Reproductive state influences the degree of risk tolerance for a seasonally breeding mesopredator

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Data Accessibility Statement

Analyses reported in this article can be reproduced using the data provided by Marneweck et al. (2021).

Acknowledgements

Abstract

The risk of predation can alter the way animals perceive costs and benefits in their environment, on which foraging decisions are made. To maximize fitness, animals with offspring show the most pronounced alteration in behavior because mothers experience increased nutritional requirements and increased vulnerability to predation. Therefore, the tolerance of risk is shaped, in part, by reproductive state. Like prey species, mesopredators balance a trade-off between food and predation to maximize fitness. However, few studies have acknowledged its importance. We investigated how mesopredators may alter their space use between periods when young are and are not vulnerable. Investigating the fine-scale space use of 19 packs of African wild dogs Lycaon pictus in the Kruger National Park, we found lower risk tolerance of denning packs; they re-visited area less frequently as lion and impala density increased and thus reduced the likelihood of risky encounters by avoiding areas where both risk and reward were high. By contrast, non-denning packs re-visited area less frequently as lion density increased and impala density decreased and thus avoided areas where reward was low, especially if risk was high. These results suggest that wild dogs shift their patterns of space use when the pack is most vulnerable. Ultimately, we found evidence of decreased risk tolerance by denning packs, likely because of increased vulnerability of lactating mothers and immobile pups. More broadly, our findings suggest that risk tolerance is dependent on reproductive state for mesopredators and should be considered as a possible mechanism for other mesopredators as well.

Introduction

The top-down effects of predators on lower trophic levels can be direct (i.e. predation) or indirect (i.e. the risk of predation influencing movement, or affecting fitness; Orrock et al. (2008)). Direct predation can reduce herbivore abundance, while the risk of predation alters foraging decisions by herbivores which can create a landscape of fear (Brown, 1999; Laundré et al., 2001), which can carry the cost of decreased feeding rates (Brown and Kotler, 2004; Kotler et al., 1991) or compositional shifts in diet (Christianson and Creel, 2010). Some prey species select areas of lower predation risk even if they are areas of poorer resource quality/availability. For example, elk *Cervus elaphus* sacrifice using high-quality foraging areas to avoid wolves *Canis lupus* (Hernández and Laundré, 2005).

Animals with offspring may show the most pronounced alteration in behavior in response to predators because, to maximize fitness, lactating mothers must both provision and protect young and thus face a trade-off between meeting the increased nutritional requirements of lactation and avoiding the increased risk of predation. Reproductive state can therefore affect the degree of tolerance of risk and subsequent use of space. For example, when at the base of a slope, female bighorn sheep *Ovis canadensis* with lambs are three times more vulnerable to predation compared to when they are on slopes (Berger, 1991). Considering this vulnerability, female mountain goats *Oreamnos americanus* with young trade forage abundance for safety, by foraging in areas with less plant biomass but closer to escape terrain (i.e. cliff faces/slopes; Hamel and Côté (2007)). Thus, reproductive state in herbivores influences changes in space use because of changing tolerance of risk. This changing tolerance of risk is not black and white (i.e. tolerant or not) but likely a gradient of tolerance from low (selecting very safe areas) to high (selecting unsafe areas).

It is not only herbivore species that are faced with the top-down limiting effect of predation. Sympatric predators use the same space and food resources, and some species outcompete others. Apex predators tend to exert strong negative effects on mesopredators through intraguild predation (Palomares and Caro, 1999; Polis and Myers, 1989), the restriction of access to prey-rich areas, and reducing food intake due to kleptoparasitism (Dröge et al., 2017; Mills and Gorman, 1997; Vanak et al., 2013). This competition ultimately imposes risk for mesopredators and consequently affects their

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distribution, population dynamics, and habitat selection (Heithaus, 2001; Swanson et al., 2014; Vanak et al., 2013). Like herbivores, mesopredators avoid direct and risky encounters by forgoing access to prey-rich areas to avoid apex intraguild competitors. For example, the nocturnal activity of stone martens *Martes foina* is driven by a trade-off between consuming less prey but avoiding diurnal predators that are less active at night (Roy et al., 2019). In addition, cheetahs *Acinonyx jubatus* generally avoid hunting at night to reduce potential contact with lions *Panthera leo* (Dröge et al., 2017), or only hunt during moonlit nights to reduce the risk of encountering night-active competitors (Cozzi et al., 2012).

When mesopredators have dependent young, they also experience the increased nutritional requirements of lactation. During this nutritionally strained period, access to prey needs to be offset by the risk of predation and competition, as prey-rich areas are often frequented by apex predators. Consequently, reproductive state may strongly affect how mesopredators modify their behavior in response to risk. As the degree of risk tolerance has been shown to be dependent on reproductive state in herbivores (Hamel and Côté, 2007; Viejou et al., 2018), we can use this as a predictive framework to generate hypotheses about how mesopredators may alter their strategies of risk tolerance, being less tolerant of risk when they have dependent young and more tolerant of risk when they have less vulnerable young.

As a mesopredator in the African large carnivore guild, African wild dogs *Lycaon pictus* avoid contact with the apex predator, lions, both reactively and proactively. Reactive avoidance occurs when wild dogs come into direct contact with lions and they react by fleeing (Webster et al., 2012). Proactive avoidance uses cues (e.g. olfactory, auditory, and/or visual) to gain information about the environment and use this long-term information to subsequently avoid risky areas (Cozzi et al., 2012; Darnell et al., 2014; Davies et al., 2021; Dröge et al., 2017; Swanson et al., 2014; Vanak et al., 2013). Wild dogs have become locally extirpated in some areas of high lion density (Swanson et al., 2014). Additionally, a large proportion of both adult (15%; Woodroffe et al. (2007a)) and pup (69%) mortality is due to lions (Groom et al., 2017), where it is estimated that lion-related mortality is the highest cause of natural mortality for wild dogs (Woodroffe et al., 2007a). The indirect effects of reduced access to herbivore-

rich areas (Dröge et al., 2017; Mills and Gorman, 1997) is an additive effect of the costs of intraguild competitor avoidance, mainly centered around lions. Thus, wild dogs need to offset the potential costs of risky interactions with lions in order to access enough prey to fulfill metabolic requirements, resulting in lions being the main risk factor in natural wild dog populations (Creel and Creel, 1998; Mills and Gorman, 1997).

