Spatial heterogeneity facilitates carnivore coexistence

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Abstract. Competitively dominant carnivore species can limit the population sizes and alter the behavior of inferior competitors. Established mechanisms that enable carnivore coexistence include spatial and temporal avoidance of dominant predator species by subordinates, and dietary niche separation. However, spatial heterogeneity across landscapes could provide inferior competitors with refuges in the form of areas with lower competitor density and/or locations that provide concealment from competitors. Here, we combine temporally overlapping telemetry data from dominant lions (*Panthera leo*) and subordinate African wild dogs (*Lycaon pictus*) with high-resolution remote sensing in an integrated step selection analysis to investigate how fine-scaled landscape heterogeneity might facilitate carnivore coexistence in South Africa's Hluhluwe-iMfolozi Park, where both predators occur at exceptionally high densities. We ask whether the primary lion-avoidance strategy of wild dogs is spatial avoidance of lions or areas frequented by lions, or if wild dogs selectively use landscape features to avoid detection by lions. Within this framework, we also test whether wild dogs rely on proactive or reactive responses to lion risk. In contrast to previous studies finding strong spatial avoidance of lions by wild dogs, we found that the primary wild dog lion-avoidance strategy was to select landscape features that aid in avoidance of lion detection. This habitat selection was routinely used by wild dogs, and especially when in areas and during times of high lion-encounter risk, suggesting a proactive response to lion risk. Our findings suggest that spatial landscape heterogeneity could represent an alternative mechanism for carnivore coexistence, especially as ever-shrinking carnivore ranges force inferior competitors into increased contact with dominant species.

Key words: African wild dog; Hluhluwe-iMfolozi Park; intraguild predation; LiDAR; lion; nonconsumptive effects; predation risk.

Introduction

Competition and predation among top predators are recognized as key drivers of carnivore population dynamics and resource use (Palomares and Caro 1999, Ritchie and Johnson 2009, Prugh and Sivy 2020). Competitively dominant carnivore species can limit the

population sizes and behavior of inferior competitors through interspecific competition and direct killing, sometimes leading to the local extinction of subordinate predator populations (Linnell and Strand 2000, Swanson et al. 2014). Key mechanisms enabling the coexistence of multiple carnivore species include spatial and temporal avoidance of dominant predator species by subordinates (Hayward and Slotow 2009, Vanak et al. 2013), and dietary niche separation (Owen-Smith and Mills 2008, du Preez et al. 2017; but see Vogel et al. 2019). However, most large carnivores are threatened by human-induced habitat loss and fragmentation,

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resulting in widespread range contractions and prey depletions that force carnivores to occupy ever-shrinking areas and target similar prey species (Ripple et al. 2014). These range contractions and expanded dietary overlap can increase the frequency and intensity of antagonistic interactions, making it increasingly challenging for subordinate species to rely on spatial and temporal avoidance of dominant competitors, exacerbating subordinate carnivore declines.

Spatial landscape heterogeneity is a key facilitator of species coexistence across trophic levels (Palmer 2003, Tews et al. 2004). Through the availability of varied physical features and nonuniform resource distributions, heterogeneous landscapes have greater niche availability that facilitates higher species diversity and the coexistence of competing species (Chesson 2000, Stein et al. 2014). For carnivores, spatial heterogeneity across landscapes can provide inferior competitors with refuges in the form of areas with lower competitor density and/or locations that provide concealment from competitors (Durant 1998, Davies et al. 2016a). In landscapes where a variety of physical features occur over small spatial scales, subordinate carnivores could potentially exist in close proximity to competitors by using landscape features to avoid detection. For example, experimental studies of invertebrate systems show that habitat structure facilitates mesopredator coexistence by reducing the frequency of aggressive encounters between competing species (Finke and Denno 2002, Janssen et al. 2007). For mammalian predators, kleptoparasitism of cheetah (Acinonyx jubatus) kills by lions (Panthera leo) is lower in landscapes with a high availability of patchy dense vegetation that provides increased cover for kill concealment (Bissett and Bernard 2007). Interactions between fine-scale habitat heterogeneity and avoidance behavior among top predators warrants further investigation to understand and predict mechanisms of carnivore coexistence better.

Subordinate species can respond to risk from dominant competitors in contrasting ways, categorized as proactive and reactive response types. A proactive response type is where repeated behavioral modifications to anticipated risk are based on a priori assessments founded on prior experience of predator behavior, whereas a reactive response type occurs when short-lived behavioral adjustments are made to an immediate threat (Creel 2018). Proactive response types are more likely to lead to food-mediated costs in subordinate predators or prey species because of systematic resource losses, whereas reactive responses to risk induce stress-mediated risk effects and are suggested to have weaker ecosystem-level effects because of their intermittent and fleeting nature (Creel 2018). The way in which subordinates respond to risk posed by dominant species has important implications for species coexistence, yet our understanding of how and when each response type arises, especially among carnivore species, remains underdeveloped. Studies examining the drivers and implications of

risk response types are only just appearing, but suggest that they depend on spatial context (Courbin et al. 2016), and that response types can interact in a hierarchical manner (Broekhuis et al. 2013, Dröge et al. 2017b). The emergence of either response type is also likely to interact with landscape characteristics.

African savanna ecosystems are among the last landscapes on Earth to contain a diverse suite of indigenous predators and their prey (Ripple et al. 2014), and therefore represent exemplary systems within which to investigate mechanisms underlying predator coexistence. Lions are dominant competitors in these environments, with their behavior and distributions largely unaffected by other predators (Mills and Gorman 1997). In contrast, competitively inferior African wild dogs (Lycaon pictus) are subject to intense competition with lions, and adjust their spatial and temporal activities in response to lions (Mills and Gorman 1997, Darnell et al. 2014, Swanson et al. 2014). Lions are the largest contributors to wild dog mortality in free-ranging populations (Woodroffe and Ginsberg 1999), and have been the driving force behind local extinctions of wild dog populations (Swanson et al. 2014, Jackson et al. 2019). Wild dogs therefore spend considerable effort avoiding lions, including being active at times of day when lions are not (Hayward and Slotow 2009, Rasmussen and Macdonald 2012) and occupying habitats with inferior prey density but lower lion abundance (Mills and Gorman 1997, Groom et al. 2017, Marneweck et al. 2019a). However, most studies of wild dog–lion interactions have focused on broad-scale patterns of proactive wild dog avoidance of lions in space and time, with comparatively little emphasis on the fine-scale use of landscape features that aid in lion avoidance, or on reactive responses to lion risk.

