

**Spatiotemporal resource partitioning  
of water sources by African carnivores on Namibian commercial farmlands**

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**Abstract**

Interspecific competition often occurs when sympatric carnivores compete for the same, limited resources, although the degree of competition between species pairs may vary with biotic factors such as body-size, diet and population density. Avoidance of dominant competitors along the axes of space and time is a potential mechanism for reducing chances of direct encounters between species. However, when resources are essential and spatially fixed, options for spatial partitioning may be limited. We examined resource partitioning within a guild of eight carnivore species at water sources across two commercial farmlands in southwest Namibia. In this semi-desert environment, surface water is scarce and farmers are forced to provision water for livestock through artificial means. Camera traps were used to record spatial and temporal activity patterns of carnivore species at artificial

and natural permanent water sources. We found carnivores to use either spatial or temporal resource partitioning, with temporal partitioning being most frequently seen. An association was seen between difference in body mass and degree of spatial partitioning, where species pairings with larger differences in body mass showed the greatest degree of partitioning. These results show that whilst in arid environments water is rare and used by a number of carnivore species, resource partitioning allows a guild of carnivores, including species of conservation concern, to coexist outside of protected areas.

Keywords: activity pattern, camera trapping, carnivores, partitioning, interspecific competition, Namibia

## **Introduction**

In ecosystems with multiple carnivore species, interspecific competition for the same limited resources such as food and habitat can occur. Such competition can have a strong and widespread impact on community composition, ultimately determining which species are able to coexist (Begon *et al.* 2006). Such an impact can have direct consequences for the conservation of rare species, for example densities of both wild dog *Lycaon pictus* and cheetah *Acinonyx jubatus* show a negative association with the densities of lions *Panthera leo* and spotted hyaenas *Crocuta crocuta* across their range (Durant, 2000). The competitive exclusion theory suggests that species with similar ecology cannot coexist (Hardin, 1960). However ecological separation, occurring on the axes of space, time and diet, can provide a mechanism for species coexistence (Schoener, 1974). The ways in which multiple carnivore species utilise and partition resources, are currently poorly understood (Vanak *et al.* 2013),

but can be important for understanding which mechanisms structure communities (Vieira & Port, 2007).

Schoener (1974) argued that although temporal resource partitioning is rare in ecology, it is seen more frequently in carnivores than other groups. Hayward & Slotow (2009) examined temporal overlap between cheetah, wild dog, spotted hyaena and lion and found subordinate guild members use temporal resource partitioning, having evolved activity patterns which minimise overlap with dominant species, to avoid both kleptoparasitism and intraguild predation. Similarly Di Bitetti *et al.* (2010) found temporal partitioning in the activity patterns of the most morphologically similar species in a community of six species of neotropical felids. Spatial partitioning is also seen between carnivores; Swanson *et al.* (2014) recorded spatial avoidance of lion by wild dog, and Kamler *et al.* (2012) found spatial avoidance of black-backed jackal *Canis mesomelas* by Cape fox *Vulpes chama*.

Carnivore species may be able to coexist and avoid the effects of competition by utilising different prey. Hayward (2006) found that although lions and spotted hyaena had high levels of dietary overlap, the unselective nature of hyaenas allowed the two species to coexist. Similarly, leopards *Panthera pardus* were found to take smaller prey items than other guild members allowing them to coexist with competitors (Hayward and Kerley, 2008). Within a diverse carnivore community, competition is likely to differ between each species pair, for example competitive theory predicts species that differ significantly in body mass do not compete (Wilson, 1975). Larger species benefit from size (Persson, 1985), meaning smaller species often have decreased access to limited resources (Amarasekare, 2003). However smaller species may avoid larger species as they are more at risk from

intraguild predation (Woodward & Hildrew 2002), an extreme form of interference competition where two species that compete for the same resources kill and sometimes eat each other (Polis, Myers & Holt, 1989). Therefore examining partitioning in a sympatric carnivore assemblage where a range of body sizes, diets and densities are present, is likely to advance current knowledge in the field of ecological community structure.

Africa presents the perfect opportunity to study carnivore guild interactions as it is the only continent with an intact carnivore guild (Cozzi *et al.* 2012). Furthermore, Namibia is the ideal place to examine resource partitioning at water sources as one of the driest climates in sub-Saharan Africa. Such locations represent important and spatially fixed resources for a number of species, and as a result these water sources become high risk areas for predation (Valeix *et al.* 2009). How carnivores avoid each other at water sources in such arid environments has received little attention (but see Atwood, Fry & Leland, 2011).

This study used camera traps to examine temporal and spatial resource partitioning at 13 permanent water sources in a sympatric guild of 11 carnivore species on two commercial farmlands in southwest Namibia. In this environment natural permanent water sources are rare, with most rainfall water seeping underground and ephemeral pools seen only in the wet season. Temporal and spatial activity patterns of carnivores were determined over the period of one year. As water sources are both scarce and spatially fixed, it was hypothesised that temporal partitioning would be the main method used by guild members to avoid direct encounters. Furthermore it was hypothesised that associations between differences in body mass and degree of resource partitioning would be observed, with species pairings with large differences in body mass showing higher levels of partitioning than species pairs of similar size.

