, 1999; Schaller, 1972), and leopards may actively avoid close proximity to lions (du Preez, Hart, Loveridge, & Macdonald, 2015; Vanak et al., 2013). However, recent findings from a single study site in South Africa suggest that lions may not suppress leopard populations or limit their distribution (Balme, Pitman et al., 2017), warranting an investigation into the population-level outcomes of competition between these threatened carnivores across a wider range of environmental conditions.

Using 3 years of camera-trap data from 10 protected areas in South Africa, we investigated three hypotheses about how lion dominance might affect leopard spatiotemporal patterns and demography. First, we hypothesized that leopard occupancy would vary with the presence or absence of lions, and that lion occupancy would be independent of leopard presence. We applied multispecies occupancy modelling (Rota et al., 2016) to explore this using four categories of environmental covariates based on predictions from competition theory about how subordinates might coexist with dominant species (Creel, 2001):

1. *Habitat:* Subordinate predators are known to use "safer" (lower risk) habitats to reduce the probability of encounters with, and attacks by, dominant competitors (Palomares et al., 2016; Wilson, Blankenship, Hooten, & Shivik, 2010). Given that leopards use trees to cache prey and seek refuge from other predators (Balme, Miller et al., 2017), we predicted that leopards would avoid harmful interactions with lions by occupying habitat in which they could climb or hide rather than open habitat, where they would be less able to escape (Balme, Pitman et al., 2017).
2. *Human*: We anticipated that leopards might be forced to use suboptimal areas with high human presence to avoid lions (Harihar, Pandav, & Goyal, 2011). These could be areas inside protected areas that experience high human activity, or areas closer to the periphery of protected area boundaries where leopards would be vulnerable to detrimental edge effects associated with human settlements but safer from lions (Balme, Slotow, & Hunter, 2010; Harihar et al., 2011; Mcdougal, 1988; Valeix, Hemson, Loveridge, Mills, & Macdonald, 2012; Woodroffe & Ginsberg, 1998).
3. *Terrain*: We expected leopards would occupy rougher terrain where it is easier to hide from lions (Hopcraft, Sinclair, & Packer, 2005; Loarie, Tambling, & Asner, 2013).
4. *Prey*: We predicted that leopards would avoid areas with high levels of preferred lion prey (large- and very large-sized prey; Hayward & Kerley, 2005) conditional on the presence of lions. As lions are the dominant competitor, their occupancy should match that of their preferred resources (Vanak et al., 2013). Therefore, the likelihood of leopards encountering lions will be highest in areas with abundant lion prey, and leopards should consequentially avoid these areas (but only where lions are commonly present).

Second, we hypothesized that leopards would reduce temporal overlap with lions to minimize risk of negative interactions.

Temporal avoidance is a strategy commonly used by subordinate carnivores, such as wild dogs (*Lycaon pictus*) and cheetahs (*Acinonyx jubatus*), to facilitate coexistence with dominant competitors (Hayward & Slotow, 2009). We tested this by estimating lion and leopard activity patterns and overlap from our camera-trap data.

Third, we predicted that dominant competitors would suppress subordinates (Prugh et al., 2009; Ritchie & Johnson, 2009) and consequently that the densities of lions and leopards would be inversely related. Strong negative relationships between the population densities of dominant and subordinate competitors have been observed for numerous carnivore competitors, including lions and wild dogs (Swanson et al., 2014), wolves (*Canis lupus*) and coyotes (*Canis latrans*; Berger & Gese, 2007) and Eurasian badger (*Meles meles*) and red fox (*Vulpes vulpes*; Trewby et al., 2008). We applied spatial capture–recapture (SCR) modelling (Royle, Karanth, Gopalaswamy, & Kumar, 2009) to estimate leopard population densities at each site and compared these to known lion population densities.

Through analysing a large regional dataset with robust monitoring techniques, we offer novel insights on interspecific competition between large carnivores that can inform their management and conservation at a rangewide scale.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was conducted in 10 protected areas distributed across KwaZulu-Natal and Limpopo provinces, South Africa (Figure 1), which represent highly suitable leopard and lion habitat (Di Minin & Moilanen, 2014; Riggio et al., 2013; Swanepoel, Lindsey, Somers, van Hoven, & Dalerum, 2013). Study sites were state-run (n = 3) and private (n = 7) protected areas that form part of a national leopard monitoring initiative established to systematically assess leopard population status across South Africa. The initiative started in 2013 and expanded through time to include more sites, such that three sites were sampled in all 3 years of the study period (2013–2015), three sites were sampled for 2 years, and four sites were sampled for 1 year (Supporting Information Table S1). Both lions and leopards were present throughout all study sites. Site were on average 390 km^2 in size (range = 216–900 km^2) and collectively covered 5,070 km^2 (Supporting Information Table S1). Sites were characterized by wooded savanna vegetation with structure consisting of open grassland (Zululand Rhino Reserve), mixed grassland and woodland (Makalali Private Game Reserve, Timbavati Private Game Reserve, Venetia-Limpopo Nature Reserve, Welgevonden Private Game Reserve), thicket interspersed with grass and low shrubland (Mkhuze Game Reserve, Phinda Private Game Reserve), thicket interspersed with woodland (Hluhluwe-iMfolozi Park, KwaZulu Private Game Reserve) or forest with thicket and low shrubland (Tembe Game Reserve) (Department of Environmental Affairs, 2015). All sites were surrounded by electrified boundary fences that constrained lion but not leopard movements (Balme et al., 2010). Lions and leopards were fully protected in all sites except for Venetia-Limpopo Nature Reserve, Timbavati Private Game Reserve and KwaZulu Private Game Reserve, which permitted limited offtake (one or two individuals per year) through legal trophy hunting.

2.2 | Camera trapping

Each site was sampled at most once per year, with 30–62 camera-trap stations deployed per site for an average of 47 ± 5 days (range 42–58 days; see Supporting Information Table S1 for sampling details; data available in Miller, Pitman, Mann, Fuller, & Balme, 2018). Stations consisted of a pair of unbaited, motion-triggered PantheraCam V-series camera-traps (Olliff et al., 2014) positioned opposite to each other and fixed approximately 40 cm above the ground. Cameras were set to have a minimum of 8 s between trigger events, and were continuously active during the survey period. To maximize the probability of detecting our target species, camera-trap stations were spaced 1–3 km apart (the size of one male home range; Tobler & Powell, 2013) and placed along dirt roads, animal trails and drainage lines commonly used by lions and leopards. Camera traps were mounted on trees or steel poles located 2–4 m from the anticipated travel route. To reduce false detections, we cleared any vegetation that might obstruct the camera's field of view. Camera traps were not moved during the individual surveys. We defined an independent capture as (a) consecutive images of different individuals of the same or different species, (b) consecutive images of individuals of the same species taken more than ≥30 min apart or (c) nonconsecutive images of individuals of the same species (O'Brien, Kinnaird, & Wibisono, 2003; Si, Kays, & Ding, 2014).

2.3 | Analysis

Statistical tests and models were run in R v. 3.3.2 (R Core Team, 2015) and spatial analyses were conducted in ArcMap v.10.2.2.

