



Novel predators and anthropogenic disturbance influence spatio-temporal distribution of forest antelope species



Yvette C. Ehlers Smith^a, David A. Ehlers Smith^a, Tharmalingam Ramesh^{a,b}, Colleen T. Downs^{a,*}

^a School of Life Sciences, University of KwaZulu-Natal, Private Bag X01, Scottsville, Pietermaritzburg 3209, South Africa

^b Sâlim Ali Centre for Ornithology and Natural History, Anaikatty, Coimbatore, Tamil Nadu, India

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ABSTRACT

Understanding the effects of anthropogenic disturbance on species' behaviour is crucial for conservation planning, considering the extent of habitat loss. We investigated the influence of anthropogenic disturbances including agriculture, urbanisation, protected areas, and the presence of novel predators, on the temporal and spatial behaviour of sympatric forest antelope (*Tragelaphus scriptus*, *Philantomba monticola*, *Sylvicapra grimmia*, and *Cephalophus natalensis*) in an anthropogenic matrix containing forest fragments in the Indian Ocean Coastal Belt of South Africa. We integrated land-use types with camera-trap data and compared activity patterns using circular statistics and occupancy modelling. Antelope species overlapped in temporal and spatial distribution and exhibited diurnal activity for 50% of the time. All species exhibited nocturnal activity for ~25–33% of all observations, except for *C. natalensis*. Nocturnal activity varied between species and land-use types. The predators *Canis familiaris*, *C. mesomelas* and *Caracal caracal* negatively influenced occupancy of *P. monticola*, *S. grimmia* and *C. natalensis*. Humans negatively influenced temporal activity of *P. monticola*, and spatial distribution of *T. scriptus* and *S. grimmia*. *C. familiaris* had an overall negative influence on *S. grimmia*. We found spatial, and to a lesser extent temporal, segregation between species. However, plasticity in activity patterns existed, which varied in response to anthropogenic effects and novel predators.

1. Introduction

Interspecific competition is one of the most important mechanisms of community organisation, as it restricts the number of species within an assemblage through overlapping ecological niches (Tokeshi, 2009). Spatial and temporal segregation of activities acts as a measure of competitive avoidance in sympatric species that exploit a common resource base (Schoener, 1974) or similar functional traits by decreasing the frequency of interspecific encounters (Kronfeld-Schor and Dayan, 2003). How sympatric species spatio-temporally overlap is influenced by their territoriality, body size (Ramesh et al., 2015; Sunarto et al., 2015), physiological adaptations, feeding niche, availability of preferred food items (Sushma, 2006) and predation pressures in a natural ecosystem (Koivisto et al., 2016).

Carnivores are often used as models to understand the effects of competition in community structure, including predator-prey interactions and how predator activity patterns shift around competitors (intra- and interspecific, native and exotic; Harrington et al., 2009; Di Bitetti et al., 2010; Farris et al., 2015; Koivisto et al., 2016) and their

prey (Ramesh et al., 2012). Camera-trap surveys are increasingly employed to assess changes in spatial and temporal patterns (Harmsen et al., 2009; Sollmann et al., 2012; Sunarto et al., 2015), and to model meso-predator release, incorporating landscape-scale factors (Oliveira-Santos et al., 2012; Schuette et al., 2013; Wang et al., 2015). Research often focuses on documenting species' activity patterns using telemetry or global positioning systems (GPS) collaring (Coates and Downs, 2005, 2006; Wronski et al., 2006), but relatively few studies have investigated influences holistically, by incorporating anthropogenic disturbance, land use and predation factors that may influence species' spatial and temporal behaviours.

Global development growth is exponential to support the burgeoning human population, and natural ecosystems are becoming more isolated (Prugh et al., 2008). An increase in the number of physical obstructions, such as fences and road networks, are inhibiting natural behaviours (McAlpine et al., 2006; Baigas et al., 2017). Habitat loss through urban expansion and agricultural extensions is increasing encounter rates between humans, domesticated animals and wildlife (McKinney, 2006; Goad et al., 2014; Johnson et al., 2017; Baigas et al.,

* Corresponding author at: School of Life Sciences, University of KwaZulu-Natal, Private Bag X01, Scottsville, Pietermaritzburg, 3209, South Africa.

E-mail addresses: EhlersSmithY@ukzn.ac.za (Y.C. Ehlers Smith), smithd1@ukzn.ac.za (D.A. Ehlers Smith), ramesh81ngl@gmail.com (T. Ramesh), downs@ukzn.ac.za (C.T. Downs).

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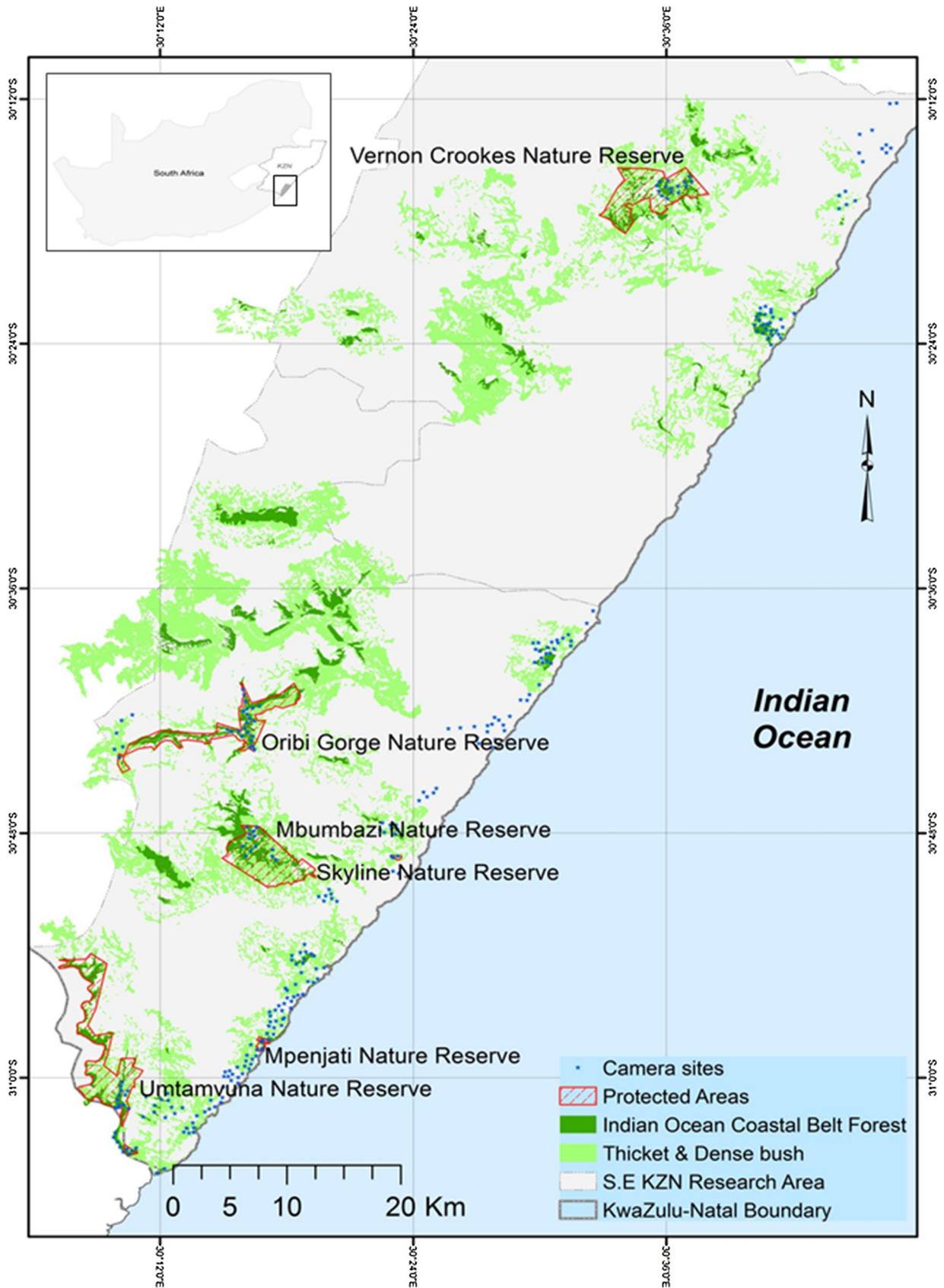


Fig. 1. The study area within the Indian Ocean Coastal Belt of southern KwaZulu-Natal Province, South Africa. The most dominant land-use classifications and survey points are indicated.

