BEHAVIORAL ECOLOGY – ORIGINAL RESEARCH

Spatial partitioning by a subordinate carnivore is mediated by conspecific overlap

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Abstract
There are several hypotheses that could explain territory size in mammals, including the resource dispersion hypothesis (RDH), the intruder pressure hypothesis (IPH), and the intraguild predation hypothesis (IGPH). In this study, we tested predictions of these three hypotheses regarding territories of 19 packs of endangered African wild dogs (*Lycaon pictus*) over 2 years in the Kruger National Park, South Africa. If territory size was supported by the RDH, then we would observe (1) wild dog territories would be larger when resource patches were more dispersed, (2) pack sizes would be larger when resource patches were rich, and (3) pack size would not affect territory size. If supported by the IPH, then we would observe (4) larger territories would experience less intrusions, and (5) there would be an increase in territory overlap in areas of low resource dispersion. Finally, if supported by the IGPH, we would observe (6) territories would be larger in areas of higher lion (*Panthera leo*) density, as evidence of a spatial avoidance strategy. We found that the IGPH was fully supported (6), the IPH half supported (5), and the RDH partially supported (1 and 3), where we found spatial partitioning of wild dogs with lions, potentially mediated by resources and territory overlap with conspecifics. Ultimately, our results show that subordinate carnivores must balance a trade-off between dominant interspecific competitors and conspecifics to successfully coexist in areas with dominant carnivores.

Keywords African wild dog · Intraguild predation · Intruder pressure · Resource richness · Resource dispersion · Territory overlap · Territory size

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Introduction

A territory can be defined as an area from which an individual or group actively excludes competitors from a specific resource(s) (Maher and Lott 1995). The resources from which to exclude competitors can be diverse, such as food, water, refugia, or nest sites. Several hypotheses have been put forward to explain the interaction of territories with these resources. The resource availability hypothesis suggests that species will utilise areas that simply maximise use of resources (Stamps and Buechner 1985). As such, it predicts that an increase in resource abundance will result in a decrease in territory size (Stamps and Buechner 1985; Hayward et al. 2009; Loveridge et al. 2009), because individuals can meet their needs in a much smaller area. The resource dispersion hypothesis (RDH) suggests that the territory size is dependent on the spatial dispersion of the resources within (Macdonald 1983). Specifically, it predicts larger territories when resource patches are more dispersed and increasing group size with the richness of those patches. Because the

RDH suggests that resources drive the formation of groups and territory size, it also suggests that group size has no effect on territory size. European badgers (*Meles meles*) fit the RDH, where territory size is positively correlated with resource (earthworms) patch dispersion and is unaffected by group size, and group size is positively correlated with resource patch richness (Kruuk and Parish 1982).

In contrast, the intruder pressure hypothesis (IPH) proposes that territory size is ultimately constrained by the energetic costs of defending a territory (Stamps 1990). It predicts a negative relationship between territory size and conspecific density (Stamps 1990) and, consequently, that larger territories then experience fewer intrusions due to their location in areas of lower conspecific density. It also predicts higher territory overlap in areas of high resource availability (as the cost of defence is not worth the effort). Coyotes (*Canis latrans*) fit the IPH, where territory size is determined by intruder pressure when resources are available and they are unable to defend large areas (Wilson and Shivik 2011). Considering the aforementioned hypotheses, one may expect a territory to be large enough as to maximise the effective utilisation of resources, but small enough to be defendable (Myers et al. 1979).

The relationships between carnivores and their resources are complex. This is especially true when carnivores are competing for the same shared resources, and a dominant carnivore can kill the subordinate [i.e. intraguild predation; Polis and Myers (1989)]. The intraguild predation hypothesis (IGPH) predicts that a subordinate carnivore will be forced to utilise areas with lower or poorer resources [i.e. spatial partitioning; Vanak et al. (2013)]. However, dominant and subordinate carnivore species can coexist if there are behavioural adjustments, such as subordinates having larger territories in areas of high dominant density to facilitate spatial avoidance (St-Pierre et al. 2006), temporal avoidance of the dominant carnivore [i.e. temporal partitioning; Hayward and Slotow (2009)], or alternative prey use by the subordinate [i.e. resource partitioning; Balme et al. (2017)]. Considering this behavioural plasticity, we can predict that in areas where both dominant and subordinate carnivores coexist, subordinate territories may be unaffected by dominant predator density if they avoid the dominant carnivore on a spatial or temporal scale or utilise different resources. Subordinate kit foxes (*Vulpes macrotis*) fit the IGPH, where they coexist with dominant coyotes, by avoiding vegetation types that the dominant coyotes favour (Lonsinger et al. 2017). Consequently, subordinate carnivores must balance the risk of dominant carnivores with the benefit of quality food resource intake.