Wild dog packs hold territories on average 393–559 km^2 (this study area; Marneweck et al. (2019)). In southern Africa, packs breed annually and, for a three-month period between May–August (Supplementary Table S1; occurring within the dry season which is approximately May–November (MacFadyen et al., 2018)), immobile pups are raised at a den site (Creel and Creel, 2002; Malcolm and Marten, 1982). Dens are usually located within the core 50% of the territory (average 66–83 km^2 in the KNP; Marneweck et al. (2019)) and the movement of the pack is greatly constrained because during this time wild dogs act as central place foragers, leaving the den site in hunting groups to kill and eat, and then returning to the den site to regurgitate for pups, the alpha female, and other individuals guarding the den (Malcolm and Marten, 1982; Mbizah et al., 2014; Pomilia et al., 2015). Although the daily distance travelled is similar during the denning and non-denning periods (Pomilia et al., 2015), returning to the den site restricts wild dog packs from utilizing their full territory over these few months. Since having vulnerable young may alter the degree of risk tolerance, and that wild dogs are not able to utilize their full territory during the denning period and reactive avoidance of competitors is limited, one would expect that wild dogs with immobile pups would adopt altered spatial strategies to reduce the risk of mortality (to both pups and adults). Wild dogs select den sites that are in areas of more rugged terrain and dense vegetation than the immediately surrounding area (up to 500 m radius) to avoid lions and promote concealment (Davies et al., 2016; Jackson et al., 2014; van der Meer et al., 2013). The area around the den (~5 km radius) also tends to have lower impala density than the rest of the territory, which has been suggested to further reduce the probability of encountering other predators (Mbizah et al., 2014). We can use this evidence on the landscape features of den sites to predict how they might use the landscape at the scale of the denning territory area and then compare this to the non-denning territory area which would provide insight into their tolerance of risk. Although wild dog den site

selection has been explored, little is known about the use of space within the denning season territory during this critical life history stage while contrasting it against the non-denning period when packs use larger areas (Mbizah et al., 2014; Pomilia et al., 2015).

The behavioral changes associated with having dependent young could provide key insights into avoidance mechanisms at a crucial time for the pack. It is clear that avoiding lions while denning would hold reproductive benefits, but it is unclear how wild dogs utilize their restricted territory while denning with respect to meeting additional nutritional requirements and offsetting increased vulnerability to predation. Behaviors such as the frequency of re-visits to an area, and the amount of time spent within an area, can help us to understand how wild dogs balance the need to forage and avoid predation while denning and how this might change as packs shift to their non-denning season.

We investigated the effect of reproductive state (denning vs. non-denning) on wild dog space use to understand how wild dog packs trade-off the risk of predation with nutritional requirements while denning, compared to non-denning, by using time allocation to measure the degree of risk tolerance. Specifically, we compared space use between reproductive states by testing measures of re-visitation and duration of visits that can act as key metrics of spatial behavior. High re-visitation is characteristic of regular exploitation of resources, while long visit duration is characteristic of territorial or station-holding behavior (Lyons et al., 2013). Thus, we would expect that longer visits indicate areas of perceived greater safety (i.e. lower risk). We expected a stronger spatial response to risk during the period of higher pack vulnerability (denning) compared to the less vulnerable period (non-denning) as evidenced by packs using the available space differently in each season. Specifically, we predicted that denning packs would re-visit areas of lower lion density (i.e. foraging in areas of reduced apex predator density; Mbizah et al. (2014)). Further, as wild dogs use landscape features to proactively avoid lions (Davies et al., 2021), we also predicted that visits would be longer in areas of rugged terrain, dense vegetation, and closer to den sites (i.e. areas unfavored by lions and that promote concealment; (Davies et al., 2016; Davies et al., 2021; Jackson et al., 2014; Mills and Gorman, 1997)). In contrast to these patterns, when packs return to their usual spatial behavior when they have mobile pups (i.e. non-denning), packs should display a reduced trade-off between food and safety as the fitness consequences

should be lower. We thus predicted that during this non-denning period, packs would display greater risk tolerance. This should be evident by the lack of dependency on more rugged and densely vegetated areas and use of higher impala density areas regardless of lion risk.

Materials and Methods

Study site and population

We conducted this study in the 19,142 km^2 Kruger National Park (KNP), South Africa. The landscape has an increasing north to south rainfall gradient (Joubert, 1986), and two major soil types of basalts in the east and granite in the west (Venter, 1986). The KNP holds an intact carnivore guild, with the largest contiguous population of wild dogs in South Africa, estimated to be ~250 individuals (adults and yearlings) during the study (Nicholson et al., 2020). We GPS collared wild dogs (n = 23 individuals, n = 19 packs: African Wildlife Tracking) between August 2016 and June 2018 (Supplementary Table S1) as part of the State Veterinary Services, South African National Parks (SANParks), and Endangered Wildlife Trust disease and health survey (SANParks Project VSCHL1372 with addenda, SANParks Animal Use and Care Reference 013/16). Collars weighed a maximum of 550 g (i.e. < 5% wild dog body weight of ~ 25 kg (Gannon and Sikes, 2007; Gorman et al., 1998)) and were fitted to wild dogs sedated with a combination of fentanyl (0.1 mg/kg) and xylazine (1 mg/kg), fully reversible with yohimbine (0.125 mg/kg) and naltrexone (0.3 mg/kg). The GPS fix schedule was set to 4 – 8 per day giving us a rich spatial data set covering two consecutive denning and non-denning periods (Supplementary Table S1).

