

African wild dog movement ecology in a small protected area in South Africa

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Dramatic population declines of African wild dogs (*Lycaon pictus*) led to a managed metapopulation approach for wild dog conservation in South Africa. Monitoring the survival and habitat use of packs reintroduced into protected areas (PAs) is an essential part of adaptive management and improving the health and, ultimately, the survival of the metapopulation. Our study describes the territoriality and habitat selection of a pack of wild dogs reintroduced into Manyoni Private Game Reserve (219 km²) in northern KwaZulu-Natal, South Africa. Despite being introduced into a small PA, the pack only utilized half their available space (121 km²) and avoided the central areas of the reserve. *Post hoc* analysis of African lion (*Panthera leo*) localities suggested competitive avoidance was a strong factor in shaping the habitat usage of the pack; however, further research is required. Habitat selection also varied seasonally and with denning. Ultimately, we showed that spatio-temporal analyses can help identify high-risk areas within wild dog territories, such as hotspots of activity along fencelines. These analyses can then be used to increase targeted management of these areas, such as improving the maintenance of well-used fencelines, which is an important consideration for the sustained success of the metapopulation across small PAs.

Keywords: African wild dogs, metapopulation, territory, T-LoCoH, habitat selection, competitive avoidance.

INTRODUCTION

Many factors dictate how carnivores use their available space, including resource availability (Reich, 1981), climate (Rabaiotti & Woodroffe, 2019; Woodroffe, Groom & McNutt, 2017), landscape features (O’Neill, Durant & Woodroffe, 2020), population density (Woodroffe & Sillero-Zubiri, 2012), inter- and intra-specific interactions (Davies *et al.*, 2021; Creel *et al.*, 2019; Marneweck, Marneweck *et al.*, 2019), life history characteristics (Marneweck, Becker *et al.*, 2019; Marneweck, Druce & Somers, 2019) and the life stage of the individual (Schradin *et al.*, 2010). Understanding the drivers of movement patterns is important for the conservation of any species, but especially for

endangered species with large territories, such as African wild dogs (*Lycaon pictus*) hereafter referred to as wild dogs. The wide-ranging behaviour of wild dogs is thought to be a critical determinant of their endangered status (Mottram, Mann, Snyman & O’Riain, 2019; Woodroffe & Sillero-Zubiri, 2012).

The greatest source of mortality for wild dogs is direct persecution for livestock depredation (Davies-Mostert, Mills & Macdonald, 2009) mostly outside of protected areas (PAs). However, population decline has also been attributed to increased habitat fragmentation, decreased prey availability and infectious disease (Barbault & Sastrapradja, 1995; Mills & Gorman, 1997; Potgieter, Whittington-Jones, Gusset, Mills & Davies-Mostert, 2012), with global climate change threatening future population resilience (Rabaiotti & Woodroffe, 2019). In South Africa, prior to 1997, the only naturally occurring, viable population of wild dogs resided within the Kruger National Park (KNP).

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With human–wildlife conflict, and possible disease outbreaks, posing a threat to the entire country's population, the South African Wild Dog Metapopulation (SAWDM) was established to increase wild dog numbers and broaden their distribution (Mills *et al.*, 1998). This conservation initiative involves reintroducing wild dog packs into several small (<1000 km²), geographically isolated conservation areas, between which natural gene flow is mimicked through translocation.

Although wild dogs do not defend their territories as fiercely as African lions, *Panthera leo*, (Mosser & Packer, 2009) or wolves, *Canis lupus*, (Schläge, Merrill & Lewis, 2017), they do actively scent-mark (Jordan, Golabek, Apps & McNutt, 2013; Parker, 2010), have defined areas they utilize and generally have exclusive core areas (Mills & Gorman, 1997; Reich, 1981), which are all hallmarks of a territory (Burt, 1943).

The study of territorial characteristics of reintroduced packs, and how this varies temporally and with the distribution of competitors, is important for informed reintroduction planning and management, as their movement and use of available space and resources directly affects their reintroduction success within the SAWDM programme (Gusset, Stewart, Bowler & Pullin, 2010; Potgieter, O'Riain & Davies-Mostert, 2015). Wild dogs have the highest energetic costs of gestation among all group-living carnivores (Creel, Creel, Mills & Monfort, 1997). As such, pack movement can be greatly restricted around the den during this time (Pomilia, McNutt & Jordan, 2015). Understanding habitat selection, ranging and activity patterns of reintroduced packs over time, and with changing life stages, will further help in our understanding of key demographic events, *e.g.* breakouts from fenced PAs and population fluctuations within isolated reserves (Lindsey, Alexander, Du Toit & Mills, 2005). This in turn can inform management actions such as expanding the current metapopulation network or limiting introductions into reserves that cannot sustain additional packs including those with larger predators that wild dogs choose to avoid (Marneweck *et al.*, 2021).

The goal of our study was to determine the territory characteristics and habitat use of a single pack of wild dogs reintroduced into Manyoni Private Game Reserve (219 km²). Given the presence of competing species, we predicted that the pack would actively avoid areas intensively used by lions, such as open savanna vegetation (Cozzi *et al.*, 2012; Creel & Creel, 2002; Darnell,

Graf, Somers, Slotow & Gunther, 2014; Davies *et al.*, 2021; Marneweck *et al.*, 2019; Vanak *et al.*, 2013). As such, we predicted that the pack would utilize landscape features (such as denser vegetation and more rugged terrain) to help them avoid lions which favour open and less rugged terrain (Davies *et al.*, 2021; Mills & Gorman, 1997). This closed vegetation would be especially important during the denning period when concealment is important, and thus we predicted that use of dense vegetation would increase during the denning period.

Although, in isolation, our study lacks an adequate sample size for making broader inferences concerning the spatial ecology of this species, when combined with similar studies in other reserves, the collective data can be used to improve our understanding of how wild dogs use space within small PAs that form part of the metapopulation. Within Manyoni itself, this information can help identify hotspots of activity and potential sources of conflict with other predators or PA edges allowing for adaptive management and improved success in reintroductions.