African wild dogs (*Lycaon pictus*) are a subordinate carnivore relative to lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*) (Creel and Creel 1996; Dröge et al. 2017). They are group living, with packs [sizes ranging from two to 30; Frame et al. (1979)] defending a territory (Parker 2010). Larger packs are generally more successful at hunting, raising pups, and avoiding threats from other predators (Courchamp and Macdonald 2001; Buettner et al. 2007; Rasmussen et al. 2008; Marneweck et al. 2019). Lions, the dominant carnivore in African terrestrial systems, contribute significantly to wild dog mortality (Creel and Creel 1996), and wild dogs have been shown to actively avoid lions (Darnell et al. 2014; Swanson et al. 2014; Dröge et al. 2017), or avoid areas of high prey density that may be favoured by lions (Mills and Gorman 1997). Such findings suggest spatial separation as per the IGPH. However, it is unclear how wild dogs adjust their behaviour regarding territory size in relation to the RDH, IPH, and IGPH.

Although wild dog pack size has been reported to have no effect on annual territory size (Mills and Gorman 1997; Creel and Creel 2002), which aligns with the RDH, it has been suggested that wild dogs fit the RDH poorly as their avoidance of lions consequently means avoidance of quality prey resources (Mills and Gorman 1997). Also, the general difference in preferred prey species and weight ranges of lions and wild dogs (Hayward and Kerley 2005; Hayward et al. 2006) suggests that this resource partitioning may structure spatial avoidance. However, although Mills and Gorman (1997) found a negative relationship between territory size and prey biomass, this has not been definitively tested in conjunction with the other predictions of the RDH. Wild dog territories naturally, and sometimes extensively, overlap (Creel and Creel 2002), especially when neighbours are related (Jackson et al. 2017). Also, larger packs tend to outcompete smaller packs when it comes to inter-pack disputes (Creel and Creel 1995). Yet, the effect of intruder pressure remains untested when it comes to wild dog territories. Using GPS collar data from resident wild dog packs in the Kruger National Park, South Africa, we aimed to investigate with which of these three competing hypotheses, and their associated predictions, wild dog territory size and overlap fit.

As well as an area from which to actively exclude competitors, a territory can also be defined as an area of exclusive use (Maher and Lott 1995). Wild dog territories are often described at both the outer 95% and the core 50% level, where territory overlap is often observed at the 95% (and thus not exclusive) but infrequently at the 50% (Creel and Creel 2002). Hence, should a wild dog territory be defined at its 95% or 50% level? We expected that the outer and the core may be affected differently. As an increase in resource dispersion leads to increased foraging distances (Kowalczyk et al. 2006; Valeix et al. 2012), we would expect the RDH to affect the overall territory size (i.e. 95%). Wild dog packs do not patrol their territory boundary, rather they scent mark throughout so that intruders encounter an increasing number of scent marks as they infiltrate a territory (Parker 2010).

Wild dog territories also often overlap at the 95% and, as such, we would not expect intruder pressure to affect the 95% territory isopleth. When there is intraguild competition, safe areas of refugia become patchy. To coexist with dominant carnivores, subordinate carnivores can increase their territory size to encompass more of these patchy refugia (Yunger 2004; St-Pierre et al. 2006). Thus, we would expect the IGPH to affect overall territory size (i.e. 95%). Wild dog dens are located in the core of their territory, in rugged areas of low prey and low lion density to further avoid detection (van der Meer et al. 2013; Jackson et al. 2014; Mbizah et al. 2014; Davies et al. 2016). Thus, if the core represents an area of refugia for wild dogs, we would expect that prey and lion density would be low and thus have no significant effect on the 50% territory. As defence of the 50% appears to be more important than at the 95% (Parker 2010) and overlap at the 50% occurs only if the packs are related (Jackson et al. 2017), we would expect that the IPH would affect the 50% territory.