We defined a pack as at least one male and one female of >1 year old (Creel and Creel, 2002). Where possible, we fitted collars to males focusing predominantly on subordinate males (Supplementary Table S1) to avoid any potential negative effects of capture on the reproductive physiology of females. Over the course of the study, some of these collared subordinate individuals dispersed from their natal packs (n = 2 groups). However, data from these individuals were excluded from our analyses subsequent to them leaving and being outside of the normal territory range and away

from the pack for >14 days as per focal observations and GPS locations. Furthermore, we did not collar alpha females as they tend to remain at the den site with pups during the lactation period (Malcolm and Marten, 1982) and would thus not give us an accurate representation of the pack's space use of the denning season territory. In some cases, a pack chose a den site outside of the KNP boundary (and thus no corresponding environmental data were available; n = 3 denning seasons for three different packs) or a collar ceased functioning over the denning period and could not be replaced as the pack was inaccessible (n = 12 denning seasons for 11 different packs). In these cases (see Supplementary Table S1 for more details), these spatial data over the denning season were not included in our analyses. Consequently, over the study period, we utilized data for 29 non-denning periods and 15 denning periods from the 19 packs, i.e. all data from inside the boundary of KNP (Supplementary Table S1). Generally, wild dog packs were concentrated in the south-west region of KNP during the study period, with relatively few packs in the north (see Fig. S3 in Marneweck et al. (2019)).

Re-visitation and visit duration

To calculate re-visitation and visit duration, we used Time Local Convex Hulls using the R package *T-LoCoH* (Lyons and Getz, 2014). Time Local Convex Hull (i.e. T-LoCoH) constructs convex hulls around GPS point sets that are localized in space and time, incorporating the time stamp of each location rather than using that information to control for autocorrelation (Lyons et al., 2013). We set the time-space scaling parameter (*s*) to 0.01 based on selection procedures in Lyons and Getz (2014) and we selected the nearest neighbors using the *k* (i.e. nearest-neighbor) method to construct hulls. We selected a value of *k* (non-denning k = 18, denning k = 24) dependent on the size of the area used by each pack, the dispersion of points within that area, and if those hulls minimized encompassing widely scattered outlying data points while also covering holes within the core areas of activity. Lastly, T-LoCoH computes metrics for re-visitation and duration based on an inter-visit gap (IVG). We set the IVG to 12 hours, to match the temporal difference between two consecutive yet different wild dog crepuscular activity periods (Woodroffe et al., 2017) and therefore avoided spatial and temporal pseudo-replication. As such, points separated by more than 12 hours in time are not considered nearest neighbors, regardless of their proximity in space (i.e. separate events from one active period to the next). T-LoCoH then

allowed us to analyze all locations within a hull and use the IVG to compute the total number of separate visits to the hull (i.e. re-visitation) as well as the mean number of occurrences per visit (i.e. duration of visit). We calculated these metrics (re-visitation and duration) for each pack's specific reproductive state of denning and non-denning. We defined the start of a denning period as the known date of a pack with a pregnant female going underground via GPS collars, focal monitoring, and citizen science reports. We defined the end of the denning period as the known date of a pack leaving a den with pups and not returning for ≥2 consecutive days via GPS collars, focal monitoring, and citizen science reports. We then defined the period in between denning periods as the non-denning period (i.e. the pack is not restricted to a den site and pups are mobile). We used the *pointDistance* function in the *raster* package (Hijmans, 2020) to calculate the distance of each point in the denning season to its corresponding den site. In some cases, packs moved den sites within a single denning season (Creel and Creel, 2002), as evident from GPS location clusters and focal monitoring. When den relocation occurred, the location was updated for the assignment of distance to den.

Environmental covariates

Wild dogs prefer prey within the weight range of 16 – 32 kg and 120 – 140 kg, in contrast to lions which prefer prey within the weight range of 190 – 550 kg (Hayward and Kerley, 2005; Hayward et al., 2006). For wild dogs, this equates to selection for species such as bushbuck *Tragelaphus scriptus*, impala *Aepyceros melampus*, and Greater kudu *Tragelaphus strepsiceros* (Hayward et al., 2006). For lions this equates to selection for species such as African buffalo *Syncerus caffer* and avoidance of smaller species such as impala (Hayward and Kerley, 2005). In the KNP, impalas make up 81% of their dietary biomass (Hayward et al., 2006; Mills and Gorman, 1997). Hence, we used impala density as a proxy for wild dog prey density. To estimate impala density, we used data from distance sampling via aerial transect counts that were conducted in July (dry season, and the wild dog denning season) of 2016 and 2017 by SANParks (SANParks, 2016, 2017). We first calculated a half-normal detection function with cosine adjustment using the R package *Distance* (Miller, 2017). We then converted detection-adjusted data through a generalized additive model with restricted maximum likelihood smoothing into a density surface (impalas/km^2; see Fig. S2 in Marneweck et al. (2019)), using the *dsm* package (Miller et al.,

2013; Miller et al., 2019). Aerial transect counts were not conducted in 2018 but, as there was no significant difference in the impala density between 2016 and 2017 (see Supplementary Material in Marneweck et al. (2019)), we assumed that impala density for 2018 was similar to 2017. This is further supported by the fact the climatic changes in the KNP in 2016 and 2017 did not alter impala distribution in the study area (Abraham et al., 2019). Using the smoothed density surface, we extracted a value of impala density for each GPS point (denning n = 3,583 and non-denning n = 16,740 GPS collar locations) according to the closest date of the impala count (either July 2016 or July 2017).

To estimate lion density, we used data from the SANParks lion survey conducted in July 2015 (dry season; SANParks (2015)) and estimated the number of lions in the thiessen polygon around each calling station, based on the pride structure, following Ferreira and Funston (2010). We then generated a smooth kernel density map (lions/km^2; see Fig. S4 in Marneweck et al. (2019)) using the *density.ppp* function with a cross validated bandwidth selection in the *spatstat* package (Baddeley et al., 2015). The KNP appears to have a stable lion population, with numbers invariable from 1975 – 2005 (Ferreira and Funston, 2010) and, as the estimated number of lions from the 2015 survey was similar to the result from the 2005 survey (Ferreira and Funston, 2010), we assumed that the 2015 estimate would be an accurate reflection for our 2016 – 2018 study period of a stable lion population. Using the smoothed density surface, we extracted a value of lion density for each GPS collar location, in the same way as we did impala.