METHODS

Study site

This study was conducted in Manyoni Private Game Reserve (previously known as Zululand Rhino Reserve), which lies within the Msunduzi valley in northern Zululand, KwaZulu-Natal, South Africa (Fig. 1). Located in a summer rainfall region, the area has an average temperature of 21.8 C and average annual rainfall of 592 mm. The PA comprises Mkhuze Valley low-veld vegetation, varying from open savanna thorn-veld and bush-veld to riverine woodland, characterized primarily by *Vachelia*, *Combretum* sp. and Marula (*Sclerocayra birrea*) woodland (Acocks, 1975).

This 219 km² PA was established in 2004 when 17 adjacent landowners removed over 200 km of fences to construct a single large PA. Various species have been reintroduced and monitored since the reserve's formation, including black rhinoceroses (*Diceros bicornis*) in 2004, cheetahs (*Acinonyx jubatus*) in 2009, lions in 2011 and wild dogs in 2014.

Data collection

A pack of six wild dogs (Table 1) was monitored in Manyoni since their reintroduction in August 2014. Upon arrival, the pack was held in a temporary

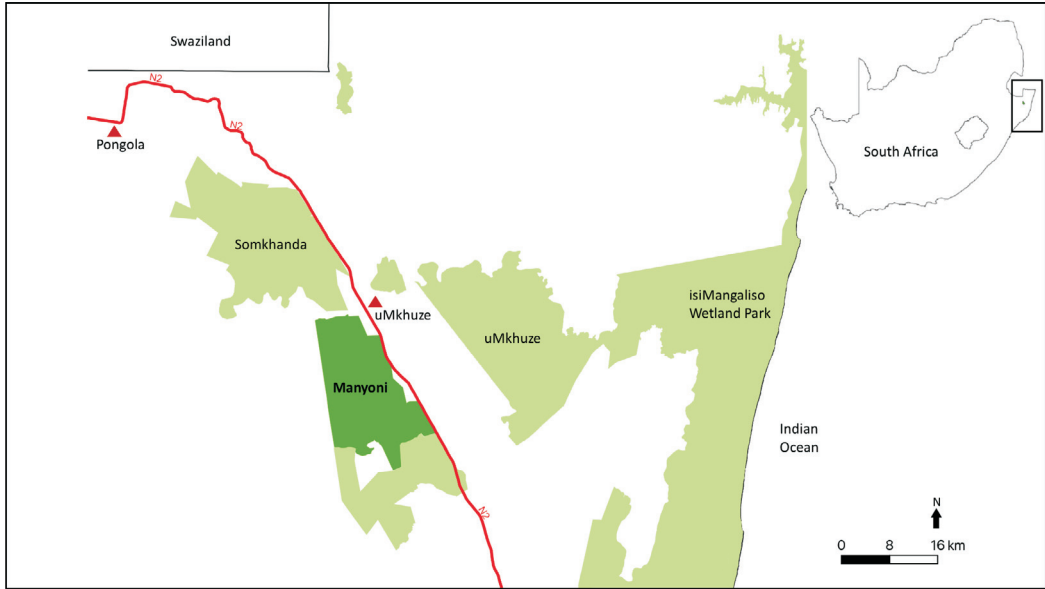


Fig. 1. Map showing South Africa (right) and the study site, Manyoni Private Game Reserve (dark green), in relation to other PAs (light green) in northern KwaZulu-Natal, South Africa. Surrounding PAs include Somkhanda Game Reserve and iSimangaliso Wetland Park. uMkhuze comprises the northeastern section of iSimangaliso. Red triangles represent locations of local towns, Pongola and uMkhuze.

enclosure (boma) for approximately 7 months, to allow for artificial pack bonding, learning to avoid electrified fencing, habituation to game vehicles, and the affixing of VHF collars which formed part of the routine management practices of the reserve. All reintroduction activities were performed in accordance with the Wild Dog Advisory Group South Africa and KwaZulu-Natal Wild Dog Advisory Group guidelines (WAG-SA, 2005). Although con-

trapection was administered while the dogs were in the boma, it was administered too late and did not prevent conception. There was no evidence that the failed contraception had behavioural effects, but this is currently being explored further in another study.

The pack was released into the wider PA in May 2015. Therefore, we restricted movement analyses to the period from May 2015 to May 2017, to exclude the time spent in the boma. A minimum of two dogs were fitted with Sirtrack VHF radio collars (one with a satellite component) at any given time which were used to locate the pack *via* radio-telemetry. The pack was located twice daily, in the early morning and late afternoon/evening, when wild dogs are typically most active (Fuller, Kat, Ginsberg & Mills, 1992). The monitoring team used a four-wheel-drive vehicle and the extensive reserve road network to get close to the pack. The wild dogs were then observed from an average distance of approximately 50 m, although in some areas of thick bush, closer following was required. Upon locating the pack, three types of sightings were recorded: (1) visual sightings with a close and accurate GPS location; (2) non-visual but strong VHF signal, indicating close proximity with an estimated GPS location; and (3) non-visual triangulations from three compass bearings. GPS points falling outside of the reserve boundary (391

Table 1. Life history of a single wild dog pack from May 2015 to May 2017 in Manyoni Private Game Reserve. The two males were sourced from Zimanga Private Game Reserve, KZN, while the four females were sourced from Madikwe Game Reserve, North West Province. Reintroduced individuals were not genetically related. Individual rank was inferred by trained Wildlife ACT monitors based on mating behaviour and dominance interactions at kills. During the breeding season, both F_3 and F_4 were observed being mounted and were thus listed as being reproductively active.

Sex_ID	Rank	Birth year	Breeding year	Mortality
F_1	Dominant	NA	NA	Yes; 2015
F_3	Dominant	2010	2016	No
F_2	Subdominant	2010	NA	No
F_4	Subdominant	2010	2016	No
M_1	Subdominant	2010	NA	No
M_2	Dominant	2012	2016	No

of a total 2404 points) were assumed to result from errors in triangulation or data recording, as no breakouts were reported during the study period. These data points were thus removed from the dataset.