If territory size was supported by the RDH, then we would expect that (1) wild dog 95% territories would be larger when resource patches were more dispersed, (2) pack sizes would be larger when resource patches were richer, and (3) pack size would not affect territory size. If supported by the IPH, then we would expect that (4) larger 95% territories would experience less intrusions, and (5) there would be an increase in 95% territory overlap in areas of low resource dispersion. Finally, if supported by the IGPH, we would expect that (6) 95% territories would be larger in areas of higher lion density. Consequently, we predict that wild dogs would fit with some predictions of the RDH (1 and 3), some predictions of the IPH (5), and the prediction of the IGPH (6).

Materials and methods

We conducted this study in the 19,142 km^2 Kruger National Park (KNP), South Africa, using data collected from GPS satellite collared packs ($n = 19$), collared 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) under the SANParks Animal Use and Care Reference 013/16). All applicable institutional and national guidelines for the care and use of animals were followed. The collars used comprised a range of makes and models, each weighing a maximum of 550 g [i.e. < 5% wild dog body weight of ~25 kg (Gorman et al. 1998; Gannon and Sikes 2007)]. Where possible, we collared males over females to avoid any potential negative effect of stress on reproductive output (Supplementary Table S1). To calculate wild dog territory sizes, we used GPS points (acquired every 4–8 h; Table 1)

from the date the pack left the den (usually around September each year), to the date that they began denning the subsequent season (usually around April each year), giving an ecological year. We calculated the territory sizes of 16 packs for the 2016–2017 ecological year, and 13 packs for the 2017–2018 ecological year (Table 1). Using the *adehabitatHR* package (Calenge 2006) in R Version 3.5.3 (R Core Team 2019), we estimated the area of the 95% and 50% territory per pack per year using the k-LoCoH method (Getz et al. 2007), where $k = \sqrt{n}$, and $n =$ the number of data points per pack per year. We defined a pack as at least one adult male and one adult female (Creel and Creel 2002). We defined pack size as the number of adults and yearlings at the start of the ecological year (i.e. after the pack leaves a den), excluding pups as they do not contribute to hunting, territory maintenance, or defence (Frame et al. 1979). Pack size was obtained from Wild Dog Advisory Group reserve reports detailed in meeting minutes (WAG-SA 1998–2019).

We extracted data on impalas [*Aepyceros melampus;* the dominant prey species for wild dogs in the KNP comprising 81% of the diet biomass; Mills and Gorman (1997)] from distance sampling via aerial transect counts that were conducted in July (coinciding with the end of the wild dog denning season) of both 2016 and 2017 by SANParks (SANParks 2016, 2017). As the best fit, we fitted a half-normal detection function with cosine adjustment through the *Distance* (Miller 2017) package in R to these data. Detection-adjusted data were converted through a generalised additive model with restricted maximum likelihood smoothing into a density surface (impala km^{-2}; Supplementary Fig. S1), using the *dsm* package (Miller et al. 2019). For the ecological year 2016–2017, we used counts from the 2016 survey. Similarly, for the 2017–2018 ecological year, we used counts from the 2017 survey. We defined a resource patch as a herd (> 1 individual) of impalas, and created a kernel-smoothed surface based on the distance between two neighbouring herds along a transect (i.e. resource patch dispersion) with a ten kilometre bandwidth (approximately three inter-transect widths), using the *smooth.ppp* function of the *spatstat* package (Baddeley et al. 2015). We then extracted the mean herd dispersion for each territory polygon. For herd biomass (i.e. resource patch richness), we calculated biomass per herd along a transect as average adult female body weight × the number of individuals × 0.75, using an average female weight of 45 kg for impalas as per Owen-Smith (1988). Using the same workflow as described above, we created a detection-adjusted density surface model of biomass (kg km^{-2}; Supplementary Fig. S2) and extracted the mean biomass for each territory polygon. The associated private nature reserves (APNR) adjoining (and open to) the KNP were assumed to have similar densities of impalas. Peel (2015) reports a density of 17 impalas/km^2 in the APNR, similar to the adjoining areas of the KNP [10–19 impalas/

Table 1 Wild dog territory sizes and overlap in the Kruger National Park across the study period

