Moving to stay in place: behavioral mechanisms for coexistence of African large carnivores

ABI TAMIM VANAK,[1,2] DANIEL FORTIN,[3] MARIA THAKER,[1,4,6] MONIKA OGDEN,[5] CAILEY OWEN,[1,5] SOPHIE GREATWOOD,[1] AND ROB SLOTOW[1]

[1]*School of Life Sciences, University of KwaZulu-Natal, PB x54001, Westville 4000 South Africa*
[2]*Ashoka Trust for Research in Ecology and the Environment, Bangalore 560064 India*
[3]*Départment de Biologie, Université Laval, Québec G1V 0A6 Canada*
[4]*Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560012 India*
[5]*Karongwe Ecological Research Institute, Schagen 1207 South Africa*

Abstract. Most ecosystems have multiple predator species that not only compete for shared prey, but also pose direct threats to each other. These intraguild interactions are key drivers of carnivore community structure, with ecosystem-wide cascading effects. Yet, behavioral mechanisms for coexistence of multiple carnivore species remain poorly understood. The challenges of studying large, free-ranging carnivores have resulted in mainly coarse-scale examination of behavioral strategies without information about all interacting competitors. We overcame some of these challenges by examining the concurrent fine-scale movement decisions of almost all individuals of four large mammalian carnivore species in a closed terrestrial system. We found that the intensity of intraguild interactions did not follow a simple hierarchical allometric pattern, because spatial and behavioral tactics of subordinate species changed with threat and resource levels across seasons. Lions (*Panthera leo*) were generally unrestricted and anchored themselves in areas rich in not only their principal prey, but also, during periods of resource limitation (dry season), rich in the main prey for other carnivores. Because of this, the greatest cost (potential intraguild predation) for subordinate carnivores was spatially coupled with the highest potential benefit of resource acquisition (prey-rich areas), especially in the dry season. Leopard (*P. pardus*) and cheetah (*Acinonyx jubatus*) overlapped with the home range of lions but minimized their risk using fine-scaled avoidance behaviors and restricted resource acquisition tactics. The cost of intraguild competition was most apparent for cheetahs, especially during the wet season, as areas with energetically rewarding large prey (wildebeest) were avoided when they overlapped highly with the activity areas of lions. Contrary to expectation, the smallest species (African wild dog, *Lycaon pictus*) did not avoid only lions, but also used multiple tactics to minimize encountering all other competitors. Intraguild competition thus forced wild dogs into areas with the lowest resource availability year round. Coexistence of multiple carnivore species has typically been explained by dietary niche separation, but our multi-scaled movement results suggest that differences in resource acquisition may instead be a consequence of avoiding intraguild competition. We generate a more realistic representation of hierarchical behavioral interactions that may ultimately drive spatially explicit trophic structures of multi-predator communities.

Key words: carnivore community; cost–benefit trade-off; interference competition; intraguild competition; Karongwe Game Reserve, South Africa; movement ecology; predator–prey interactions; top-down effects.

Predation and competition are key drivers that shape community structure and function, strongly affecting the distribution, population dynamics, and behavior of interacting species (Chase et al. 2002, Chesson and

Kuang 2008, Hopcraft et al. 2010). These drivers combine most spectacularly within the same guild in the mammalian Carnivora, where some of the largest terrestrial predators share similar resources and space (Palomares and Caro 1999, Linnell and Strand 2000, Ritchie and Johnson 2009). Apex carnivores can be keystone components in ecosystem functioning, not only because of their role in driving trophic cascades (Schmitz et al. 2004, Steneck and Sala 2005, Elmhagen et al. 2010, Terborgh and Estes 2010), but also because of their top-down competitive effects on sympatric carnivores (Linnell and Strand 2000, Caro and Stoner 2003, Ritchie

and Johnson 2009). These antagonistic interactions between multiple species of sympatric predators go beyond "eating and being eaten" (Johnson 2010), because subordinate carnivores live under the risk of interference competition and intraguild killing (Holt and Polis 1997, Donadio and Buskirk 2006). Classic ecological theory based solely on predator–prey interactions may thus be inadequate to understand trophic dynamics in many ecological systems (Elmhagen et al. 2010, Johnson 2010). Indeed, the behavioral games that predators play to coexist can be as important as those between predators and prey (Johnson 2010).

Game theoretic models that examine the space use of multiple competing predators and mobile prey generally predict that top predators are unrestricted and will match the distributions of their prey, whereas subordinate predators balance the trade-off between resource acquisition and risk (Heithaus 2001, Rosenheim 2004). These models, however, poorly match systems with large mammalian carnivores because they make key simplifying assumptions about the nature of the interactions between competing predators, as well as the composition of the resource base. All models only consider two predators competing for the same basal resource, where the dominant intraguild predator also preys on the subordinate predator (intraguild prey; Rosenheim 2004) or utilizes an alternative resource (Heithaus 2001). Many terrestrial ecosystems have more than two species of large mammalian carnivores competing for multiple prey species (Woodroffe and Ginsberg 2005). More importantly, subordinate carnivores are not the main prey for dominant carnivores, although they may be killed as an extreme form of interference competition (Palomares and Caro 1999, Donadio and Buskirk 2006). Even empirical studies that examine the competitive effects of top predators on subordinate predators typically focus on a subset of the interacting species (Creel et al. 2001, Vanak and Gompper 2010), or only examine some localized aspects of behavior (e.g., home range overlap, kleptoparasitism, harassment, foraging–vigilance trade-offs; Creel et al. 2001, Ritchie and Johnson 2009).

Some of the most diverse and complex terrestrial assemblages of large carnivores in the world occur in African savannas, with up to five species of large carnivores, *Panthera leo* (lion), *P. pardus* (leopard), *Crocuta crocuta* (spotted hyena), *Acinonyx jubatus* (cheetah), and *Lycaon pictus* (African wild dog), occurring sympatrically. Interference competition among these species is well documented in the literature (Creel et al. 2001). For example, both cheetahs and wild dogs suffer negative consequences from competition with lions and spotted hyenas. These include reduced access to high-resource areas, reduced food intake due to kleptoparasitism, direct harassment, and increased mortality of cubs and adults due to intraguild killing (Durant 1998, Creel et al. 2001, Webster et al. 2012). Thus far, temporal partitioning of activity has been

postulated as the principal behavioral mechanism that allows these subordinate carnivores to coexist with dominant carnivores (Hayward and Slotow 2009). However, recent evidence suggests that there may be greater temporal overlap between these predator species than previously detected (Cozzi et al. 2012), requiring further examination of the behavioral mechanisms that permit sharing of space. Additionally, most studies of intraguild competition examine interactions between pairs of species and ignore interactions between the subordinate carnivores, inadvertently assuming that behavioral decisions are mainly a function of avoiding competition from the most dominant carnivore. This assumption is likely to be invalid in many cases because subordinate carnivores also compete with each other for similar resources (Owen-Smith and Mills 2008), and therefore must simultaneously balance the risk of competition from multiple carnivore species.