## Methods

### Study area

The study was conducted across two bordering commercial farmlands Tsirub (S 26°49'14", E 16°05'55") and Klein Aus Vista (KAV)(S 26°42'00", E 16°06'09") near the settlement of Aus, Karas region, southwest Namibia (Fig. 1). The farms directly border the Tsau//Khaeb (Sperrgebiet) National Park and total 400 km<sup>2</sup> and 500 km<sup>2</sup> respectively. The area consists of Namib Desert and Nama Karoo biomes (Giess, 1971), characterised by mountains and flat grassy plains dominated by *Stipagrostis* grass species with relatively few trees and shrubs. The mean annual rainfall is 80 mm and the mean annual temperature is 17.5 °C (22.8 °C summer, 15.2 °C winter), ranging from -5 °C to 42 °C (Namibia Weather Network, 2014). Altitude lies between 1 000 - 1 500 m. The area is positioned within a winter-summer rainfall transitional zone (Burke, 2004), although most rain falls during the summer months (November to March).

The main agricultural activity was livestock and game production for meat, Tsirub farmed game, namely springbok *Antidorcas marsupialis* and oryx *Oryx gazella*, whilst KAV farmed cattle *Bos taurus* but also had oryx and springbok present. Tsirub had no internal fences, whilst KAV was divided into four main grazing camps through which cattle were rotated. However, spacing of wires within the fence line was wide enough to allow passage of carnivores through and was not considered a barrier to movement. Density of artificial water sources varied between farms with Tsirub having a density of 7.25 points/100 km<sup>2</sup>, whilst KAV had 3.92/100 km<sup>2</sup>.

Previous studies have shown differences between domestic livestock and game farmers in tolerance levels of carnivores which in turn affect removal (Lindsey *et al.* 2005). However, during the study period no carnivores were killed on either farm with the exception of Tsirub's owner occasionally shooting black-backed jackals during normal game hunting activities. Blaum *et al.* (2009) found the stocking density and associated changes in vegetation structure to have a negative relationship with abundance of small carnivores. Due to the arid environment, both farms stocked at low density (KAV stocked cattle at a density of 80 cattle/100 km<sup>2</sup>) and the density of wild game across the two farms was similar. Therefore the differences between the farms in stocking density were not believed to affect the carnivore guild.

## **Methods**

A total of 12 artificial water sources (Tsirub n=7, KAV n=5) and one natural, permanent spring on KAV, were chosen randomly and monitored by camera trap from May 2013 to May 2014. A single Scoutguard SG560V (HCO Outdoors, Georgia, USA) camera trap was positioned at an average height of 40 cm from the ground and angled so the entire water source was in view. Camera traps were spaced at least 4 km apart, which was considered as spatially independent, and programmed to take one photo per trigger, with a minute delay between and checked every two weeks when batteries and SD cards were changed.

## **Statistical Analysis**

Temporal partitioning was analysed separately for each farm. Due to small sample sizes data were combined for the two farms to test for spatial partitioning and the association between difference in body mass and resource partitioning. Because the 2014 rains only reached 50 % of the annual mean of 80 mm, and the seasonal pools only filled for a few days at a time (S. Edwards, pers. obs), differences in natural water availability were thought to be minimal and thus seasons were not controlled for. Carnivore images were identified to species level and classed into independent events, using a criterion of a minimum of 30 minutes between consecutive photos of the same species (O'Brien *et al.*, 2003), except for species with individual markings where detection of a different individual was always recorded, but the criterion above hold valid for same individual detection. Analyses to examine temporal and spatial partitioning between each carnivore species pair were conducted using R 3.1.1 (R Development Core Team, 2014).

## **Temporal and Spatial Resource Partitioning**

Temporal partitioning activity patterns at water sources were compared with the non-parametric circular Mardia-Watson Wheeler test (Batschelet, 1981) using Oriana (Kovach Computing Services, 2013), to test the null hypothesis that activity patterns were identical for each species pair. As the test requires  $n \geq 10$ , not all species could be analysed.

Additionally Oriana was used to calculate the mean vector (activity time), length of mean vector which ranges from 0 to 1, where a higher value indicates that the observations are clustered more closely around the mean and circular variance, standard deviation and 95 % confidence intervals, which are equivalent to their linear counter parts. Secondly, independent events for each species and camera trap location were grouped into two hour

time periods (i.e. 00:00 h – 02:00 h etc) and the proportion of events in each period calculated. Pianka's index of niche overlap (Pianka, 1973) was then calculated for each species pair using R package 'pgirmess' version 1.5.9 (Giraudoux, 2014).

Finally, in order to examine if different carnivore species avoid using the same water point on the same day, a bootstrapping procedure was used to test if the number of joint occurrences observed differed from the number expected randomly. For each species pair and camera trap location two sets of random numbers were generated, the  $n$  of the first set equal to the number of days the first species had been detected at that particular camera trap and the  $n$  of the second set equal to the number of days the second species in the pair had been detected. The total number of operational camera trap nights determined the range the random numbers were generated from. For example, if a camera trap had 250 camera trap nights and cheetah had been detected there on 50 nights and aardwolf on 100 nights, one set of 50 random numbers between 1 and 250 would be generated, and another set of 100 between 1 and 250 would be generated. The number of times the same number was seen in each set of random numbers represented the number of joint occurrences expected to occur at random. Each re-sampling procedure was repeated 10 000 times for each species pair at each camera trap location and the mean was used for analysis. Wilcoxon matched pairs tests were then used to examine differences between observed and mean expected joint occurrences for each species pair.

To examine spatial resource partitioning between species the proportion of independent events at each water source was calculated for each species. Spearman's rank correlation was used to examine associations in the relative abundance of each species pair



at camera trap locations. Relative abundance was calculated as the number of operational camera trap nights, using the formula from Negroes *et al.* (2010):

$$RAI_i = (g_i \sum_j P_{ij} / \sum_j t_{nj}) * 100$$

Where  $g_i$  = average group size for the  $i^{\text{th}}$  species,  $P_{ij}$  = number of independent events for the  $i^{\text{th}}$  species,  $t_{nj}$  = total number of trap nights at the  $j^{\text{th}}$  location. For social species, such as black-backed jackal, bat-eared fox *Otocyon megalotis* and brown hyaena *Hyaena brunnea*, mean group size was determined from the literature, or where possible from direct field observations across the study sites.