Despite its moderate area and entirely fenced boundary, the Hluhluwe-iMfolozi Park (HiP) in South Africa supports surprisingly high densities of lions and wild dogs. The high wild dog density (the highest recorded across their range; Marneweck 2020) is particularly unexpected because high lion densities, which in HiP are amongst the highest in Africa (Marneweck 2020), usually preclude simultaneously high wild dog densities (Swanson et al. 2014, Marneweck et al. 2019a). Both predators were reintroduced to the park in recent decades, and despite some initial setbacks, their populations have grown and are relatively stable (Somers et al. 2017). The high predator densities and enclosed boundary should increase antagonistic interactions between lions and wild dogs, yet both species thrive. The HiP landscape is highly heterogeneous compared with most other savanna ecosystems, with large variation in rainfall, vegetation types, geology, and topography over small spatial scales (Beale et al. 2013, Howison et al. 2017, Veldhuis et al. 2017), which we hypothesize facilitates wild dog coexistence with lions through effective use of the spatially varied landscape.

Here, we combine temporally overlapping global positioning system (GPS) telemetry data from lions and wild

dogs with high-resolution remote sensing to investigate how fine-scaled landscape heterogeneity might facilitate carnivore coexistence, using wild dogs and lions as a model pairing. Using integrated step selection analysis (iSSA), which enables the simultaneous evaluation of both habitat selection and animal movement (Avgar et al. 2016), we ask whether the primary lion-avoidance strategy of wild dogs is spatial avoidance of lions and areas frequented by lions, or if wild dogs selectively use landscape features to avoid detection by lions when in high-risk areas or in close proximity to lions. Furthermore, we test whether wild dog responses to lion risk are proactive (i.e., exhibit strongest responses when in areas and during times frequently used by lions) or reactive (i.e., exhibit strongest responses when in close proximity to lions). We predicted that lions would elicit strong behavioral responses in wild dogs, and that wild dogs would combine spatial avoidance with selection for landscape features generally avoided by lions, such as rugged terrain and very dense vegetation (Mills and Gorman 1997, Davies et al. 2016b). We further predicted that behavioral responses by wild dogs would vary temporally, with stronger lion-avoidance behavior at night when lions are most active, and that response type would be mostly proactive given the high risk lions pose to wild dogs and the predictable nature of these ambush predators.

Methods

Study area

The 89,600-ha HiP (Fig. 1) consists mostly of undulating hills and savanna vegetation with highly varying levels of woody cover, and some forest and open grassland patches at higher elevations. There is a wide range of elevation (60–580 m above sea level [a.s.l.]) and precipitation (650–1,000 mm/yr), with summer rainfall occurring primarily between October and April (Cromsigt et al. 2017). The mean wild dog population over the study period (2014–2016) consisted of 53 (range: 42–66) adults and yearlings in a mean of 6.5 (range: 6–8) packs, with a mean pack size of 7.81 (range: 2–17) adult and yearling wild dogs. Wild dog density was 5.88 adults and yearlings/100 km^2, the highest in Africa (Marneweck 2020). Approximately 120 lions in 11 prides were present at a density ranging from 11.9 to 12.3 lions/100 km^2 (Marneweck 2020). Spotted hyena (*Crocuta crocuta*), leopard (*Panthera pardus*), and cheetah are other resident large predators. A near full suite of indigenous mammalian herbivores is present in the park (Cromsigt et al. 2017).

Wild dog and lion GPS telemetry

Spatial data from wild dogs were obtained from GPS collars deployed on wild dogs between September 2014 and August 2016 (GPS satellite units, Sirtrack Iridium,
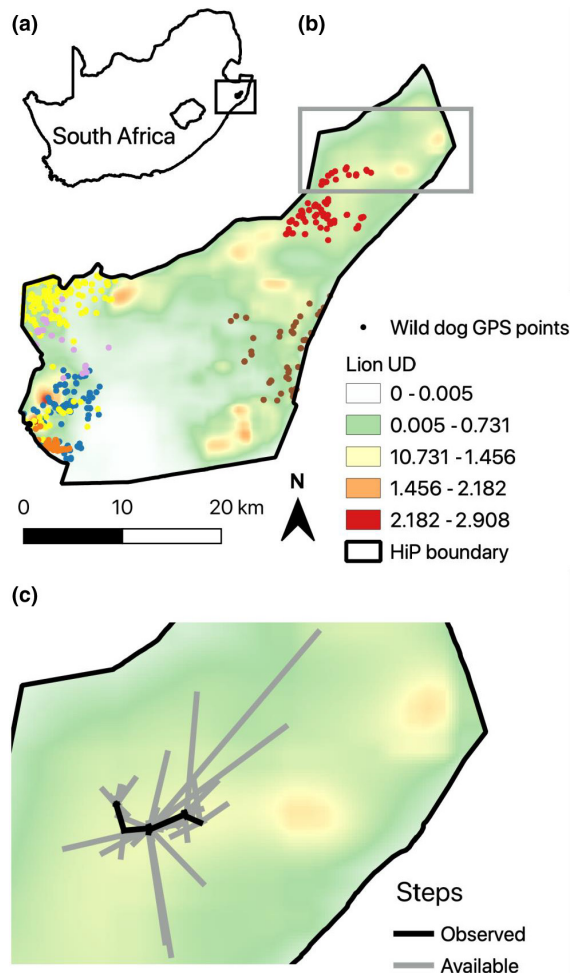

Fig. 1. (a) Location of the Hluhluwe-iMfolozi Park (HiP) within South Africa (inside the rectangle), (b) lion utilization distribution across the park generated from GPS relocations of 17 lions, with the colored points displaying the GPS relocations of the six wild dog individuals used in the study (each color represents a different individual, each representing a separate pack apart from the individuals coloured in purple, blue, and orange who were from the same pack but temporally separated [see text]) and (c) an example of the observed and available steps used in the iSSA (inset from the gray rectangle in (b)). The apparent low lion utilization in the southern region of HiP in (b) does not reflect low lion densities there, but is rather an artifact of no lion GPS data being available from this region; available wild dog GPS data from this area were therefore excluded from the study.