Pack ID	No fixes (mean fixes/day)	Pack size	Outer 95% Size (km^2)	% Overlap	Core 50% Size (km^2)	% Overlap
2016–2017						
Afsaal	781 (3)	12	500	41	83	0
Berg-en-Dal	656 (4)	11	154	45	13	0
Croc Bridge	398 (4)	8	183	10	42	1
Hamiltons	831 (4)	9	481	41	85	8
Imbali	442 (4)	6	435	33	62	0
Kwaggaspan	545 (4)	6	565	38	117	0
Leeupan	578 (5)	9	186	45	41	16
Letaba	471 (4)	11	477	9	79	0
Matekenyane	844 (5)	3	222	74	41	19
Numbi	1110 (4)	4	272	35	45	17
Orpen	909 (5)	8	767	23	128	0
Phabeni	1380 (5)	8	296	83	41	24
Phalaborwa	276 (3)	7	432	10	73	0
Pretoriuskop	652 (4)	4	475	12	87	0
Toulon	520 (5)	13	572	67	76	44
Toulon split	598 (4)	6	263	90	40	78
Mean ± SE	687 + 70	8 ± 1	393 ± 43	41 ± 6	66 ± 8	13 ± 5
2017–2018						
Afsaal	1108 (5)	10	494	2	83	0
Delaporte	1074 (5)	7	905	32	191	9
Hamiltons	560 (4)	9	401	28	85	0
Kwaggaspan	1168 (5)	11	192	54	117	0
Leeupan	1060 (5)	16	354	26	41	0
Matekenyane	1017 (4)	3	675	82	41	34
Nandzana	1360 (4)	12	634	22	106	1
Northern	1109 (4)	9	781	0	91	0
Numbi	371 (4)	2	272	24	45	14
Orpen	1360 (5)	30	491	17	128	0
Phabeni	1118 (5)	8	387	69	41	44
Phalaborwa	665 (3)	14	942	15	73	2
Toulon split	1212 (4)	13	740	66	40	36
Mean ± SE	1014 + 83	11 ± 2	559 ± 67	34 ± 7	83 ± 13	11 ± 5

km^2 (SANParks 2017; Marneweck et al. this study)]. As such, we assumed similar impala densities for sections of territories extending beyond the KNP boundary to avoid introduction of bias by truncating data. Further, as impala are water dependant, they are generally sedentary and do not often move long distances [average home range size 1.7 km^2; Dunham (1979)], so we are confident that our herd distance metrics are an appropriate estimate for the year following the survey.

We defined an intrusion as a pack being located within the 95% or 50% territory of another at least once, and converted this to a rate of the number of intrusions per day (i.e. if a pack was located in another territory four times in one day it would be one intrusion). We did this using the *over* function in the *sp* package (Bivand et al. 2013). We

determined territory overlap (Supplementary Fig. S3) using the *gIntersection* function of the *rgeos* package (Bivand and Rundel 2018), by calculating the focal territory area minus the area exclusive.

To estimate lion density across the KNP, we used data from the SANParks 2015 lion survey (SANParks 2015) and following Ferreira and Funston (2010), we estimated the number of lions in the Thiessen polygon around each calling station, based on the pride structure. With these estimates, we created a smooth kernel density surface (lions km^{-2}; Supplementary Fig. S4) 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 fairly static from 1975 to 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. The APNR has similar densities of lions to the adjoining areas of the KNP (Dyer 2012). As such, we assumed similar lion densities for sections of territories extending beyond the KNP boundary and we did not truncate data to the border of the KNP.

From 2014 to 2016, the KNP experienced a severe but heterogenous drought, where the diets and distributions of herbivores were affected (Abraham et al. 2019). Our study incorporates data from the end of this drought (i.e. September 2016). To ascertain if the drought had an impact on the impala metrics we used in this study, we tested impala herd dispersion and impala herd biomass within the 95% territories against each of the ecological years. To do this, we ran two generalised linear mixed effects models with a quasi-poisson distribution. We found no significant difference between the years regarding impala herd dispersion ($t = -0.90$, $p = 0.39$, Supplementary Table S2) or impala herd biomass ($t = 1.74$, $p = 0.12$, Supplementary Table S2). Although the drought may have affected the distribution and density of herbivores, we found no such impact on the density or distribution of impalas within our study range (i.e. wild dog territories) or time period (mid 2016–mid 2018). This is further supported by the Abraham et al. (2019) study that found impalas in the KNP did not move in response to the drought, but rather changed their diet to incorporate more browse compared to grass.