2.3.1 | Spatial occupancy

We used a Bayesian multispecies conditional occupancy modelling approach developed by Rota et al. (2016) to concurrently study lion and leopard spatial patterns. The approach assumes that the latent occupancy state (ψ) is a multivariate Bernoulli (MVB) random variable, such that $Z_i \sim \text{MVB}(\psi_i)$, where $Z_i = \{Z_{1i}, Z_{2i}, \ldots, Z_{Si}\}$ represents a S-dimensional vector of 1's and 0's. Defining the latent occupancy state in this way permits the modelling of species detection data without assuming which species is dominant or subordinate, and overcomes the limitations of previous two-species conditional models which required a priori assumption about species' dominant and subordinate status (e.g. Richmond, Hines, & Beissinger, 2010; Waddle et al., 2010). This is because a MVB distribution readily generalizes to >1 dimension (Dai, Ding, & Wahba, 2013). When modelling two species,

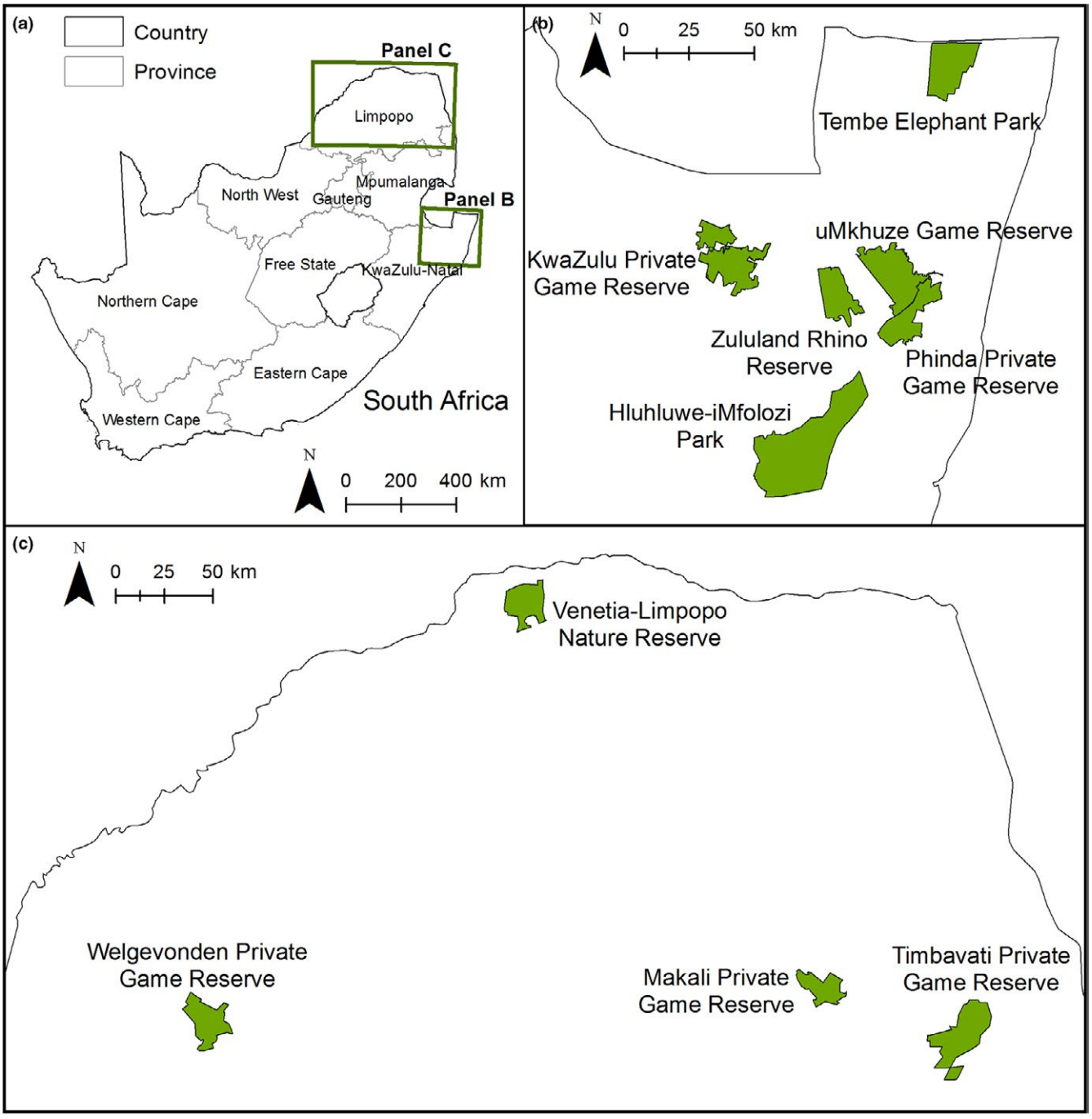

FIGURE 1 Map of the study area in South Africa (a), showing study sites in KwaZulu-Natal (b) and Limpopo provinces (c)

$$Z \sim \mathrm{MVB}\left(\psi_{11},\psi_{10},\psi_{01},\psi_{00}\right),$$

together with the probability mass function

$$f\left(Z|\psi_{11},\psi_{10},\psi_{01},\psi_{00}\right) = \psi_{11}^{z_1 z_2}\psi_{10}^{z_1(1-z_2)}\psi_{01}^{(1-z_1)z_2}\psi_{00}^{(1-z_1)(1-z_2)}$$
$$= \exp\left(\log\left(\psi_{00}\right) + z_1\log\left(\frac{\psi_{10}}{\psi_{00}}\right) + z_2\log\left(\frac{\psi_{01}}{\psi_{00}}\right) + z_1 z_2\log\left(\frac{\psi_{11}\psi_{00}}{\psi_{01}\psi_{10}}\right)\right),$$

where the latent occupancy state is represented as ψ_{11} when both species are present, ψ_{10} when species one is present but species two is absent, ψ_{01} when species one is absent but species two is present and ψ_{00} when both species are absent; and where f represents natural parameters, defined as

$$f_1 = \log\left(\frac{\psi_{10}}{\psi_{00}}\right),$$

$$f_2 = \log\left(\frac{\psi_{01}}{\psi_{00}}\right),$$

$$f_{12} = \log\left(\frac{\psi_{11}\psi_{00}}{\psi_{01}\psi_{10}}\right).$$

The natural parameters can be modelled as linear functions of covariates, such that

$$f_1 = x'_\alpha \alpha,$$

$$f_2 = x'_\beta \beta,$$

$$f_{12} = x'_\gamma \gamma,$$

where x_α, x_β and x_γ are covariates of class vector, while α, β and γ represent conformable vectors of slope parameters. To obtain the probability of each latent occupancy state using a multinomial logit link, we use the natural parameters, such that:

$$\psi_{11} = \frac{\exp(f_1 + f_2 + f_{12})}{1 + \exp(f_1) + \exp(f_2) + \exp(f_1 + f_2 + f_{12})},$$

$$\psi_{10} = \frac{\exp(f_1)}{1 + \exp(f_1) + \exp(f_2) + \exp(f_1 + f_2 + f_{12})},$$

$$\psi_{01} = \frac{\exp(f_2)}{1 + \exp(f_1) + \exp(f_2) + \exp(f_1 + f_2 + f_{12})},$$

$$\psi_{00} = \frac{1}{1 + \exp(f_1) + \exp(f_2) + \exp(f_1 + f_2 + f_{12})}.$$

This modelling approach enables simultaneous evaluations of the latent occupancy state of multiple species in relation to both environmental variables and the presence or absence of other interacting species. Modelling marginal probability of occurrence for a particular species is given as:

$$P(z_1 = 1) = \psi_{11}\psi_{10},$$

while pairwise covariance is given as:

$$\text{cov}(z_1, z_2) = \psi_{11}\psi_{00} - \psi_{10}\psi_{01},$$

and the probability of occurrence of one species, conditional on another species, is given as:

$$P(z_1 = 1 | z_2) = \frac{\psi_{1z_2}}{\psi_{1z_2} + \psi_{0z_2}}.$$

We fit a series of models to test our predictions with regard to the effects of environmental covariates on marginal and conditional species occupancy. Four categories of 10 environmental covariates were calculated at a station level using photographs from camera traps or by extracting mean covariate pixel values within a buffer (500 m radius, which captured the unique characteristics of each station without overlap) around camera-trap stations (geospatial data) using the following methods:

1. *Habitat:* We grouped vegetation classes in the 2013–2014 Geoterraimage South African National Land-cover Dataset (Department of Environmental Affairs, 2015) (30 m resolution) into three nonmutually exclusive "climbable" (vegetation with thick branches), "hideable" (bush) and "exposed" (open) vegetation categories based on in-person observations of habitat structure during ground truthing of study area. Climbable vegetation typically consisted of indigenous forest and woodland/open bush; hideable vegetation consisted of indigenous forest, woodland/open bush, thicket/dense bush and low shrubland; and exposed vegetation consisted of low shrubland and grassland. Minor variation across study sites in vegetation (and misrepresentation of habitat in the original dataset, e.g. thick bush as grassland) necessitated minor reclassification of some categories: in KwaZulu Private Game Reserve, Makalali Private Game Reserve, Timbavati Private Game Reserve, Welgevonden Private Game Reserve and Zululand Rhino Reserve, climbable consisted of indigenous forest, woodland/open bush, thicket/dense brush and grassland (see Supporting Information Table S2 for habitat percentages by site). Original land-cover data were reclassified into these categories using the Reclassification Tool in ArcMap.
2. *Human*: We measured human presence using two proxies: i) human relative abundance index (RAI), calculated as the number of independent photograph captures of people (on foot or in vehicles) per 100 trapping days (O'Brien et al., 2003), and ii) distance to study site edge (as human density increased outside study site boundaries), calculated as the smallest Euclidian distance from a camera-trap station to the study site boundary.
3. *Terrain*: We used raster data from the USGS Shuttle Radar Topographic Mission (U.S. Geological Survey, 2000) (30 m) to calculate a topographic ruggedness index as the square root of the summed squared difference of a pixel and its eight neighbours in ArcMap (Riley, DeGloria, & Elliot, 1999).
4. *Prey*: We estimated relative abundance of prey similarly to our human RAI, as the number of independent captures per 100 trap days. Prey RAI shares a close monotonic relationship with independent estimates of prey abundance in at least two of our sites (Balme et al., 2010). We grouped prey species into four size categories based on their body mass (following Balme, Pitman et al., 2017): small = <25 kg, medium = 25–99 kg, large = 100–349 kg and very large = >350 kg (Supporting Information Table S3).

We also calculated one detection covariate to examine whether seasonal differences in precipitation and temperature affected detection rates of carnivores. We assigned this covariate based on whether the camera-trap sampling period occurred during the wet (December–April) or dry (May–November) season (Supporting Information Table S3).

We evaluated levels of interspecific interactions by conducting two modelling approaches, which were analysed together as part of an integrated modelling framework (Rota et al., 2016). The first comprised a set of marginal occupancy models that assumed lions and leopards occur independently. The second comprised a set of conditional occupancy models that assumed occupancy probability of lions and leopards varies in the presence or absence of one another. To maintain computational efficiency, we adopted a two-stage model fitting approach (Richmond et al., 2010). In stage one, we evaluated whether "season" was an informative detection covariate on both the global and minimum marginal and conditional occupancy models. The outcome of this stage determined whether

season would be retained as a covariate for detection. In stage two, we conducted marginal occupancy models using only those predictor variables shown to be important in the global models, and conditional occupancy models using predictor variables that were based on our 10 environmental covariates (related to habitat, human, terrain or prey, as described above). We controlled for geographical variation in occupancy probabilities by including latitude, longitude and their interaction as covariates in all models (Rota et al., 2016).

We fit Bayesian multispecies conditional occupancy models in STAN v.2.8.0 (Stan Development Team 2015) via the RSTAN v.2.8.0. interface in R. We ran four chains of 1,000 Markov chain Monte Carlo (MCMC) iterations with a burn-in phase of 200 for each model. Convergence of the MCMC chains was assessed using the Brooks–Gelman–Rubin convergence diagnostic ($\hat{R} \leq 1.1$; Gelman et al., 2014). As our approach represented an integrated modelling framework (i.e. both marginal and conditional models were analysed concurrently), and therefore allowed for cross-model comparisons (Rota et al., 2016), we ranked and compared candidate models based on Watanabe–Akaike Information Criterion (WAIC; Gelman et al., 2014). We considered models with ≤2 ΔWAIC from the lowest-WAIC model as supported. We assessed model fit using Bayesian *p*-value, where values around 0.5 indicated strong model fit and values approaching 0 or 1 indicated poor fit. Model covariates with credible intervals of slope parameters that did not overlap 0 were considered strong environmental predictors (Rota et al., 2016). We plotted posterior marginal and conditional occupancy probabilities for covariates by fixing other covariates at their observed means.

2.3.2 | Temporal overlap

To test whether leopards adjusted temporal activity with lion presence, we used camera-trap records to compare overlap in activity patterns between species. We estimated temporal activity overlap by calculating the coefficient of change ($\hat{D}_4$) and 95% confidence intervals based on circular kernel density statistics. The coefficient of change ranges from 0, representing no overlap, to 1, representing complete overlap (see Ridout & Linkie, 2009 for details). As a preliminary test of variation in activity patterns between study sites, we calculated activity overlap between lions and leopards in each study site and year. This revealed that temporal activity patterns and overlap between lions and leopards were similar across all sites (see Results). Therefore, we combined data from all sites to calculate activity overlap between lions and leopards. To account for the predominantly nocturnal behaviour of the species, we investigated activity overlap separately for the night (18:00–05:59) and daylight (06:00–17:59) hours. As occupancy models indicated that season had a detectable effect on detection rate (see Results), we compared temporal overlap between the seasons by conducting separate analyses using photographs taken during the wet and dry seasons. At last, to further explore whether temporal patterns of prey explained carnivore activity, we examined the seasonal overlap of lion and leopard activity with prey by size category. Temporal analyses were conducted using the R package *Overlap* (Meredith & Ridout, 2016) following Ridout and Linkie (2009) parameter recommendations and ANOVA to test for differences.

2.3.3 | Population effects

To evaluate evidence of competition at a population level, we compared lion and leopard population densities across study sites and years (data available in Miller et al., 2018). Lions are managed intensively in eight of the 10 study sites as part of a national metapopulation strategy (Miller et al., 2013). In these reserves, lion population sizes are known with certainty based on counts of known individuals. In the two remaining, larger sites (Timbavati Private Game Reserve and Hluhluwe-iMfolozi Park), lion population abundance is estimated annually using systematic call-up surveys (Ferreira & Funston, 2010; Midlane, O'Riain, Balme, & Hunter, 2015). Excluding estimates from these two sites had no impact on the overall results (see Results). To estimate lion population density at each site and for each year, we divided the known or estimated population size of lions by the area of the study site.