### **Association between differences in body mass and degree of resource partitioning**

To examine associations between differences in body mass between species pairs and the degree of resource partitioning, Spearman's rank correlation was used with the Pianka's indices for both temporal and then spatial partitioning against the difference in relative body mass (taken from Estes (1992)) for all carnivore species pairs.

### **Results**

A total of 11 species were detected over 4 507 camera trap nights across the two farms. Species detected were Cape fox (n = 140), bat-eared fox (n = 376), black-backed jackal (n = 4482), honey badger *Mellivora capensis* (n = 46), aardwolf *Proteles cristata* (n = 12), spotted hyaena (n = 11), brown hyaena (n = 399), leopard *Panthera pardus* (n = 148), cheetah (n = 22), caracal *Caracal caracal* (n = 8) and African wild cat *Felis lybica* (n = 52). Due to low

sample sizes and presumed low densities, spotted hyaena, aardwolf, and caracal across the two sites and African wild cat on KAV were excluded from analysis.

### **Temporal and Spatial Resource Partitioning**

Almost all species showed predominant nocturnal activity (between 18:00 h and 6:00 h) with less than one hour differences in within species mean activity times across study sites (Table 1). Cape fox showed strictly nocturnal activity patterns with peaks of activity around midnight and dawn (Figs. 2 and 3). Bat-eared fox was mainly nocturnal, but showed some activity during the day at Tsirub, but was strictly nocturnal at KAV with a peak in activity at 21:00 h. At both sites black-backed jackal showed activity throughout the day and night, but with the least activity recorded from mid-morning to late afternoon. Honey badger at Tsirub showed activity throughout the day and night, with peaks in the early morning and early evening, whilst on KAV nearly all activity was nocturnal. Brown hyaena at both sites showed predominant nocturnal activity, with peaks on Tsirub around 22:00 h and 3:00 h, and similar peaks between 21:00 h and 22:00 h and at dawn at KAV. On both sites leopards were most active during the first half of the night and dawn, with some activity throughout the day. Cheetah and African wild cat were predominately nocturnal. Cheetah showed increased activity in the early evening, at dawn and early morning, whereas African wild cat had a clear peak in activity at 1:00 h.

Mardia-Watson Wheeler tests revealed significant differences in temporal activity between species at water points across both sites. On Tsirub brown hyaena temporal activity was significantly different to the temporal activity of leopard ( $W = 13.17$ ,  $P = 0.002$ ),

black-backed jackal ( $W = 94.61, P < 0.001$ ), bat-eared fox ( $W = 12.52, P = 0.001$ ) and honey badger ( $W = 36.3, P < 0.001$ ). Leopard temporal activity was significantly different from Cape fox ( $W = 6.84, P = 0.03$ ) and honey badger ( $W = 6.52, P = 0.04$ ), black-backed jackal was significantly different from African wild cat ( $W = 10.6, P = 0.005$ ), bat-eared fox ( $W = 20.53, P = 0.002$ ) and Cape fox ( $W = 10.08, P = 0.006$ ) and honey badger temporal activity was significantly different from African wild cat ( $W = 12.03, P = 0.002$ ), bat-eared fox ( $W = 13.54, P = 0.04$ ) and Cape fox ( $W = 20.92, P < 0.001$ ) (Table 2).

At KAV, there were significant differences in temporal activity at water points between all carnivore species, with the exception of brown hyaena and honey badger ( $W=1.63, p=0.44$ ) and honey badger and Cape fox ( $W = 0.07, P = 0.95$ ) (Table 2).

Bootstrapping procedures showed significant differences in the number of observed and expected numbers of joint occurrences for only three of the 28 species pairs; bat-eared fox and African wild cat ( $V = 0, P = 0.03$ ) honey badger and African wild cat ( $V = 0, P = 0.03$ ) and honey badger and cheetah ( $V = 0, P = 0.03$ ) on Tsirub. This meant the number of days the two species were seen at the same water source was significantly different than would be expected to happen at random. Observed values were always less than expected for significant values, suggesting avoidance at water points. No species pairs showed significant differences between the number of observed and expected joint occurrences on KAV. It should be noted as Cape fox was only recorded at one location on KAV, paired t-tests could not be performed for this species.

Spearman's rank correlation tests showed significant, negative associations between difference in body mass and degree of spatial partitioning for only three species pairs out of

28: black-backed jackal and leopard, brown hyaena and cheetah and between leopard and cheetah (Table 2).

### **Association between differences in body mass and degree of resource partitioning**

Spearman's rank correlation showed no significant association between difference in body mass and Pianka's index of temporal overlap for data combined from all two study sites ( $r_s = -0.15$ ,  $P = 0.33$ ). However, a significant, negative correlation was seen between difference in body mass and Pianka's index of spatial overlap for all data combined ( $r_s = -0.43$ ,  $P = 0.004$ ).