Multivariate behavioral interactions are notoriously difficult to study empirically, mainly because the motivation or causes of behavioral tactics of free-ranging carnivores may remain unrecognized without extensive knowledge of all possible interacting individuals. Furthermore, intraguild competition can alter population sizes and demography of sympatric carnivores, and hence cause levels of intra- and interspecific competition to vary dynamically across space and time (Creel et al. 2001). Here, we overcome some of these challenges by studying free-ranging lions, leopards, cheetahs, and African wild dogs in a fenced reserve in South Africa, where predator and prey densities were relatively stable and the locations of almost all individuals of all focal carnivore species were known. This controlled environment allowed us to examine the effect of intraguild competition from multiple carnivores without the confounding effects of incomplete information about the number of interacting individuals, and of density-dependent changes in demography and levels of competition.

Based on concurrent consecutive locations of almost all focal carnivore individuals over a four-year period, we assessed the movement decisions of each focal species as a multivariate function of the presence of interspecific and intraspecific competitors, prey selection strategies, and land cover types. Carnivores can reduce the risk of encounters with other competitors by avoiding direct encounters (Creel et al. 2001), or by avoiding predictable activity areas (core home range) or predictable time periods (but see Cozzi et al. 2012). We examined behavioral mechanisms of coexistence at two scales: in response to the location of the nearest individual competitor and the long-term activity area of each competitor species. Resource selection is also a key driver of movement and we accounted for prey acquisition as well as selection of land cover types in our analysis of movement decisions. Depending on their hunting mode, carnivores use different tactics to acquire prey. Cursorial predators typically range widely, select-

ing for areas of high prey availability, whereas sit-and-pursue predators select for ambush sites or areas of high prey vulnerability (Schmitz 2005). By including land cover type as a predictor of movement decisions, we were able to test for other aspects of habitat selection (e.g., microclimate or breeding refuge), independent of prey selection. Because all of these factors are affected by seasonal variation, we examined these movement tactics in wet and dry seasons separately. We thus performed a comprehensive movement analysis that was based on the spatial dynamics of carnivore competitors, together with the spatial organization of prey, vegetation, and abiotic habitat features.

METHODS

Study area

This study was conducted in Karongwe Game Reserve (KGR; center 24°13′ S and 30°36′ E), South Africa. In brief, this 85-km^2 fenced conservancy consists of savanna habitats structurally classified into: closed woodland (54.4% of the area) consisting mainly of *Combretum* and *Mopane* woodlands with closed tree canopies; open woodland (24.1%) consisting mainly of *Acacia* spp. with separated tree canopies; open riverine (15.8%) consisting of open-canopy forest with thick understory along drainage lines; closed riverine (1.6%) consisting of gallery forests along rivers; and open scrub (4.1%) consisting of old agricultural lands now reverting to open scrub habitat. The reserve has two major rivers and numerous artificial water holes that are perennial sources of water. The reserve experiences two main seasons (dry season, generally between April and October; wet season, generally between November and March). For this study, seasons were designated based on actual rainfall data (similar to Birkett et al. 2012) because the timing and duration of rainfall varied between years. Further details about the study area are available in Thaker et al. (2011).

Carnivore guild

Almost all adults of the focal carnivore species within the reserve were fitted with VHF transmitters (Telonics SB2 Transmitter, Africa Wildlife Tracking, Pretoria, South Africa) during the study period, 2001–2005. The number of individuals present and radio-tagged in the reserve varied over the years. Lions formed a single pride of five, of which two of three adult males and both adult females were tagged. African wild dogs formed a single pack, of which one of two adult males and the single adult female were tagged. For leopards, all resident adult males ($n = 2$) and females ($n = 7$) were tagged. Similarly, all adult male ($n = 2$) and female ($n = 4$) cheetahs were tagged. We assumed that the movements of the collared individuals were also a fair representation of non-tagged adults and young, because >90% of observations of tagged animals had them associated with non-tagged animals. Locations for each tagged animal were collected multiple times (2–48

points; mean 5.9 ± 3.6 points SD) daily. Spotted hyenas were also present in the reserve ($n = 5$, of which two were tagged). Although predatory in some parts of their distribution (Mills 1990, Kolowski and Holekamp 2006), hyenas were mainly scavengers and not part of the active hunting guild in this reserve (Thaker et al. 2011), similar to Kruger National Park (Owen-Smith and Mills 2008). We recognize that hyenas may still have an influence on the movement decisions of the other carnivores in the reserve, but we did not have sufficient movement data for all years to include them in this analysis.

Prey availability and vulnerability

Twelve ungulate species were recorded in the reserve, but here we focused on the top five principal prey species (>75% contribution to diet), based on numbers and biomass consumed by each carnivore species: impala (*Aepyceros melampus*), blue wildebeest (*Connochaetes taurinus*), waterbuck (*Kobus ellipsiprymnus*), Burchell's zebra (*Equus burchelli*), kudu (*Tragelaphus strepsiceros*), warthog (*Phacochoerus africanus*), and giraffe (*Giraffa camelopardalis*) (see Appendix A for percentage contribution to the diet of each carnivore species). Population sizes of these ungulate species were relatively stable over the study period (see Appendix B for prey population sizes). Thus, the biomass of ungulates (mean 4064 kg/km^2, range 3703–4532 kg/km^2) and the population densities of large carnivores (mean 0.05 individuals/km^2) in this fenced reserve were within the range reported from other African savannas (see reviews in Carbone and Gittleman 2002, Hayward et al. 2007).

Species-specific distributions of the principal prey species were relatively stable throughout the five-year study period, as determined from annual aerial surveys. See Appendix B for the VI (volume of intersection) index of overlap in utilization distributions of each ungulate species. We generated maps of ungulate prey availability using location data of ungulates determined from a road-strip census procedure (Hirst 1969). The reserve was sampled four times for five consecutive days each in both the wet and dry seasons from November 2004 to September 2005. The survey was conducted by two teams, each of which traveled half the reserve roads daily (80 km total) and recorded the geographic coordinates of all ungulates sighted using a handheld GPS. The start and end points of each drive were alternated daily to ameliorate time bias. Because the road network of this reserve is extensive, we were able to create a probability distribution map of each ungulate species for each season using a fixed-kernel density estimator (least-squares cross validation bandwidth selection). This provided us with a seasonally explicit estimate of the probability of encountering any given ungulate species. Bushbuck and duiker were also killed by the focal carnivore species (Appendix A), but their location data were insufficient to generate probability distribution maps. Although bushbuck and duiker are

considered important prey species for cheetahs, leopards, and wild dogs, their total energy contribution is much lower than that of larger prey such as kudu, waterbuck, and wildebeest (Appendix A; C. Owen et al., *unpublished data*).