Leopard population density for each site and year was estimated using a SCR model framework (Royle et al., 2009). We identified individual leopards from camera-trap data based on their unique pelage patterns, both visually and using pattern recognition software (Crall, Stewart, Berger-wolf, & Rubenstein, 2013) to ensure accuracy. The sex of each individual was determined by the presence or absence of testes, as well as other morphological characteristics (Balme, Hunter, & Braczkowski, 2012). Photographs in which individual leopards could not be identified were excluded from the analyses, but these typically constituted a small proportion of leopard captures (<10%). When simultaneous photographs of both flanks of an individual were not recorded, we identified individuals by a single flank. We identified a "best flank," by which the highest number of single-flank individuals could be identified per survey (either left or right flank). These best flank individuals were included in the SCR model together with individuals that could be identified by both flanks. We discarded captures of individuals that were only identifiable by the other flank. Following the capture–recapture analytical methods and hierarchical model formulation described by Goldberg et al. (2015) and Royle et al. (2009), our sex-specific SCR models were implemented within a Bayesian framework using data augmentation (Goldberg et al., 2015; Royle & Young, 2008). Data augmentation adds a sufficiently large number of all-zero capture histories to create a dataset of size *M* individuals (Royle et al., 2009). Augmentation is considered sufficient when the number of augmented individuals does not truncate the posterior estimates on population size (Goldberg et al., 2015; Proffitt et al., 2015). Data augmentation for our study sites ranged from 200 to 500. We chose a uniform prior distribution from 0 to *M* on population size (Goldberg et al., 2015). Starting values for parameters were as follows: $\sigma = 1$, $\theta = 0.75$, $\ln(\alpha_0) = 0$, $\beta = 0$, $\psi = 0$, ψ_{sex} = proportion of males sampled (Goldberg et al., 2015; Proffitt et al., 2015). We used improper priors $(-\infty, \infty)$ for α_0 and all β parameters, $(0, \infty)$ for σ, (0.5, 1) for θ and (0, 1) for ψ and ψ_{sex} (Goldberg et al., 2015; Proffitt et al., 2015).

Leopard models were fitted using MCMC methods in the R package *SCRbayes* (available at: https://www.usgs.gov/software/scrbayes). The models include a measure of effort through a matrix of camera station activity, where active stations were represented with a "1" and inactive stations with a "0" for each 24-hr capture period for the duration of the survey. To account for individual, sex-specific effects, we included a sex covariate within all models. Although nonindependent cubs (<12 months old) were occasionally detected, we only included adults and subadults within our analyses (Karanth & Nichols, 1998). All analyses were run using a statespace of 20 km from the edge of our camera array to ensure that all potential activity centres were included. Models were run for 30,000 iterations with a burn-in of 5,000. To reduce autocorrelation, we thinned the MCMC chains by skipping every other iteration, resulting in 12,500 iterations in our posterior sample. We evaluated model goodness of fit using a standard Bayesian *p*-value approach (Royle, Chandler, Sollmann, & Gardner, 2013), while convergence of the MCMC chains was assessed by examining posterior parameter-wise traceplots and histograms. The mean and 95% credible intervals for each model parameter were then computed from these converged samples (Goldberg et al., 2015).

To test the relationship between lion and leopard density, we ran a linear mixed-effects model with species density data from each site and year using the R package *nlmer*, with "leopard density" as our dependent variable and "lion density" as a fixed effect. We also included "site" and "year" as random intercept effects (this model structure accounted for longitudinal change equivalent to incorporating autoregressive correlation structure with the corAR1 function; $AIC_{site/year} = 97.26$, $AIC_{AR} = 97.23$; Swanson et al., 2014).

3 | RESULTS

Using 800 camera stations over 719,200 trap days, we recorded 2,011 independent captures of lions (range of 0–387) and 2,321 independent captures of leopards (range of 43–226 across study sites/years).

3.1 | Spatial occupancy

Occupancy probabilities of lion and leopard were independent of each other, and there was no evidence to suggest conditional occupancy based on competitor presence. The first stage of our model fitting procedure found that season as a covariate on detection consistently improved model fit and indicated that detection probability of both lions and leopards was higher during the dry season (Table 1). Results from the second stage showed that the top-ranking model with the lowest WAIC was the global marginal model (M1 in Table 1), providing strong evidence of independence between the two species. The conditional global model (C1) ranked second and showed substantially poorer fit than the global marginal model (ΔWAIC = 4.8); furthermore, the credible intervals of all covariates in C1 overlapped 0, indicating that they were weak predictors of occupancy (Supporting Information Figure S1; Supporting Information Table S4). There was less support for our prediction-driven models than the global marginal model (Table 1), which suggests that a combination of environmental covariates is more likely to explain species occupancy than one covariate alone.

Marginal occupancy for the two carnivores varied with four covariates (Figure 2). Leopards were more likely to occupy areas with greater hideable habitat, human activity (RAI) and topographic ruggedness. Marginal occupancy probability of lions decreased with increasing hideable habitat and increased with higher abundance of very large prey. We found no evidence to suggest that occupancy of lions or leopards varied with exposed or climbable habitat, distance to boundary or small, medium or large prey RAI.

3.2 | Temporal overlap

Temporal activity overlap and patterns between lions and leopards were similar across sites ($F_{9,8} = 0.57$, $p = 0.79$; $\hat{D}$ mean = 0.76 ± 0.07; Supporting Information Table S5; Supporting Information Figure S2). Analysis of data from all sites and years revealed that lion and leopard showed high (>0.70) overlap in activity patterns that was similar between day and night ($F_{1,1} = 25$, $p = 0.13$) and the wet and dry seasons ($F_{1,1} = 9$, $p = 0.21$; Table 2). Both species demonstrated similar broad-scale temporal patterns, with peak activity during the night and least activity during the day in both seasons (Figure 3). At a finer temporal scale, the predators showed minor temporal partitioning that became more distinct in the wet season (Figure 3). During the night hours, lion activity peaked in the early morning *c*. 01:00 in the wet season and *c*. 03:00 and *c*. 07:00 in the dry season, whereas leopard activity peaked at slightly offset hours, *c*. 05:00 in the wet season and *c*. 03:00–05:00 in the dry season. In the daytime, lion and leopard temporal patterns were closely aligned during the dry season but slightly offset in the wet season, with lion activity peaking *c*. 14:00 and leopard activity peaking *c*. 11:00 (Figure 3). In contrast to carnivore activity, prey were most active during the day (Supporting Information Figures S3 and S4). Therefore, lions and leopards showed similar patterns of activity overlap with all prey sizes ($F(1,11)_{carnivore} = 2.78$, $p = 0.12$, $F(3,11)_{prey\ size} = 43.84$, $p < 0.001$). Both carnivores showed low-to-moderate activity overlap with their preferred size of prey ($\hat{D}$ range = 0.44–0.72, mean = 0.57 ± 0.11) except for leopard, which showed high overlap with small prey ($\hat{D}_{wet} = 0.85$, 95% CI = 0.82–0.91; $\hat{D}_{dry} = 0.75$, 95% CI = 0.74–0.79). Activity overlap between carnivores and prey increased slightly in the wet season (mean increase in $\hat{D}$ = 0.07 ± 0.03; lion: $F(1,3)_{season} = 18.36$, $p = 0.02$, $F(3,3)_{prey\ size} = 172.91$, $p < 0.001$; leopard: $F(1,3)_{season} = 34.35$, $p = 0.01$, $F(3,3)_{prey\ size} = 102.91$, $p = 0.002$), however carnivore activity peaks did not closely match prey activity peaks (Supporting Information Figures S3 and S4).