To investigate which of the three hypotheses best explained territory size, pack size, and territory overlap, we ran five generalised linear mixed effects models with a Poisson distribution using the *lme4* package (Bates et al. 2015). For our first model, we set 95% territory size as the response plus impala herd dispersion (RDH), pack size (RDH), intrusion rate (IPH), and lion density (IGPH) as explanatory variables. We repeated this for 50% territory size (second model). For our third model, we set pack size as the response plus impala herd biomass (RDH) at the 95% and the 50% territory as explanatory variables. For our fourth model, we set 95% territory overlap as the response plus impala herd dispersion (IPH) as an explanatory variable. We repeated this for 50% territory overlap (fifth model). For all models, we set the pack ID nested within ecological year as a random factor to account for multiple sampling of the same pack in consecutive years. We conducted all analyses and created all figures in RStudio for Windows (R Core Team 2019).

Results

Territory size

The 95% territory size was affected by impala herd dispersion ($z = 4.14$, $p < 0.01$, Fig. 1a), intrusion rate ($z = 4.00$, $p < 0.01$, Fig. 1b), and lion density ($z = 2.51$, $p = 0.01$, Fig. 1c). All factors had a positive effect on territory size, where increasing impala herd dispersion, increasing intrusion rate, and increasing lion density resulted in larger territories. Pack size did not affect the 95% territory size ($z = -0.05$, $p = 0.96$). None of the explanatory variables affected the 50% territory size (impala herd dispersion $z = 0.29$, $p = 0.77$; pack size $z = 1.32$, $p = 0.19$; intrusion rate $z = 0.21$, $p = 0.83$; lion density $z = 0.87$, $p = 0.38$).

Pack size

Pack size was unaffected by resource patch richness (i.e. impala herd biomass) at either the 95% ($z = -0.87$, $p = 0.38$) or 50% level ($z = 0.41$, $p = 0.69$).
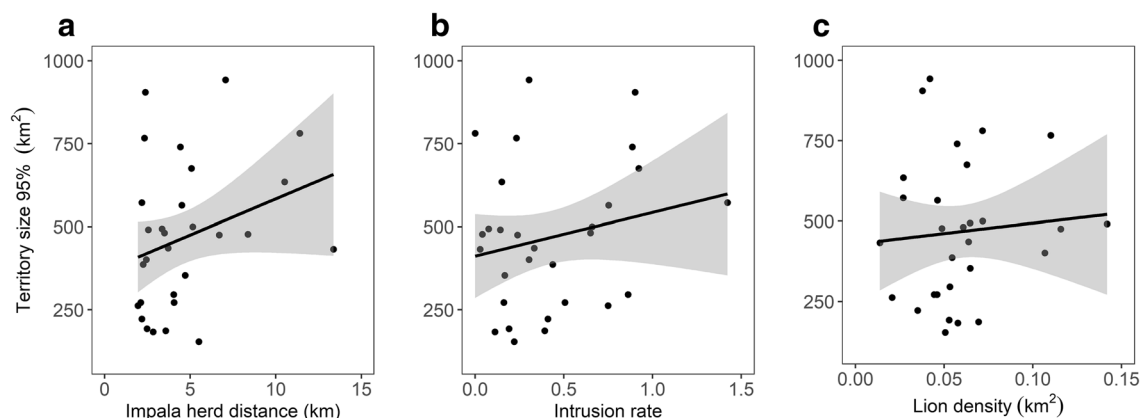
Fig. 1 The effect of **a** impala herd dispersion, **b** intrusion rate, and **c** lion density on wild dog 95% territory size. Shaded regions represent the 95% confidence intervals

Territory overlap

Impala herd dispersion affected the amount of territory overlap at both the 95% ($z = -3.43$, $p < 0.01$, Fig. 2a) and the 50% level ($z = -2.25$, $p = 0.02$; Fig. 2b), where decreasing herd dispersion (i.e. greater availability) caused an increase in overlap at both territory levels.