New Zealand). Collars were placed on at least one individual per pack and programmed to take GPS relocations every 2–6 h. However, for consistency in the analysis and because we expected wild dog responses to lions to occur in a narrow temporal window, we restricted our analysis to 2-h relocation data only. This restriction resulted in spatial data from six individual wild dogs from four packs being available. Although three collared individuals were from the same pack,

there were intervals of 11 and 7 months between these three data sets, and the pack composition between the three sampling periods differed in terms of individuals present, pack size, and home range, with little spatial overlap between the three collared individuals (Fig. 1b). We therefore treated them as independent movement data sets. All spatial data used were from nondenning periods, because of large differences in space use between denning and nondenning periods (O'Neill et al. 2020) and a paucity of 2-h spatial data from denning packs. We further restricted the wild dog data used to those that overlapped temporally and spatially with collared lions. We therefore only used wild dog data where we were confident that the movements of the majority of lion groups were known (see below and Fig. 1b). We also only used movement data from continuous strings of at least 10 movement steps to remove the influence of missed relocations. We further excluded GPS relocations outside the park (wild dogs occasionally break through the fence and remain outside the park until they either voluntarily return or are retrieved) because of large differences in the environment, including an absence of lions.

Lion spatial data were acquired from GPS collars (African Wildlife Tracking, Pretoria, South Africa) placed on 17 lions (10 females and 7 males from nine prides and seven coalitions, respectively) between April 2013 and April 2017. Two female lions from the same pride were collared, but with a 17-month interval between collaring periods. Spatial data from these two lions were combined so that lion movements were considered at the pride or coalition level. Hourly relocation data over the course of 24 h were available for all lions apart from three females, for which there were hourly relocations between 17:00 and 06:00 (when lions are most active), and two additional relocations at 10:00 and 14:00. We subsampled all lion GPS data sets to this lower temporal resolution.

Airborne LiDAR

We surveyed all of HiP with discrete-return airborne light detection and ranging (LiDAR) in March 2015 using the Global Airborne Observatory (GAO), formally known as the Carnegie Airborne Observatory. The GAO LiDAR subsystem provides three-dimensional structural information of vegetation canopies and the underlying terrain surface. The GPS-IMU subsystem provides position and orientation data for the GAO sensors, allowing for highly precise and accurate positioning of LiDAR observations on the ground. The GAO data were collected from 2000 m above ground level, using a scan angle of 36° and a side overlap of 50%. The aircraft velocity was 130 knots, and the LiDAR pulse frequency was 250 kHz, resulting in an average point density of 5.81 pulses (7.47 points)/m^2. Horizontal and vertical error estimates were 16 and 7 cm root mean square error (RMSE), respectively. The LiDAR data provided maps of ground elevation (digital elevation model, DEM), woody canopy height, and three-dimensional vegetation structure at 1-m spatial resolution. Vegetation height measurements from the GAO have been field validated for savanna vegetation (Asner et al. 2009). We did not expect overall or seasonal variation in vegetation between the LiDAR data collection (March 2015) and the rest of the study period (September 2014 to August 2016) to affect our results substantively, because >60% of the wild dog relocations used were during the wet season (October–April), thereby coinciding with the LiDAR data-collection season. Furthermore, perennial woody biomass accounts for a large proportion of savanna vegetation (Venter et al. 2003), resulting in similar overall vegetation structure during the wet and dry season.

Integrated step selection analysis

We used an integrated step selection analysis (iSSA; Avgar et al. 2016) to describe wild dog resource selection in relation to both lions and landscape features. An iSSA allows the joint estimation of movement and resource selection parameters as an extension of step selection functions, a case-control resource selection function where the step selected (defined as the straight-line path between successive GPS relocations) is the dependent variable (Fig. 1c) (Thurfjell et al. 2014). Wild dog GPS relocations were converted into steps and the probability of a wild dog selecting a step was estimated by comparing each observed step with a matched sample of 10 randomly drawn available steps. Available step lengths were sampled from a gamma distribution (short steps are mostly taken, with occasional longer steps) parameterized using the observed step length distribution of all wild dogs (shape = 0.226652359, scale = 2176.222043). Turn angles (in radians) for available steps were sampled from values between π and $-\pi$ following a uniform distribution. The median number of available observed steps per wild dog was 144 (range: 43,503).

Seven population-level iSSA models were fitted to the wild dog movement data using the *clogit* function in the R (version 3.6.0) *survival* package (Therneau 2015) to fit a conditional logistic regression, with start point ID as the strata for all models. We did not fit individual models to each wild dog separately because of the low number of steps for several individuals. However, we tested for effects of variable sample sizes between individuals in a separate analysis by subsampling 43 sets of steps (observed and associated available steps) from each wild dog, matching the individual with the fewest observed steps, and applying the seven models to these subsets. We then bootstrapped this procedure (10,000 iterations) to produce mean parameter estimates and model weights. To verify that between-individual variability in wild dog responses did not affect the findings of our population-level models, we constructed a mixed-effects model with random slopes for the key variables driving

wild dog habitat selection (i.e., lion utilization and view-shed) in the top supported model (representing the habitat [encounter] hypothesis; see Results) using the glmmTMB R package version 1.0.2.1 (Magnusson et al. 2017) and following Muff et al. (2020).

Core model covariates

A consistent core model that included covariates expected to influence wild dog movement was used as the foundation for the seven models designed to test hypotheses related to wild dog behavior in response to lion risk (Table 1). Support for inclusion of the core model covariates comes largely from wild dog studies conducted in the presence of lions (because of the paucity of wild dog populations in areas without lions), thereby likely reflecting wild dog behavior relative to broad-scale lion presence. The inclusion of this core model as the basis for the seven models enabled us to investigate contrasting hypotheses of how wild dogs respond to fine-scaled variation in lion risk, in terms of both risk intensity and the type of risk (short vs. long term).