2017), which may impede natural behaviours. It is critical to understand the various factors that influence species activity patterns within a changing environment for effective conservation management of disturbed landscapes. Certain areas still maintain certain levels of naturally-occurring, free roaming species despite the reduction in natural habitats and the compartmentalisation of continuous habitats through fencing, whether to demarcate boundaries or to keep animals in or out.

The south-eastern coastal region of KwaZulu-Natal, South Africa (KZN, Fig. 1) does not have large expanses of wilderness areas or an interconnected Protected Area Network, and subsequently no longer contains large charismatic mammalian species. The region's biome, the Indian Ocean Coastal Belt (hereafter termed Coastal Belt), was once dominated by a forest-grassland habitat mosaic (Cooper, 1985; Lawes, 2002; Berliner, 2009; Olivier et al., 2013), but various factors are responsible for the current fragmented distribution of forests, including paleo-climatic change, biogeographic impacts, climatic history, and anthropogenic influences (Lawes, 1990; Eeley et al., 1999; Lawes et al., 2007). Coastal development has resulted in the large-scale conversion of the natural landscape for agriculture, forestry, rural development and exurban expansion within an area that is also a popular holiday destination (Geldenhuys and MacDevette, 1989; Midgley et al., 1997). Forest mammals persist in the habitat patches within the land-use mosaic, despite the anthropogenic land-use change. Free roaming sympatric forest antelope species occur within the region, including *Tragelaphus scriptus* (southern bushbuck), *Philantomba monticola* (blue duiker), *Sylvicapra grimmia* (grey duiker), and *Cephalophus natalensis* (red duiker) following reintroductions from the early 1990's into the region (Venter et al., 2016).

In recent years, *Canis mesomelas* (black-backed jackal) and *Caracal caracal* (caracal) have expanded their range into Coastal Belt Forest patches (Jones, 2016; P. Massyn, Ezemvelo KZN Wildlife, pers. comm.). Both species are widespread, highly adaptable, medium-bodied, nocturnal carnivores (Rowe-Rowe, 1978, 1992; Kaunda and Skinner, 2003; Skinner and Chimimba, 2005; Humphries et al., 2015). Both are opportunistic predators, capable of exploiting a wide variety of prey and forage items (Avenant and Nel, 1998; Kaunda and Skinner, 2003; Humphries et al., 2015). Caracal can hunt larger-bodied mammals in comparison with black-backed jackal (Kok and Nel, 2004; Melville et al., 2004). These carnivores are novel predators to the region, but may be considered major predators (Humphries et al., 2015), and in the absence of leopard (*Panthera pardus*; not detected within our camera-trap surveys) the apex predator within these forest patches. Caracals, in particular, flourish in the absence of large predators and have expanded their historic distribution from the western highlands of KZN to its south coast and therefore overlap considerably with forest-duiker distributions within southern KZN's coastal forests (Rowe-Rowe, 1992; Jones, 2016). Exurban expansion has introduced domestic dogs (*Canis familiaris*), which may influence forest mammals' behaviour. Free-ranging dogs may interact with wildlife in a variety of ways (Lessa et al., 2016): they are predators (Srbek-Araujo and Chiarello, 2008), potential prey items (Athreya et al., 2016), competitors (Vanak and Gompper, 2009), disease vectors (Viana et al., 2015), or disturbance factors (Doherty et al., 2017). Though their impact is as a direct result of human action (or lack thereof), it is difficult to classify them as a direct predation threat or as an anthropogenic disturbance. Despite the potential influence that domestic dogs could have on wildlife, their direct influence on ungulates and native predators within Africa (except as disease vectors) is not well documented (Hughes and MacDonald, 2013; Doherty et al., 2017).

Blue and red duikers are classified as vulnerable, and near-threatened, respectively within South Africa (Ehlers Smith et al., 2016; Venter et al., 2016). Anecdotal declines have been linked to the expansion of caracal into forested regions. This scenario provided the opportunity to investigate spatial and temporal activity patterns between sympatric browsing antelope species within an anthropogenic

land-use mosaic of varying levels of human disturbance, and the influences therein of novel meso-predators in the absence of large carnivores. Over a two-year period, within the Coastal Belt of southern KZN, we hypothesised that i) both abiotic (land use types, anthropogenic disturbances and seasonal effects) and biotic factors (novel predators) would influence activity patterns and spatial overlap of sympatric antelope species, and that ii) niche separation between forest antelope would be facultative, through spatial and temporal segregation of activities. To test our hypotheses we assessed the influence of a) seasonality on activity patterns of forest ungulates, considering our study sites fell within sub-tropical latitudes; b) anthropogenic landscape-scale factors, such as agriculture and urban development on temporal activity patterns of antelope and novel predators, and c) land-use and anthropogenic disturbance, in combination with predator pressures, on the spatial distribution (i.e. site occupancy) of antelope species.

2. Material and methods

2.1. Study area

Our study area was a ~120 km-long x 30 km-wide strip of the Coastal Belt in the southern coastal region of KZN, South Africa, between the Umkomazi River in the north (30°12'1" S 30°48'4" E) and the Umtamvuna River in the south (31°04'46.69" S, 30°11'39.87" E; Fig. 1). Temperatures ranged between 4–32 °C throughout the region, and daily temperatures peaked around mid-day. Rainfall occurs year-round but is more frequent during the summer (November–February). The annual rainfall varies between 440–1400 mm, and the climate is sub-tropical. (Mucina and Rutherford, 2011).

Two suitable habitat classes were within our study region: 1) Indian Ocean Coastal Belt Forest (comprising of Coastal Scarp and Lowland Coastal Forest) and 2) Coastal Thicket/Dense Bush (hereafter Dense Bush; Eeley et al., 1999; Mucina and Rutherford, 2011; GeoTerraImage, 2014), which has habitat structures and plant composition that resemble secondary forest regeneration (Ehlers Smith et al., 2017). These habitat patches are nested within a heterogeneous landscape of anthropogenic and natural land-use types. There are four large (forest) nature reserves within the study region that are managed by the local wildlife authority (Ezemvelo KZN Wildlife): Oribi Gorge; Mbumbazi; Umtamvuna, and Vernon Crookes Nature Reserves, and two smaller reserves: Skyline and Mpenjati.

2.2. Study species

The blue duiker is the smallest antelope of the region (Table 1). Pairs hold strict territories (Bowland and Perrin, 1995). Food items include tannin-rich, mature fallen leaves, growing shoots, flowers, and fruits (Jarman, 1974; Field, 1975; Jarman and Sinclair, 1979; Spinage, 1986; Bowland, 1990). The high tannin leaf preference is an indication that blue duikers are high Carbon:Nutrient dietary selectors (a diet consisting of high total non-structural carbon content; Seydack and Huisamen, 1999). This degree of selectivity implies a highly specialised diet. Blue duikers are considered to be diurnal, with some activity peaks at dawn and dusk, but also spend a large proportion of the day resting or ruminating (Bowland and Perrin, 1995).

The red duiker is the "intermediate" duiker of the region, large than blue duiker, but smaller than the grey duiker (Table 1). They are considered to be diurnal but spend 24–69% of the day resting or ruminating (Bowland and Perrin, 1995). Unlike the blue duiker, they are not territorial (Bowland and Perrin, 1995). Food items include fallen leaves, fruits, flowers and fine stems of low-growing shrubs (Bowland and Perrin, 1998).

The grey duiker has general habitat requirements, reflected in its broad distribution range (Skinner and Chimimba, 2005). Unlike the true forest duiker, grey duikers are not reliant on forest habitats and are

Table 1

Species attributes derived from published literature associated with the antelope species naturally occurring within the IOCB region (Elder and Elder, 1970; Jarman, 1974; Field, 1975; Waser, 1975; Jarman and Sinclair, 1979; Spinage, 1986; Bowland, 1990; Wronski et al., 2006).