### **Discussion**

Partitioning between carnivores has been documented for a number of species, either temporally (Di Bitetti *et al.*, 2010; Ramesh *et al.* 2012), spatially (Schwartz *et al.* 2010, Vanak *et al.* 2013), and occasionally both (Atwood *et al.* 2011). Our results show carnivores exhibited either temporal or spatial resource partitioning at water points, with a significant, negative association between spatial overlap and difference in body mass between species pairs. Only leopard and black-backed jackal showed both temporal and spatial resource partitioning, whilst some of the species pairings involving cheetah and African wild cat showed no resource partitioning. Most previous studies have focused on two or three species or multiple species of the same family, this study is the first to focus on a guild of eight sympatric carnivore species representing the Canidae, Felidae, Hyaenidae and Mustelidae families.

Temporal partitioning was more common than spatial resource partitioning; of the 28 species pairs, 17 showed temporal partitioning, compared to three showing spatial. Schoener (1974) stated temporal partitioning to be less common than spatial, whilst Hayward & Slotow (2009) predicted temporal resource partitioning being the main mechanism for the coexistence of large African carnivores. Partitioning at spatially fixed resources may represent a special case; Atwood *et al.* (2011) also recorded temporal partitioning between three carnivore species at artificial water points. As the two dominant species were recorded at all and most of the water points it was argued there was little opportunity for spatial partitioning by subordinate species. Romero-Muñoz *et al.* (2010) also suggested spatial rarity of travel routes to explain the wide overlap between puma *Puma concolor* and jaguar *Panthera onca* on roads and trails. As carnivore species occurred at 46% - 100% of water points monitored, limited opportunity for spatial resource partitioning existed, meaning carnivores must use another mechanism to avoid direct carnivore encounters at water.

Differences in the density of water points between the two farms might affect the degree of partitioning seen, for example a higher density of water may be expected to be associated with lower levels of temporal partitioning as more options for spatial partitioning are available. Density of water on Tsirub was almost twice that of KAV, and had a total of 57% of species pairs showing temporal partitioning compared to KAV where 86% of pairings exhibited temporal partitioning. Differences in water density and options for partitioning may also explain why certain species, for example cheetah, were not detected on KAV.

Temporal partitioning occurred on a finer scale than simple nocturnal, crepuscular and diurnal partitioning recorded in other studies (e.g. Crooks & Vuren 1995). All carnivores

showed the majority of activity to occur at night, with the exception of black-backed jackal and honey badger which showed activity throughout both day and night. Harrington *et al.* (2009) recorded American mink *Neovision vision* switching from primarily nocturnal to diurnal behaviour with increasing abundance of competitors. Whilst it may aid temporal partitioning for some species to show diurnal activity at water points, Daan (1981) argued diurnal and nocturnal activity require very different evolutionary adaptations and that recorded shifts in activity patterns are usually seen within the normal diel cycle of the species. Furthermore increased daytime activity may result in increased contact and conflict with humans; carnivores have been shown to shift activity patterns in order to avoid human activity (e.g. Henschel & Ray 2003). In this study cheetah were seen to be primarily nocturnal, although usually described as diurnal (Cooper *et al.* 2007), such a difference in behaviour could be a tactic to avoid persecution.

More species pairs showed temporal partitioning in the form of significant differences in activity patterns rather than complete avoidance of a water point on the same day another carnivore species was present. Data pertaining to the water requirements of carnivores is scarce, with Bothma (2005) recording Kalahari leopards drinking, or having access to moisture in the form of kills, at intervals of 2.5, 2.2 and 1.6 days for males, females without cubs and females with cubs respectively. Metabolic water requirements may halt avoidance of water points on the same day as competitors, alternatively fine scale shifts in temporal activity at water points may be sufficient to minimise risk of intraguild predation.

No partitioning at either scale was seen between cheetah and Cape fox, and between African wild cat and Cape fox, bat-eared fox, leopard or cheetah. Abundance of

competitors has been cited as the most important factor influencing competition between interacting species (Creel, Spong & Creel 2001). Romero-Muñoz *et al.* (2010) suggested low densities of competitors decrease the probability of encounter, making partitioning unnecessary. This may explain the lack of partitioning between species pairings involving cheetah and African wild cat; cheetah only occurred on Tsirub where just two individuals were recorded, whilst African wild cat had a mean photographic rate of just 3.05 events per 100 trap nights.

A significant, negative association between spatial, but not temporal, overlap and difference in body mass between species pairs was recorded. Relative body mass is cited as one of the most important factors influencing interspecific competition (Polis *et al.* 1989). Whilst closely related species are prime candidates for competition (Wilson, 1975), carnivores with relatively large differences in body size are prime candidates for intraguild predation. As there is a risk of intraguild predation for carnivores at water points, a negative association between spatial partitioning and difference in body mass may be expected. Prior to data collection camera traps were positioned and tested so that all movement was believed to trigger, as sample sizes were too small for occupancy analysis, therefore differences in detection rates between species were believed to reflect differences in visits to water rather than in detection probabilities. This result could suggest carnivores are able to partition themselves in a way that incorporates risk of intraguild predation in relation to body-size. However such a result was also expected for temporal resource partitioning, yet no significant association was seen, which may mean resource partitioning is not the reason for the spatial association.

The results of this study show temporal resource partitioning to be the main driver for coexistence of a large number of sympatric carnivore species, and suggest commercial farmlands have the potential to accommodate a diversity of carnivore species, even with limited water resources. As some of the species recorded are of conservation concern these results are encouraging and highlight the importance of farmlands and their management strategies for wildlife. Further studies to investigate partitioning of home ranges around water sources both within and between species would be of interest as home range size variations have been related to water availability (De Beer & van Aarde 2008). As a result density and positioning of artificial water points may influence spatial ecology of species and ultimately the carrying capacity of an area.