We predicted that wild dogs would prefer less rugged, flatter areas because they are easier and less energetically costly to traverse and hunt in for a cursorial predator (Halsey 2016). We resampled the 1-m LiDAR-derived DEM using bilinear interpolation to a 10-m cell size, and from this calculated terrain ruggedness, measured as vector ruggedness measure (VRM; Sappington et al. 2007) using a 3×3 cell neighborhood. Ruggedness was chosen over metrics of slope and elevation (which were correlated with VRM) because it has been shown in previous studies to influence wild dog habitat selection (Mills and Gorman 1997, Groom et al. 2017). Ruggedness at the end of a step (i.e., selection for that location) was included in the core model.

Being cursorial hunters, we also expected wild dogs to select areas of open vegetation (see O'Neill et al. 2020) that aid in hunting coordination. Alternatively, because the primary prey of wild dogs in HiP consists of nyala (*Tragelaphus angasii*) and impala (*Aepyceros melampus*; Krüger et al. 1999, Somers et al. 2017), selection for areas with increased browse (denser vegetation) that favors high abundance of these prey species could be expected (see Jenkins et al. 2015). Vegetation cover was measured as visibility in the form of viewsheds (Aben et al. 2018) following Davies et al. (2016*a*,*b*). Viewsheds were modeled by calculating the visible area from each wild dog GPS relocation within a 50-m radius in a three-dimensional field of view (i.e., capturing horizontal line of sight as well as lower vegetation strata and below canopy area), assuming a height of 0.75 m, which approximates the eye level of an alert wild dog. Visible area included areas up and/or downslope and could be obstructed by both vegetation and terrain. Visible pixels within tree canopies taller than 1 m were excluded because these areas would not be occupied by prey species or lions, resulting in a three-dimensional measurement of vegetation between 0 and 1 m above the ground at a 1-m^2 resolution. Viewshed area at the end of a step (i.e., selection) was included in the core model.

We further expected wild dogs to move and select habitats differently throughout the day. Wild dog hunting is typically restricted to crepuscular time periods (Hayward and Slotow 2009, Woodroffe et al. 2017), with resting and socializing generally occurring during the day and at night, although nighttime hunting can occur during full moon (Rasmussen and Macdonald 2012). We constructed a time-of-day category, roughly corresponding to daylight, crepuscular light, and darkness, to reflect these temporal behavioral differences using the *sun-methods* functions in the *maptools* R package (Bivand and Lewin-Koh 2018). Any GPS fix taken

TABLE 1. Candidate models used to evaluate the relative influence of habitat (viewshed and ruggedness) and time of day in relation to wild dog space use and lion avoidance in Hluhluwe-iMfolozi Park, South Africa. SL = step length (m), ToD = time of day defined as night, day, or twilight, RG = ruggedness of the terrain measured with vector ruggedness measure (VRM), VS = viewshed (m^2), DistLion = log-transformed distance to the nearest lion (m), LionUD = utilization distribution of all known lions (a measure of long-term lion-encounter risk), 'start' and 'end' designate that the point value comes from the start and end of the step, respectively.

Model	Explanatory variables
Core	[lnSL × ToD] + [lnSL × RG(start)] + VS(end) + RG(end)
Avoidance (proximity)	Core + [DistLion(end) × ToD] + [ln(SL) × DistLion(start) × ToD]
Avoidance (encounter)	Core + [LionUD(end) × ToD] + [ln(SL) × LionUD(start) × ToD]
Habitat (proximity)	Core + [DistLion(end) × RG(end) × ToD] + [DistLion(end) × VS(end) × ToD]
Habitat (encounter)	Core + [LionUD(end) × RG(end) × ToD] + [LionUD(end) × VS(end) × ToD]
Avoidance and habitat (proximity)	Core + [DistLion(end) × ToD] + [ln(SL) × DistLion(start) × ToD] + [DistLion(end) × RG(end) × ToD] + [DistLion(end) × VS(end) × ToD]
Avoidance and habitat (encounter)	Core + [LionUD(end) × ToD] + [ln(SL) × LionUD(start) × ToD] + [LionUD(end) × RG(end) × ToD] + [LionUD(end) × VS(end) × ToD]
Avoidance and habitat (proximity and encounter)	Core + [DistLion(end) × ToD] + [ln(SL) × DistLion(start) × ToD] + [DistLion(end) × RG(end) × ToD] + [DistLion(end) × VS(end) × ToD] + [LionUD(end) × ToD] + [ln(SL) × LionUD(start) × ToD] + [LionUD(end) × RG(end) × ToD] + [LionUD(end) × VS(end) × ToD]

between the onset of civil dawn and 2 h after sunrise or 1 h before sunset and 5 min before the end of astronomical dusk was classified as twilight (crepuscular), following activity data from observations of wild dog hunting behavior (Rasmussen and Macdonald 2012). Steps classified as day occurred between 2 h after sunrise and 1 h before sunset, and steps taken between 5 min prior to astronomical dusk and civil dawn were classified as night.

Within an iSSA, the ß coefficient of the ln-transformed step length (hereafter ln*StepLength*) represents the modification of the gamma distribution shape parameter originally used to generate the available steps (Avgar et al. 2016). We expected that temporally varied wild dog activity patterns would translate into varying movement rates throughout the day, with increased movement while hunting during twilight relative to lower day and nighttime movement rates (Hayward and Slotow 2009, Rasmussen and Macdonald 2012). We therefore included time-of-day categories as an interaction with the ln*StepLength* in the core model to account for differing movement rates throughout the day. In addition, we expected terrain ruggedness to interact with movement rate, with increased ruggedness slowing movement. We therefore included the interaction between ruggedness (VRM) at the start point of each step and the ln*StepLength* of the step in the core model. We did not include the cosine of the turn angle in the core model (i.e., we did not account for directional persistence) because we did not assume wild dogs to show important directional persistence between 2-h relocations.

Lion risk covariates

We measured lion risk to wild dogs in two ways: proximity to the nearest known lion at the time of each GPS relocation and the long-term lion-encounter risk in a given area. Responses to lion proximity represent reactive response to risk (an immediate threat of a lion close by), whereas responses to long-term lion-encounter risk represent proactive responses to an a priori assessment of risk. Lion proximity was measured as the Euclidean distance in meters between each wild dog relocation and the nearest known lion (male or female) at the time. These distance measurements were then log-transformed to allow the effect of lion proximity to decay with increasing distance. Wild dog and lion GPS relocations were temporally well aligned, with 54% of wild dog relocations within 5 min of the nearest lion relocation, and 81% within 10 min. The median difference between wild dog and lion relocations was 54 s.