	Blue duiker		Red duiker		Grey duiker		Southern bushbuck	
	Male	Female	Male	Female	Male	Female	Male	Female
Mean weight (kg)	4.1 (range: 3.2–4.9)	4.6 (range: 3.4–5.9)	11.7 (range: 9.8–12.6)	11.9 (range: 10.3–13.2)	17.6 (range: 15.3–21.2)	17.8 (range: 10–25.4)	60 (range: 40–80)	42.5 (range: 25–60)
Mean home range (ha)	0.75	0.75	2–15	2–15	21 (range: 12.1–27)	21 (range: 12.1–27)	33.9 (range: 25.2–43.3)	12 (range: 6.3–18.8)
Activity pattern	Diurnal (peaks at dawn and dusk)		Diurnal (peaks at dawn and dusk)		Diurnal (peaks at dusk)		Nocturnal / Diurnal (peaks at dawn)	
Diet	Specialised concentrate selective browser		Concentrate selective browser		Concentrate browser		Selective browser	
Body size (relative to other study ungulates)	Small		Medium		Medium		Large	

the largest of the three-duiker species within the study region (Table 1). In areas of high disturbance, they become more nocturnal (Skinner and Chimimba, 2005). Their mean home range is ~21 ha but may vary from 12.1 to 27.4 ha depending on the time of the year (Allen-Rowlandson, 1986). Food items include leaves, twigs, flowers, fruits, seeds, tubers and bark, and also raid cultivated crops, timber seedlings and ornamental gardens (Hofmann, 1973; Allen-Rowlandson, 1986).

Although southern bushbuck is a medium-sized antelope, it was the largest naturally occurring forest antelope within the study region (Skinner and Chimimba, 2005). Their diet consists of leaves, twigs, buds, flowers and fruits (Hofmann, 1973; Allen-Rowlandson, 1986; Skinner and Chimimba, 2005). They are low carbon/nutrient dietary selectors, the inverse to blue duiker. All four species are classified as browsers; however, they differ in terms of body size and dietary preference (Table 1).

2.3. Survey site selection

We identified all suitable habitat patches of Coastal Belt Forest and Dense Bush within the study region, using the Geographic Information System (GIS) program, ArcGIS v10.2 (ESRI, 2011), as described in the latest land-cover GIS layer map (GeoTerraImage, 2014). We overlaid a 400 m x 400 m grid over each patch that was logistically accessible with the relevant permits and permissions, and allocated survey points at the intersection of grid lines. This guaranteed proportional representation across habitat patches (Ehlers Smith et al., 2017, 2018). We projected survey locations onto a Global Positioning System (Garmin GPSmap 62; Garmin© USA) as a navigational aid for survey-site selection in the field. Individual survey locations within habitat patches were subsequently classified according to surrounding land-use type: farmland, residential or nature reserve. Each land-use classification was ordered according to its level of disturbance, based on the anthropogenic infrastructure present. As a proxy for infrastructure we used the number of roads within a 1 km buffer of each selected site; quantifying how differently roads were used (e.g. volume of traffic and hours of utilisation) was problematic. However, roads act a proxy for anthropogenic infrastructure or human disturbance level. An alternative proxy is number of households per km² under the assumption that the more houses that need to be linked, the more roads there will be, but these data are not available for our study region area. Distances between farm houses are greater than those within residential areas and roads on reserves are access roads, which allows for road density to be ranked accordingly by level of disturbance.

2.4. Camera trap surveys

We deployed 30 infrared motion-detection camera traps (Moultrie®

M-880, EBSCO Industries, Inc., U.S.A) during each survey period to assess presence and activity patterns of antelope and carnivore species at each survey location within the Coastal Belt Forest and Dense Bush habitat patches. We deployed the camera traps for a minimum of 21 days for 24 h/day, utilising a motion triggered delay of 30 s. The camera traps were attached to a robust tree at an approximate height of 30 cm above ground on a game trail, or on hiking trail where available, with an open glade to allow the camera sensor its maximum range. For full methods see Ramesh and Downs (2013, 2015) and Ehlers Smith et al. (2017, 2018). Surveys were conducted between June 2014 and May 2016, resulting in one spring-summer survey (September – February) and one autumn-winter survey (March – August) for each camera-trap site.

2.5. Analyses: activity patterns – diel phase selection

Each individual photograph provided information on date and time that was used to assess the temporal and seasonal activity patterns of antelope and predator species over a 24-h period. To avoid pseudo-replication, and to align with instantaneous scan sampling methods designed to quantify activity budgets and behavioural ethograms, we only considered the first photograph of an animal within a 5-min interval as an independent record (Altmann, 1974; Pullin et al., 2017).

We classified animal activity patterns based on the daily diel phases. Diurnal activities were classed as daytime activities (one hour after sunrise to one hour before sunset), and nocturnal activities as night-time activities (one hour after sunset to one hour before sunrise). Cathemeral activities were classified where no differences were observed between diurnal and nocturnal activity patterns. Crepuscular activities were assigned as showing peak activity at dawn (from one hour before to one hour after sunrise), and dusk (from one hour before to one hour after sunset) (Michalski and Norris, 2011; Oliveira-Santos et al., 2012; Ikeda et al., 2016). We estimated the mean annual sunrise (06:00) and sunset (18:00) for our study area. The mean autumn-winter sunrise (06:56) and sunset (17:05) times are based on the shortest day (21 June) and the mean spring-summer sunrise (04:52) and sunset (18:59) are based on the longest day (21 December), as provided by © 2016 South African Astronomical Observatory.

We used the non-parametric Mardia-Watson-Wheeler test (M-W-W test) within the circular statistics program Oriana (Kovach, 2011) to assess the difference in activity patterns of individual species between seasons (spring-summer and autumn-winter) and different land-use classifications (farmland, nature reserves and residential areas). Significant differences between vector lengths would result in a high W statistic and a subsequent rejection of the null hypothesis of identical distributions (Kovach, 2011). We applied non-parametric Watson's U tests to assess whether the distribution of records for each species

throughout the day was random. A high U value and a low probability ($P < 0.05$), indicates non-uniformity within the data (Kovach, 2011), which provides evidence for a specific temporal activity pattern.

To assess the overall activity pattern favoured by each species within each land-use classification, we utilised The Manly's Selectivity Measure, using the package 'adehabitats' (Calenge, 2006) within the program R (R Core Team, 2013). It calculates w_i (the selection ratio) and B_i (the Manly's Selectivity Index) which enabled direct comparison between selection ratios within each resource unit (time phase) and can be interpreted as the probability that for any selection event, an animal would choose a specific time phase over all others (Manly et al., 2007). A w_i value greater than 1 indicated a positive selection for the phase, less than 1 indicated avoidance of the phase and ~ 1 indicated that the time phase was used in proportion to its availability and no selection was noted. We calculated each species' preference for, or avoidance of, each diel phase based on the selection ratio w_i and tested for each species in each habitat using a chi-square test with Bonferroni adjustments. Time phases with the highest Manly's Selectivity Index (B_i) were considered key activity periods (Manly et al., 2007).

2.6. Analyses: temporal overlap – seasonal & land use

We converted all times of photographs captured to radians to calculate the overlap coefficient (Δ) for comparison of diel activity patterns between species, based on kernel density functions. These coefficients ranged between 0 (indication of no overlap) to 1 (indication of identical activity distributions). We obtained 95% confidence intervals for each coefficient by performing 1000 bootstrap iterations. The package 'overlap' (Meredith and Ridout, 2014) within the statistical program R (R Core Team, 2013) was utilised. Care is needed when comparing coefficients of overlap between different study areas, periods of time or varying degrees of heterogeneity, because pooled data give higher estimates of overlap than the original, unpooled data (Ridout and Linkie, 2009). The package overlap provides coefficient estimates based on sample size, where the minimum sample size is 50. Capture rate over a 24 h period for each species was tested through Spearman's rank correlation coefficient tests after determining non-normal distribution of the data-set's means, to assess significant temporal time overlap among antelope species and between antelope and predators, and human presence. For this we pooled our data across land-use types to avoid sample size issues. We compared overlap for each antelope species according to season. The Spearman's rank correlation coefficient test was carried out using the program SPSS version 24 (IBM Corp., 2013).