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**Table 1:** Circular descriptive statistics for carnivore species across Tsirub and KAV commercial farmlands, southwest Namibia

Variable	Tsirub								KAV					
	Cape fox	Bat-eared fox	Black-backed jackal	Honey badger	Brown hyaena	Leopard	Cheetah	African wild cat	Cape fox	Bat-eared fox	Black-backed jackal	Honey badger	Brown hyaena	Leopard
# of events	19	358	3332	34	265	55	22	51	121	18	1150	12	134	93
Mean vector	01:17	23:48	00:47	02:11	01:23	01:03	02:14	23:23	01:26	22:21	23:57	02:33	01:42	00:18
Length of mean vector	0.69	0.36	0.25	0.08	0.63	0.32	0.45	0.55	0.63	0.80	0.18	0.73	0.58	0.40
Circular variance	0.31	0.64	0.76	0.93	0.37	0.68	0.55	0.45	0.69	0.20	0.82	0.27	0.42	0.60
Standard error of mean vector	00:45	00:22	00:11	06:09	00:13	01:06	01:11	00:37	00:20	00:36	00:26	01:00	00:21	00:39
95% confidence interval	23:48-02:45	23:03-00:33	00:25-01:09	14:06-14:16*	00:56-01:50	22:53-03:12	23:53-04:35	22:09-00:37	00:46-02:06	21:10-23:32	23:05-00:50	00:35-04:31	01:00-02:25	23:00-01:36

\* Oriana cautioned value may be unreliable due to low concentration/uniform distribution

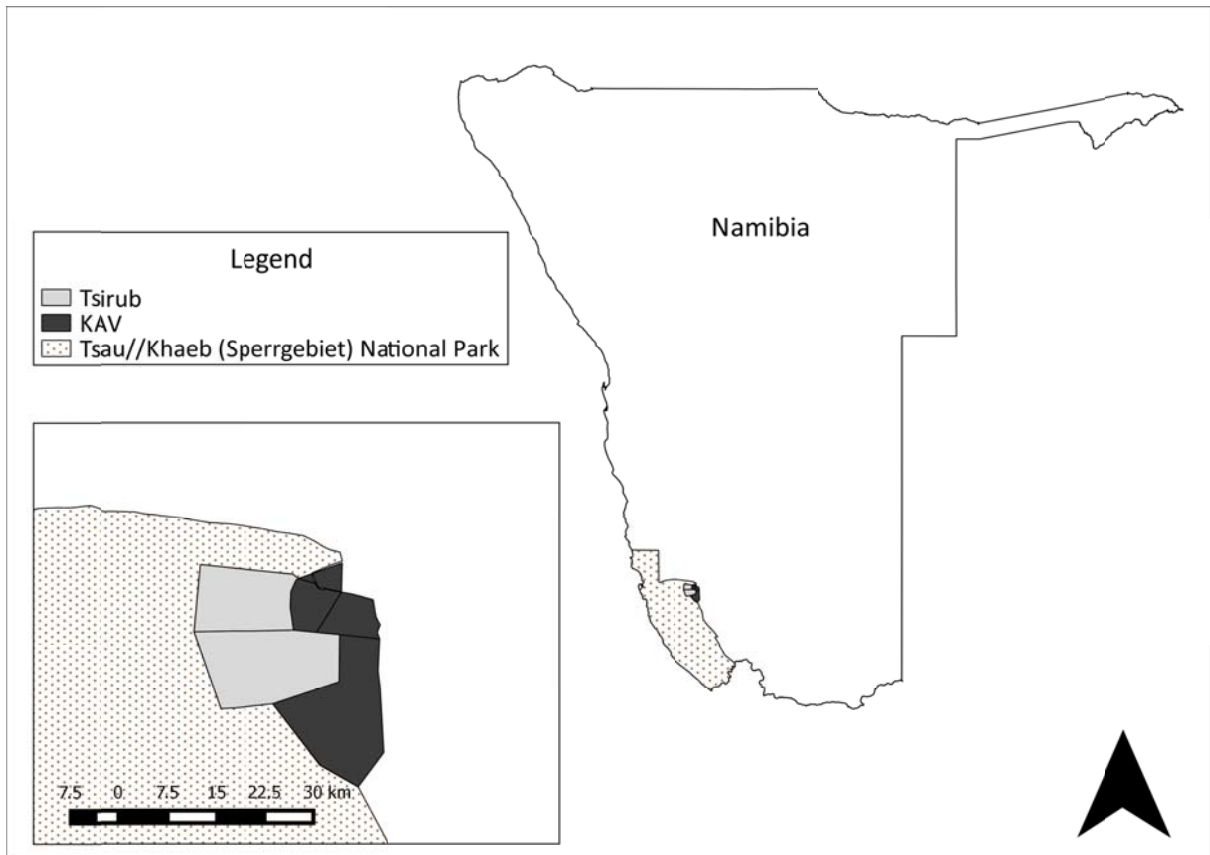
**Table 2:** Results of temporal and spatial resource partitioning analyses between carnivores on commercial farmlands, southwest Namibia. Significant results shown in bold.