Wild dogs are cooperative, seasonal breeders, usually denning between May and June, producing litters of 8–12 pups (Courchamp & Macdonald, 2015). As the pack was only released in May, 2015 was excluded as a potential breeding year. A denning period was estimated from the first time a den was located to when pups either left the den to travel with the pack or mortality was confirmed and the pack did not return to the den for more than two consecutive days. According to this definition, the pack successfully denned in 2016, producing a litter of 10 pups though none survived the first year.

Territorial extent and characteristics

The utilization distribution (UD) is a bivariate function yielding a probability density for locating the pack at any given place according to the coordinates (x, y) (Kernohan, Gitzen & Millsaugh, 2001). Several methods are available to estimate the territory of an animal, ranging in their definition of 'space use' and complexity. Kernel density estimates (KDEs) are a popular choice in home range modelling; however, various limitations with KDEs have been identified. Firstly, the models treat all locations as independent, which is often not the case with regularly sampled GPS points, resulting in over-smoothing of locations that are naturally clumped. Additionally, these simpler models fail to incorporate complex boundaries, thus including areas that cannot be used by the animal into the UD estimate (Getz *et al.*, 2007), an important consideration in our study. Other methods, such as Brownian movement models (Horne, Garton, Krone & Lewis, 2007), Local Convex Hull unions (Getz & Wilmers, 2004; Lyons, Turner & Getz, 2013) and autocorrelated kernel methods (Fleming & Calabrese, 2017) have allowed for more realistic and robust space use estimations.

Ultimately, we selected T-LoCoH (Time Local Convex Hull; Lyons *et al.*, 2013) to calculate the territory size of the pack (2015–2017) and explore habitat usage. T-LoCoH is an effective space use estimation method that can be used to identify complex barriers or inaccessible areas and is not overly sensitive to changing sample size or sampling frequency. This method is suitable for analysing core areas and spatial avoidance along sharp barriers (Stark, Vaughan, Saldivar, Nathan

& Goossens, 2017), such as fencelines, and allows spatial patterns in time strategies (*i.e.* revisitation and duration of visit) to be analysed easily within the model.

T-LoCoH methods outlined by Lyons *et al.* (2013) incorporate user-defined elements such as the time-space scaling factor (s) which scales the relationship between time and space when creating hulls (or localized home range estimates around a selected number of locations), and nearest neighbour selection which determines how many locations are required to form a hull. To remove this potential user-bias, we selected our model parameters using cross-validation-based k -LoCoH methods outlined by Dougherty, Carlson, Blackburn & Getz (2017) and Dougherty, de Valpine, Carlson, Blackburn & Getz (2018). This process involved a grid-based exploration of parameter space whereby the training/testing datasets were analysed at every combination of k (x -axis) and s (z -axis) to identify the maximum probability for the test points (y -axis), thus, denoting the optimal parameter set. We used an adaptive scaling of the pack's maximum theoretical velocity (v_{max}) to transform temporal distance between points into units of space. Training datasets were created using 80% of the original data with model testing conducted on the remaining 20%. To ensure independence between the testing points, 50 points preceding and following the selected test points were removed from the full data set. To minimize variation, the selection of test vs training sets was repeated 100 times. Optimal parameters identified by our cross-validation methods were $s = 0$ and $k = 17$. Therefore, nearest neighbour selection and hull creation was based solely on space rather than a Time-Scaled Distance (TSD; Lyons *et al.*, 2013). All data manipulation and analyses were done in program 'R' (v. 4.0.2) and the 'tlocoh' package (Lyons & Getz, 2018). We described our territory estimates using isopleth levels which indicated the proportion of points enclosed along a gradient of hull unions. Specifically, we referred to the outer 0.95 isopleth level as the total territory, and the 0.5 isopleth level as the core territory.

Re-visitation rate (nsv , *i.e.* number of separate visits) and duration of each visit ($mnlv$, *i.e.* mean number locations per visit) were assigned to each hull. We selected a time interval of 12 hours to define the period that must pass before another occurrence in the hull is considered a separate visit as this aligns with the crepuscular nature of

wild dog movement (Fuller *et al.*, 1992). To better visualize the spatial distribution of our behavioural metrics, we used the 'tlocoh.dev' package (Lyons, 2018), to build time-use grids for the pack. Therefore, *nsv* and *mnlv* were calculated per 1 km² grid cell rather than as individual hulls.

Post hoc analyses of lion localities were also conducted in an attempt to explain the observed wild dog habitat use. Lion location data were opportunistically recorded by WildlifeACT monitors while searching for the pack. Sixteen adult lions were located within the PA during the study period, organized in seven groupings (or prides). The largest grouping consisted of five individuals (two males and three females) whilst the smallest grouping comprised a single female. The lion data were analysed using the same estimation methods as the wild dog pack (*i.e.* T-LoCoH with *k*-method cross-validation parameter selection). Optimal parameters for the lion territories were identified as *s* = 0 and *k* = 22. Total and core territory spatial overlap between the wild dog pack and the lions were estimated by calculating the area of intersection using the 'gIntersection' function from the 'rgeos' package (Bivand & Rundel, 2019). Temporal overlap between the two species was estimated using 'lhs.to.stats' function from the 'tlocoh.dev' R package. This approach compared the centroid-to-centroid distances of a random selection of hulls from the two species to that of time-overlapped hulls. We used the Welch two-sample *t*-test to test if the distribution for the time-overlapped, and randomly paired hulls, had statistically different means.