2.7. Analyses: spatial overlap

We created a binary (presence:absence) detection history of each camera for each antelope, predator species (native and domestic) and human from the 21-day survey period (each day was represented as a calendar day, starting at midnight for a full 24-h period). We contracted three days to constitute a "survey day" for each species at each camera trap site for each sampling cycle, respectively (MacKenzie et al., 2006). This results in a 7-day detection history of each camera, thus increasing the detection probability of each survey period (as per Ramesh and Downs, 2015). Using each predator's detection history, we repeated a single season occupancy model for each sampling cycle using the package 'unmarked' (Fiske and Chandler, 2011) within the program R (R Core Team, 2013). We incorporated land-use covariates extracted from the latest land-cover GIS layer map (GeoTerraImage, 2014) within a 1-km buffer: % farmland (F) and % urban land (U), as well as nature reserve (R) as a binary variable and depending on whether a camera-trap site was situated within a nature reserve (1) or not (0). We calculated the occupancy probability (Ψ) for each predator species at each camera trap site as following: $\Psi (F + U + R)$, $P(.)$, whilst keeping the detection probability constant. The individual predator species

occupancy probability was then incorporated alongside the land-use covariates, into single species occupancy models for each antelope species, to estimate the influence of predators (both natural and domestic) on the occupancy (Ψ) and detection probability (P) of the antelope species. A maximum model was created, combining all covariates (COV), and we modelled the influence of each covariate individually and in combination on Ψ while maintaining P as constant, and vice versa, e.g., $\Psi (COV1)$, $P (.)$ or $\Psi (.)$, $P (COV1 + COV2)$. We then combined various covariates on Ψ and P concurrently, e.g., $\Psi (COV1 + COV2)$, $P (COV1 + COV2)$; thus, we calculated the influence of each covariate separately or in combination with other covariates, on both Ψ and P (Ramesh and Downs, 2015). We assessed model fit using a Pearson's chi-square goodness-of-fit, using 1000 parametric bootstraps, where values > 0.95 and < 0.05 indicated poor fit (MacKenzie and Bailey, 2004; Fiske and Chandler, 2011; Tobler et al., 2015; Wright et al., 2016). The top model that best described the influence of a covariates on Ψ and P was determined using the lowest Akaike's Information Criterion (AIC) value, while the simplest model can be ascribed to the constant parameters $\Psi (.) P (.)$ (Burnham and Anderson, 2002; Ramesh and Downs, 2014).

3. Results

We incorporated only 250 out of 270 survey sites into the analysis across the two survey cycles, because of camera theft or change in land ownership between seasons/years. Of the 250 sites, 69 survey sites were classified as farmland, 97 as residential and 84 as nature reserves, according to the land-use type in which the survey patch resided. We considered residential areas to have the highest level of disturbance based on the anthropogenic infrastructure present, followed by farmland and nature reserves (km of road per km² of land-use area: residential area = 65.71; farm = 26.71; nature reserve = 0.06). After removing duplicate photographs of individuals within a 5-min time-frame, 21 days of camera trapping at 250 sites yielded 5250 photographs. The number of photographs varied according to land-use type for each antelope species (Appendix A) The following number of independent photographs of predators was recorded: Black-backed jackal (Pooled = 79, Farm = 50, Residential = 3, Nature Reserve = 26); Caracal (Pooled = 104, Farm = 23, Residential = 2, Nature Reserve = 79), and Domestic dog (Pooled = 154, Farm = 41, Residential = 95, Nature Reserve = 18). For a full list of species, including other meso-carnivores encountered see Ehlers Smith et al., 2017, 2018).

3.1. Activity patterns - diel phase selection

The Watson's U test result indicated that the activities of ungulate species across all land-use types differed from the uniform distribution ($P < 0.005$), indicating preference for specific diel phases (Appendix A–E). The percentage of nocturnal activities differed between species and across land-use classifications. Of the four antelope species, red duiker was the least active at night. Nocturnal activity was more prevalent within farmland and residential settings compared with nature reserves, except for southern bushbuck, which exhibited higher activity (26%) within nature reserves (Table 2; Appendix C). Dusk was the key activity period for all three-duiker species (Table 2). Southern bushbuck activity periods varied between dawn and dusk based on the land-use type (Table 2). Dawn and dusk diel phases were positively selected across all land-use types for blue and red duiker, but the Manly's selectivity index (B_i ; Table 2; Appendix B and E) indicated that dusk was the key activity period. Grey duiker was the only species for which the diurnal phase was the key activity, but only within nature reserves (Appendix D).

A higher percentage of total diel activities were noted within the diurnal, dawn and dusk phases of caracal and black-backed jackal activities, where dawn and dusk diel phases were found to be key activity

Table 2

Activity pattern of target species at survey sites: % (μ) = % of total diel activity (μ). A w_i (the selection ratio) value greater than 1 indicates a positive selection for the diel phase, less than 1 indicates avoidance of the phase and ~ 1 indicates that the time phase was used proportionally to its availability and no selection was noted. Time phases with the highest Manly's selectivity index (B_i) were considered key activity periods. (Significant P – values are based on Bonferroni level = 0.0125).

Sps.	Diel	Pooled					Farm					Residential					Nature reserve				
		% μ	w_i	SE	P	B_i	% μ	w_i	SE	P	B_i	% μ	w_i	SE	P	B_i	% μ	w_i	SE	P	B_i
BB	Noc	23	0.56	0.01	0.00	0.12	23	0.43	0.02	0.00	0.08	22	0.54	0.02	0.00	0.11	26	0.62	0.03	0.00	0.14
	Di	49	1.23	0.02	0.00	0.25	54	1.15	0.02	0.00	0.20	50	1.19	0.02	0.00	0.24	51	1.23	0.03	0.00	0.27
	Da	11	1.63	0.06	0.00	0.34	12	1.93	0.08	0.00	0.34	15	1.83	0.08	0.00	0.36	11	1.38	0.11	0.00	0.30
	Du	17	1.44	0.05	0.00	0.30	11	2.19	0.08	0.00	0.38	13	1.52	0.08	0.00	0.30	12	1.39	0.11	0.00	0.30
BD	Noc	23	0.43	0.01	0.00	0.08	18	0.43	0.02	0.00	0.08	18	0.44	0.01	0.00	0.08	17	0.41	0.02	0.00	0.07
	Di	51	1.12	0.01	0.00	0.19	48	1.15	0.02	0.00	0.20	46	1.10	0.01	0.00	0.19	50	1.21	0.03	0.00	0.22
	Da	14	1.98	0.04	0.00	0.34	16	1.93	0.08	0.00	0.34	17	2.04	0.05	0.00	0.35	15	1.81	0.10	0.00	0.33
	Du	12	2.24	0.04	0.00	0.39	18	2.19	0.08	0.00	0.38	19	2.29	0.05	0.00	0.39	18	2.13	0.10	0.00	0.38
GD	Noc	31	0.55	0.03	0.00	0.11	13	0.32	0.05	0.00	0.07	27	0.65	0.04	0.00	0.12	22	0.53	0.17	0.01	0.14
	Di	44	1.17	0.04	0.00	0.23	61	1.47	0.07	0.00	0.31	43	1.03	0.05	0.52	0.19	64	1.53	0.19	0.01	0.41
	Da	14	1.36	0.12	0.00	0.27	10	1.23	0.21	0.28	0.26	12	1.43	0.15	0.00	0.27	8	1.00	0.55	1.00	0.27
	Du	11	2.03	0.14	0.00	0.40	15	1.80	0.25	0.00	0.37	18	2.19	0.17	0.00	0.41	6	0.67	0.46	0.47	0.18
RD	Noc	1	0.55	0.03	0.00	0.11	10	0.23	0.02	0.00	0.05	15	0.37	0.05	0.00	0.07	0	0.00	0.00	0.00	0.00
	Di	96	1.17	0.04	0.00	0.23	63	1.50	0.04	0.00	0.30	56	1.33	0.06	0.00	0.26	0	0.00	0.00	0.00	0.00
	Da	1	1.36	0.12	0.00	0.27	13	1.54	0.14	0.00	0.31	14	1.67	0.22	0.00	0.32	0	0.00	0.00	0.00	0.00
	Du	2	2.03	0.14	0.00	0.40	15	1.78	0.15	0.00	0.35	15	1.83	0.23	0.00	0.35	0	0.00	0.00	0.00	0.00
BJ	Noc	18	0.67	0.12	0.01	0.10	32	0.77	0.16	0.14	0.13	0	0.00	0.00	0.00	0.00	23	0.55	0.20	0.02	0.08
	Di	47	0.67	0.12	0.01	0.10	30	0.72	0.16	0.07	0.12	0	0.00	0.00	0.00	0.00	27	0.65	0.21	0.09	0.09
	Da	17	2.13	0.52	0.03	0.32	14	1.68	0.59	0.25	0.28	33	4.00	3.27	0.36	0.33	23	2.77	0.99	0.07	0.39
	Du	19	3.19	0.60	0.00	0.48	24	2.88	0.73	0.01	0.48	67	8.00	3.27	0.03	0.67	27	3.23	1.04	0.03	0.45
CC	Noc	11	0.74	0.11	0.02	0.15	43	1.04	0.25	0.86	0.26	50	1.20	0.85	0.81	0.17	27	0.64	0.12	0.00	0.13
	Di	61	1.06	0.12	0.60	0.22	39	0.94	0.24	0.80	0.23	0	0.00	0.00	0.00	0.00	47	1.12	0.14	0.36	0.23
	Da	13	1.73	0.41	0.08	0.36	13	1.57	0.84	0.50	0.39	0	0.00	0.00	0.00	0.00	15	1.82	0.49	0.09	0.37
	Du	15	1.27	0.36	0.46	0.26	4	0.52	0.51	0.35	0.13	50	6.00	4.24	0.24	0.83	11	1.37	0.43	0.39	0.28
DD	Noc	28	0.27	0.06	0.00	0.07	5	0.12	0.08	0.00	0.02	16	0.02	0.09	0.00	0.11	0	0.00	0.00	0.00	0.00
	Di	28	1.73	0.09	0.00	0.43	61	1.46	0.18	0.01	0.26	74	0.26	0.11	0.00	0.52	89	2.13	0.18	0.00	0.62
	Da	18	0.86	0.25	0.57	0.21	17	2.05	0.71	0.14	0.36	3	0.36	0.22	0.00	0.11	6	0.67	0.65	0.61	0.19
	Du	27	1.17	0.29	0.56	0.29	17	2.05	0.71	0.14	0.36	7	0.36	0.32	0.72	0.26	6	0.67	0.65	0.61	0.19
H	Noc	11	0.02	0.01	0.00	0.01	3	0.08	0.06	0.00	0.03	1	0.02	0.01	0.00	0.01	1	0.01	0.01	0.00	0.01
	Di	72	2.30	0.01	0.00	0.84	92	2.20	0.08	0.00	0.77	94	2.26	0.03	0.00	0.77	97	2.33	0.01	0.00	0.88
	Da	7	0.24	0.04	0.00	0.09	0	0.00	0.00	0.00	0.00	2	0.29	0.09	0.00	0.10	2	0.22	0.05	0.00	0.09
	Du	10	0.19	0.04	0.00	0.07	5	0.59	0.33	0.22	0.21	3	0.35	0.10	0.00	0.12	1	0.09	0.03	0.00	0.03