We also generated a map of prey vulnerability for each of the carnivore species based on four years (2001–2005) of kill location data from the reserve (Thaker et al. 2011). Because of the opportunistic nature of kill data and the typical bias toward larger prey species (Mills 1992), we included the location of all kills, regardless of prey species, to ensure that we had the most complete carnivore-specific estimate of the probability of killing prey (similar to catchability; sensu Hopcraft et al. 2005). We also examined the relationship between the relative probability of occurrence of each predator species (utilization distribution) and the relative probability of occurrence of each of their principal shared prey species to illustrate level of spatial overlap at the home range scale.

Statistical analyses

We examined the effect of intraguild competitors for each of the carnivore species at multiple spatial scales. At a coarse spatial scale, we determined the extent of overlap in home ranges between competing species, using the volume of intersection (VI) index (Fieberg and Kochanny 2005). At finer scales, the spatial determinants of predator movements were modeled using modified step selection functions (SSFs; Fortin et al. 2005). We treated lions and wild dogs as a single group each because movements of individuals were not independent of each other, but individual variability in movement was incorporated into the SSFs for cheetahs and leopards. Instead of being based on steps, the functions derived for all carnivore species were based on moves, i.e., segments linking two successive locations where the organism interrupted its motion. Unlike steps, the duration of moves can be variable (Turchin 1998). Nevertheless, the general statistical principles of SSF apply (Fortin et al. 2005, Forester et al. 2009). The SSFs contrasted the characteristics of each observed move with the characteristics of five moves expected if the animal traveled randomly with respect to habitat features. Based on principles of correlated random walk (Turchin 1998), lengths and turning angles (i.e., the angle between previous and next locations) of random moves were drawn based on the two observed distributions. Because individual moves lasted different lengths of time, we needed to determine how each distribution was linked to move duration.

First, we estimated the relationship between log(movement length) and log(movement duration). The model included move duration and season as main effects, together with the interaction of season × move duration. If no seasonal effects were detected ($P > 0.10$), the related terms were dropped from the final model. From these final models, we determined the precision

associated with the predicted values of the observed moves. We then drew, for each observed move, five random move lengths from the Normal distribution N (M, SD), where M is the predicted move length and SD is its associated standard deviation. Second, we determined whether the turning angle distribution varied as a function of move duration. We used the Kolmogorov-Smirnov statistic to test whether the distributions of turning angles were different between distance categories, and we grouped distances with similar distributions ($P > 0.10$). We ended up with 18 observed distributions of different ranges in hours of observation for the wet and dry seasons for lion (0–0.99 h, 1–4.99 h, >5 h for both seasons combined); leopard (0–0.99 h, 1–18.99 h, >19 h for both seasons combined); wild dog (0–0.99 h, >1 h separately for each season); and cheetah (0–0.99 h, 1–4.99 h, 5–18.99 h, >19 h separately for each season). We then drew, for each observed move, five random turning angles from the relevant distribution. In the end, each actual move was paired with five random moves sharing the same starting point, but differed in their length or direction, or both.

The attributes of observed and random moves were contrasted using conditional logistic regression (PHREG procedure; SAS Institute 2008) for lions and wild dogs, with the resulting SSF taking the structure:

$$w(\mathbf{x}) = \exp(\mathbf{x}_{njt'}\boldsymbol{\beta}) \quad (1)$$

where $\boldsymbol{\beta} = (\beta_1, \ldots, \beta_m)'$, with $\beta_1, \ldots, \beta_m$ being the fixed regression coefficients for m covariates; $\mathbf{x}_{njt} = (x_{njt1}, \ldots, x_{njtm})'$, with $x_{njt1}, \ldots, x_{njtm}$ being the values of m covariates estimated at the jth location available to animal n at time step t. To account for individual variability in movement of cheetahs and leopards, we used *random effects* conditional regressions, conducted using R 2.11.1 (R Core Development Team 2010) with the R package TwoStepCLogit (Craiu et al. 2011). This yielded an SSF taking the structure:

$$w(\mathbf{x}) = \exp(\mathbf{x}_{njt'}\boldsymbol{\beta} + \mathbf{z}_{njt'}\mathbf{b}) \quad (2)$$

where $\mathbf{z}_{njt} = (z_{njt1}, \ldots, z_{njtq})'$, with $z_{njt1}, \ldots, z_{njtq}$ being fixed values specifying the structure of the random effects; and $\mathbf{b} = (b_{n1}, \ldots, b_{nq})'$, with $b_{n1}, \ldots, b_{nq}$ being animal-level random effects. Because conditional regressions have no intercept, random effects are included as random regression coefficients. With both Eqs. 1 and 2, moves with higher SSF score $w(\mathbf{x})$ have higher odds of being chosen by an animal.