It has been suggested that wild dogs use dense vegetation and rugged terrain to avoid detection (during both denning and non-denning seasons), when lion density or risk of encounter is high (Davies et al., 2016; Davies et al., 2021; Jackson et al., 2014). Thus, ruggedness and vegetation density are important landscape features for wild dogs to use to reduce the likelihood of risky encounters. We used woody cover as a proxy for vegetation density, utilizing the percentage woody cover projected at a 1 km pixel resolution generated by calibrating remote sensing images with field measurements from Bucini et al. (2009). Using the woody cover layer, we extracted a value of woody cover for each GPS point. To calculate terrain ruggedness, we first obtained a digital elevation model (1 km resolution) of the study area from the United States Geological Survey EarthExplorer (USGS, 2011). Using the digital

elevation, we then calculated the Vector Ruggedness Measure (VRM), using QGIS (QGIS Development Team, 2019). The VRM captures variability in slope and aspect into a single measure, and quantifies local variation in terrain more independently of slope than other methods (Sappington et al., 2007) and has been used to successfully show the impact of ruggedness on wild dog den site selection and space use (Davies et al., 2016; Davies et al., 2021). Using the VRM surface layer, we extracted a value of VRM for each GPS point.

Between 2014 and 2016, the KNP experienced a severe but heterogenous drought. Although the drought may have affected the overall distribution and density of herbivores (Abraham et al., 2019), we found no such impact on the density or distribution of impalas within our study range (i.e. wild dog territories) or time period (see Supplementary Table S2 in Marneweck et al. (2019)). This is further supported by Abraham et al. (2019) who found that impalas in the KNP did not move in response to the drought, but rather changed their diet to incorporate more browse compared to grass. Although woody vegetation was damaged during the 1991 – 1992 KNP drought, Viljoen (1995) reports that this was localized and, overall, woody vegetation was not significantly affected during that drought period. Furthermore, as trees benefit from reduced competition from grass during drought periods (Eckhardt et al., 2000), we did not assume a significant difference in the woody vegetation as a result of the 2014 – 2016 drought.

Statistical analyses

We created two candidate model sets: one with re-visitation as the response and the other with visit duration as the response, using generalized linear mixed effects models with a negative binomial distribution for re-visitation and a poisson distribution for visit duration. Both responses were count data (poisson), however, models with re-visitation as the response were overdispersed and thus we used a negative binomial. Each model set tested impala density, lion density, woody cover, and terrain ruggedness as explanatory variables, plus distance to den for the denning season. We also included the potential additive effects of impala density and woody cover, impala density and ruggedness, woody cover and ruggedness, woody cover and lion density, ruggedness and lion density, interactions between impala density and lion density, and a null model. We set pack ID (denning n = 10 packs, non-denning

= 19 packs) as a random variable in all candidate models. We repeated this procedure for denning (n = 3,583 data points) and non-denning (n = 16,740 data points) periods. We assessed collinearity between independent explanatory variables prior to analysis using variance inflation factors (VIF) and Spearman rank correlation tests. All correlations had Spearman's rho < 0.5 and all variables had VIF values < 2. Lions occur in areas of high overall herbivore density and, in the KNP, the area of highest lion density has a high prey biomass of 2,749 kg/km^2 (comprising the species; African buffalo, giraffe *Giraffa cameloparadalis*, impala, Plains zebra *Equus quagga*, warthog *Phacochoerus africanus*, blue wildebeest *Connochaetes taurinus*, Greater kudu, and waterbuck *Kobus ellipsiprymnus*; (Creel and Creel, 1996; Ferreira and Funston, 2010)).. Thus, although lions can occur in the high herbivore biomass regions of the KNP, lion density and impala density were not correlated in our study (r < -0.01, p = 0.36). While impalas can occur at high densities in areas of high lion density, high impala densities can also occur in areas of low lion density (for impala and lion density maps, see Supp Figs. S2 and S4 in Marneweck et al. (2019)). This demonstrates the spatial disassociation between the biggest risk for wild dogs (i.e. lions) and their biggest reward (i.e. impalas). To identify the best model(s), we used model selection based on Akaike's information criterion adjusted for small sample size (AIC*c*), where models within 2 ΔAIC*c* of the top model were considered important (Burnham and Anderson, 2002).

Finally, we mapped the seasonal difference in habitat suitability of wild dogs based on the factors from top model affecting re-visitation (i.e. impala and lion density, see *Results*) for both denning and non-denning. We did this using two random forest classification algorithms, utilizing impala and lion density as predictor variables for wild dog locations each season (denning n = 3,583 locations, non-denning n = 16,740 locations). We used 5,000 random locations to represent pseudo-absence, 2,000 trees, and selected the optimal value of mtry using the *tuneRF* function of the *randomForest* package (Liaw and Wiener, 2002). The out-of-bag (OOB) error rate and area under the curve (AUC) were 8.37% and >0.99 for denning, and 14.27% and >0.99 for non-denning, respectively. We conducted all analyses in R version 3.6.3 (R Core Team, 2020), using packages *MuMIn* (Barton, 2020), *lme4* (Bates et al., 2015), and created figures with *ggplot*2 (Wickham, 2016) and *visreg* (Breheny and Burchett, 2017).

Results

Denning

The top model explaining re-visitation for denning packs contained an interaction between impala density and lion density (Table 1, Fig. 1a). We found a strong negative relationship between the number of visits with both lion and impala density, where the number of re-visits decreased (i.e. negative co-efficient, Table 1) as both impala and lion density increased (Fig. 1a). Notably, no visits occurred in areas where the lion density exceeded 26 lions/100 km^2. The top model explaining visit duration for denning packs contained an interaction between impala density and distance to the den (Table 1, Fig. 1b). Wild dogs decreased visit duration (i.e. negative co-efficient, Table 1) as impala density increased and distance to the current den site decreased (Fig. 1b). The habitat suitability for wild dogs during the denning season, as based on impala and lion density, revealed small suitable areas (Fig. 2), consistent with literature on territory reduction during the denning season (Pomilia et al., 2015).