Discussion

Territory size

As predicted, wild dog territory size was explained by impala herd dispersion (RDH; 1) and lion density (IGPH), and unaffected by pack size (RDH; 3). Contrary to our prediction, intrusion rate also affected territory size (IPH; 4). As predicted by the RDH, we found larger territories where prey was more dispersed, and pack size did not affect territory size. The RDH predicts that increased dispersion will lead to increased foraging distances required and thus larger territories (Kowalczyk et al. 2006). Our finding of increased impala herd dispersion leading to larger territories is in contrast to previous findings concluding that prey availability does not affect wild dog territory size (Creel and Creel 2002). We suggest that this discrepancy may be due to the high prey encounter rates in that study [3.75–16.40 prey individuals encountered per km travelled; Creel and Creel (2002)], which could be a proxy for high prey availability and thus low dispersion all together. However, this is difficult to compare as no studies use a metric of herd dispersion for wild dogs. Nevertheless, resource dispersion has been investigated in lions, where lion territory size increased as resource patches were more dispersed (Valeix et al. 2012). Similarly, wolf (*Canis lupus*) territories were larger where the probability of moose (*Alces alces*) occupancy was lower (Kittle et al. 2015).

If following the RDH, territory size is affected by resources and thus no relationship between territory size

and group size. Our findings support this and are in line with previous studies that have found that wild dog pack size does not affect territory size (Mills and Gorman 1997; Creel and Creel 2002), and a similar finding for lions (Spong 2002). It is suggested that territory size in wild dogs is related to habitat and subsequent prey encounter rates within those habitat types (Creel and Creel 2002), which we support with higher dispersion of impala herds resulting in larger territories.

If following the IPH, territories will be smaller in areas of high conspecific density due to the costs of territory defence (Stamps 1990) and, thus, smaller territories will receive fewer intrusions. Our results do not support this, where intrusion rate increased with territory size in wild dogs. Woodroffe (2011) found that although wild dog densities tripled over a nine-year study period, territory sizes remained the same, but territory overlap increased. Wild dogs often settle in areas with close relatives present (Girman et al. 1997), and there is a strong positive effect of relatedness on territory overlap (Jackson et al. 2017). Therefore, territory overlap in wild dogs can be extensive, but offset by temporal avoidance (Creel and Creel 2002), and direct encounters between packs in the KNP are uncommon as neighbours rarely use an overlapping area simultaneously (Mills and Gorman 1997). Although Girman et al. (1997) found relatedness between neighbouring packs in the KNP, our study represents wild dogs from 4 to 5 generations later, where likely much change in the population has occurred (Wilkinson 1995; Davies 2000; Kemp and Mills 2005; Marnewick and Davies-Mostert 2012; Marnewick et al. 2014). A recent genetic study of wild dogs across South Africa showed that overall relatedness in the KNP was low ($r = 0.06$; typical of fourth-order relatives), and the same as the metapopulation of smaller, fenced reserves (Tensen et al. 2019). As Tensen et al. (2019) utilised genetic samples collected from the same wild dogs as those used in our study, we are confident that the KNP wild dogs have low relatedness. This is further supported by the fact that between-pack relatedness of the metapopulation was 0.04 (Tensen et al. 2019). Considering that the overall relatedness was the same

Fig. 2 The effect of impala herd dispersion on wild dogs **a** 95% and **b** 50% territory size. Shaded regions represent the 95% confidence intervals
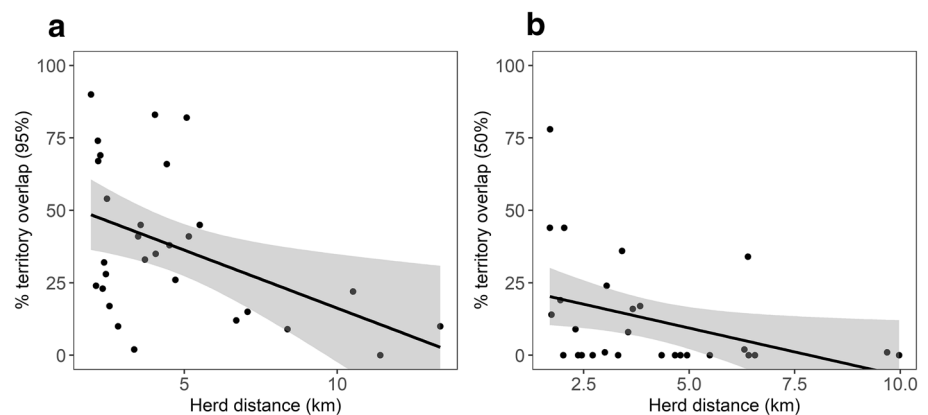
between the metapopulation and the KNP ($r = 0.06$), we can infer that it is likely that the between-pack relatedness would also be similar to the metapopulation ($r = 0.04$), highlighting low relatedness. Consequently, our data support high degrees of territory overlap in this species, but not facilitated by relatedness. We suggest that the large overlap of wild dog territories negates this aspect of the IPH.