Habitat selection

Habitat was classified into six vegetation types: thicket, open savanna, closed savanna, riparian, rocky hills and old (modified) lands, as defined by reserve managers in 2012 (Supplementary Fig. S1; T. Gilroy, pers. comm., May 2017). To explore habitat selection over the entire study period, and to incorporate habitat availability, we applied χ^2 goodness-of-fit tests that compared observed counts of the pack in each habitat with the expected use of a habitat based on its availability. Relative availability of each habitat was calculated as the proportion of cover (area in km²; Supplementary Table S1) of a given habitat type relative to the total reserve area. Expected counts were then calculated by simulating 2013 randomly distributed points, matching the number of pack locations, through the reserve, independent of

habitat type. From the χ^2 test, we inferred preference (+) or avoidance (-) of the pack for a certain vegetation type based on deviations from expected values. We then used T-LoCoH to determine seasonal changes in habitat selection by exploring visitation and duration of time spent in the different vegetation types. This analysis was achieved by assigning *nsv*, *mnlv* and dominant vegetation type to each hull.

RESULTS

Territorial extent and characteristics

A total of 2013 GPS fixes were recorded within the PA boundaries spanning 755 days from May 2015 to May 2017. The majority of GPS points (77%) were visual sightings with an accurate GPS location (type 1); while 20% of locations were from non-visual triangulations (type 3) and only 3% were from non-visual recordings with a strong VHF signal (type 2). Using T-LoCoH methods, the estimated total territory size (0.95 isopleth level; Fig. 2A) was substantially smaller (121 km²) than the total PA size (219 km²). Space use patterns showed low intensity usage in the centre of the PA with high intensity usage along the edges, and the core territory located in the corners of the PA, the easternmost location coinciding with the den site. A total of 414 GPS fixes were used to construct the estimated lion territory (Fig. 2B). Territory overlap between the two species did occur (Fig. 2C), covering 27 km² and amounting to 20% of the pack's total territory. Core territory overlap was substantially smaller, with an area of 0.14 km², which accounted for only 3% of the pack's core territory. The distribution for the time-overlapped and randomly paired hulls had statistically significant means (*t* = 3.661, d.f. = 75.575, *P* < 0.001), with the density of time-overlapped hulls increasing the further the hull centroids were located in space (Fig. 3).

Assessing the spatial distribution of visitation and duration highlighted where the pack spent most of their time. The majority of frequently visited sites were located along the edges of the PA (Fig. 4A), with substantially lower visitation rates to the interior, again corresponding with the estimated lion territory (Fig. 2B). The area of highest visitation was strongly associated with the den site in the northeastern region of the PA. The time-use map displaying duration of visit (Fig. 4B) highlighted areas the pack may not visit frequently but upon arrival stayed for extended periods of time.

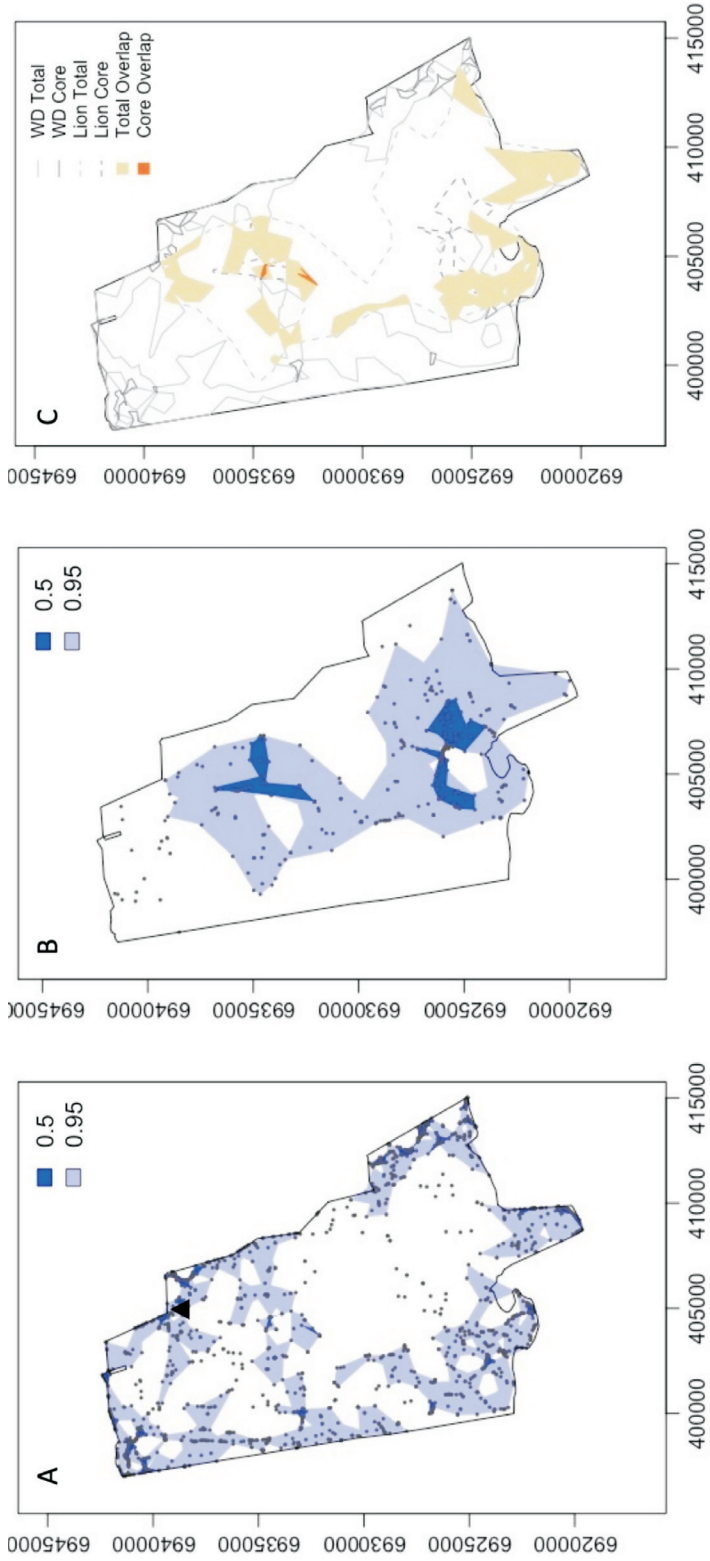


Fig. 2. T-LoCoH estimated territory size (km²) for (A) single pack of wild dogs, (B) lions and (C) total and core area overlap between the wild dog pack and lions in Manyoni Private Game Reserve. Isopleth levels (a and b) indicate the proportion of total points enclosed by the hulls with red isopleths indicating high-density areas. Hulls were constructed using the Fixed *k*-method (a) *k* = 17, *s* = 0 and (b) *k* = 22, *s* = 0; duplicate points offset by 1 map unit. Total and core HR represents the 0.95 and 0.5 isopleth levels, respectively.