Species	Temporal				Spatial
	Activity patterns		Joint occurrence		Spatial avoidance
	Mardia-Watson-Wheeler test		Wilcoxon matched pairs test		Spearman's rank correlation
	Tsirub	KAV	Tsirub	KAV	$r_s$
Cape fox & bat-eared fox	2.34	<b>8.08</b>	12	NA	<b>0.78</b>
Cape fox & black-backed jackal	<b>10.08</b>	<b>52.87</b>	10	NA	0.44
Cape fox & honey badger	<b>20.92</b>	0.07	4	NA	0.16
Cape fox & brown hyaena	0.20	<b>8.00</b>	0	NA	0.28
Cape fox & leopard	<b>6.74</b>	<b>20.09</b>	0	NA	-0.38
Cape fox & cheetah	2.49		4	NA	0.42
Cape fox & African wild cat	0.48		0	NA	-0.18
Bat-eared fox & black-backed jackal	<b>20.53</b>	<b>15.54</b>	15	4	<b>0.61</b>
Bat-eared fox & honey badger	<b>13.54</b>	<b>7.33</b>	11	0	0.38
Bat-eared fox & brown hyaena	<b>12.52</b>	<b>8.83</b>	0	3	0.47
Bat-eared fox & leopard	1.36	<b>8.92</b>	6	0	-0.53
Bat-eared fox & cheetah	1.12		11		<b>0.63</b>
Bat-eared fox & African wild cat	2.33		<b>0</b>		-0.40
Black-backed jackal & honey badger	4.66	<b>10.26</b>	17	4	-0.20
Black-backed jackal & brown hyaena	<b>94.61</b>	<b>43.64</b>	17	7	0.24
Black-backed jackal & leopard	0.76	<b>8.41</b>	5	7	<b>-0.79</b>
Black-backed jackal & cheetah	2.32		20		<b>0.61</b>
Black-backed jackal & African wild cat	<b>10.60</b>		8		-0.53
Honey badger & brown hyaena	<b>36.30</b>	1.63	18	4	0.15
Honey badger & leopard	<b>6.44</b>	<b>6.69</b>	0	1	0.25
Honey badger & cheetah	2.49		<b>0</b>		0.05
Honey badger & African wild cat	<b>12.03</b>		<b>0</b>		-0.07
Brown hyaena & leopard	<b>13.17</b>	<b>6.98</b>	8	9	0.03
Brown hyaena & cheetah	3.64		6		<b>-0.79</b>



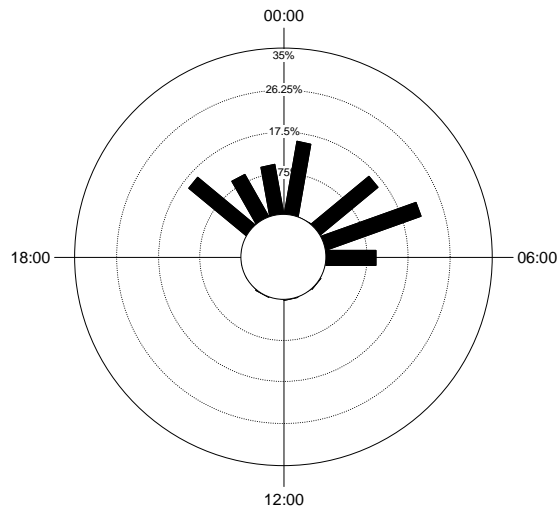
Brown hyaena & African wild cat	1.67	<b>0</b>	-0.11
Leopard & cheetah	1.22	0	<b>-0.79</b>
Leopard & African wild cat	2.75	4	0.12
Cheetah & African wild cat	3.74	5	-0.34

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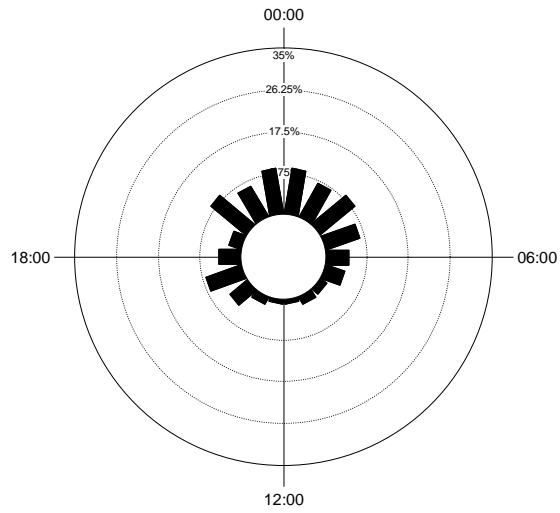


**Figure 1:** Study farms Tsirub and Klein Aus Vista, Karas region, southern Namibia.

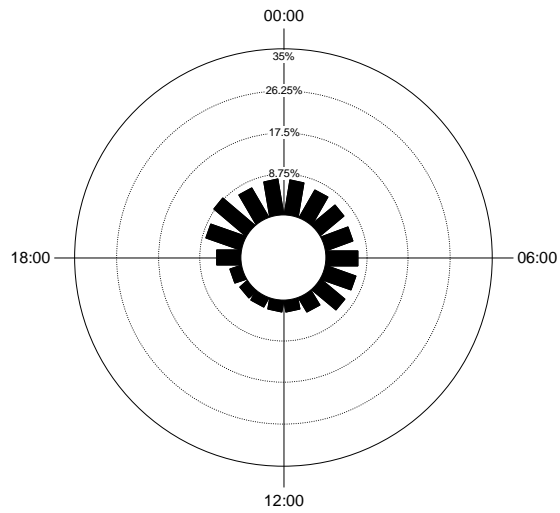
### Cape fox (n=19)