We built multivariate models reflecting the fact that moves could be influenced by multiple habitat attributes. The baseline model included a set of continuous covariates determined at the end of the move: prey vulnerability (0–1 scale), competitor utilization distribution (three covariates on a 0–1 scale), and a set of categorical (0 or 1) land cover variables: closed riverine, closed woodland, open woodland, open scrub, with open riverine as the reference category. Because this is an enclosed reserve with an extensive network of roads,
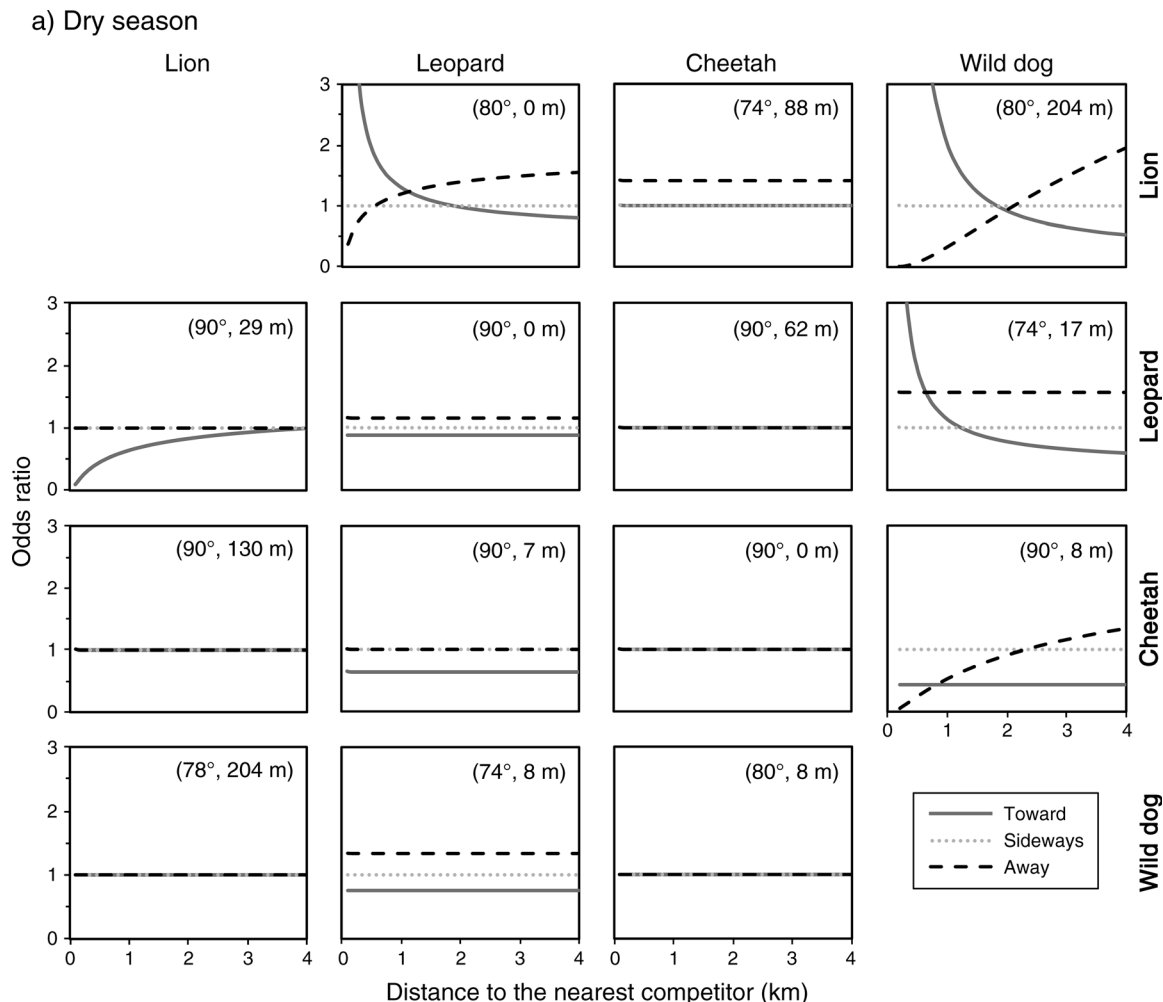
FIG. 1. Distance-dependent responses of carnivores to the presence of competitors at the fine spatial scale during the (a) dry season and (b) wet season in Karongwe Game Reserve, South Africa. Shown are the odds that a given predator species (right-hand y-axis) moved in a particular direction with respect to another species (top labels) as a function of the distance between the two. Line types distinguish movement directions: toward, away, and sideways. Responses start within the range of observed distances (x-axis). Opening angles and minimum observed distances used to define toward and away movements (see *Methods* for details) are inset in parentheses at the top of each graph.

we included distance to the border fence and roads in our models to account for their effects before making inferences about the other parameters. In general, carnivores are known to use roads to travel across their home ranges (e.g., Funston et al. 2010), and some carnivores, such as lions and wild dogs, have been shown to use boundary fences as an aid when hunting large prey (Van Dyk and Slotow 2003).

We also added an index of prey availability consisting of the utilization distributions of the top five prey species for each carnivore species. Because of multicollinearity, the availability index of all principal prey species could not necessarily be a part of the SSFs. We began by including all of them, but removed variables with VIF > 6 (which is lower than the threshold of 10 often suggested, (e.g., Cohen et al. 2003), but higher than VIF > 2 (suggested by Graham 2003). We also tested

whether the removal of a covariate among a set influenced the sign of the others. If this was the case (indicative of multicollinearity), the covariate was either removed or it was kept while excluding the one for which the sign changed. For predators other than lions, we also included interaction terms to determine whether they adjusted their movement biases with respect to blue wildebeest, waterbuck, and warthog, depending on the risk of lion encounter. In the reserve, these ungulates are mostly killed by lions, but they are also consumed by the other large carnivores (Thaker et al. 2011; Appendix A). The interaction with waterbuck exceeded the multicollinearity threshold and thus was not included in the models.

Finally, one of the key interests here was to determine whether a given predator selectively moved away from or toward the nearest competitor, and whether this
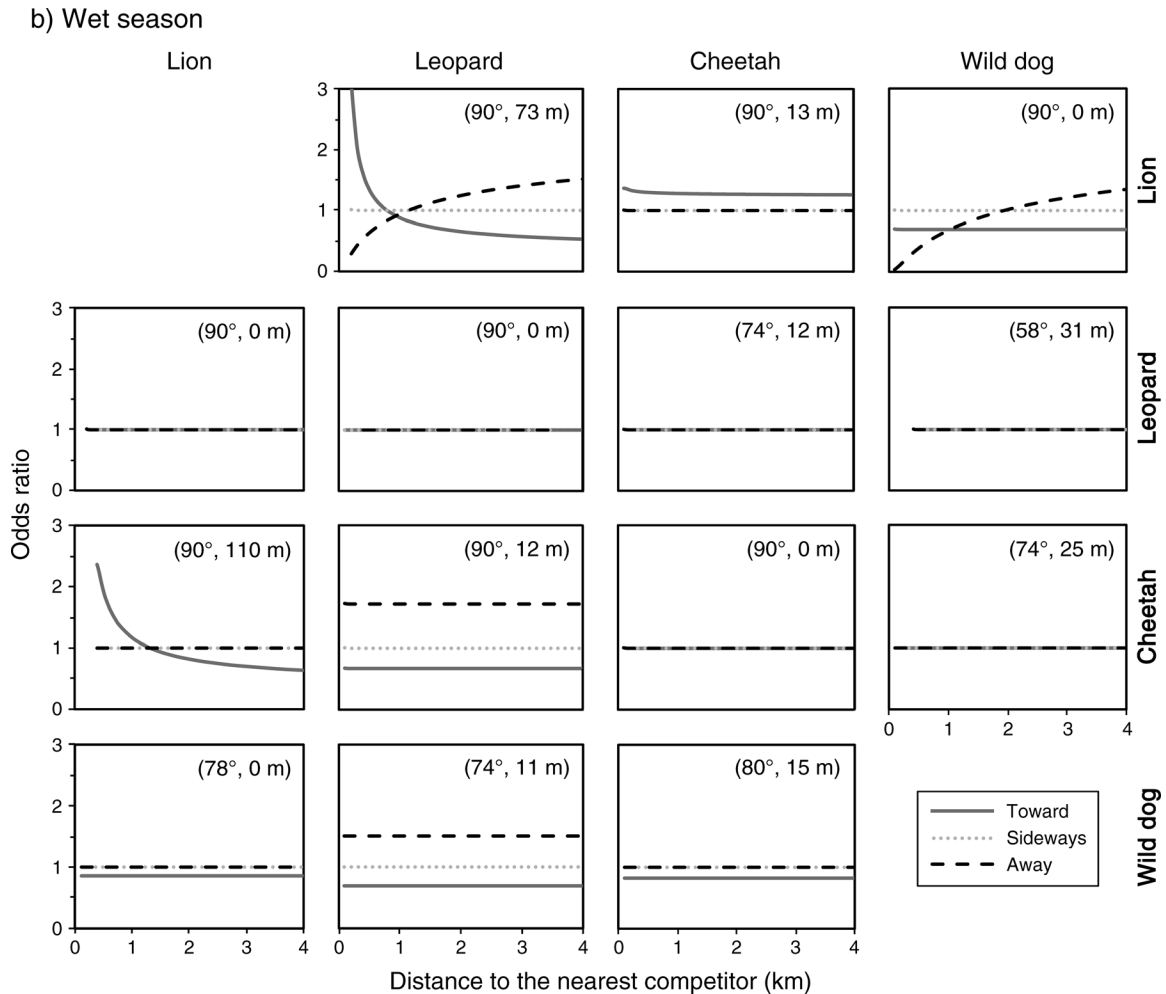
b) Wet season