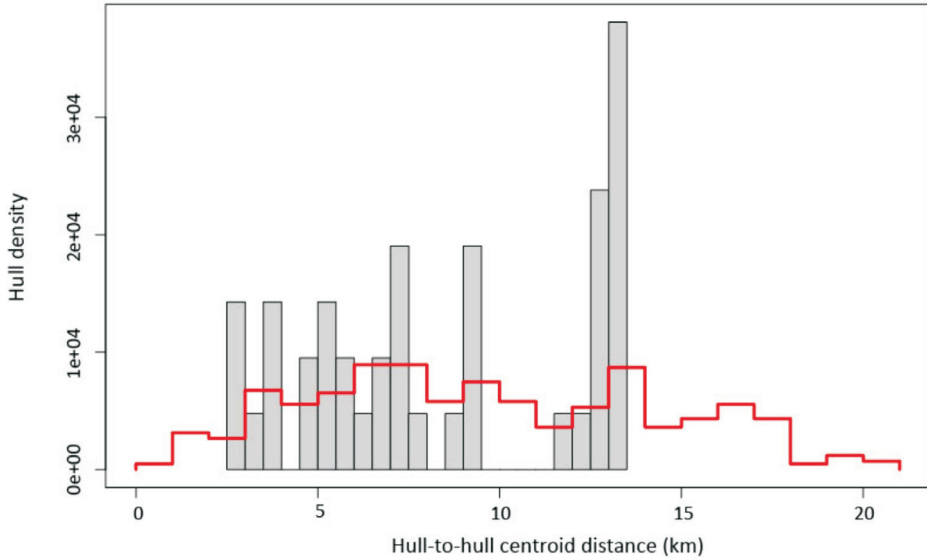


Fig. 3. Density of time-overlapped hulls and hull-to-hull centroid distance (km) between a single pack of wild dogs and lions in Manyoni Private Game Reserve (2015–2017). The red line indicates the centroid distance of randomly selected hull pairs.

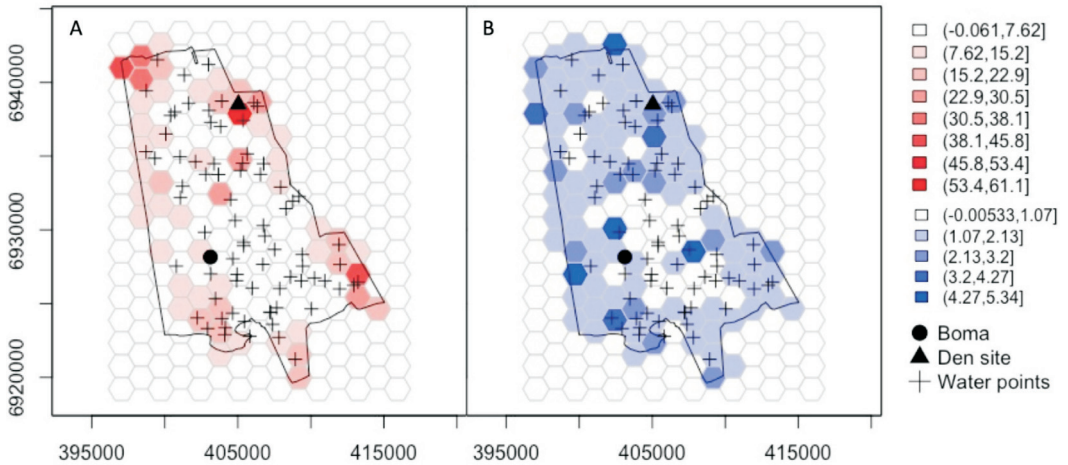


Fig. 4. Time-use metrics for a single pack of wild dogs in Manyoni Private Game Reserve (2015–2017). (A), Number of separate visits (*nsv*) to each grid cell (1 km² areas with an intervisit gap of 12 hours apart); (B), mean number of locations per visit (*mnlv*) to each grid cell.

These areas were more spread out through the reserve; however, there were still unused patches in the centre of the PA, corresponding to the core area of the lion territory (Fig. 2B,C). Areas of longest duration were generally associated with water sources, with an area of medium duration surrounding the boma (Fig. 4B).

Habitat selection

There were marked differences between habitat selection over the entire study period and seasonal

preferences. In total, the pack showed a strong preference for riparian vegetation ($P < 0.001$; Table 2), whilst they appeared to avoid closed savanna ($P < 0.001$; Table 2). There was also some evidence for the pack avoiding thicket ($P = 0.043$), open savanna ($P = 0.021$) and rocky hill vegetation ($P = 0.027$; Table 2). Using T-LoCoH time-use metrics there was evidence for seasonal differences in visitation rate and duration of time spent by the pack in the different vegetation types. The pack showed relatively high revisitation and

Table 2. χ^2 evaluations for habitat preference for an wild dog pack (2015–2017) within Manyoni Private Game Reserve. Expected counts were calculated by simulating 2013 randomly distributed points throughout the reserve, with points located either inside or outside of the respective vegetation type. Significance of preference or avoidance of the pack for a certain vegetation type were then based on deviations from this random distribution. Significant preference (P) is indicated by symbols: (+) selection/preference for vegetation, (–) avoidance of vegetation, (0) no preference/significance.