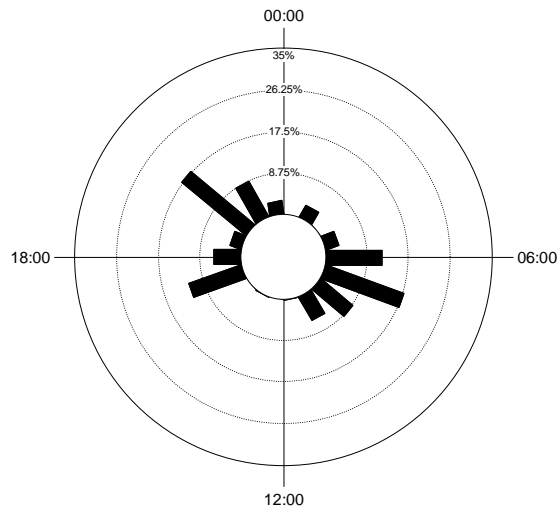
### Bat-eared fox (n=358)



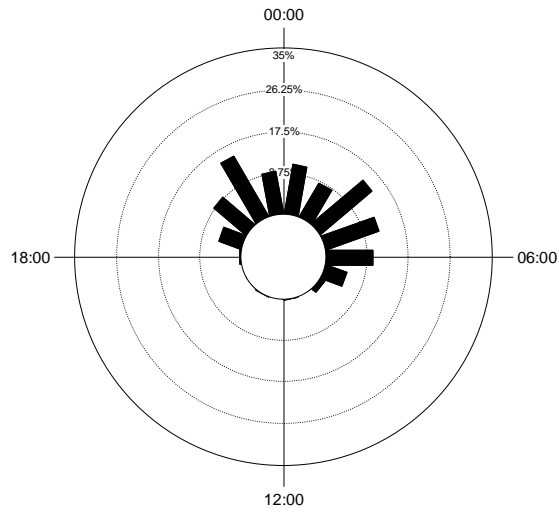
### Black-backed jackal (n=3,332)



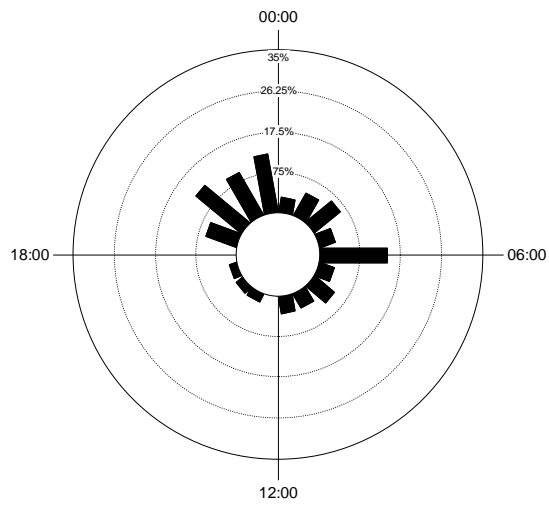
### Honey badger (n=34)

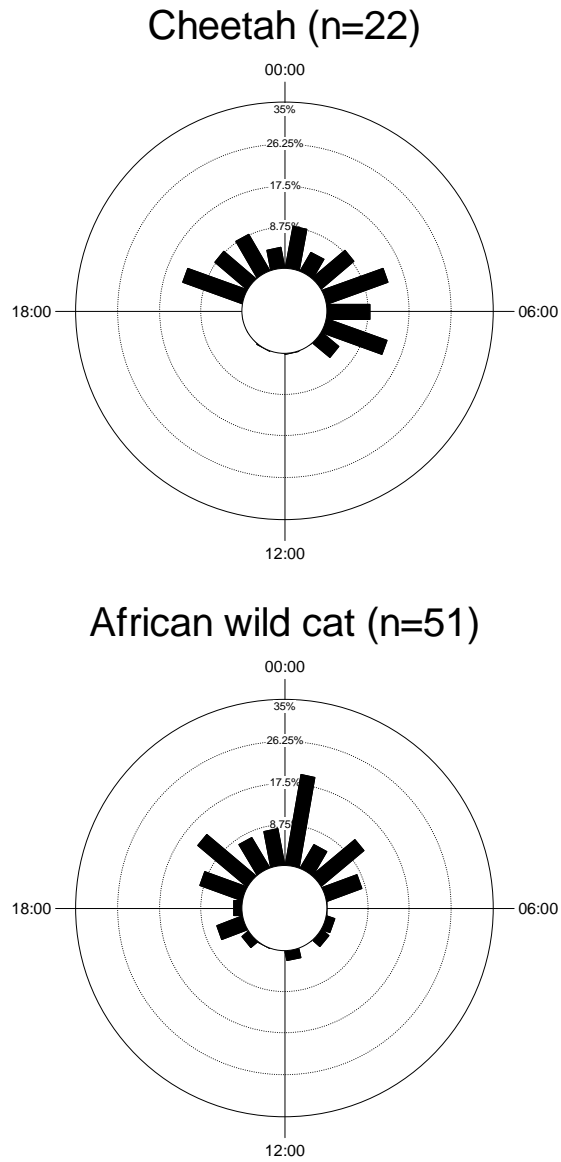


### Brown hyena (n=265)



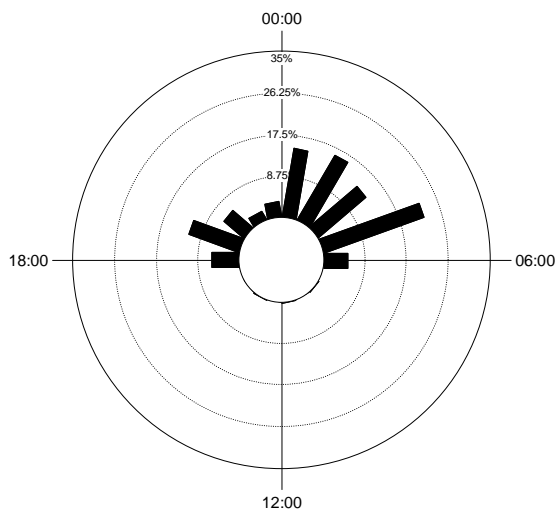
### Leopard (n=55)