Noc = Nocturnal; Di = Diurnal; Da = Dawn; Du = Dusk.

phases, respectively. The diurnal phase was calculated as the key activity period for both humans and domestic dogs.

3.2. Temporal overlap – seasonal & land use

The results from the M-W-W test for nonparametric data indicated that the distribution of activities between seasons was equal for all species, except for red duiker (M-W-W test, $W = 9.91$; $P = 0.01$). Red duiker activity patterns varied significantly between seasons, with the lowest $\Delta = 0.68$ (CI: 0.61-0.76; Fig. 2), compared with other sympatric antelope. This was apparent when comparing the number of observations for each season (Autumn/Winter = 1092 and Spring/Summer = 134) for red duiker. When contrasting differences in activity patterns between seasons, bushbuck activity patterns varied the least ($\sim 7\%$ difference between seasons), $\Delta = 0.93$ (CI: 0.91-0.95; Fig. 2). Grey duiker and blue duiker displayed similar seasonal patterns, $\Delta = 0.86$ (CI: 0.81-0.91) and $\Delta = 0.82$ (CI: 0.81-0.84) respectively.

The estimated Δ for each pairwise species comparison varied between land-use type in the amount of overlap (Table 3; Fig. 3). Blue duiker (M-W-W test; farm and nature reserve: $W = 7.33$; $P = 0.03$; residential and nature reserve $W = 14.92$; $P < 0.001$), grey duiker (M-W-W test; farm and nature reserve: $W = 12.87$; $P < 0.001$; residential and nature reserve $W = 6.06$; $P = 0.05$), and domestic dog (M-W-W test; farm and nature reserve: $W = 6.03$; $P = 0.05$; residential and nature reserve $W = 7.92$; $P = 0.02$), exhibited different distributions of circadian activity between land-use types. Similarly, when comparing overlap between the sympatric antelope (Fig. 3; Table 3) and between antelope and predators/humans there was a significant difference between coefficients (antelope: $t = 69.37$; with predators/humans:

$t = 27.47$; $P < 0.0001$) respectively.

There was a large degree of overlap between the various antelope species and similarities in activity peaks (relating to diel phase selection; Table 3; Fig. 3). Based on the Δ estimated (Fig. 4–7), the overlap patterns between each antelope with carnivores and humans varied greatly between land-use type, though only significantly for blue duiker, grey duiker and domestic dog. The patterns of overlap were further explored according to seasonality for red duiker within Appendix F.

3.3. Spatial overlap

The analyses were limited to sites that fell on farmland (69) and nature reserves (84), because of low predator occupancy within residential areas ($n = 5$). Humans were present at 51 sites, and caracal was present at 39, black-backed jackal was present at 29, and domestic dog at 23. For the final modelling, we incorporated the calculated occupancy for each of humans (H), caracal (C), black-backed jackal (J), and domestic dog (D) at each site in addition to land-use covariates % farmland (F) and whether the site was classified as a nature reserve (R).

We calculated top models for each species and their mean untransformed parameter estimates of Ψ and P (Tables 4 and 5) for each survey cycle, respectively. There were marked differences in Ψ and P for individual species between survey cycles. Southern bushbuck had overall the highest occupancy throughout the study region ($\Psi = 0.87 \pm 0.05$) and red duiker exhibited the lowest ($\Psi = 0.16 \pm 0.06$). The number of covariates used within the models ranged between 4 and 9. Those that featured most often in the occupancy estimation were jointly domestic dog and caracal, followed by

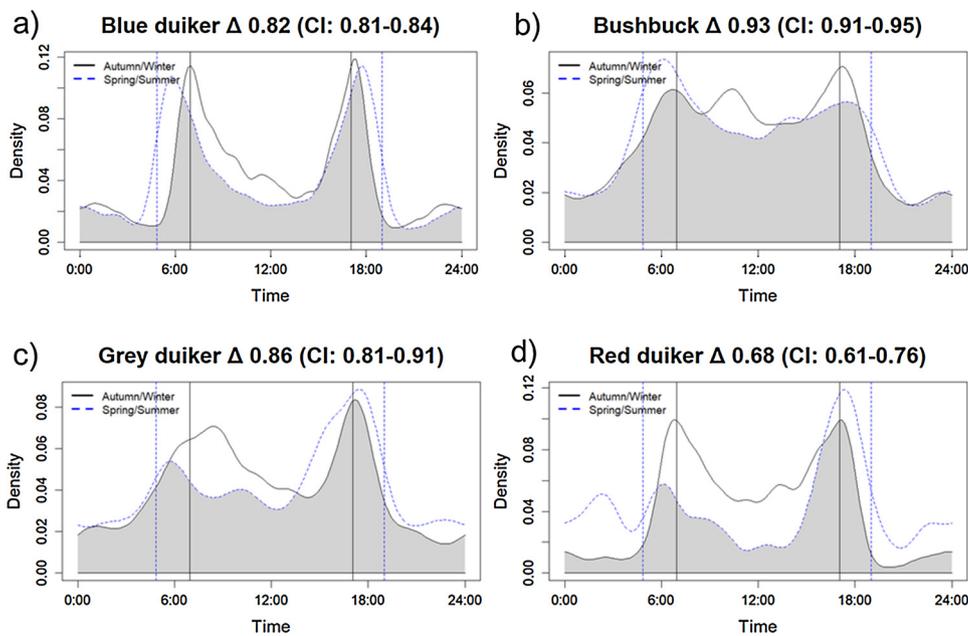


Fig. 2. Ungulate activity curves by season. Solid line = Autumn/Winter and dotted line = Spring/Summer: a) blue duiker; b) southern bushbuck; c) grey duiker; d) red duiker across all land-use types. The coefficient of overlapping equals the area below both curves, shaded grey in this diagram. The vertical dotted lines mark summer solstice sunrise (04:52) and sunset (18:59) and the solid vertical lines mark winter solstice sunrise (06:56) and sunset (17:03).

Table 3

The coefficient of overlap Δ estimated for each pairwise species comparison across each land-use type surveyed within the IOCB, including 95% confidence intervals (bias corrected for non-normally distributed data). The coefficients range between 0 (indication no overlap) to 1 (indication identical distributions).