As predicted, none of our variables explained the size of the 50% territory. If we use den sites as a proxy for core territory characteristics, average prey biomass and lion density are low (van der Meer et al. 2013; Jackson et al. 2014; Mbizah et al. 2014). If the low density is consistent, then we would expect no effect on territory size but rather location.

In line with the IGPH, we found larger territories in areas of higher lion density. There is high competition between lions and wild dogs, where lions outcompete wild dogs (Creel and Creel 1998; Darnell et al. 2014; Swanson et al. 2014; Dröge et al. 2017), and account for significant wild dog mortality both within the KNP (van Heerden et al. 1995) and elsewhere (Woodroffe et al. 2007; Groom et al. 2017). Wild dogs in the KNP adjust territory size to facilitate avoidance of a high likelihood of interactions with lions (i.e. high lion density). We did not observe any wild dog territories on the eastern boundary, an area of high prey availability also coinciding with the highest lion density, further suggesting strong spatial avoidance. The eastern boundary of the KNP supports very high prey biomass [2749 kg 100 km^{-2}; comprising buffalo (*Syncerus caffer*), giraffe (*Giraffa giraffa)*, impala (*Aepyceros melampus*), zebra (*Equus quagga*), warthog (*Phacochoerus africanus*), wildebeest (*Connochaetes taurinus*), kudu (*Strepsiceros strepsiceros*), and waterbuck (*Kobus ellipsiprymnus*); Ferreira and Funston (2010)], which suggests a high density of lion preferred prey. Lions prefer larger prey species, ranging from 190 to 550 kg (Hayward and Kerley 2005). The megaherbivores [i.e. herbivores weighing > 1000 kg; Owen-Smith (1988)] and generally high numbers of medium–large prey (i.e. 190–550 kg) available to lions in this area of the KNP may lead to natural resource partitioning with wild dogs who prefer prey species ranging from 16 to 32 kg and 120 to 140 kg (Hayward et al. 2006). This conforms to the earlier suggestion by Mills and Gorman (1997) that wild dogs avoid lions via avoidance of vegetation types with high prey densities (i.e. spatial niche partitioning). Although there is also low lion density in the northern region of the KNP, we did observe any resident packs in that region. It is possible that we were unaware of resident packs, but due to intensive monitoring, citizen science reports, and surveys (Marnewick et al. 2014), we do not believe that this is a likely scenario. We suggest rather that the historical decline of wild dogs in that region (Wilkinson 1995; Davies 2000; Marnewick and Davies-Mostert 2012), and subsequent lack of recovery, has led to a vacuum effect (Mihoub et al. 2011), preventing the colonisation of this

empty patch that appears to be ideal for wild dogs with low inter and intraspecific competitors.

Hayward and Slotow (2009) provide evidence for temporal partitioning of activity periods among Africa's large predator guild, where wild dog activity peaks differ from those of lions. Our results suggest spatial avoidance, but we do not have data on simultaneous temporal lion or wild dog activity so temporal avoidance should be an avenue for future research. We propose that wild dogs fit with the IGPH via spatial partitioning potentially facilitated by resource partitioning more than temporal niche partitioning (Cozzi et al. 2012). If this is correct, any change in ecological conditions leading to a reduction or redistribution of the KNP megaherbivore guild and subsequent change in the density and/or distribution of lions would require wild dogs to alter their spatial strategy and coexist with lions via temporal partitioning. For example, in India, dholes (*Cuon alpinus*), leopards (*Panthera pardus*), and tigers (*Panthera tigris*) adapt their mechanisms of coexistence across a gradient of resource availability (Karanth et al. 2017). Specifically, temporal and spatial overlap was higher when prey densities were lower, and less spatial overlap occurred when prey densities were higher (Karanth et al. 2017). Furthermore, behavioural plasticity has been demonstrated in wild dogs where, in areas of high human density, packs offset the risk of human encounter with activity during the night (Rasmussen et al. 2012).