FIG. 1. Continued.

tendency depended on the distance of each competitor. For all species, the location of the nearest individual competitor of each species was included. We also included the location of the nearest intraspecific competitor only for leopards and cheetahs, as lions and wild dogs each consisted of a single group. When animals were in close proximity to each other (within ~200 m based on actual observed distances; see Fig. 1), directed movements toward competitors were expected to reflect aggression (i.e., interference, harassment, kleptoparasitism), whereas movements away reflected avoidance. For analysis, we defined the opening angle for which a movement could be considered as directed toward or away from the conspecific. The opening angle was assumed to be symmetrical between forward and backward movement biases (e.g., an opening angle going from −45° to +45° for forward movement was associated with an opening angle from −135° to +135° for backward movement). We determined the opening angle that best fitted the data, based on the negative log-likelihood profile provided by different values (Hilborn

and Mangel 1997). Then, distance effects were modeled according to $D_i' = (D_i + 0.01)^k$, where D_i is the distance (km) to the nearest competitor of species i, and k is a parameter controlling for distance-dependent changes in the strength of movement biases with respect to the nearest competitor's location. We tested multiple k values (i.e., −2, −1, −0.5, 0, 0.5, 1, 2) and retained the one minimizing the SSF's negative log-likelihood for each predator and each season. No autocorrelation was detected in successive moves. The robustness of SSF was assessed based on k-fold cross validation for conditional logistic regression (Fortin et al. 2009).

RESULTS

The three felid species, lions (~200 kg), leopards (~60 kg), and cheetahs (~50 kg), showed considerable overlap in home ranges with each other (Table 1). At the fine spatial scale, however, the dominance of lions over the other carnivores emerged more clearly. Lions were more likely to move toward the recent locations of leopards (both seasons) and cheetahs (wet season) when

TABLE 1. Mean 95% fixed-kernel home range size and overlap in home ranges between carnivore species in Karongwe Game Reserve, South Africa.

Predator	Home range size (km²)	VI index		
		Leopard	Cheetah	Wild dog
Lion	60.1 ± 4.9	0.61 ± 0.11	0.58 ± 0.08	0.40 ± 0.17
Leopard	38.5 ± 2.8	0.07 ± 0.08	0.57 ± 0.09	0.52 ± 0.10
Cheetah	41.5 ± 24.1	—	0.32 ± 0.10	0.45 ± 0.18
Wild dog	51.6 ± 15.3	—	—	—

Note: Values (mean ± SD) for home range sizes and volume of intersection (VI) indices are shown for the 4-year study period (three wet seasons and four dry seasons).

in close proximity to them (Fig. 1). As expected, leopards were less likely to move toward the recent location of lions, but this pattern was only apparent in the dry season (Fig. 1a), when habitat selection between these two species was most similar (Appendix C). Contrary to expectation, cheetahs showed a high probability of moving toward recent locations of lions (wet season, Fig. 1b), but still maintained a minimum distance of 110 m from the dominant felid (99% of the time). Intraguild interactions between leopards and cheetahs were only apparent at the fine spatial scale. Although leopards did not respond to the recent locations of cheetahs, cheetahs were more likely to move away from the recent location of leopards (Fig. 1). For leopards, intraspecific interactions were also in the final model for the dry season (Fig. 1a; Appendix C), which was expected, given that leopards showed little overlap in home ranges with other conspecifics (Table 1).

The only canid species in the large carnivore guild, African wild dogs (~25 kg), had low overlap in home range with all three competitors (Table 1). The dominance of the other carnivores over wild dogs was most apparent at the fine scale, with the strength of these intraguild interactions dependent on the season. In the dry season, when competitors were more likely to move toward than away from the recent locations of wild dogs (Fig. 1a), wild dogs strongly avoided the activity centers of all other carnivores (Appendix C). In the wet season, however, wild dogs showed finer-scaled risk-averse tactics by being less likely to move toward the recent location of all other competitors than in other directions (Fig. 1b).