Farm	Black-backed jackal	Caracal	Domestic dog	Human	Bushbuck	Grey duiker	Red duiker
Blue duiker	0.72 (CI: 0.62-0.81)	0.69 (CI: 0.54-0.80)	0.71 (CI: 0.61-0.81)	0.62 (CI: 0.53-0.70)	0.80 (CI: 0.78-0.83)	0.82 (CI: 0.78-0.87)	0.83 (CI: 0.80-0.87)
Southern bushbuck	0.65 (CI: 0.64-0.89)	0.72 (CI: 0.64-0.89)	0.79 (CI: 0.64-0.89)	0.70 (CI: 0.64-0.89)	–	0.86 (CI: 0.81-0.91)	0.84 (CI: 0.81-0.87)
Grey duiker	0.66 (CI: 0.55-0.76)	0.67 (CI: 0.50-0.83)	0.81 (CI: 0.70-0.90)	0.76 (CI: 0.66-0.84)	–	–	0.85 (CI: 0.81-0.89)
Red duiker	0.61 (CI: 0.51-0.70)	0.61 (CI: 0.45-0.75)	0.76 (CI: 0.65-0.86)	0.74 (CI: 0.64-0.82)	–	–	–
Black-backed jackal	–	0.71 (CI: 0.56-0.85)	0.58 (CI: 0.44-0.71)	0.48 (CI: 0.34-0.60)	–	–	–
Caracal	–	–	0.63 (CI: 0.44-0.88)	0.53 (CI: 0.34-0.71)	–	–	–
Domestic dog	–	–	–	0.78 (CI: 0.66-0.88)	–	–	–
Residential	Black-backed jackal	Caracal	Domestic dog	Human	Bushbuck	Grey duiker	Red duiker
Blue duiker	–	–	0.70 (CI: 0.63-0.77)	0.55 (CI: 0.51-0.58)	0.86 (CI: 0.84-0.88)	0.83 (CI: 0.80-0.86)	0.88 (CI: 0.84-0.93)
Southern bushbuck	–	–	0.78 (CI: 0.64-0.89)	0.62 (CI: 0.64-0.89)	–	0.87 (CI: 0.84-0.91)	0.86 (CI: 0.82-0.90)
Grey duiker	–	–	0.76 (CI: 0.67-0.83)	0.55 (CI: 0.51-0.60)	–	–	0.81 (CI: 0.48-0.83)
Red duiker	–	–	0.73 (CI: 0.65-0.80)	0.61 (CI: 0.56-0.66)	–	–	–
Domestic dog	–	–	–	0.77 (CI: 0.68-0.84)	–	–	–
Nature reserve	Black-backed jackal	Caracal	Domestic dog	Human	Bushbuck	Grey duiker	Red duiker
Blue duiker	0.74 (CI: 0.59-0.86)	0.82 (CI: 0.75-0.87)	0.51 (CI: 0.35-0.67)	0.51 (CI: 0.48-0.54)	0.84 (CI: 0.81-0.87)	0.77 (CI: 0.64-0.86)	–
Southern bushbuck	0.76 (CI: 0.64-0.89)	0.86 (CI: 0.64-0.89)	0.55 (CI: 0.64-0.89)	0.57 (CI: 0.64-0.89)	–	0.76 (CI: 0.62-0.88)	–
Grey duiker	0.66 (CI: 0.48-0.83)	0.76 (CI: 0.61-0.89)	0.53 (CI: 0.34-0.72)	0.54 (CI: 0.42-0.67)	–	–	–
Black-backed jackal	–	0.75 (CI: 0.60-0.88)	0.39 (CI: 0.21-0.59)	0.40 (CI: 0.26-0.55)	–	–	–
Caracal	–	–	0.51 (CI: 0.34-0.69)	0.52 (CI: 0.44-0.62)	–	–	–
Domestic dog	–	–	–	0.81 (CI: 0.61-0.94)	–	–	–

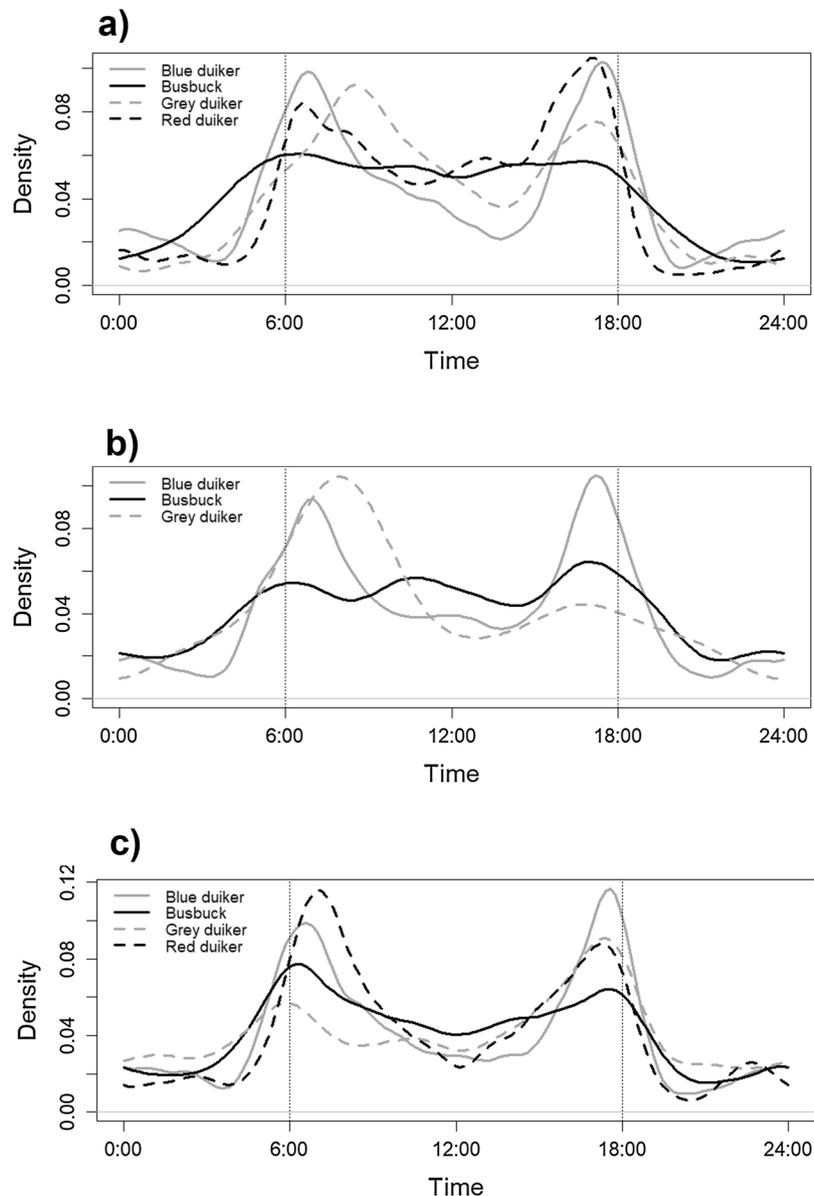


Fig. 3. Ungulate activity curves by land use. Solid grey line = blue duiker; solid black line = southern bushbuck, dotted grey line = grey duiker and dotted black line = red duiker: a) farmland; b) nature reserves, and c) residential areas. The vertical dotted lines mark the mean annual sunrise (06:00) and sunset (18:00).

black-backed jackal and human, whereas farmland only featured twice. The covariate ‘residential’ only had an influence on the Ψ and P of southern bushbuck (Table 4). Both abiotic and biotic factors in combination influenced each species differently, highlighting the varied ecology of each species.

4. Discussion

4.1. Seasonal influences on activity patterns and temporal overlap

Spring-summer months had a maximum of 14:07 h daylight per day and autumn-winter months had a minimum of 10:09 h. Despite the 03:58 h of difference in daylight hours between the seasons, there was little variation in activity time for all species other than red duiker. There were differences in activity peaks for certain species, which were related to the shifts in sunrise and sunset times across the year, depending on the species’ preferential diel phase selection.

Southern bushbuck, the largest bodied species, exhibited only a 7% difference in activity between seasons and did not exhibit distinct peaks

in activity patterns. They were more active in the early morning hours during the spring-summer months, which corresponds with observed peaks in lambing (Odendaal and Bigalke, 1979). Wronski et al. (2006) also found a lack of seasonal variation in activity patterns, though they suggest that bushbuck may have a relatively fixed time budget because of the necessity to forage and ruminate at certain intervals.