Non-denning

Like denning packs, the top model explaining re-visitation for non-denning packs also contained an interaction between impala density and lion density (Table 2, Fig. 1c). There was a negative relationship between the number of re-visits and both lion and impala density (i.e. negative co-efficient, Table 2) where, in contrast to the denning period, the number of re-visits decreased with increasing lion density and decreasing impala density (Fig. 1c). Visits occurred in areas of higher lion density than the denning season, but no visits occurred in areas where the lion density exceeded 41 lions/100 km^2. The top model for explaining non-denning visit duration also contained an interaction between impala density and lion density (Table 2, Fig. 1d). We found a positive relationship between lion and impala density (i.e. positive co-efficient, Table 2) where wild dogs made longer visits in areas of increasing impala and increasing lion density (Fig. 1d). The habitat suitability for wild dogs, based on impala and lion density, showed a larger suitable area compared to the denning season (Fig. 2), consistent with literature on larger ranges during non-denning (Pomilia et al., 2015).

Discussion

We found that the reproductive state of wild dog packs played a strong role in how packs used space as a mechanism for tolerating varying degrees of risk posed to them by lions. Specifically, during the vulnerable denning period, wild dogs displayed a lower degree of tolerance towards risk compared to their non-denning period where they tolerated higher degrees of risk. For example, wild dogs during denning re-visited areas of lower impala density as lion density increased and made shorter visits to areas of higher impala density, especially if they were close to the den. By contrast, wild dogs that were not denning appeared to take more risks by maximizing resource acquisition (i.e. high re-visits) and decreasing safety (i.e. high duration of visits) in areas of higher impala density even though lion density was high in these patches. This is evidence that wild dogs alter their spatial behavior depending on the presence of immobile and highly dependent young. These results support other studies identifying the location of den sites to be associated with predator avoidance (Davies et al., 2016; Jackson et al., 2014; Mbizah et al., 2014) but improve our understanding of which landscape factors influence their degree of risk tolerance. In addition, our results are the first to highlight the shifting degree of risk tolerance that is dependent on reproductive state for a mesopredator.

Denning

Despite the importance of impala in their diet (Hayward et al., 2006; Mills and Gorman, 1997), denning wild dogs avoided re-visiting areas with higher impala density if the lion density was also high. Thus, wild dogs forego impala-rich areas to increase safety from lions which suggests that the risk of predation outweighs the benefit of food resources during denning. This finding is not unexpected; however, it may indicate that acquiring sufficient food while denning is difficult. Wild dogs regurgitate meat for pups and other members of the pack who remain at the den (Malcolm and Marten, 1982). Consequently, if finding food is difficult, provisioning for the lactating alpha female as well as pups might be compromised. Yet, wild dogs have been recorded to persist on smaller prey items (Woodroffe et al., 2007b) and show preference for species as small as 16 kg (Hayward et al., 2006). Hunting smaller prey that can be consumed rapidly may be a strategy to promote concealment during this time, or reduce the energy expended (Embar et al., 2014). It is therefore possible that wild dogs could alter their prey

consumption to offset the increased vulnerability of the pack when pups are present and immobile. Season-specific prey selection is a key area to explore for wild dogs in future studies. Alternatively, they may spend less time at carcasses while denning as they need to return to the den to feed pups and avoid detection. However, further research into diet composition while denning would be required to validate this assertion. The alteration of feeding behavior when young are present has been recorded in other carnivores. Female cheetahs alter their behavior at kills (e.g. moving kills, increased vigilance) to reduce predation of both cubs and self (Hunter et al., 2007). Also, female brown bears *Ursus arctos* reduce their salmon *Oncorhynchus gorbuscha* consumption to avoid the risk of infanticide (Nevin and Gilbert, 2005). These behavioral modifications support the notion that the cost of encountering an apex predator is greater than the cost of not encountering food (Vanak et al., 2013), which is likely amplified when vulnerable young are present. As re-visitation represents the exploitation of resources, then wild dogs' lack of re-visitation to areas of high impala density while denning may represent a lack of resource exploitation because these areas are risky. A similar finding was reported by O'Neill et al. (2020), where wild dogs avoided risk (in this case, human density) more strongly in the denning season.

Lions contribute significantly to both wild dog pup and adult mortality (Groom et al., 2017; Woodroffe et al., 2007a). As such, among other decisions driving den site selection and subsequent area use, the risk of predation from lions likely takes a significant priority (Darnell et al., 2014; Davies et al., 2016; Groom et al., 2017; Jackson et al., 2014). Our results reveal that denning wild dogs were not present in areas exceeding 26 lions/100 km^2. Swanson et al. (2014) found a similar limit for wild dogs in the Serengeti, where they did not occupy areas above 20 lions/100 km^2. Wild dogs made shorter visits in areas of higher impala density, especially when close to the den. This suggests that an area with higher impala density could be perceived as risky while denning, as it may increase the risk of encountering any other predator. Although common for wild dogs to return to the den after each hunt, in cases where a pack has moved far (ca 10 km) or failed to kill during a hunt, they may not return (Creel and Creel, 2002). We suggest that our findings may also represent some members of the pack spending periods of time (~1–2 days) away from the den (>10 km) when in areas of low impala density because of the likely unsuccessful hunts in these areas. As long visit duration may represent increased

safety, then our results suggest that areas of lower impala density are valuable to wild dogs while denning even if the effort to obtain enough food resources in these areas is very high, the costs of foraging in impala-rich areas could be lethal.

Non-denning

Mesopredators must trade-off food acquisition and avoid predation to persist sympatrically with apex carnivores. This trade-off has been identified in several systems. For example, the presence of apex coyotes *Canis latrans* in prey rich areas displaces the mesopredators San Joaquin kit foxes *Vulpes macrotis mutica* (Nelson et al., 2007). Apex lions anchor themselves in areas of high herbivore density (Creel and Creel, 1996; Ferreira and Funston, 2010)) and, although not always the case (Comley et al., 2020), avoiding lions may mean avoiding resource-rich areas (Mills and Gorman, 1997). However, because impala density and lion density were not correlated in our study (the KNP is very heterogenous (Biggs et al., 2003)), and likely because lions avoid impalas (Hayward and Kerley, 2005), it was therefore possible for wild dogs to utilize impala-rich patches while still avoiding areas of high lion density. Non-denning wild dogs re-visited areas of high impala density even when this was synonymous with high lion density, thus, their willingness to risk encountering a lion is increased when they are not denning and is associated with the likely benefit of access to more overall resources that inhabit the areas frequented by lions (e.g. other prey such as bushbuck and kudus). As re-visitation represents the exploitation of resources, then non-denning wild dogs increased re-visitation to areas of increasing impala density (comparative to denning) likely represents the exploitation of preferred food resources. Interestingly, this exploitation occurs despite the higher risk of encountering lions which suggests that packs take increase their risk tolerance when they are non-denning. We hypothesize that this is because pups are mobile during this time, and consequently packs are likely better able to avoid direct, costly, and lethal encounters with lions (or take effective evasive action when they do come into direct contact) thus enabling packs to take more risks.