To quantify spatial variation in long-term lion-encounter risk, we constructed a utilization distribution (UD) for each lion using the *adehabitatHR* package (Calenge 2011) in R, with a grid cell size of 500 m. This spatial scale was fine enough to provide meaningful descriptions of variation in lion space corresponding

with the 2-h temporal resolution of the wild dog movement data. We used the standard reference bandwidth h_{ref} as our smoothing parameter, because it yielded continuous UDs that better fit the GPS relocations than alternative methods (e.g., using the 90th percentile of daily lion displacement distance; Dröge et al. 2017b). We normalized the UD of each lion so that each was scaled from 0 to 1, and then combined them to yield a parkwide lion UD, which appropriately resolved areas of high and low lion use.

Model development and evaluation

We constructed seven iSSA models to quantify behavioral responses of wild dogs to lion risk (Table 1). All continuous predictor variables included in the models were scaled and centered prior to model implementation. The first two models tested the hypothesis that wild dogs adjust their behavior to avoid lions spatially. The "avoidance (proximity)" model represents the hypothesis that the primary response of wild dogs to lions is spatial avoidance of lion proximity (a reactive response), whereas the "avoidance (encounter)" model represents the hypothesis that wild dogs avoid areas with high long-term lion-encounter risk (a proactive response). These models included, in addition to all the variables in the core model, an interaction between lion risk at the step's end point (defined as the distance to the nearest lion for the "avoidance [proximity]" model and long-term lion-encounter risk for the "avoidance [encounter]" model) and time of day (to evaluate selection relative to lion risk and how this might vary throughout the day) and a three-way interaction between lion risk at the step's start, time of day, and ln*StepLength* (to evaluate movement rate in relation to lion risk and time of day). We predicted that wild dogs would spatially avoid lions or areas of high lion-encounter risk by selecting locations further from lions or with lower lion-encounter risk at the end point of steps (positive coefficients) and increase their movement rate (ln*StepLength*) when in close proximity to lions or when in areas of high lion-encounter risk (at the start of steps). Because lions hunt primarily at night (Hayward and Slotow 2009), we further predicted that wild dog responses to lion proximity or encounter risk (in terms of both avoidance [reflected through increased distance from the nearest lion or decreased lion-encounter risk at step end points] and increased movement speed [increased ln*StepLength* when lions were close by or when in areas of high lion-encounter risk, i.e., at the start of a step]) would be stronger at night (larger positive coefficients).

The next two models (the "habitat [proximity]" and "habitat [encounter]" models) tested hypotheses that wild dogs adjust their behavior to avoid detection by lions by modifying their habitat selection when lion risk is high. The "habitat (proximity)" model represents the hypothesis that the primary response of wild dogs to lion risk is avoidance of detection through altered habitat

selection when close to lions (a reactive response), whereas the "habitat (encounter)" model represents the hypothesis that wild dog's primary response to lion risk is avoidance of detection through modified habitat selection when in areas of high long-term lion-encounter risk (a proactive response). In addition to the core model variables, these models included two three-way interactions between (1) lion risk at the steps' end point (defined as distance to the nearest lion for the "habitat [proximity]" model and lion-encounter risk for the "habitat [encounter]" model) and ruggedness at the step's end point and time of day, and (2) lion risk at the steps' end point, viewshed area at the step's end point, and time of day. These interactions evaluated whether wild dogs select rugged terrain and/or dense vegetation to avoid detection by lions when in close proximity or in areas of high lion-encounter risk, and how this behavior varies throughout the day. We predicted that wild dogs would decrease the likelihood of being detected by lions through selection for increased ruggedness and smaller viewsheds (denser vegetation) when lions were in close proximity (shorter distance to the nearest lion at a step's end point) or where lion-encounter risk was high. We further predicted that habitat selection for these landscape characteristics would be strongest at night when lion activity is highest.

The fifth and sixth models combined the avoidance and proximity models introduced above. The "avoidance and habitat (proximity)" model represented the hypothesis that wild dogs avoid lion proximity by both moving away (spatial avoidance) and by selecting habitats that reduce detection by lions (detection avoidance) when in close proximity to lions. This model included all the variables in the core, "avoidance (proximity)," and "habitat (proximity)" models. The "avoidance and habitat (encounter)" model represented the hypothesis that wild dogs avoid lions in high-risk areas by both moving away (spatial avoidance) and by selecting habitats that reduce detection by lions (detection avoidance) when in areas of high lion-encounter risk. This model included all the variables in the core, "avoidance (encounter)," and "habitat (encounter)" models. Finally, the seventh "avoidance and habitat (proximity and encounter)" model tested whether wild dogs employ both spatial avoidance and altered habitat selection to reduce lion risk in response to both lion proximity and when in areas of high lion-encounter risk. This model included all variables in the previous six models and the core model.

After fitting the seven models to the population-level wild dog movement data, we used sample size adjusted Akaike information criterion (AIC_c) and model Akaike weights to assess which model best described wild dog behavior. To visualize effects of the measured covariates on wild dog habitat selection, we plotted the marginal covariate effects on wild dog relative probability of use. To test whether our results were heavily skewed by individual wild dogs with substantially larger sample sizes, we repeated the model selection analysis using the bootstrapped results. For this analysis, we tallied the instances of a model having the lowest AIC_c value from the 10,000 bootstrapped iterations and calculated the mean Akaike weight of each model over the 10,000 iterations. The model with the highest mean Akaike weight and the highest minimum AIC_c tally was selected as the top model, with the mean coefficient value and confidence intervals (from the 10,000 iterations) calculated for each explanatory variable.

To obtain mean wild dog movement rates (meters/ 2 h), we added the iSSA coefficient of ln*StepLength* to the original gamma distribution of step lengths to modify its shape, and then multiplied this modified distribution by the original scale parameter (Prokopenko et al. 2017). This process was repeated for the three times of day using the coefficients of the interaction between ln*StepLength* and time-of-day category to estimate the movement rate across each time category. To compare finer-scaled movement patterns (two hourly) and assess the validity of our modeled movement rate estimates, we calculated the measured step lengths for each 2-h time interval and compared these to the broader time periods (day, night, and twilight).