There was an 18% difference in activity between seasons for blue duiker. They were active for longer during the day within the cooler autumn-winter months, though not significantly so. Their morning activity peaks continued for longer periods of time, corresponding with an increase in temperature as the day progressed. Crawford and Robinson (1984) also found that their morning activity peaks were extended in winter, while the afternoon active period began earlier. Blue duikers appear to be sensitive to peaks in temperature and show signs of hyperthermia at temperatures above 30 °C (Haim and Skinner, 1991), which was reflected in our study in an activity lull at mid-day, during the hottest periods of the spring-summer months.

Only red duiker exhibited significant seasonal differences in activity overlap, with a lower photographic rate during the Spring/Summer

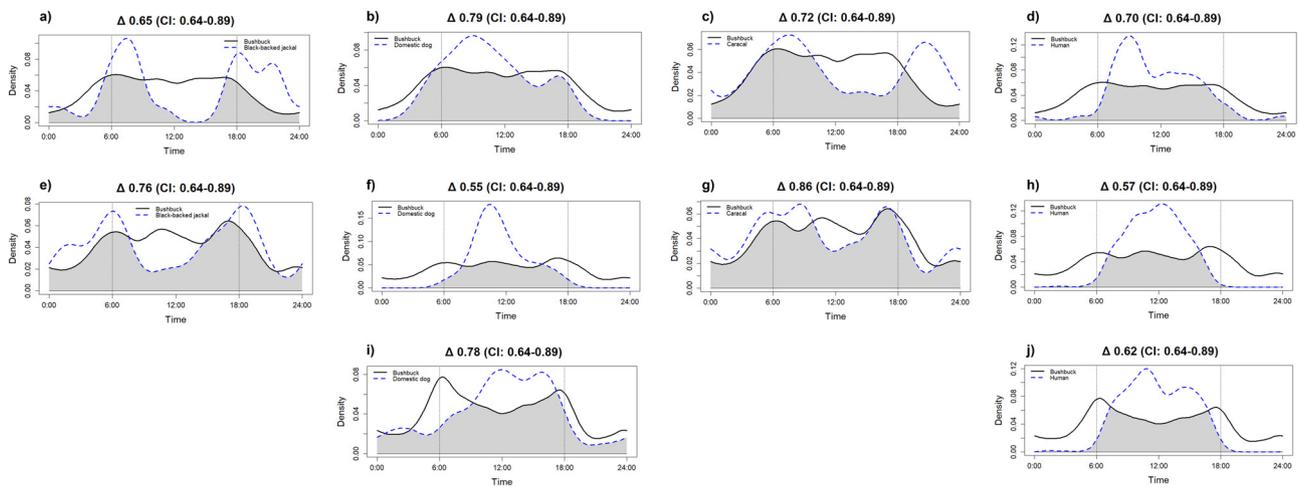


Fig. 4. Activity curves for southern bushbuck (solid line) with other species (dotted line) within farmland [TOP]: a) black-backed jackal; b) domestic dog; c) caracal, and d) human. Nature reserves [MIDDLE]: e) black-backed jackal; f) domestic dog; g) caracal, and h) human. Residential areas [BOTTOM]: i) domestic dogs, and j) human. The coefficient of overlap (presented in Table 3) equals the area below both curves, shaded grey in this diagram. The vertical dotted lines mark the mean annual sunrise (06:00) and sunset (18:00).

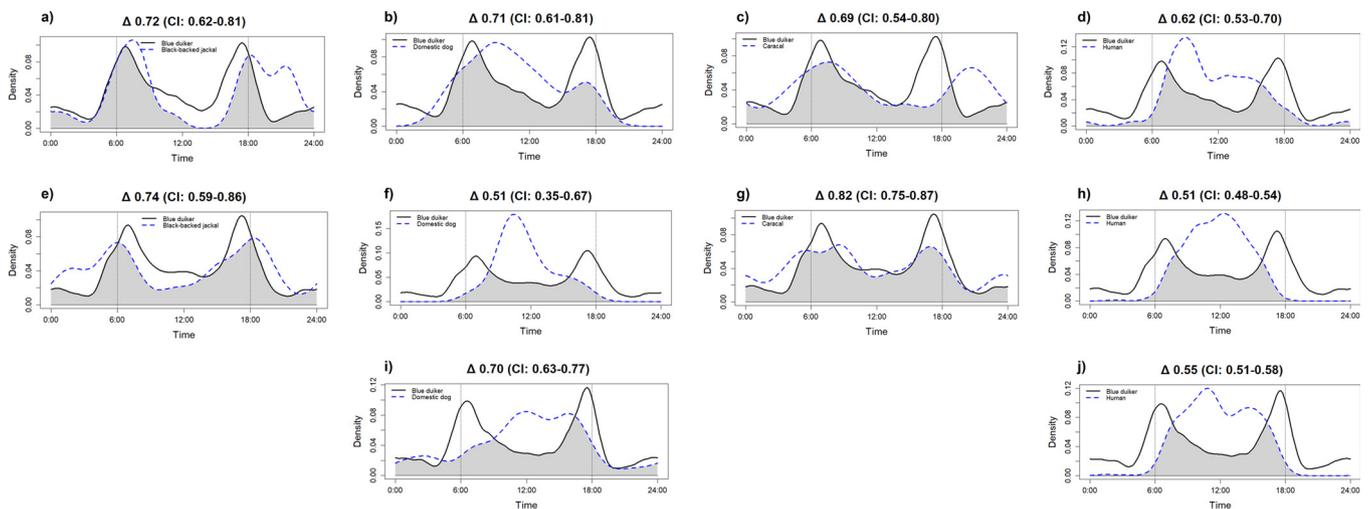


Fig. 5. Activity curves for blue duiker (solid line) with other species (dotted line) within farmland [TOP]: a) black-backed jackal; b) domestic dog; c) caracal, and d) human. Nature reserves [MIDDLE]: e) black-backed jackal; f) domestic dog; g) caracal, and h) human. Residential areas [BOTTOM]: i) domestic dogs, and j) human. The coefficient of overlap (presented in Table 3) equals the area below both curves, shaded grey in this diagram. The vertical dotted lines mark the mean annual sunrise (06:00) and sunset (18:00).

months. The increase in red duiker activity during winter months may be in relation to the availability of food sources. Red duikers do not hold defended territories (unlike blue duiker), allowing the species to move and shift around according to food availability. Plant fruiting phenology drives the availability of preferred food sources, which is thus seasonally mediated; Bowland (1990) found that blue and red duikers were relatively more active in habitats of higher quality. The autumn-winter months are the driest months of the year, and for species that are not reliant on drinking water (Skinner and Chimimba, 2005) an increase in foliage intake would be required to meet their water requirements, which necessitates being active for longer. A study of forest duikers within central Africa related small increases in the midday activity in the dry season in response to reduced food resources (Dubost, 2010).

4.2. Anthropogenic influences on activity patterns and temporal overlap

Differences in temporal activity patterns were related to the type of land use and disturbance effects. Based on road density as a proxy for anthropogenic infrastructure, residential areas, followed by farms were

the most disturbed. The activity of dogs and humans in combination resulted in highly disturbed land-use types. Although nature reserves had the lowest anthropogenic infrastructure, a larger number of people are encountered within nature reserves, where people participate in outdoor activities and use small walking trails. Residential areas had the highest number of dogs photographed in comparison with farms and nature reserves, which is indicative of the associated human population density within the study area (Ehlers Smith et al., 2018). We may view domestic dogs as a direct predator of antelope, particularly in residential areas, where residents have witnessed dogs killing bushbuck (n = 2) and blue duiker (n = 2) from two villages within the study area over a one-year period.