Non-denning wild dogs visited areas up to 40 lions/100 km^2 (where denning packs did not exceed 26 lions/100 km^2), providing further evidence that wild dogs were more tolerant of lion risk when they were not denning compared to when they were denning. Interestingly, the maximum lion

density visited by non-denning wild dogs (41 lions/100 km^2) was double that of Swanson et al. (2014), who found that 20 lions/100 km^2 was the limit for wild dogs in the Serengeti. Lions are held responsible for the disappearance and continued absence of wild dogs in the Serengeti (Swanson et al., 2014), yet our results show that wild dogs utilized areas of much higher lion density than that recorded in the Serengeti. We suggest that the high density of preferred wild dog prey availability in the KNP (e.g. up to 4,500 impalas/100 km^2; SANParks (2017) as well as general high herbivore biomass (Ferreira and Funston, 2010)), coupled with more complex vegetation structure than the Serengeti, may offset the risk and allow wild dogs to coexist with lions, likely through proactive avoidance, without being locally extirpated (Davies et al., 2021).

Non-denning wild dogs made their longest visits in areas of both higher impala and lion density. With pups mobile and the packs less vulnerable, wild dogs can tolerate more risk to obtain adequate food resources in these areas comprising high impala density in areas of high lion density. This is supported by Cozzi et al. (2012), who found that wild dogs are starvation driven and will exploit every opportunity to hunt. Our results suggest that this is more likely to occur during non-denning periods. As increased visit duration may represents station-holding behavior (a proxy for safety), then non-denning wild dogs likely perceive areas of higher impala density as valuable enough to run the risk of potentially costly and lethal lion encounters.

During a time of restricted space available with an increased need for resource acquisition, denning wild dogs take fewer risks. Our results highlight that lion density alters access to prey for wild dogs, supporting the conclusions of Creel and Creel (1998) who suggested that interference competition is a strong determinant of wild dog population dynamics. We found that, in the KNP, wild dogs never visited areas exceeding 41 lions/100 km^2. The lion densities spanning the areas visited by wild dogs in this study (<1 – 41 lions/100 km^2) are relatively low compared to the highest lion density occupied in the KNP (75 lions/100 km^2; SANParks (2015)). Thus, in general, it appears that the KNP is large enough for wild dogs to avoid the areas of highest lion density, which may be facilitated by territory overlap with other wild dogs (Marneweck et al., 2019) and/or a heterogeneous and complex vegetation structure (Davies et al., 2021). However, a caveat of our study is that our environmental variables did not

completely overlap temporally with our response variables. The lion data were from 2015 and impala data from 2016 – 2017, while wild dog data were from 2016 – 2018. Further, both lion and impala data were collected in the dry season, which would align with denning space use but not with non-denning space use. However, due to densities of both lions and impalas not showing significant shifts over time/seasons in our study area (Abraham et al., 2019; Ferreira and Funston, 2010; Marneweck et al., 2019), we are confident that our results do provide important insights into wild dog space use but urge further study of all covariates simultaneously.

In an era of environmental change, having accurate descriptions of habitat use is imperative for successful conservation efforts (Hefty and Stewart, 2018). Knowledge of fine scale movements and area selection is also important for selecting suitable areas for protection and/or reintroduction. Furthermore, understanding drivers of movement is essential for endangered species with large territories, such as the wild dog. Monitoring lion density and distribution is crucial in areas where wild dogs are present, to ensure their ongoing persistence and survival. This is particularly relevant for smaller protected areas, where wild dogs might not be able to avoid areas of high lion density while still meeting their metabolic requirements. Ultimately, our findings provide correlational evidence of shifting priorities in habitat use by wild dogs between their denning and non-denning seasons. This shift is suggestive of plasticity in their degree of risk tolerance mediated by reproductive state of these mesopredators.

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Table 1. Coefficients from the 13 candidate generalized linear mixed models describing the effects of impala density, lion density, woody cover, terrain ruggedness, and distance to den site on the re-visitation (negative binomial distribution) and visit duration (poisson distribution) of denning African wild dogs (n = 3,583 data points) between 2016 and 2018 in the Kruger National Park, South Africa. Wild dog pack ID (n = 10 packs) was set as a random variable for all models. Top models (i.e. those within 2 ΔAIC_c of the top model) are highlighted in bold.

	Model	Estimate	Std Error	AIC_c	ΔAIC_c	Weight	R^2
Re-visitation							
1	**Lion density +**	**5.036**	**0.551**	**26275.86**	**0.00**	**>0.99**	**0.67**
	impala density +	**0.848**	**0.046**				
	lion density*impala density	**-14.439**	**0.804**				
2	Distance to den +	-0.162	0.010	26506.04	230.18	<0.01	0.34
	impala density +	0.088	0.028				
	distance to den*impala density	0.015	0.008				
3	Lion density +	6.587	0.527	26511.43	235.57	<0.01	0.34
	woody cover	0.120	0.011				
4	Distance to den	-0.154	0.009	26536.07	260.21	<0.01	0.28
5	Lion density	6.668	0.548	26622.58	346.72	<0.01	0.32
6	Lion density +	6.663	0.549	26624.61	348.75	<0.01	0.32
	terrain ruggedness	-0.003	0.033				