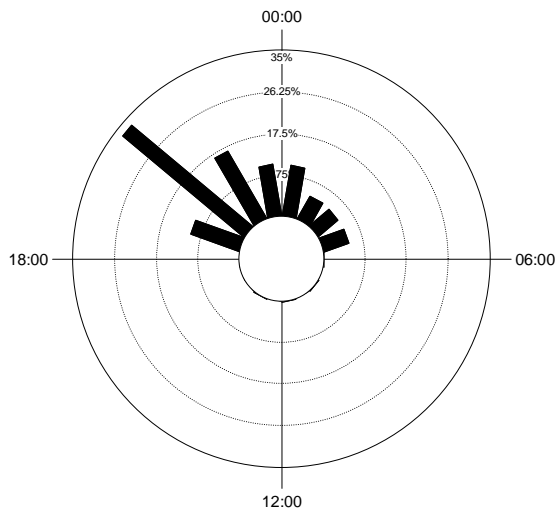


**Figure 2:** Temporal activity of carnivores on Tsirub, black bars show activity seen throughout the 24 hour period, with length of black bars representing the proportion of activity seen. Longer bars represent peak times of activity.

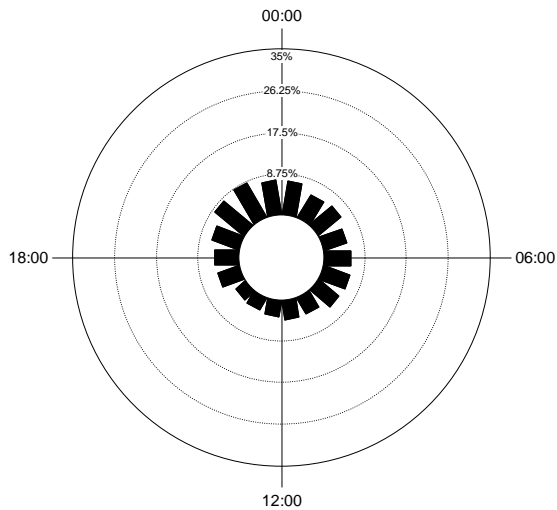
### Cape fox (n=121)



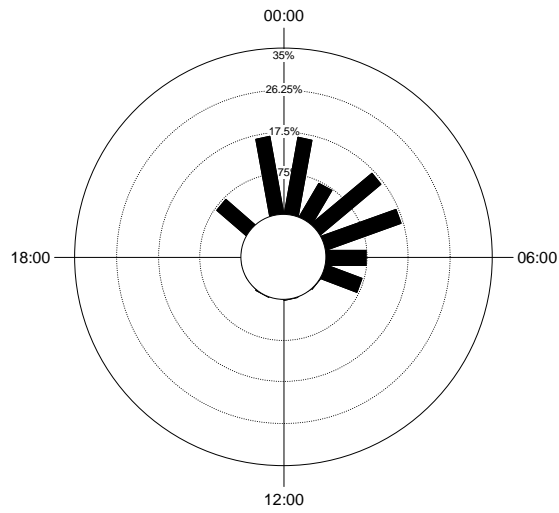
### Bat-eared fox (n=18)



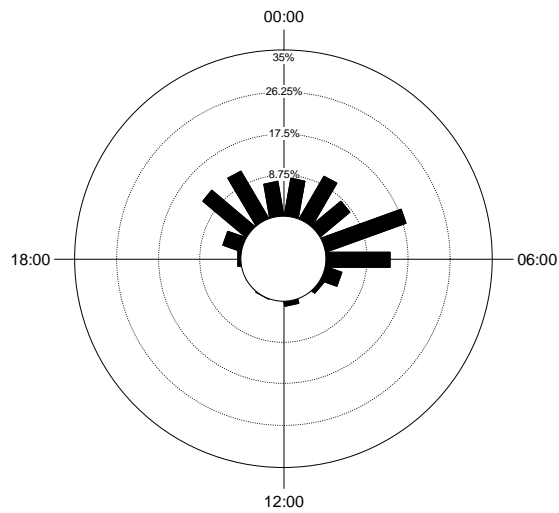
### Black-backed jackal (n=1,150)



### Honey badger (n=12)



### Brown hyena (n=134)



### Leopard (n=93)

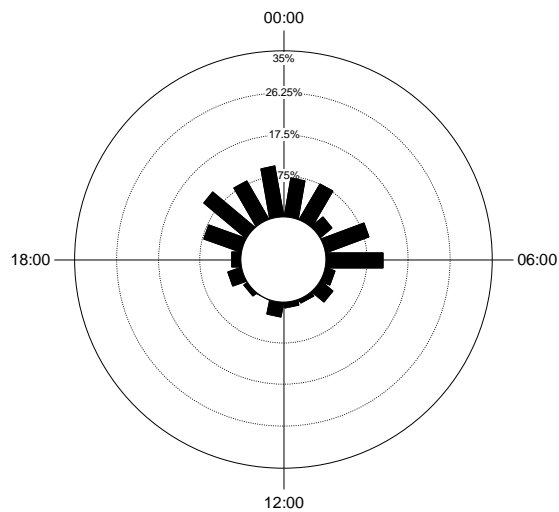


Figure 3: Temporal activity of carnivores on KAV black bars show activity seen throughout the 24 hour period, with length of black bars representing the proportion of activity seen. Longer bars represent peak times of activity. 31