Pack size

As predicted, patch richness did not affect pack size (RDH; 2). If following the RDH, an increase in patch richness (prey biomass in our study) would lead to an increase in group size, because more resources lead to higher rates of reproduction and recruitment (Macdonald 1983; Valeix et al. 2012). However, we found no such effect in wild dogs. Larger packs can have increased hunting success and are better able to defend kills from kleptoparasites (Creel and Creel 1995; Carbone et al. 2005). Further, packs prioritise pups and alphas at kills (Malcolm and Marten 1982; Forssman et al. 2018). Thus, one would expect an increase in food to lead to an increase in reproduction and recruitment. However, an increase in food intake does not necessarily equate to successful recruitment in wild dogs, which are constrained by several other factors, for example, the cost of territorial defence, finding appropriate den sites, raising pups, and having access to spatial refugia (Creel and Creel 1995).

Territory overlap

As predicted, prey availability affected territory overlap at the 95% level (IPH; 5). Unexpectedly, it also explained

territory overlap at the 50% level. Resource availability has been shown to affect territory overlap for other similarly cooperatively breeding canids. For example, areas of Ethiopian wolf (*Canis simensis*) territory overlap had significantly more predictable and higher biomass than exclusive areas (Tallents et al. 2012). It may be that packs in areas of high resource availability are more tolerant of overlap, over and above normal degrees of overlap observed among wild dog packs, as there is less net competition to food availability. The mean 95% territory overlap in this study was 38%, similar to the 30–35% reported in the KNP (Reich 1981), and 35% in northern Botswana (Jordan et al. 2017), but higher than most other reports [22% Selous (Creel and Creel 2002); 22% northern Botswana (Parker 2010); 22% Kenya (Woodroffe 2011); 20% related neighbours and 7% unrelated neighbours, southern Africa (Jackson et al. 2017); and 13% Hluhluwe–iMfolozi Park (Marneweck 2018)]. Further, the mean 50% territory overlap in our study was 12%, considerably higher than the 0.5% reported in the Selous (Creel and Creel 2002), 3% in Hluhluwe–iMfolozi Park (Marneweck 2018), and 1–6% in northern Botswana (Parker 2010). Wild dogs defend territories with scent marks but, instead of marking at territory boundaries, they mark throughout their territories and intruders encounter an increasing number of scent marks as they infiltrate a territory (Parker 2010). It is thus expected that overlap of the 50% core territory would have a greater impact on pack-specific processes than that of the 95% (Creel and Creel 2002). It may be that packs are simply unable to monopolise these quality areas as the cost of defence (traversing territory) may outweigh the benefit of more energy intake, even at the 50% level. Conversely, this high degree of intraspecific tolerance (high inter-pack overlap) may be a strategy to avoid areas of high lion density; wild dogs rather tolerate conspecifics than lions because the ultimate cost of any potential interactions may be lower with other wild dogs than it is with lions. This is supported by wild dogs in the KNP that have low overall relatedness (Tensen et al. 2019), so the overlap cannot be fully explained by tolerance of kin. It is possible that the different methodologies used to calculate the territories and overlap in the studies to which we refer are the reasons for such discrepancies in overlap reported. However, as the method we used (LoCoH) is likely the most conservative method for estimating territory size (Scull et al. 2012; Bryant et al. 2017), we are confident that our result of high territory overlap is an accurate reflection of wild dog territories in the KNP.

In conclusion, our results suggest that wild dogs fit best with the IGPH (1/1), fit partially with the RDH (2/3) and less so with the IPH (1/2). Essentially, wild dogs avoid areas of high lion density in the KNP via spatial partitioning potentially mediated through resource partitioning and conspecific overlap. Consequently, as wild dogs are constrained by human pressure outside of the KNP and APNR to the

west and south, and restricted by prey availability within the KNP and APNR, wild dog territories overlap considerably with conspecifics with the highest overlap recorded for the species in Africa. The general good prey availability for wild dogs in the KNP and APNR (especially southern KNP) facilitates this overlap, where higher prey availability leads to higher degrees of territory overlap. Ultimately, our results highlight the trade-offs that subordinate carnivores face to successfully persist in areas with dominant carnivores; subordinate carnivores avoid the dominant and tolerate conspecifics as the lesser of two evils.

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