Vegetation		Expected	Observed	χ^2	P	Preference
Riparian	Inside	64	180	57.698	$P < 0.001$	+
	Outside	1949	1833			
Thicket	Inside	852	779	4.086	0.043	–
	Outside	1161	1234			
Closed savanna	Inside	220	106	42.620	$P < 0.001$	–
	Outside	1793	1907			
Rocky hills	Inside	412	356	4.867	0.027	–
	Outside	1601	1657			
Open savanna	Inside	852	779	5.343	0.021	–
	Outside	1161	1234			
Old lands	Inside	146	123	1.928	0.165	0
	Outside	1867	1890			

duration of time in rocky hills, thicket and open savanna, with spikes in usage around both dry seasons (Fig. 5). Both revisitation rate and duration of visit peaked in riparian vegetation during the denning period.

DISCUSSION

Our T-LoCoH estimates showed that despite being introduced into an area smaller than the estimated home range for the species (278–665 km²; Woodroffe, 2011) the pack utilized only half of the space available to them (121 of the 219 km² available). When compared with studies also using T-LoCoH methods, similarly small territory sizes *e.g.* 154 km² in the KNP (Marneweck, Marneweck *et al.*, 2019) have been reported even for packs in much larger PAs and thus we suggest that the pack in our study were not restricted by PA size.

The area used by the pack appeared to be strongly influenced by the presence of lions. Wild dogs have been shown to adjust their territory size to avoid lions (Marneweck, Marneweck *et al.*, 2019). For example, in Madikwe Game Reserve the pack utilized only a third of the area available (180 km²) due to competitive exclusion from lions (Hofmeyr, 1997). We found evidence of spatial avoidance between our pack and the lions, the pack showed high intensity usage along the edges of the PA and seemingly avoided the interior of the PA which was dominated by the lion territory. Total territory overlap between the two species,

accounting for 20% of the packs total territory, occurred along the peripheries of the lion territory and along the edges of the open savanna habitat (Fig. 2C and Supplementary Fig. S1). Core area overlap was substantially more restricted, covering only 3% of the pack's core area and mostly linked to areas with permanent water from pumped water sources that the pack visited regularly (Fig. 2C and Fig. 4A). This finding suggests that the pack only risks spatial overlap to access critical resources, *e.g.* water or prey associated with predictable water sources (Marneweck *et al.*, 2021; Thrash, Theron & Bothma, 1995). We also found evidence of temporal avoidance between the pack and lions, where the density of hulls that overlapped temporally tended to decrease the closer the hulls were located spatially (Fig. 3). This result suggests that the pack may employ temporal niche partitioning allowing them to utilize the same areas as the lions but reducing the risk of an encounter. Given the limited lion data available to us, 414 locations spanning the study period, these findings should not be over-interpreted. Instead, they should be used to highlight potential interspecific relationships shaping territory and habitat selection of species within the same guild, and to propose future studies exploring spatio-temporal exclusion by competing species in small PAs.

The high overlap of the pack's territory with the reserve boundary (Fig. 2A), as well as high levels of revisitation (Fig. 4A), is a cause for concern.