Movement decisions of the carnivores were further influenced by resource selection. At the home range scale, the three largest carnivores overlapped with areas of high prey availability, with some seasonal differences (Fig. 3). The utilization distribution (UD) of lions was positively associated with the UD of impala, warthog, and wildebeest in both seasons, and with waterbuck in the wet season only. The UDs of cheetah and leopard were also positively associated with these species in both seasons. In contrast, the UD of wild dogs were negatively correlated with the availability of these prey species (Fig. 3). At the fine scale, lions were more likely to move toward areas of high availability of their principal prey, as well as areas of high prey vulnerability (Appendix C), which is expected from a sit-and-pursue apex predator. Furthermore, lions showed strong selection for closed riverine in the dry season, while avoiding woodland and open scrub areas in all seasons (Appendix C). Unlike lions, the smaller carnivores were more specific in their resource selection tactics, selecting for fewer resource-rich areas. Contrary to expectation from a sit-and-pursue predator, leopards did not select for areas of high prey vulnerability, but instead selected for some areas of high prey availability; this selection was stronger in the dry than in the wet season (Appendix C). Leopards also strongly selected for closed riverine areas in the dry season (Appendix C). Consistent with a cursorial hunting strategy, cheetahs only selected for some areas of high prey availability and open woodland areas conducive to this hunting mode (Appendix C). However, prey selection strategies of cheetahs were driven not only by hunting tactics, but also by the constraints of avoiding lions. Although cheetahs moved toward areas of high wildebeest occurrence in both seasons, these areas were avoided in the wet season when they overlapped with high risk of lion occurrence (Appendix C; Fig. 2). In the dry season, areas rich in principal prey were still selected by cheetahs, irrespective of the presence of lions (Appendix C). The restriction in space use of wild dogs was also reflected in their fine-scale movement, as they were more likely to move toward areas of high availability of only one prey species per season (Appendix C). As expected from cursorial hunters, wild dogs avoided closed land cover types, such as woodlands in both seasons and closed riverine in the wet season (Appendix C).

All carnivores also responded to the presence of anthropogenic features in the landscape. The focal carnivores were more likely to move toward roads in both seasons, except for leopards, which only moved toward roads in the wet season (Appendix C). Cheetahs and wild dogs also were likely to move toward the boundary fence in both seasons, whereas lions showed directional movement to fences only in the dry season (Appendix C).

DISCUSSION

As one of the most comprehensive empirical studies of intraguild interactions, we found that behavioral mech-
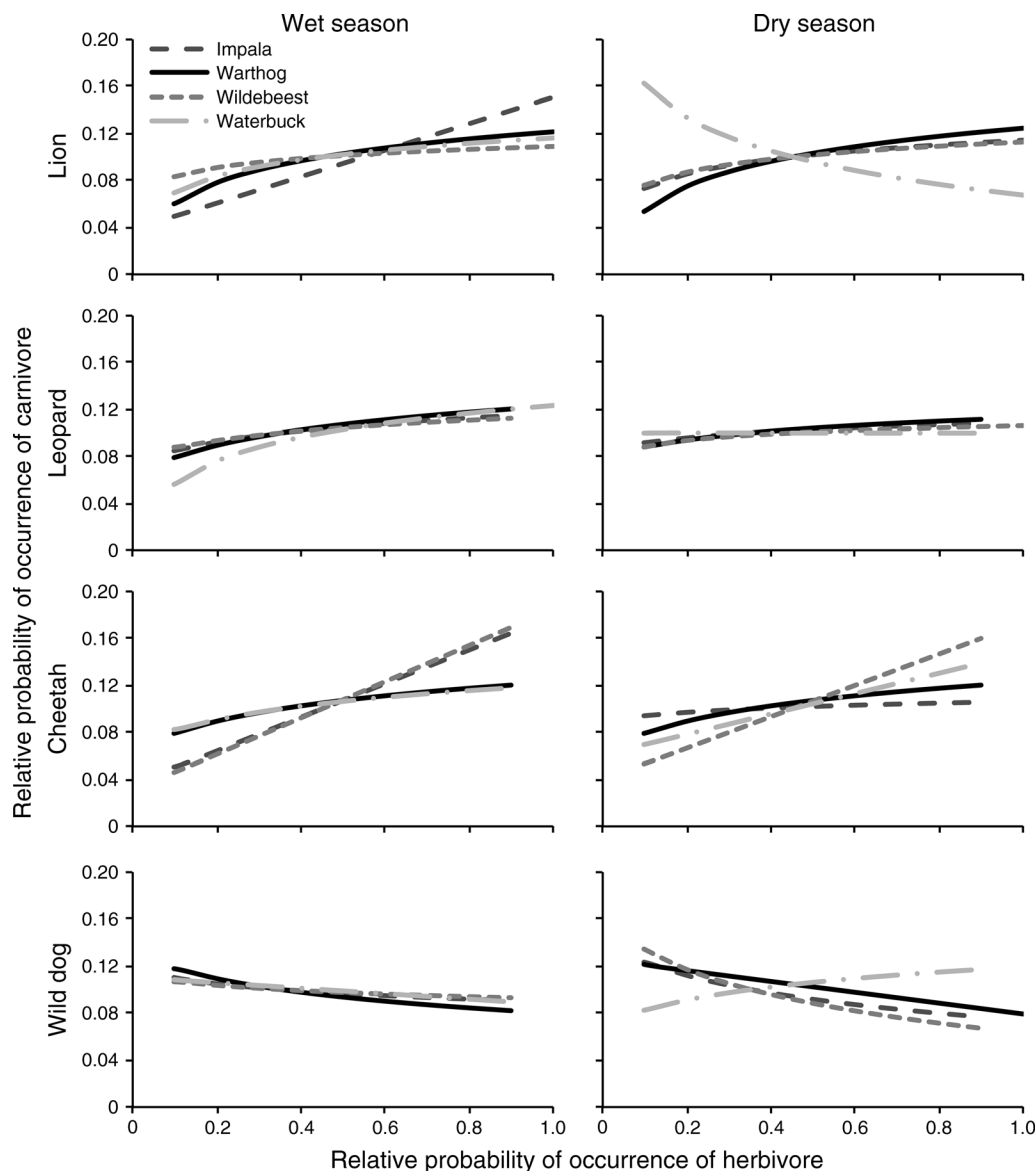
FIG. 2. Relationship between the relative probability of occurrence for the focal carnivore species and their main prey species (different line types for each herbivore) in the wet and dry seasons. Note that, while the relative probabilities of occurrence of lions, leopards, and cheetahs were positively correlated with prey occurrence, this relationship was negative for wild dog and shared prey.

anisms for coexistence of large carnivores followed a hierarchical allometric pattern, with multiple tactics at different spatial scales. These ranged from strong spatial segregation at the broad scale, to aggression and avoidance in response to the nearest recent location of competitors at the fine scale, indicating that carnivores have spatial awareness of multiple competitors at a range of distances. Movement decisions were thus an integrated reflection of the degree of threat between species as well as their resource selection tactics, which changed with season.