To test for variation in wild dog resource selection and lion-avoidance behavior with moonlight (because wild dogs are known to increase activity levels on full moon nights; Rasmussen and Macdonald 2012), we repeated our analysis for subsets of GPS relocation data from periods of high and low moon illumination (see Appendix S1: Section S1).

Results

Hypotheses representing proactive risk response types (i.e., avoidance of long-term lion-encounter risk) received substantially more support than those representing reactive response types (i.e., avoidance of lion proximity). The "avoidance and habitat (encounter)" and "habitat (encounter)" models received almost equal support when applying the models to the entire data set, suggesting that wild dogs combine spatial avoidance with altered habitat selection when in areas of high lion-encounter risk (Appendix S1: Table S1). However, the "habitat (encounter)" model was more parsimonious and received more support from the bootstrapped analysis (accounting for sample size variation; Appendix S1: Table S2) and was therefore favored over the more complex "avoidance and habitat (encounter)" model and used in further analysis. The strong support for the "habitat (encounter)" model suggests that the primary response of wild dogs to lion risk was to alter their habitat selection when long-term lion-encounter risk was high.

Among the core model variables included in the "habitat (encounter)" model, our results suggest that wild dogs consistently select habitats with low visibility (smaller viewshed area) and increased terrain ruggedness (Table 2). Wild dogs also moved further during the day

TABLE 2. Scaled mean model coefficients from the selected model ("habitat [encounter]") explaining wild dog space use in Hluhluwe-iMfolozi Park, South Africa. Bold font indicates variables where $P < 0.05$.

Explanatory variable	Population ß	SE (ß)	Z value	P value
Viewshed (end of step)	**−0.347**	**0.053**	**−6.577**	**<0.001**
Ruggedness (end of step)	**0.103**	**0.036**	**2.885**	**0.004**
ln(*StepLength*): Day	**0.162**	**0.055**	**2.937**	**0.003**
ln(*StepLength*): Night	−0.005	0.048	−0.102	0.919
ln(*StepLength*): Twilight	−0.072	0.075	−0.968	0.333
ln(*StepLength*): Ruggedness (start of step)	−0.035	0.035	−0.998	0.318
Ruggedness (end of step): Day: Lion UD (end of step)	−0.041	0.042	−0.978	0.328
Ruggedness (end of step): Night: Lion UD (end of step)	−0.054	0.058	0.936	0.349
Ruggedness (end of step): Twilight: Lion UD (end of step)	−0.055	0.043	−1.302	0.193
Viewshed (end of step): Day: Lion UD (end of step)	**0.094**	**0.032**	**2.985**	**0.003**
Viewshed (end of step): Night: Lion UD (end of step)	**0.219**	**0.062**	**3.505**	**<0.001**
Viewshed (end of step): Twilight: Lion UD (end of step)	0.008	0.074	0.106	0.915

(mean = 846.53 m/2 h; 95% CI = 726.22–966.83) relative to at night (mean = 482.53 m/2 h; CI = 377.27–587.79) or during twilight (mean = 336.21 m/2 h; CI = 173.90–498.51; Table 2), with the longest step lengths in the early morning (04:00–06:00) and early afternoon (14:00–16:00) (Fig. 2). When considering wild dog responses to lion risk covariates, the three-way interaction between viewshed area, time of day, and lion-encounter risk was significant (Table 2). In contrast to overall patterns of selection for low-visibility locations,

wild dogs selected sites with high visibility (large viewsheds) when in areas of high lion-encounter risk during the day and at night, with this pattern especially evident at night (Fig. 3). Results between the bootstrapping procedure and when applying the model to the entire data set were largely consistent, apart from larger confidence intervals with the bootstrapping results (Appendix S1: Tables S2 and S3). Similarly, results from the habitat (encounter) mixed-effect model (Appendix S1: Table S4) were highly consistent with those of the habitat (encounter) model without random slopes (Table 2).

Results during full moon (moon illumination >0.8) were highly similar to the overall results (Appendix S1, Tables S5–S8, Appendix S1: Fig. S1a), whereas during new moon conditions (moon illumination <0.2), the "habitat (proximity)" model received more support (Appendix S1, Tables S5–S7), suggesting that wild dogs were more sensitive to lion proximity during darker nights. Although responses were less clear under new-moon conditions, the bootstrapped results suggested that wild dogs increased their selection for rugged areas when lions were far away at night (Appendix S1: Table S8, Fig. S1b).

Discussion

Wild dogs are the smallest of Africa's five top predators and the most vulnerable to interference competition by competitors. Of these dominant competitors, lions represent the single biggest threat. It is therefore reasonable for wild dogs to base much of their habitat selection and movement behavior on lion avoidance, with lions shown to exert strong influences on wild dog behavior, ecology, and population demographics wherever they coexist (Creel and Creel 1996, Woodroffe and Ginsberg 1999, Swanson et al. 2014, Groom et al. 2017). In the heterogeneous Hluhluwe-iMfolozi landscape, our results suggest that wild dogs attempt to avoid lions by altering their use of the landscape, both as a general behavior and when in areas of high lion risk. Although it is well established that wild dogs avoid lions spatially (Mills and Gorman 1997, Swanson et al. 2014, Marneweck
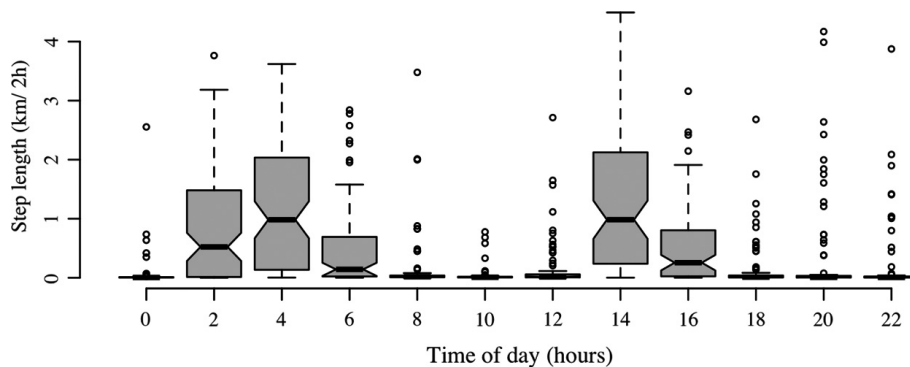