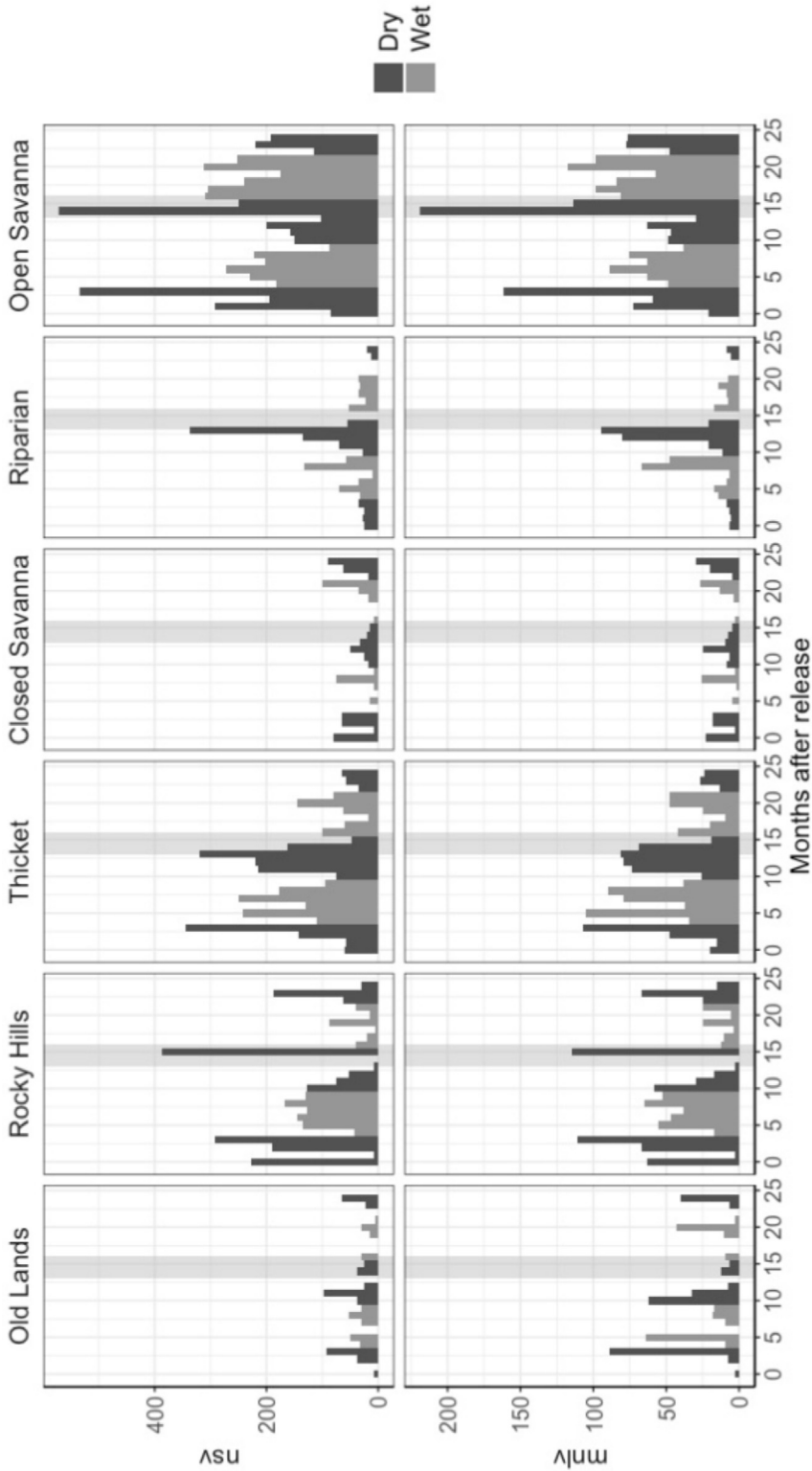


Fig. 5. Monthly and seasonal changes in revisitation (*nsv*; number of separate visits) and visit duration (*mnlv*; mean number of locations in the hull per visit) for a pack of wild dogs across different habitat types in Manyoni Private Game Reserve (2015–2017). Separate visits defined by an inter-visit gap period of 12 hours. Grey highlighted area denotes denning period.

Break-outs from PAs and associated threats of vehicle collisions, domestic canine diseases and intolerant farmers are a major source of mortality for wild dogs (Davies-Mostert *et al.*, 2009). Therefore, maintaining fence integrity is a vital part of wild dog management. Wild dogs have been shown to use fencelines to aid in hunting (van Dyk & Slotow, 2003), which can significantly increase their hunting success and exacerbate predation pressure within a PA. For this specific pack, and other packs within the metapopulation, organizations such as Wildlife ACT provide intensive monitoring which can help mitigate against these risks. However, for many PAs in South Africa, extensive time and resources cannot be allocated to monitoring packs on the ground. Therefore, by understanding pack movement, and identifying areas of high intensity usage, resources can be strategically allocated to high-risk areas (*e.g.* maintaining particular stretches of well-used fencelines and monitoring prey off-take around heavily utilized water sources). Such resource allocation can provide improved, proactive management of wild dogs within the SAWDM, and for the species as a whole.

The area with the greatest number of observations, and the highest revisitation rate, over the total study period corresponded with the core territory during denning (Fig. 2A). This supports the findings of both Reich (1981) and Mills & Gorman (1997), who have also reported a strong association between the core zones of wild dog territories and their den sites. Such a finding is understandable as the pack must regularly return to the den site to provision the lactating female and later pups. Denning occurred in the first breeding season after release, which has been linked with high ultimate reproductive success (Marneweck, Becker, *et al.*, 2019). Although the 2016 litter did not survive past a year, this is not necessarily a result of their reintroduction nor inadequacy of the PA. Smaller PAs such as Somkhanda Game Reserve (120 km²) have successfully reintroduced and maintained viable wild dog packs that routinely breed successfully (KZN-WAG, 2020; Wildlife ACT, 2020). Furthermore, the Manyoni pack successfully denned again in 2018, producing three pups. Our paper shows that, despite being restricted in size, small PAs can be valuable contributors to biodiversity objectives.

Despite accounting for less than 3% of available vegetation, the pack showed a strong preference for riparian vegetation ($P < 0.001$; Table 2), with

most of the pack's core territory being situated in this riverine habitat (Fig. 2A and Supplementary Fig. S1). Davies *et al.* (2021) showed that wild dogs in Hluhluwe-iMfolozi selected increasingly thicker vegetation to avoid lions. Furthermore, wild dogs located in open habitat areas like Liuwa (Dröge *et al.*, 2017) and the Serengeti (Swanson *et al.*, 2014) have generally fared poorly as they are easily detected by spotted hyaenas (*Crocuta crocuta*) and lions, resulting in increased competition.

Relative to its availability, the pack appeared to avoid open savanna vegetation, which corresponds to our prediction that the pack would avoid areas preferred by lions. When breaking usage down over months since reintroduction, we can see that riparian usage peaked substantially during the denning period (Fig. 5). Creel & Creel (1995) reported that although thicker vegetation may slightly impede wild dog hunting coordination, it also impedes the ability of hyaenas to locate and steal kills, thus reducing the probability of kleptoparasitism. Reduced detection by competitors would be an important factor for selecting a den site. Indeed Marneweck *et al.* (2021) showed that during the denning period, wild dogs will forgo rich resource patches to avoid lions. Additionally, selection of dense riverine vegetation for the location of the pack's den site could be due to increased vegetation complexity (Davies, Marneweck, Druce & Asner, 2016) and proximity to water (O'Neill *et al.*, 2020) during the dry season when the denning period commenced (Fig. 5). Apart from this peak in usage of riparian vegetation, habitat usage of other vegetation types did not appear to change with denning.

Despite the wild dog territory (Fig. 2A) and revisitation grid (Fig. 4A) showing reduced usage of the interior of the park, there were patches of longer duration stays located in these areas (Fig. 4B). Areas of high revisitation may indicate patches of high quality, predictable resources that the pack visits regularly, whereas areas of long duration may indicate more seasonally dependent resources, that when available, would result in the pack overdispersing in those locations. This result could also explain the peaks in visitation and duration usage of open savanna during the dry periods (Fig. 5). For example, non-denning wild dogs have been shown to re-visit areas of high impala (*Aepyceros melampus*) density (open savanna habitat) despite high lion density (Marneweck *et al.*, 2021). In our study, the pack was monitored in the early

morning and late afternoon/evening as wild dogs are typically considered crepuscular (Fuller *et al.*, 1992). This monitoring regime restricted our temporal analyses and limited our ability to explore potential changes in temporal partitioning in response to competitive pressure from more dominant carnivores (Hayward & Slotow, 2009). Though we found evidence that the pack may be utilizing coexistence mechanisms such as temporal niche partitioning (Fig. 3) to reduce their direct competition with lions in the interior of the PA, this needs to be explored further with more robust data.