TABLE 1 Model results for marginal and conditional occupancy models of lion and leopard in 10 study sites across South Africa (2013–2015). Empty cells indicate covariate was not included in the model. Values in bold indicate covariates for which the credible intervals of the slope parameters did not overlap 0, indicating strong predictors of species occupancy. Including season as a detection covariate improved model fit in all cases; for legibility, results from iterations without season are shown for the global model only

Model	Type	Species	Intercept	Exposed	Hideable	Climbable	Distance to boundary	Human RAI
Global (M1)	M	Leopard	1.47	0.44	0.96	−0.11	0.14	0.85
Global (M1)	M	Lion	0.17	−0.2	−0.5	0.24	0.08	0.13
Global (C1)	C	Both	−0.53	0.10	0.25	−0.49	−0.31	−1.18
Global (M2)	M	Leopard	1.47	0.42	0.93	−0.09	0.13	0.93
Global (M2)	M	Lion	0.21	−0.20	−0.51	0.23	0.08	0.13
Habitat (C3.1)	C	Both	−0.10		−0.16			
Human (C4.2)	C	Both	−0.47					−1.67
Prey (C6.6)	C	Both	−0.54					
Habitat (C3)	C	Both	−0.03	0.07	0.07	−0.37		
Human (C4)	C	Both	−0.51				−0.14	−1.74
Global (C2)	C	Both	−0.56	0.10	0.31	−0.48	−0.30	−1.13
Hideable (M3)	M	Leopard	0.64		0.24			
Hideable (M3)	M	Lion	0.71		0.27			
Habitat (C3.3)	C	Both	−0.13	0.18				
Prey (C6.1)	C	Both	−0.53					
Human RAI (M4)	M	Leopard	0.88					0.54
Minimum (C1.1)	C	Both	−0.1					
Prey (C6.4)	C	Both	−0.12					
Habitat (C3.4)	C	Both	−0.13			0.04		
Human (C4.3)	C	Both	−0.14				−0.19	
Terrain (C5)	C	Both	−0.08					
Prey (C6.3)	C	Both	−0.20					
Prey (C6.5)	C	Both	−0.13					
Topographic ruggedness (M5)	M	Leopard	0.79					
Prey RAI (very large) (M6)	M	Lion	0.81					

Notes. M: marginal; C: conditional; RAI: relative abundance index; WAIC: Watanabe–Akaike Information Criterion. [a]Lion and leopard analyses were run together inclusively in marginal models; consequentially, the WAIC and $\hat{R}$ values are the same for both species in these models.

3.3 | Population effects

The number of lions in each study site ranged from 4 to 120 (mean = 36.2 ± 41.6). Accordingly, lion population density ranged from 1.1 to 16.6 lions/100 km^2 (mean = 6.9 ± 5.0 individuals/100 km^2). Across all camera trapping surveys, we identified 213 male leopards, 256 female leopards and 29 leopards of unknown sex (Table 3). During each survey, on average 26.1 ± 8.3 (range = 10–41) individual leopards were captured on 111 ± 42 occasions (range = 36–197) and recaptured on 2.6 ± 0.8 occasions (range = 1.2–4.5). Based on our SCR analyses, estimated leopard population densities across sites and years ranged from 1.0 to 11.0 leopards/100 km^2 (mean = 7.2 ± 3.1 individuals/100 km^2). Assessment of posterior MCMC parameter-wise traceplots and histograms indicated that all models converged ($\hat{R}^3$ = 1.002–1.004 for all models) and that data augmentation used within each model was sufficient to prevent truncation of *N*-Super (i.e. the population size of individuals within the statespace; Gopalaswamy et al., 2012). Tests revealed no evidence of lack of fit (Bayesian *p*-value ranged 0.46–0.57 in all cases except Welgevonden Private Game Reserve in 2013, for which model fit was 0.83; Table 3).

The mixed-effects model found that leopard population densities were generally higher in study sites with higher lion densities (Figure 4), but this relationship was weak and lion density was not a strong predictor of leopard density ($\beta_{\text{lion density}}$ = 0.11 ± 0.17, t_9 = 0.63, p = 0.54; excluding Timbavati Private Game Reserve and Hluhluwe-iMfolozi Park: $\beta_{\text{lion density}}$ = 0.10 ± 0.44, t_5 = 0.22, p = 0.83).

Topographic ruggedness	Prey RAI (small)	Prey RAI (medium)	Prey RAI (large)	Prey RAI (very large)	Detection	WAIC[a]	ΔWAIC
0.44	−0.11	0.25	0.23	0.13	Season	16880.55	0
−0.06	0	0.03	−0.12	**0.5**	Season	16880.55	0
0.38	−0.29	−0.20	−0.20	−0.53	Season	16885.39	4.83
0.44	−0.11	0.28	0.25	0.12		16890.08	9.53
−0.06	0	0.03	−0.12	**0.51**		16890.08	9.53
					Season	16890.12	9.56
					Season	16892.37	11.81
				−1.20	Season	16893.43	12.88
					Season	16893.51	12.96
					Season	16895.58	15.03
0.36	−0.27	−0.19	−0.26	−0.51		16895.67	15.11
					Season	16899.07	18.51
					Season	16899.07	18.51
					Season	16905.15	24.6
	−0.41	0	−0.21	−0.91	Season	16909.8	29.25
					Season	16910.49	29.94
					Season	16910.71	30.16
		−0.20			Season	16911.1	30.54
					Season	16911.4	30.84
					Season	16911.74	31.19
0.22					Season	16912.23	31.68
	−0.66				Season	16913.83	33.28
			−0.39		Season	16914.04	33.49
0.15					Season	16918.17	37.61
				0.14	Season	16919.66	39.11

Spatial variation (i.e. using "site" as a random effect) accounted for 77% of the variance, whereas temporal variation (i.e. using "year" as a random effect) accounted for 0%.

4 | DISCUSSION

Our study revealed an unexpected lack of spatial and temporal avoidance, and associated demographic consequences, of interspecific competition between two wide-ranging, large carnivores. We expected leopards, the subordinate competitor, to exhibit conditional spatial occupancy, temporal shifts and inversely related population densities relative to lions, the dominant competitor; yet evidence suggested otherwise. Our findings demonstrate that lions do not influence leopard spatiotemporal dynamics at the scale of our analysis, even though they pose a threat to leopard survival (Balme et al., 2013; Balme, Pitman et al., 2017). In an important way, we found no evidence that lions suppress leopard populations, suggesting that these two carnivores can coexist within the same protected areas without competitive interactions seemingly contributing to their declines.

Contrary to our hypothesis about spatial avoidance, lions and leopards acted independently of one another, by prioritizing different landscape features that met their individual ecological needs. If our occupancy modelling results had been consistent with the predicted asymmetrical relationship between a dominant and subordinate competitor (Palomares & Caro, 1999), we would have expected to see changes in leopard occupancy based on the