7	Impala density +	0.062	0.023	26666.90	391.04	<0.01	0.30
	woody cover	0.115	0.011				
8	Terrain ruggedness +	-0.076	0.033	26668.96	393.10	<0.01	0.27
	woody cover	0.121	0.011				
9	Woody cover	0.118	0.011	26671.96	396.10	<0.01	0.27
10	Impala density	0.091	0.024	26762.64	486.78	<0.01	0.31
11	Terrain ruggedness +	-0.045	0.034	26762.87	487.01	<0.01	0.32
	impala density	0.094	0.024				
12	Null	2.932	0.105	26774.85	498.99	<0.01	0.25
13	Terrain ruggedness	-0.033	0.034	26775.87	500.01	<0.01	0.25
Visit duration							
1	**Distance to den +**	**0.073**	**0.007**	**14628.43**	**0.00**	**>0.99**	**0.34**
	impala density +	**-0.002**	**0.022**				
	distance to den*impala density	**-0.021**	**0.006**				
2	Distance to den	0.072	0.007	14643.61	15.18	<0.01	0.34
3	Impala density +	-0.031	0.018	14693.34	64.91	<0.01	0.35
	woody cover	-0.056	0.009				
4	Woody cover	-0.059	0.008	14694.14	65.72	<0.01	0.36

5	Lion density +	0.462	0.394	14694.78	66.35	<0.01	0.36
	woody cover	-0.060	0.008				
6	Terrain ruggedness +	0.005	0.027	14696.12	67.69	<0.01	0.36
	woody cover	-0.059	0.008				
7	Impala density +	-0.039	0.006	14696.83	68.40	<0.01	0.31
	lion density +	-4.899	0.905				
	impala density*lion density	0.644	0.100				
8	Impala density	-0.058	0.018	14733.08	104.65	<0.01	0.31
9	Terrain ruggedness +	-0.007	0.027	14735.01	106.58	<0.01	0.31
	impala density	-0.057	0.018				
10	Null	1.524	0.099	14741.17	112.74	<0.01	0.32
11	Lion density	0.373	0.402	14742.32	113.89	<0.01	0.32
12	Terrain ruggedness	-0.014	0.027	14742.88	114.45	<0.01	0.32
13	Lion density +	0.366	0.402	14744.06	115.63	<0.01	0.32
	terrain ruggedness	-0.014	0.027				

Table 2. Coefficients from the 11 generalized linear mixed models describing the effects of impala density, lion density, woody cover, and terrain ruggedness on the re-visitation (negative binomial distribution) and visit duration (poisson distribution) of non-denning African wild dogs (n = 16,740 data points) between 2016 and 2018 in the Kruger National Park, South Africa. Wild dog pack ID (n = 19 packs) was set as a random variable for all models. Top models (i.e. those within 2 ΔAIC$_c$ of the top model) are highlighted in bold.

	Model	Estimate	Std Error	AICc	ΔAICc	Weight	R^2
Re-visitation							
1	**Lion density +**	**-1.584**	**0.125**	**127748.2**	**0.00**	**>0.99**	**0.48**
	impala density +	**0.106**	**0.011**				
	lion density*impala density	**-0.731**	**0.178**				
2	Lion density	-1.386	0.114	127870.1	121.90	<0.01	0.48
3	Lion density +	-1.398	0.114	127870.8	122.66	<0.01	0.48
	woody cover	-0.006	0.005				
4	Lion density +	-1.385	0.113	127872.0	123.78	<0.01	0.48
	terrain ruggedness	-0.006	0.018				
5	Impala density	0.073	0.007	127901.3	153.09	<0.01	0.47
6	Terrain ruggedness +	-0.008	0.019	127903.1	154.89	<0.01	0.47
	impala density	0.073	0.007				
7	Null	2.742	0.143	128011.4	263.16	<0.01	0.47
8	Terrain ruggedness	-0.011	0.019	128013.0	264.85	<0.01	0.47

9	Woody cover	<0.001	0.005	128013.4	265.16	<0.01	0.47
10	Impala density +	0.114	0.006	135629.5	7881.31	<0.01	0.01
	woody cover	-0.002	0.001				
11	Terrain ruggedness +	-0.016	0.007	136110.00	8361.82	<0.01	<0.01
	woody cover	-0.003	0.001				
Visit duration							
1	**Lion density +**	**0.597**	**0.081**	**66283.89**	**0.00**	**>0.99**	**0.28**
	impala density +	**-0.074**	**0.008**				
	lion density*impala density	**0.781**	**0.114**				
2	Impala density	-0.034	0.005	66356.99	73.10	<0.01	0.27
3	Terrain ruggedness +	0.002	0.014	66358.97	75.08	<0.01	0.27
	impala density	-0.034	0.005				
4	Lion density +	0.389	0.078	66359.88	75.99	<0.01	0.27
	woody cover	-0.017	0.004				
5	Lion density	0.427	0.078	66377.05	93.16	<0.01	0.27
6	Lion density +	0.427	0.078	66379.05	95.16	<0.01	0.27
	terrain ruggedness	<0.001	0.014				
7	Woody cover	-0.019	0.004	66382.32	98.43	<0.01	0.27