From a methodological point of view, it was interesting to note that the optimal scaling parameter selected for our territory estimates was $s = 0$, and therefore, time had no influence in picking nearest neighbour GPS points, and the hulls around each point were constructed from the closest points in space only (Lyons *et al.*, 2013). One explanation for this could be that the pack's active, repetitive movement as they patrolled their limited territory size is best modelled using two-dimensional Euclidean distance, rather than incorporating time-scaled distance. A second possibility is that wild dog movement may more closely resemble diffusion dynamics rather than the maximum-velocity transformation used in this paper. Highly territorial male springbok (*Antidorcas marsupialis*) have been shown to be governed by a sub-diffusion movement pattern (Supplementary material in Lyons *et al.* (2013)). Additionally, diffusive transformations may be more suitable when modelling the movement patterns of dispersing individuals. This should be explored further in future studies where this alternative equation for TSD between points may be more accurate in predicting wild dog movement, both in free-ranging individuals and those restricted to smaller PAs.

It must be noted that although T-LoCoH is one of the best methods for estimating space use along complex boundaries (Lyons *et al.*, 2013; Stark *et al.*, 2017), over-estimation outside of the reserve still occurred (Fig. 2A). T-LoCoH methods require regular time intervals between recorded locations. This is not always possible when using telemetry data, as a monitor on the ground must first locate the pack before recording fixes. We attempted to overcome this challenge by using Kalman smoothing (Patterson, McConnell, Fedak, Bravington & Hindell, 2010) to estimate any missing data values during the sampling period. However, there were still missing data over small

temporal scales, which could lead to errors in the total territory estimation. Gaps in data are especially problematic when studying wild dogs as they are known to move large distances over a relatively short period of time (Andreka, Linn, Perrin & Maddock, 1999; Woodroffe & Sillero-Zubiri, 2012), and thus valuable information could have been unobserved.

Our preliminary findings highlight the influence dominant carnivores have in shaping the territories and spatio-temporal habitat use of subordinate carnivore species. However, territory size has been shown to vary with factors not included in this study such as rainfall, litter and pack size (Pomilia *et al.*, 2015), perennial rivers (Mottram *et al.*, 2019), social behaviour and disease (Van Heerden, Mills, Van Vuuren, Kelly & Dreyer, 1995). A more complete understanding of factors influencing the ranging patterns of reintroduced wild dogs will benefit from the inclusion of such data.

CONCLUSION

Our study explored the movement patterns of a single reintroduced wild dog pack as part of the SAWDM. The results provide support for the theory that small well-fenced PAs can sustain wild dogs. The pack appeared to be strongly influenced by the presence of lions, with the pack avoiding large areas of suitable habitat and showing temporal partitioning of shared core areas. Future studies should further explore this spatio-temporal avoidance, especially within the confines of small PAs. We showed that habitat use was far more complex than simple resource selection where similar resources were exploited differently based on seasonality, pack life-stage and interspecific competition. The high overlap of the total territory with the reserve boundaries, and the close proximity of the core area to the reserve fence, increases the threats associated with edges in small PAs. If this is a consistent feature of wild dog space use in other small reserve, then more maintenance and increased monitoring effort along fence lines is likely required to prevent potential break-outs. Such intensive monitoring will also likely reduce negative interactions between wild dogs and neighbouring land users. By incorporating temporal data, we can expand our understanding of spatial and temporal patch use, leading to better-informed inferences about endangered species habitat requirements and improved monitoring and mitigation of potential risks to species survival.

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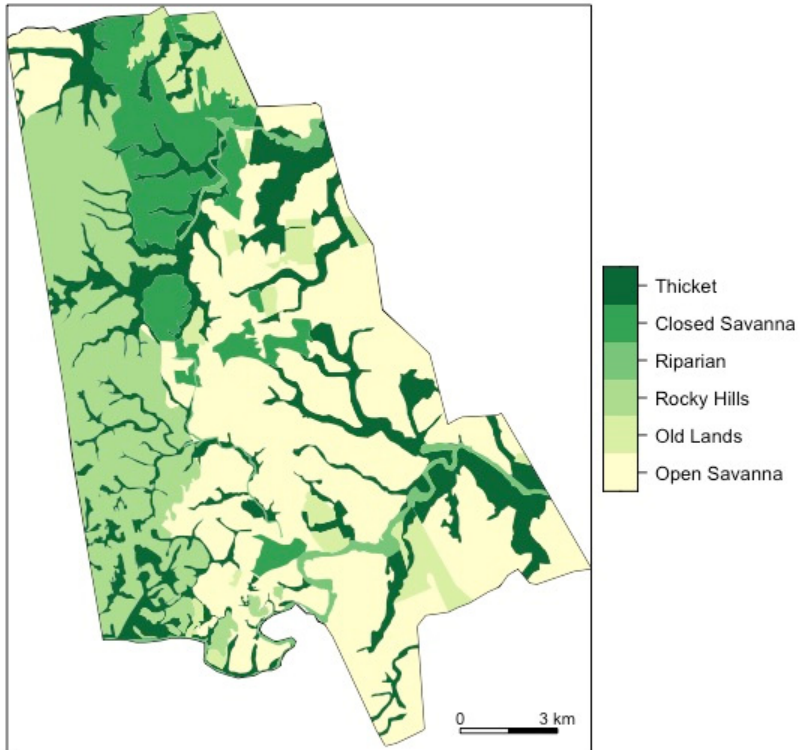
Supplementary material to:

Michelle Pretorius, Greg B. Distiller, Theoni Photopoulou,
Christopher P. Kelly & M. Justin O’Riain

African wild dog movement ecology in a small protected area in
South Africa

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SUPPLEMENTARY MATERIAL



Supplementary Fig S1. Vegetation types across Manyoni Private Game Reserve, defined in 2012 (T. Gilroy, pers. comm., May 2017).

Supplementary Table S1. The area (km²) of coverage and relative percentage (%) of the different habitat types within Manyoni Private Game Reserve defined in 2012.

Vegetation type	Area	Percentage cover
Open Savanna	90.95	41.51
Thicket	44.02	20.09
Rocky Hills	43.03	19.64
Closed Savanna	22.51	10.28
Old Lands	13.11	5.98
Riparian	5.48	2.50
Total	219.10	100.00