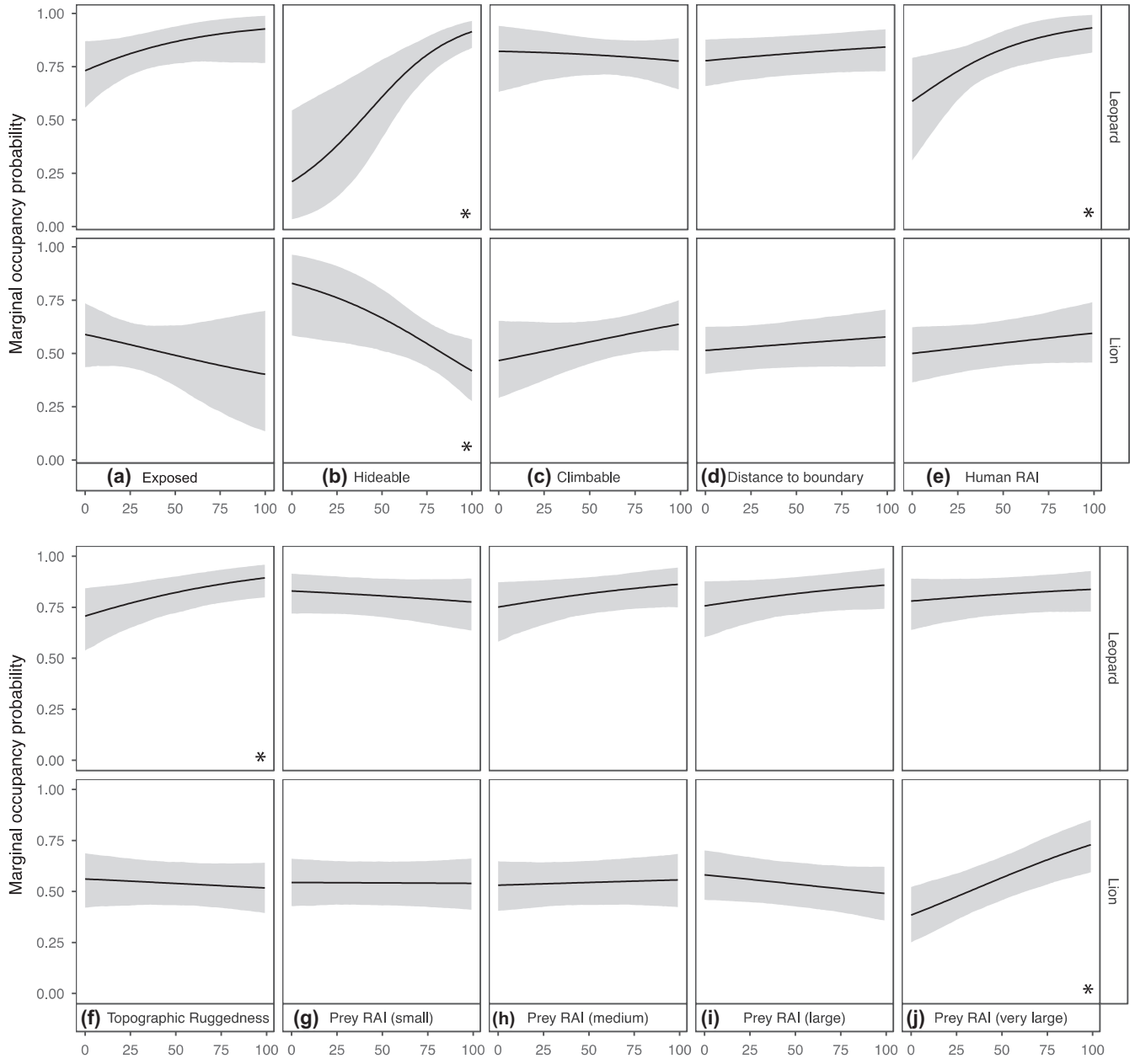

FIGURE 2 Marginal occupancy probability of leopard (rows 1 and 3) and lion (rows 2 and 4) in 10 study sites across South Africa (2013–2015) based on the top-ranking global marginal model (M1). Occupancy is shown as a function of (a) exposed (open vegetation), (b) hideable (bushy vegetation) and (c) climbable habitat (tree-height vegetation), (d) distance to study site boundary, (e) human relative abundance index (RAI, indicating activity), (f) topographic ruggedness index and the RAI of (g) small, (h) medium, (i) large and (j) very large prey. Solid lines represent the mean posterior distributions and ribbons indicate 95% credible intervals. Asterisks indicate covariates for which the credible intervals of slope parameters did not overlap 0 (Table 1), indicating a strong effect on species occupancy

presence of lions. However, we found no evidence to support conditional occupancy by either species, and the marginal models suggested that lions and leopards prefer different environmental conditions. The top-ranking model for leopards demonstrated that, regardless of lion presence, leopards were most likely to occupy areas with high human activity, rugged terrain and a high percentage of high-cover, low visibility woodland and shrubland, which we termed "hideable" habitat. Leopard preference for dense, bushy habitats and rugged terrain is likely associated with increased prey availability and hunting success (Bailey, 2005; Balme, Hunter, & Slotow, 2007; Balme, Pitman et al., 2017; Swanepoel et al., 2013), rather than as refuge from lions. Likewise, although leopards had a higher probability of using areas with more human activity, it seems unlikely that they were using human presence as a protective "shield" against lions (sensu Berger, 2007). First, lions showed no avoidance of such areas. Second, these areas likely did not represent suboptimal leopard habitat as predicted, but rather the opposite. Most (>90%) human captures by our camera traps were

TABLE 2 Temporal overlap between lions, leopards and prey by season and time of day in 10 study sites across South Africa (2013–2015)

	Temporal activity overlap ($\hat{D}$ [95% CI])					
	Wet season (December–April)			Dry season (May–November)		
Group compared	Full day (00:00–24:00)	Day (06:00–17:59)	Night (18:00–05:59)	Full day (00:00–24:00)	Day (06:00–17:59)	Night (18:00–05:59)
Lion–leopard	0.87 (0.85–0.94)	0.72 (0.67–0.87)	0.87 (0.83–0.95)	0.90 (0.87–0.93)	0.82 (0.78–0.90)	0.92 (0.88–0.95)
Lion–small prey	0.80 (0.77–0.85)			0.74 (0.73–0.78)		
Lion–medium prey	0.46 (0.44–0.52)			0.44 (0.43–0.48)		
Lion–large prey*	0.57 (0.45–0.53)			0.50 (0.49–0.55)		
Lion–very large prey*	0.72 (0.69–0.77)			0.68 (0.66–0.72)		
Leopard–small prey*	0.85 (0.82–0.91)			0.75 (0.74–0.79)		
Leopard–medium prey*	0.52 (0.49–0.58)			0.44 (0.43–0.49)		
Leopard–large prey	0.63 (0.59–0.69)			0.51 (0.50–0.56)		
Leopard–very large prey	0.78 (0.75–0.84)			0.73 (0.71–0.76)		

Note. Asterisks indicate preferred prey for the paired carnivore (Hayward & Kerley, 2005; Hayward et al., 2006).

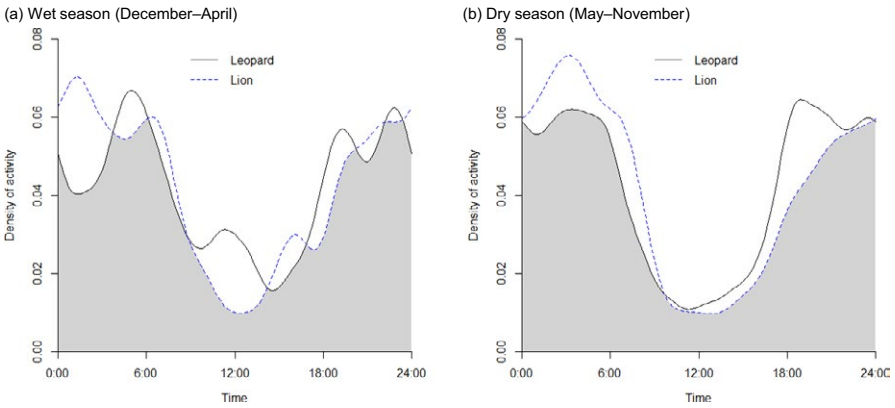

FIGURE 3 Temporal overlap of activity patterns of leopards and lions based on photograph records from camera trapping in 10 study sites across South Africa (2013–2015) during the (a) wet and (b) dry seasons

of tourist vehicles, which can deter poachers (Laurance, 2013). As leopards are increasingly being targeted by poachers for their skins for ceremonial wear (Stein et al., 2016), leopards may avoid poachers by favouring areas with high tourism traffic (Cromsigt et al., 2013; Everatt, Andresen, & Somers, 2015). Lions may not need to adopt the same strategy as they are currently less desired by poachers (although this may change as demand for lion bone increases; Williams, Newton, Loveridge, & Macdonald, 2015).