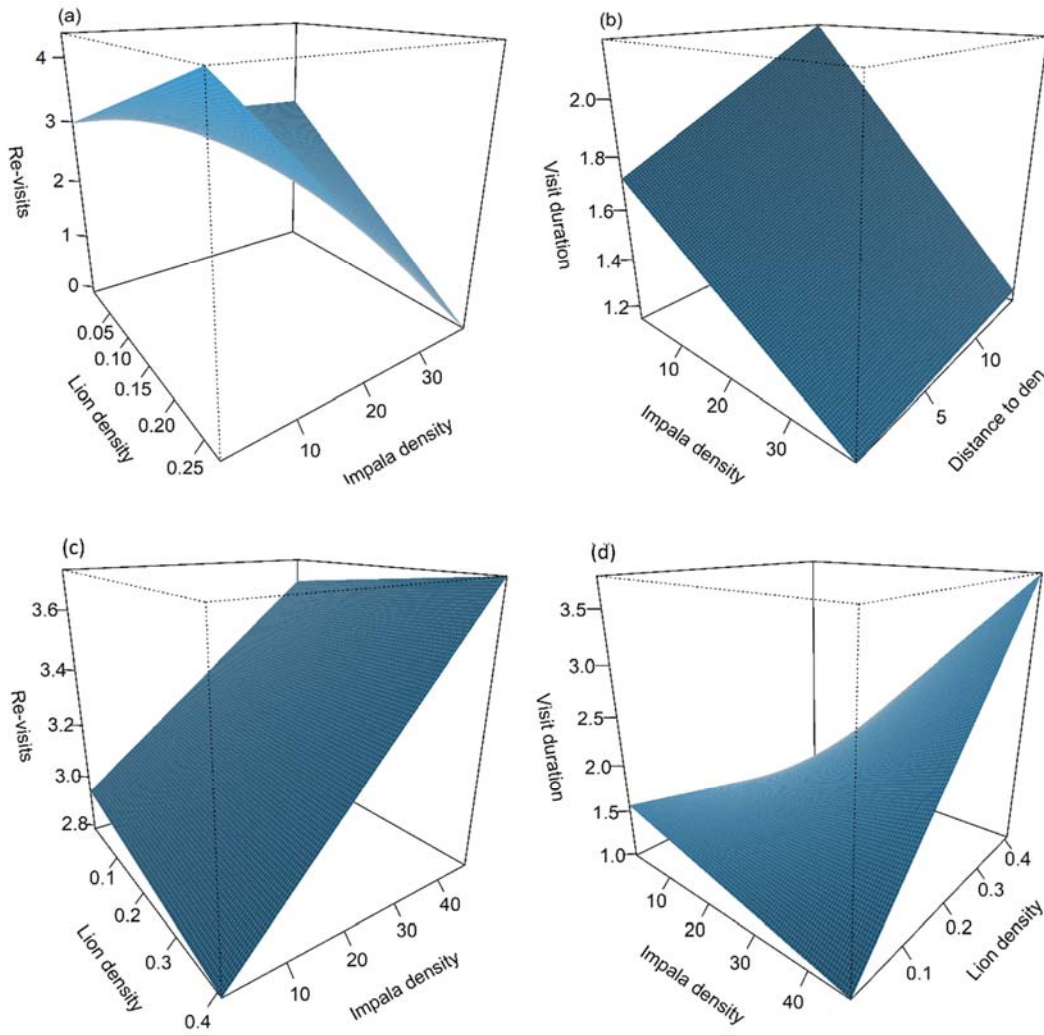|							
8	Terrain ruggedness +	<0.001	0.014	66384.32	100.43	<0.01	0.27
	woody cover	-0.019	0.004				
9	Null	1.494	0.065	66404.88	120.99	<0.01	0.27
10	Terrain ruggedness	0.002	0.014	66406.86	122.98	<0.01	0.27
11	Impala density +	-0.030	0.004	70356.90	4073.01	<0.01	<0.01
	woody cover	-0.001	0.001				

Figure 1. The effect of (a) lion density (lions/km2) and impala density (impalas/km2) on denning season re-visitation, (b) impala density (impalas/km2) and distance from the den site (km) on denning season visit duration, and the effect of impala density (impalas/km2) and lion density (lions/km2) on (c) non-denning re-visitation and (d) non-denning visit duration by 19 African wild dog packs in the Kruger National Park.
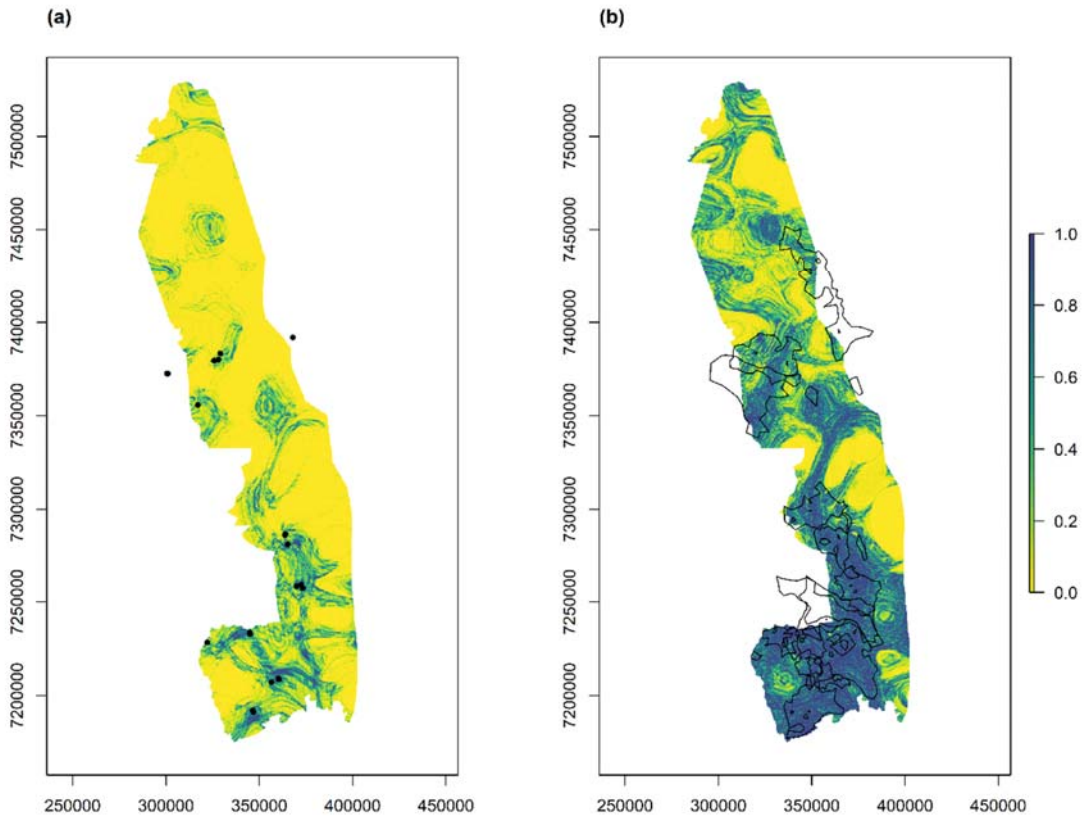
Figure 2. Spatial variation in habitat suitability for African wild dogs based on the most important variables identified in our model evaluation procedure (i.e., lion and impala density) during (a) the denning season (dots represent most recent [2018] den sites) and (b) the non-denning season (polygons represent 2017–2018 95% LoCoH wild dog territories) in the Kruger National Park.