Similar to other African savanna ecosystems, lions were the most dominant carnivore (Owen-Smith and Mills 2008) because they selected for the richest resource

areas available and were the only species that moved toward all other carnivore species. For lions, season, and the associated changes in resource availability and vegetation characteristics, only minimally affected movement tactics, presumably because their dominance enabled unrestricted access to preferred areas. As such, lions were the only carnivore that selected for areas of high cover, such as riverine habitat (similar to Spong 2002), as well as areas of high prey vulnerability (similar to Hopcraft et al. 2005). Furthermore, at the broad scale, lion activity centers also overlapped with areas of high prey availability for many species (Fig. 3), even if lions did not actively move toward these species (such as impala, which is not a major part of their diet). The
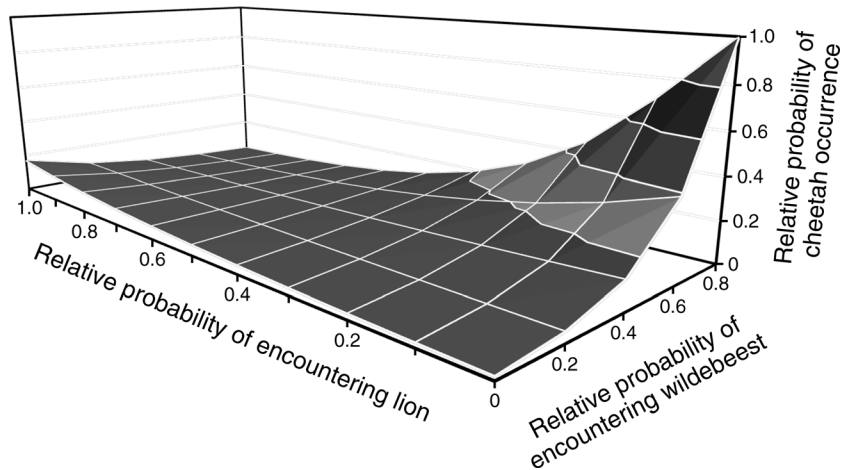
FIG. 3. Relative probability of occurrence of cheetahs in the wet season as a function of the probability of encountering of lions and wildebeest. Note that cheetah occurrence was highest in areas where the probability of encountering wildebeest was high but encountering lion was low.

unhindered access to landscape features and resources by lions seemed to have strong negative effects for the subordinate carnivores.

Unlike for lions, season played an important role for the subordinate carnivores. For leopards, interactions with other competitors were not apparent in the wet season, but in the dry season, leopards moved toward wild dogs and avoided the recent locations of lions as well as other leopards. Unlike for the other carnivore species, intraspecific killing was the greatest cause of mortality for leopards in this reserve (11 animals, including subadults and cubs, were killed during the study period); Balme et al. (2013) had similar findings. Hence, maintaining high territorial separation from conspecifics was expected, because encountering another leopard posed a real risk, especially in the dry season when visibility through vegetation and thus the probability of detection was probably higher. Leopards also selected for closed riverine areas in the dry season, but their arboreal behavior probably permitted shared use of this land cover type with lions. Cheetahs were expected to be subordinate to lions (Durant 2000, Creel et al. 2001), but their movement toward recent locations of lions in the wet season seemed counterintuitive. However, cheetahs may be using other avoidance tactics such as selecting for open woodland areas, a habitat that was avoided by lions, or by being diurnal (Hayward and Slotow 2009; but see Cozzi et al. 2012). Cheetahs also appeared to be subordinate to leopards, as they were more likely to move away from the recent location of leopards despite the lack of directed moves toward them.

As the smallest member of the large carnivore guild, African wild dogs were the most subordinate; all of the felid species were more likely to move toward them when in close proximity, especially in the dry season. To avoid these high risks of direct intraguild interactions, African wild dogs used both broad- and fine-scaled tactics, depending on the season. In the dry season, when visibility through vegetation and thus the probability of detection by competitors was high, wild dogs avoided the activity centers of the other carnivores. By contrast, in the wet season, when visibility through vegetation was at its worst, wild dogs seemed to take higher risk by mainly avoiding the recent location of the other competitors. Wild dogs have been shown to avoid areas where lions are more likely to detect them (Webster et al. 2012), but our results indicate that wild dogs also responded to the simultaneous risk from leopards and, to a lesser extent, cheetahs in the landscape.

Despite an increase in complexity, theoretical models of predator–prey spatial games (Heithaus 2001, Rosenheim 2004, Flaxman et al. 2011) still overlook behavioral processes fundamental to the functioning of ecosystems involving multiple interacting predators. The allometric hierarchy in dominance of movement decisions that we found indicates that all large carnivores cannot be considered to have a uniform effect on lower trophic levels (Schmitz and Suttle 2001). In a classic three-trophic-level system, a "leap-frog effect" can be expected (Sih 2005), in which predators match the resources of prey but not the distributions of prey themselves. This prediction is in contrast to that of a four-trophic-level system, where a top predator, especially one with no or low intraspecific competition (such as the lion in our study), has strong effects on the habitat selection decisions made by subordinate predators (Heithaus 2001, Rosenheim 2004). If top predators are more efficient competitors or if dietary overlap is high, then subordinate predators should be excluded from productive habitats (Heithaus 2001). We found that the space use patterns of the African large carnivore guild do not fully follow these theoretical predictions. Although subordinate carnivores were affected by top-down forces, in that they displayed avoidance tactics
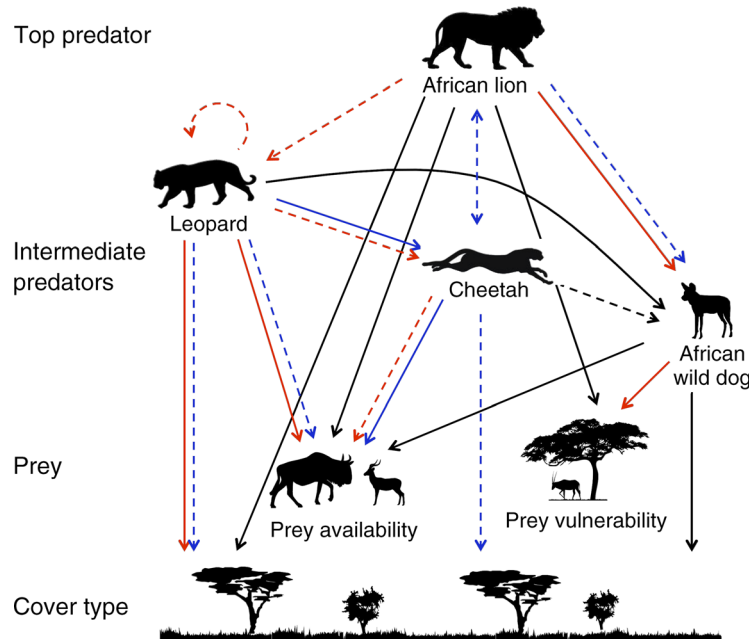
FIG. 4. Summary of the hierarchical intraguild behavioral interactions and selection of resources in African large carnivores. Lines indicate the direction and strength (solid, strong; dashed, weak) of the relationship between carnivores and prey availability, prey vulnerability, and land cover type. Blue lines (solid and dashed) indicate the wet season; red lines (solid and dashed) indicate the dry season; black lines (solid) represent both seasons.

toward other carnivores, all species, not just lion, were driven by bottom-up effects of prey and land cover selection (summarized in Fig. 4).