FIG. 2. Measured wild dog step lengths between two hourly GPS relocations in Hluhluwe-iMfolozi Park, South Africa.
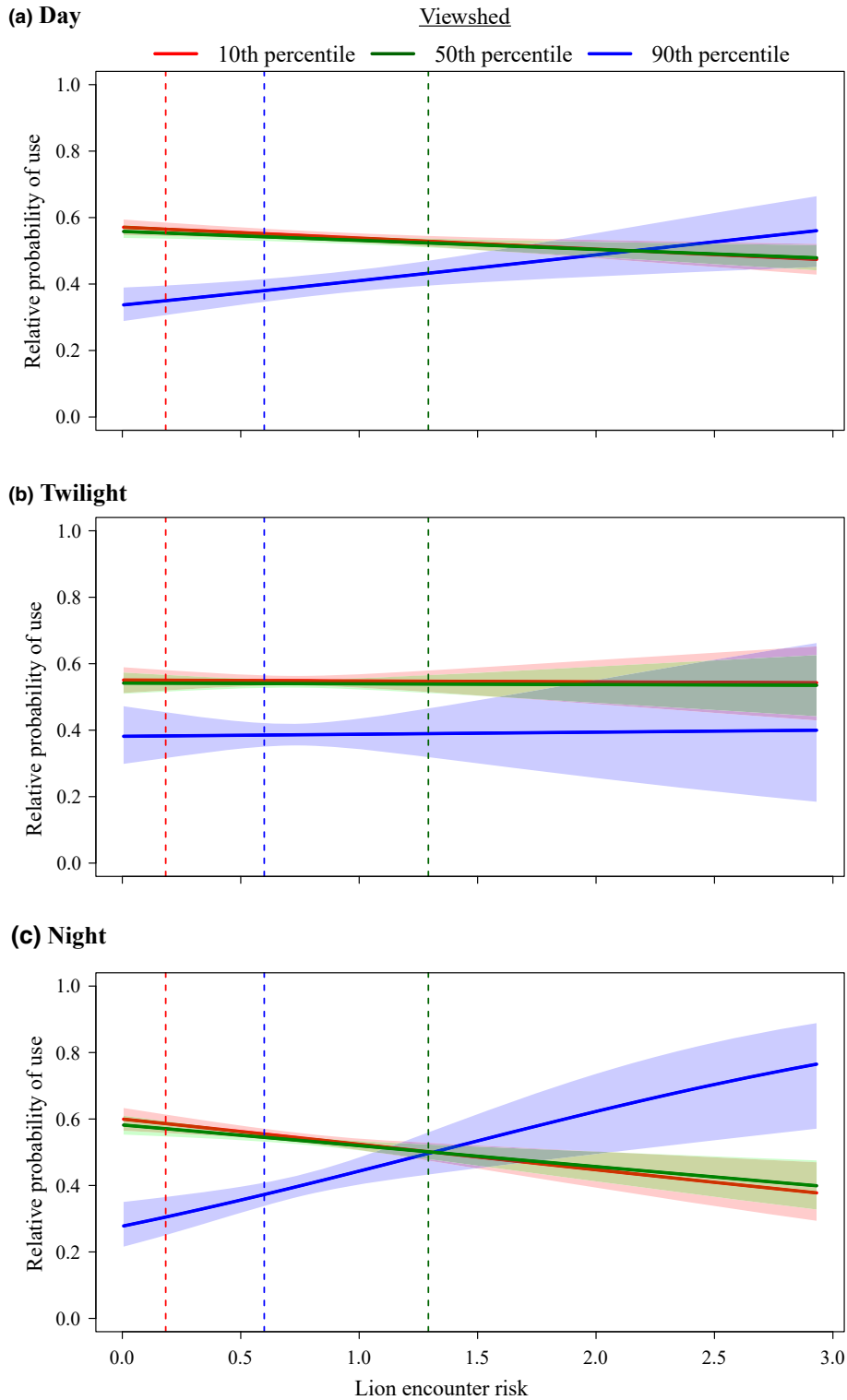
Fig. 3. Response curves displaying model predictions for wild dog viewshed selection across the three times of day (day, twilight, and night) and varying levels of lion-encounter risk. Predictions were calculated using the viewshed: time-of-day: lion utilization distribution (UD) three-way interaction from the most parsimonious model, that is, the habitat (encounter) model. Solid colored lines represent varying levels of viewshed openness, shading represents 95% confidence intervals, and dashed vertical lines represent the 10th, 50th, and 90th percentile of the observed lion-encounter risk distribution.

et al. 2019a), including in HiP historically (Darnell et al. 2014), simple spatial avoidance did not appear to be their primary strategy over our study period, with wild dogs instead using habitat structure to evade lions. Of our seven tested hypotheses, which we converted into statistical models for evaluation, those that incorporated an interaction between wild dog habitat selection and lion-encounter risk received substantially more support than models including only spatial avoidance of lion risk. The high density of lions in HiP during our study period likely makes spatial avoidance difficult and wild dogs appear to instead rely on landscape features to avoid detection or ambush by lions. That wild dogs in HiP persist at their highest densities in Africa, despite the high lion density, underscores the importance of heterogeneous landscapes for carnivore coexistence and the value of competition refuges for subordinate carnivores.

Our results also suggest that wild dogs predominantly exhibit a proactive response to lion risk, with much stronger support for hypotheses representing wild dog responses to long-term lion-encounter risk than to metrics of immediate lion proximity. Proactive responses to lion risk contrast with reactive responses observed for cheetah (Broekhuis et al. 2013, Swanson et al. 2014) and could result from stronger detrimental effects of lions on wild dogs than on cheetahs (Swanson et al. 2014), and hence the need for wild dogs to be more proactive and conservative in their response to lion risk. Reactive responses were likely also uncommon because our data set contained few examples of wild dogs in very close proximity to lions (the median distance from lions to observed step's end points was 3.59 km), suggesting that proactive responses to lion-encounter risk were effective at maintaining a large distance from lions. However, when accounting for moon illumination, our results suggest that wild dogs were more cognizant of lion proximity on new-moon nights, likely because of reduced visibility. The increased use of rugged areas when lions were far away on new-moon nights (Appendix S1: Fig. S1b) is likely an artifact of lions avoiding rugged areas (Mills and Gorman 1997) rather than wild dogs selecting these areas in response to increased distance from lions.