The marginal models suggested lion occupancy was higher in areas with a low percentage of hideable habitat and areas with high abundances of very large prey. Hideable habitat represents optimal hunting conditions for leopards which, as solitary ambush predators, rely on cover to successfully stalk prey (Balme et al., 2007). In contrast, the dense cover associated with hideable habitat may impede hunting lions, by reducing encounter rates with prey and their ability to hunt cooperatively (Hopcraft et al., 2005; Loarie et al., 2013). Intraguild predation theory predicts that in circumstances where the subordinate competitor (or intraguild prey) is more efficient than the dominant competitor (or intraguild predator) at utilizing basal prey resources, the subordinate may outcompete the dominant competitor through exploitation competition (Holt & Polis, 1997). Therefore, it is plausible that lions were outcompeted and displaced by leopards in hideable habitat, but if this were true we would expect lion occupancy in this habitat to be conditional on leopard presence, which was not the case. Lion preference for areas with a high abundance of very large prey matches their dietary niche (Hayward & Kerley, 2005).

TABLE 3 Spatial capture–recapture model statistics for leopard densities in 10 study sites across South Africa (2013–2015). σ = the scale parameter sigma (m); λ_0 = expected encounter rate of individual i in location j at sampling occasion k; ψ = fraction of the maximum allowable number representing the true population size (set via data augmentation); N Super = the estimated number of activity centres located within the statespace; D = density 1/km)

						Statistic results	
Study site	**Year**	**Stat**	σ	λ_0	ψ	*N* **super**	***D***
Hluhluwe-iMfolozi Park	2013	Mean	3584.36	0.025	0.731	310.37	0.064
		SD	530.95	0.008	0.141	59.68	0.012
	2014	Mean	3217.19	0.053	0.805	354.82	0.077
		SD	257.12	0.011	0.104	45.10	0.010
	2015	Mean	3748.41	0.028	0.697	299.54	0.065
		SD	469.36	0.008	0.138	58.64	0.013
KwaZulu Private Game Reserve	2015	Mean	3725.95	0.028	0.730	318.05	0.082
		SD	681.31	0.011	0.129	55.52	0.014
Makalali Private Game Reserve	2014	Mean	3606.05	0.028	0.405	211.09	0.063
		SD	364.90	0.012	0.095	48.60	0.014
	2015	Mean	3119.17	0.046	0.590	313.40	0.094
		SD	276.21	0.020	0.110	57.51	0.017
Phinda Private Game Reserve	2014	Mean	4117.61	0.058	0.560	240.39	0.068
		SD	217.21	0.007	0.099	41.62	0.012
Tembe Elephant Park	2015	Mean	2896.82	0.040	0.628	263.66	0.083
		SD	345.27	0.014	0.139	57.73	0.018
Timbavati Private Game Reserve	2013	Mean	6283.46	0.007	0.519	330.60	0.099
		SD	986.55	0.002	0.126	79.88	0.024
	2014	Mean	5754.00	0.009	0.491	314.89	0.095
		SD	534.74	0.002	0.083	52.13	0.016
uMkhuze Game Reserve	2013	Mean	3390.20	0.038	0.771	333.60	0.111
		SD	285.45	0.008	0.113	48.20	0.016
	2014	Mean	2542.88	0.074	0.719	307.24	0.103
		SD	173.58	0.013	0.116	48.97	0.016
	2015	Mean	3235.32	0.037	0.657	279.32	0.093
		SD	302.94	0.008	0.117	49.04	0.016
Venetia-Limpopo Nature Reserve	2014	Mean	5231.13	0.014	0.752	165.84	0.052
		SD	1169.24	0.008	0.151	32.99	0.010
	2015	Mean	3779.10	0.024	0.763	164.73	0.047
		SD	809.18	0.016	0.144	30.61	0.009
Welgevonden Private Game Reserve	2013	Mean	4153.02	0.020	0.368	153.19	0.051
		SD	524.45	0.005	0.094	38.12	0.013
	2014	Mean	4728.34	0.035	0.590	131.19	0.038
		SD	507.64	0.012	0.140	30.54	0.009
	2015	Mean	7509.50	0.031	0.429	93.40	0.027
		SD	1874.41	0.019	0.121	25.51	0.007
Zululand Rhino Reserve	2015	Mean	9156.13	0.053	0.083	33.37	0.010
		SD	1138.50	0.018	0.029	10.45	0.003

Site-level temporal activity showed no strong evidence of competition between lions and leopards. Although temporal partitioning is a common strategy for avoiding competition (Harrington et al., 2009; Linnell & Strand, 2000; Schoener, 1974), lions and leopards were active at the same times, resting during the day and moving during the night. Minor, fine-scale offsets between peak lion and

			Capture results				
Bayesian *p*-value	Captures	Mean spatial recapture ± *SD* (min–max)	Recapture range	Individuals	Males	Females	Unknown
0.50	40	1.2 ± 0.4	1–2	24	14	9	1
0.50	153	2.1 ± 1.3	1–6	40	16	24	0
0.50	109	2.3 ± 1.4	1–6	29	14	12	3
0.57	158	2.4 ± 1.9	1–10	33	11	22	0
0.53	82	2.3 ± 2.4	1–12	23	8	12	3
0.53	132	2.8 ± 2.0	1–7	32	13	13	6
0.53	197	3.3 ± 2.9	1–12	29	10	19	0
0.51	121	2.8 ± 2.0	1–8	20	8	12	0
0.52	92	1.7 ± 1.2	1–6	37	18	16	3
0.53	140	2.0 ± 1.5	1–6	41	17	24	0
0.55	135	2.5 ± 2.5	1–14	32	15	12	5
0.54	144	2.9 ± 3.3	1–17	27	7	16	4
0.56	104	2.6 ± 2.0	1–8	25	8	13	4
0.52	55	2.1 ± 1.9	1–8	20	10	10	0
0.47	36	1.8 ± 1.2	1–6	16	8	8	0
0.81	134	4.5 ± 4.0	1–14	17	7	10	0
0.49	93	2.5 ± 2.1	1–8	24	10	14	0
0.46	112	3.7 ± 3.3	1–12	19	12	7	0
0.46	75	3.3 ± 3.0	1–10	10	7	3	0

leopard activity in the wet season could reflect competitor avoidance but, given that activity overlap with prey increased in this season, more likely reflect shifts in activity to enhance opportunities for hunting prey. As with previous findings (Hayward & Slotow, 2009), most carnivore temporal patterns did not track preferred prey activity, which peaked during the day. This suggests that lions and