Distributions of predators and prey tend to be stabilized by spatial constraints (Sih 2005). When predators, but not prey, are spatially constrained, a negative relationship between predator and prey distributions is expected. Here, wild dogs were spatially constrained not only by the boundary fence, but also by all of the top predators, resulting in the expected mismatch between the distribution of wild dogs and their prey (Creel 2001). This low overlap of wild dog home ranges with high-resource areas may further explain why competitor species tended to avoid the activity centers of wild dogs; going toward the activity centers of wild dogs implied getting farther away from areas rich in principal prey. By contrast, leopards and cheetahs showed strong spatial overlap with the prey-rich home range of lions. Probably to minimize the risk of interference competition, these subordinate felid species showed fine-scaled avoidance behaviors and restricted resource acquisition tactics. This trade-off was most apparent for cheetahs during the wet season, as minimizing the chance of encountering lions outweighed the benefits of acquiring large prey such as wildebeest (similar to Durant 1998). However, in the dry season, when the distribution of prey was more heterogeneous (Owen-Smith 1982), cheetahs did not avoid resource-rich areas even if they were risky. These differences in behavioral strategy between seasons seemed to depend on the potential fitness reward, such

that greater risks were accepted when the marginal value of energy gain on fitness was higher (Lima and Dill 1990). Current theoretical and empirical studies that focus only on habitat selection of competing carnivores overlook these more subtle behavioral tactics that permit coexistence in a shared landscape.

Community-level studies that incorporate multiple predator species typically explain coexistence as a function of dietary niche separation (for African carnivores, see Sinclair et al. 2003, Owen-Smith and Mills 2008); the consequences for shared prey and resulting trophic cascade seem to be well established (Sih et al. 1998, Schmitz et al. 2004, Finke and Denno 2005). However, ignoring the structure of the predator community (Holt and Huxel 2007), competitive dynamics, and the resultant movement tactics of predators (Schmitz 2005) can lead to an oversimplification. For example, it is generally accepted that cheetahs, unlike lions, do not prefer large-bodied prey species such as wildebeest (Hayward et al. 2006a), even though they are energetically more rewarding than smaller species. These dietary preferences of carnivores all have been determined from study areas where multiple carnivore species coexist. Thus, diet selection inherently includes a trade-off between preferred prey and what can be obtained given intraguild competition. We found that cheetahs only avoided areas with high wildebeest occurrence when they overlapped considerably with the dominant competitor, lions. Hence, dietary niche separation, rather than being a mechanism that allows for coexis-

tence, may instead be a consequence of intraguild competition.

Spatial anchoring of competing predators can provide refugia for some prey (Sih et al. 1998), probably resulting in behaviorally mediated trophic cascades that are heterogeneous in their effects across the landscape (Schmitz and Suttle 2001, Schmitz et al. 2004). For example, wild dogs avoid lions (Creel et al. 2001), while kudu avoid areas used by wild dogs, one of their main predators (Hayward et al. 2006b, Thaker et al. 2011). Hence, lions are indirectly influencing the distribution of kudu, a key member of the browsing guild (Owen-Smith 1982), potentially resulting in cascading effects on vegetation structure and composition across the landscape. Furthermore, the relationship that a particular predator has with its prey depends not only on its hunting strategy (Schmitz and Suttle 2001, Schmitz 2008, Thaker et al. 2011), but also on its intraguild hierarchical rank. Indeed, the ungulates in this study area did not show threat-sensitive antipredator strategies, but rather responded to the space use patterns of the top predators: lions and leopards (Thaker et al. 2011).

Because of a lack of data, we were unable to include spotted hyenas in the models, which may partly hamper interpretation of the strategies that allow this guild of predators to coexist. Hyenas can have strong negative effects on other carnivores through intraguild killing and kleptoparasitism (e.g., Creel and Creel 1996, Durant 2000, Cooper 2008). In this reserve, intraguild killing by hyenas was never observed and kleptoparasitism was rarely observed ($n = 11$ in 4 years), and appeared to be targeted mainly at leopards ($n = 9$). Unlike in other areas, hyenas showed strong spatial separation with lions (Thaker et al. 2011) and because of the low population size, they did not have a numerical dominance over lion kills (Cooper 2008). Furthermore, hyenas showed strong spatial overlap with wild dogs (Thaker et al. 2011). Thus, we speculate that in our study area, hyenas would mostly affect leopards and wild dogs and, to a lesser degree, cheetahs. Given the infrequent records of kleptoparasitism, the negative effects of hyenas are unlikely to outweigh the intraguild interactions from the other carnivores.

In sum, the interplay between movement patterns and habitat features that emerged from our analyses suggests that, for subordinate carnivores on the move, there can be a much higher fitness cost of encountering a dominant competitor than of not encountering something to eat. Such a strong risk–benefit trade-off is typically experienced by prey (Lima and Dill 1990). However, because dominant carnivores tend to anchor themselves spatially in the most prey-rich areas (Linnell and Strand 2000), the greatest cost for some subordinate carnivores (intraguild killing) is also spatially coupled with the highest potential benefit of resource acquisition. Therefore, avoiding intraguild competition also increases the risk of starvation. We found that the trade-off between top-down competitive effects and bottom-up resource requirements for competing carnivores is dynamic and responsive to local conditions, such that greater risks were taken when resources were more of an imperative (Fig. 4). This key spatially explicit trade-off highlights the fact that assemblages of top predators cannot be considered to have homogenous effects on communities, and that maintaining intact guilds of predators is imperative for ecosystem functioning (Estes et al. 2011).

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SUPPLEMENTAL MATERIAL

Appendix A

Most-common ungulate species killed by the focal carnivore species in Karongwe Game Reserve, South Africa (*Ecological Archives* E094-240-A1).

Appendix B

Average population size of the principal prey species and the overlap in annual utilization distribution for each species over five years in Karongwe Game Reserve, South Africa (*Ecological Archives* E094-240-A2).

Appendix C

Parameter estimates for best-supported models explaining the movement of lions, leopards, cheetahs, and African wild dogs in Karongwe Game Reserve, South Africa (*Ecological Archives* E094-240-A3).