Proactive responses to risk are more likely to exert food-mediated costs in prey or subordinate carnivores compared with stress-mediated costs associated with reactive risk responses (Creel 2018). Food-mediated costs for wild dogs likely translate into them occupying areas with lower prey densities (Mills and Gorman 1997, Marnewick et al. 2019a), which can lower reproductive fitness (Groom et al. 2017, Marnewick et al. 2019b). In the case of wild dogs, proactive responses to risk could also result in some prey (e.g., impala and nyala that are targeted by both lions and wild dogs in HiP; Somers et al. 2017, Barnardo et al. 2020) being squeezed, whereby avoidance of lions leads to increased predation risk from wild dogs, because wild dogs are more likely to

be found in landscapes unoccupied by lions (e.g., rugged areas and dense vegetation). Prey squeezing has been previously suggested for prey vulnerable to both ambush and cursorial predators, based on diverging hunting strategies (Atwood et al. 2009, Lone et al. 2014), and our results suggest that risk-avoidance behavior in subordinate carnivores could be an additional mechanism (see also Davies et al. 2020).

When in riskier places (increased lion-encounter risk) and times (at night), wild dogs switched their overall selection for dense vegetation to instead select locations with increased visibility (large viewsheds), likely to enable earlier detection of potentially approaching lions during these risky and low-visibility periods. Altered habitat selection in response to lions at night suggests greater sensitivity to lion risk when lions are most active (Hayward and Slotow 2009), and suggests that HiP wild dogs utilize both landscape and temporal niche partitioning to avoid lions. Wild dogs elsewhere are known to separate their diel activity patterns from those of lions temporally, with high levels of wild dog activity during crepuscular periods and low activity at night when lions are most active (Hayward and Slotow 2009, Woodroffe et al. 2017). Our slowest recorded movement rate at twilight was therefore unexpected and seemingly contradictory to previous studies. However, these movement rates represent step length (displacement) rather than overall activity (as measured in other studies), and heightened activity does not necessarily result in increased spatial displacement. For example, wild dogs hunt most often during twilight (Rasmussen and Macdonald 2012), but in HiP they chase prey over relatively short distances and appear to be adept at ambush hunting in dense vegetation (Krüger et al. 1999), likely leading to shorter step lengths at twilight. In addition, our fine-scaled analysis of movement rates revealed a bimodal pattern of activity as recorded previously, with peaks in the early morning before sunrise and during the afternoon between 14:00 and 16:00. Increased displacement between 04:00 and 06:00 would represent some twilight movement that was characterized as nighttime (because civil dawn was never before 04:00 in our study), with movement possibly commencing after 05:00 and aligning with previously observed patterns (Hayward and Slotow 2009, Woodroffe et al. 2017). However, our results do suggest that wild dogs in HiP might begin hunting earlier than elsewhere, and the afternoon peak in movement rate could represent altered activity budgets in this high-lion-density environment. Wild dogs shift their activity to nighttime in areas of high human density (Rasmussen and Macdonald 2012) and it is possible that the afternoon peak in activity represents a behavioral modification to avoid lions, as has been documented for prey species (Tambling et al. 2015, Veldhuis et al. 2020).

Other factors not assessed here could also affect wild dog habitat selection, as well as their coexistence with lions. Prey availability affects the distribution of most predators, and although wild dogs are known to

prioritize lion avoidance over prey density (Mills and Gorman 1997, Groom et al. 2017, Marneweck et al. 2019a), prey distributions are still likely to play some role in shaping habitat selection and movement (Marneweck 2020). Dietary niche separation between wild dogs and lions could also facilitate coexistence. In HiP, lions prey predominantly on buffalo (Barnardo et al. 2020), whereas wild dogs favor nyala and impala (Krüger et al. 1999, Somers et al. 2017). Such dietary niche separation could enable wild dogs to use parts of the landscape selected by their primary prey (e.g., denser vegetation favored by browsing nyala), but with lower lion density. The location of other predators, especially spotted hyenas, and conspecifics could also affect wild dog landscape use. Spotted hyenas, however, exert considerably weaker effects on wild dogs relative to lions (Woodroffe and Ginsberg 1999, Webster et al. 2012), including in HiP (Darnell et al. 2014), and are therefore unlikely to significantly alter wild dog space use. Wild dog avoidance of lions could also place them at higher risk from other predators, for example, leopards, that favor denser vegetation. However, lions are exceedingly the dominant threat to wild dogs in natural systems (Woodroffe and Ginsberg 1999) and avoidance of them would take priority. Wild dog packs have also been found to tolerate high levels of territorial overlap (Marneweck et al. 2019a), especially with related packs (Jackson et al. 2017), suggesting that conspecifics have a weak effect on habitat selection relative to lions.

Lions have been viewed as detrimental to wild dog conservation efforts, with previous suggestions that wild dog conservation will be more successful in areas with low lion density and that future reintroductions be focused on such areas (Creel and Creel 1996, Mills and Gorman 1997). However, wild dogs have evolved under competitive suppression by lions, and there is considerable overlap in their present and historic ranges. Moreover, the presence of lions does not necessarily hinder reintroduction success (Gusset et al. 2008, Nicholson et al. 2020). Instead, our results suggest that landscape heterogeneity can facilitate carnivore coexistence and that heterogeneous environments could represent ideal sites for wild dog conservation. Indeed, wild dogs have only been intermittently present in several open ecosystems in Africa (Etosha, Scheepers and Venzke 1995; Ngorongoro, Creel and Creel 1996; Liuwa Plain, Dröge et al. 2017a; Serengeti plains, Jackson et al. 2019), suggesting that wild dogs in these homogeneous landscapes are unable to avoid dominant competitors and establish permanent populations. More broadly, the role of landscape heterogeneity in facilitating carnivore coexistence warrants further study at a wider range of sites and could represent an alternative mechanism for coexistence in addition to spatial and temporal niche separation.

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