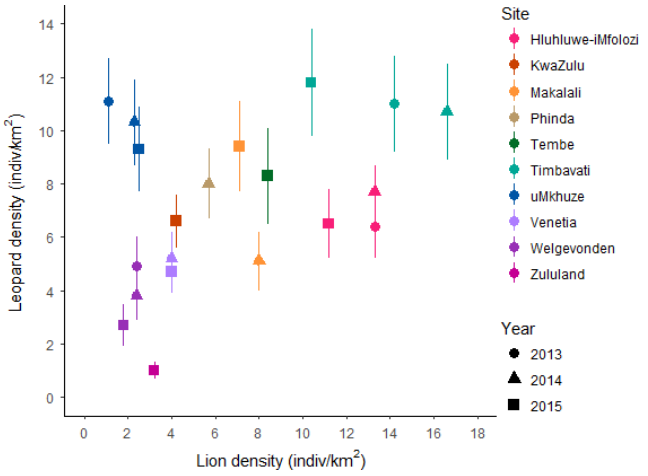

FIGURE 4 Relationship between leopard and lion density in 10 study sites across South Africa (2013–2015). Colour indicates study site, shape indicates sampling year, and vertical coloured lines represent standard deviation of leopard density. Lion density was not a statistically significant predictor of leopard density in the linear effects model

leopards are optimizing hunting conditions by taking advantage of the camouflage provided by low-light conditions and reducing physiological limitations due to daytime heat (higher temporal overlap with prey in the wet season also corresponded to higher monthly temperatures in our study region). We would expect that particularly for leopards, the foraging benefit gained through this activity pattern offsets the risk of encountering their competitor. Other subordinate carnivores (e.g. wild dogs, cheetahs, bobcats [*Lynx rufus*]) are similarly incentivized by opportune hunting conditions to risk foraging alongside dominant competitors (Cozzi et al., 2012; Wilson et al., 2010). Prey was abundant across most sites (Balme et al., 2010; Lindsey et al., 2011; Miller et al., 2013), and therefore, it is possible that our findings of temporal overlap were resource-mediated. Temporal partitioning has been a function of prey abundance in other systems with large felids (Karanth et al., 2017; Wilson et al., 2010), and thus, we anticipate that lions and leopards could exhibit increased temporal segregation at sites where low prey abundance imposes greater sharing of resources.

At last, we did not find evidence of lions suppressing leopard densities at the population level. Interference competition between intraguild competitors can have demographic consequences through reducing carrying capacity or slowing population growth due to direct aggression or the inaccessibility of resources (e.g. spatial, temporal or food avoidance or exclusion; Linnell & Strand, 2000). Yet our results suggest that lions and leopards coexist without negatively impacting each other's behaviour, distribution or density. In contrast to our original hypothesis, we found a weak (not statistically significant) positive relationship between species densities, which we attribute to environmental conditions and management rather than interspecific interactions. In a specific manner, protected areas that are effectively managed to support lions (e.g. more suitable habitat, higher prey abundance, less poaching) would similarly facilitate protection of leopards. Prior evidence suggests that the densities of both carnivore species are related to the biomass of their preferred prey (Hayward, O'Brien, & Kerley, 2007), which may have further explained our results although we did not have data to explicitly test this relationship. Although lions (and leopards) can cause mortality to individual animals (Balme, Miller et al., 2017; Palomares & Caro, 1999), these effects do not appear to scale to the population level. Our findings support recent evidence from the Sabi Sand Game Reserve (Balme, Pitman et al., 2017), pointing to the same general result across our 10 study sites: that lions and leopards coexist without having a negative effect on each other at a population scale.

The apparent lack of interspecific competition between lions and leopards at our scale of inquiry may be the result of several ecological phenomena. First, our results show that bottom-up factors play a stronger role in influencing occupancy of a subordinate predator (leopards) than top-down suppression by a dominant predator (lions). It is possible that similar relationships are present across the broader carnivore guild in these sites, calling into question the validity of the mesopredator release hypothesis as a framework for understanding carnivore interactions in relatively intact ecosystems (Ford et al., 2015). Second, lion and leopard preference for different prey species and weight ranges may be sufficient to preclude direct competition (Clements, Tambling, Hayward, & Kerley, 2014). Third, our results are consistent with Hutchinson and MacArthur's (1959) ecological theory on size distributions of animals, which predicts that mammal species with a body size ratio of 1.3 or higher will not directly compete due to niche separation. Lions and leopards have a body size ratio of 3.1 (Radloff & Du Toit, 2004), and accordingly, we can expect their coexistence in similar temporal and spatial niches, which we observed in our study, to hold in other regions across their species range. At last, lion–leopard interspecific interactions today could be a "ghost of competition past," and reflect distinct ecological niches which emerged as the species coevolved in sympatry in the Pliocene (Connell, 1980; Turner, 1990).

Global priorities and strategies for biodiversity conservation are increasingly being developed at broad scales that extend beyond single populations to encompass multiple landscapes and, in some cases, continents (Di Minin et al., 2016; Dickman, Hinks, Macdonald, Burnham, & Macdonald, 2015). Informed decision-making requires clear and generalizable understanding of the ecological principles underlying population dynamics and interspecific interactions. The extensive geographical scope of our data combined with multispecies, regional occupancy modelling offers guiding principles about how carnivores coexist across a range of environmental conditions and competitor presence. Minor differences in spatial occupancy, combined with dietary partitioning, appear to enable lions and leopards to share the same temporal niche and general habitat without suppressing each other's populations.

Our findings have several encouraging implications for management and conservation of threatened carnivores. First, subordinate carnivores may be more adaptive, and less vulnerable,

to potential behavioural and population suppression by dominant competitors than previously thought. Emerging evidence from a broader array of geographic regions and ecosystems is offering new understanding about the diverse strategies that subordinate carnivores such as cheetahs, bobcats and now leopards use to navigate competition (Balme, Pitman et al., 2017; Lewis et al., 2015; Mills & Mills, 2017; Wilson et al., 2010). Second, multiple large carnivores may be able to coexist in the same protected areas. This is critical information for two reasons: (a) maintaining intact ecosystems with large carnivores is vital for maintaining healthy ecosystem functioning and community structure (Ripple et al., 2014) and (b) preserving intact sympatric carnivore guilds is a priority for promoting biodiversity conservation (Dalerum, Somers, Kunkel, & Cameron, 2008). As a charismatic, threatened keystone species, lions are increasingly the sole focus of highly funded, continental-wide conservation efforts (Lindsey, Balme, Funston, Henschel, & Hunter, 2016; Wildlife Conservation Network & Leonardo DiCaprio Foundation, 2017), but these funds can and must be allocated strategically to protect "lionscapes" that can simultaneously support other sympatric threatened species, including leopards. Our study provides evidence that lions and leopards—and potentially other competing large carnivores globally—can be concurrently managed in the same protected areas without negative repercussions from interspecific competition, enabling an aligned, cost- and space-efficient carnivore conservation strategy.

ACKNOWLEDGEMENTS

We thank the managers at our study sites for providing data and for logistical support during camera trapping. We are grateful for logistical and technical assistance from Jim Hines, Daryl McKenzie, Lindsey Rich, Matt Rogan, Gareth Whittington-Jones, Almero Bosch, WildlifeACT and Wildlife and Ecological Investments. Sahas Barve and Dan Linden provided valuable feedback on the manuscript. J.M. was supported in part by Panthera postdoctoral funding and by National Science Foundation Coupled Human and Natural Systems Grant 115057. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

AUTHORS' CONTRIBUTIONS

G.B. conceived the ideas and designed methodology; R.P. and G.M. collected the data; J.M., R.P. and G.M. analysed the data; J.M. led the writing of the manuscript. J.M., R.P., G.M., A.F. and G.B. contributed critically to the writing of the manuscript.

DATA ACCESSIBILITY

Data used in this study are archived in the Dryad Digital Repository: https://doi.org/10.5061/dryad.396v8n4 (Miller et al., 2018).

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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: Miller JRB, Pitman RT, Mann GKH, Fuller AK, Balme GA. Lions and leopards coexist without spatial, temporal or demographic effects of interspecific competition. *J Anim Ecol*. 2018;00:1–18. https://doi.org/10.1111/1365-2656.12883