Three of the four antelope (red duiker being the exception) performed approximately a quarter to one-third of their activities at night, which varied based on land-use type, suggesting that species are more frequently active at night in response anthropogenic disturbance. Dawn (within residential) and dusk (within farmland and reserves) were key activity periods for bushbuck, but when comparing nocturnal activity between the three land-use types, southern bushbuck were more active at night within nature reserves. The higher number of humans utilising

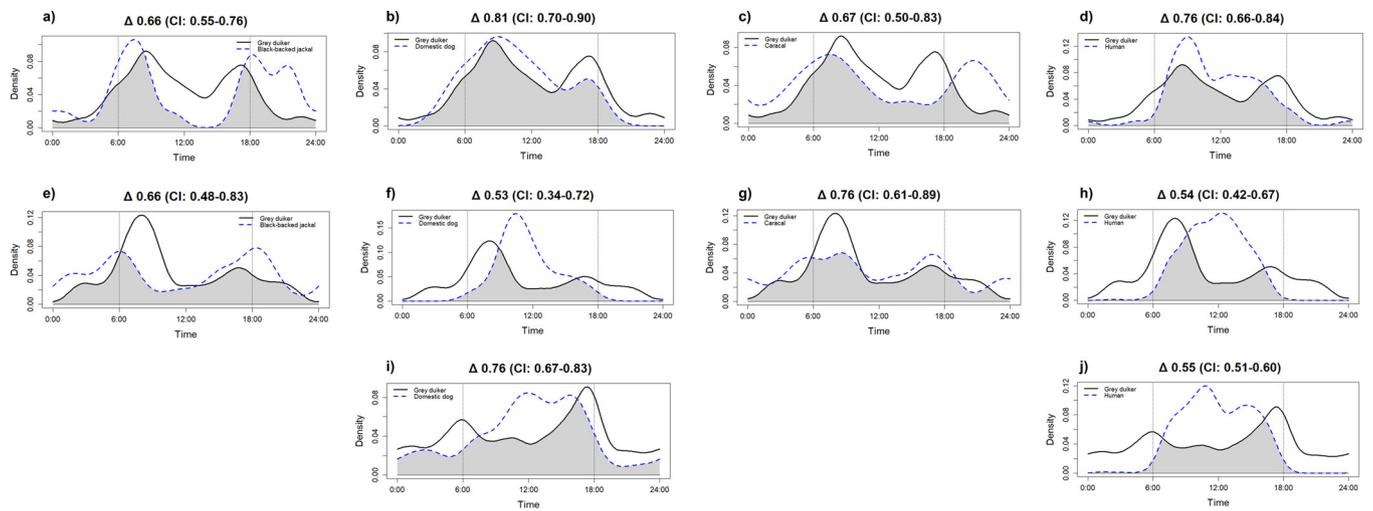


Fig. 6. Activity curves for grey duiker (solid line) with other species (dotted line) within farmland [TOP]: a) black-backed jackal; b) domestic dog; c) caracal, and d) human. Nature reserves [MIDDLE]: e) black-backed jackal; f) domestic dog; g) caracal, and h) human. Residential areas [BOTTOM]: i) domestic dogs, and j) human. The coefficient of overlap (presented in Table 3) equals the area below both curves, shaded grey in this diagram. The vertical dotted lines mark the mean annual sunrise (06:00) and sunset (18:00).

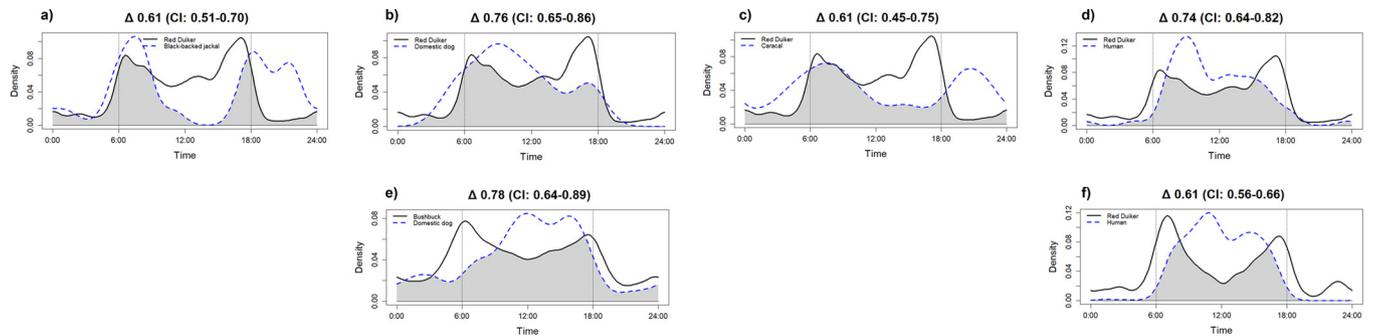


Fig. 7. Activity curves for red duiker (solid line) with other species (dotted line) within farmland [TOP]: a) black-backed jackal; b) domestic dog; c) caracal, and d) human. Residential areas [MIDDLE]: e) domestic dog, and f) human. The coefficient of overlap (presented in Table 3) equals the area below both curves, shaded grey in this diagram. The vertical dotted lines mark the mean annual sunrise (06:00) and sunset (18:00).

nature reserves may be contributing to the greater nocturnal activity within this land-use type. Jacobsen (1974) attributes nocturnal bushbuck activity in most areas because of human persecution, though the data were only collected within day-light hours and the observations remain untested. Wronski et al. (2006) also provided evidence that bushbuck were active at night and were least active in the daytime, with a dawn activity peak. However, their results may be misleading as they describe dawn as the period around sunrise and sundown, and do not assess them separately.

Contrary to the results found by Bowland (1990), blue duikers were active at night for 18% of the time. Our study area overlapped with one of Bowland’s study sites (Umdoni Park), which relative to his other sites

could be considered the most disturbed. Duikers become more nocturnal in areas with high disturbance (Skinner and Chimimba, 2005) and Bowland’s (1990) results may be limited by the ad-hoc nature of the night-time surveys conducted.

All antelope species exhibited the lowest coefficient of temporal overlap with humans. Stankowich (2008) found in a meta-analysis a greater flight response in ungulates in hunted populations. Furthermore, humans on foot had a greater influence on flight response. However, ungulates in areas with higher levels of human traffic showed reduced wariness but a lack of alternative sites to retreat to may explain some of this effect (Stankowich, 2008). Our field observations showed that all antelope species were skittish and easily flushed. Each

Table 4

Top logistic models ($\Delta AIC = 0$) for assessing the influence of carnivores, humans and domestic dogs on the occupancy and detection probability of four antelope species across farmland and nature reserves* across the survey region (* excluding red duiker, which was not photographed in any reserves).

Species	Cycle	Model	No. Par	AIC	AIC wgt.	$\Psi \pm SE$	$P \pm SE$
Blue duiker	1	$\Psi (J + C + D), P(J + H)$	7	1058.4	0.47	0.69 ± 0.06	0.65 ± 0.03
	2	$\Psi(J + C + D), P(F + J + C + H)$	9	1223.6	0.31	0.80 ± 0.06	0.60 ± 0.04
Southern bushbuck	1	$\Psi (R + D + H), P(\cdot)$	5	1395.7	0.41	0.87 ± 0.05	0.54 ± 0.02
	2	$\Psi (I), P(F + R + H)$	5	1287.8	0.46	0.78 ± 0.03	0.47 ± 0.03
Grey duiker	1	$\Psi (J + H), P(\cdot)$	4	457.1	0.32	0.25 ± 0.05	0.32 ± 0.03
	2	$\Psi (F + D), P(D + H)$	6	382.0	0.4	0.20 ± 0.05	0.51 ± 0.08
Red duiker	1	$\Psi (C + H), P(F)$	5	236.5	0.48	0.16 ± 0.06	0.71 ± 0.07
	2	$\Psi (F + C), P (I)$	4	242.0	0.57	0.20 ± 0.07	0.71 ± 0.04

Abbreviations: F = % farmland; R = nature reserve; C = caracal occupancy; D = domestic dog occupancy; H = human occupancy, J = jackal occupancy.

Table 5

Parameter estimates (including direction of relationship) for explanatory variables from the best occupancy and detection probability models for ungulate species across nature reserve and farmland survey sites within the study region per survey cycle.

Species	Cycle	Site occupancy			Site detection probability			
		Covariates	Estimate	Standard error	Covariates	Estimate	Standard error	
Blue duiker	1	(Intercept)	42.3	17.05	(Intercept)	6.41	1.05	
		J	−215.8	95.47	J	−11.92	3.08	
		C	−22.2	9.92	H	−7.44	1.39	
	2	D	73.7	37.26				
		(Intercept)	34.9	16.24	(Intercept)	−125.55	55.3	
		J	−178	91.4	F	7.77	3.51	
Southern bushbuck	1	C	−15.3	9.71	J	266.61	119.99	
		D	59.5	36.11	C	−12.95	4.12	
					H	169.02	70.01	
	2	(Intercept)	14.4	5.4	Constant	0.179	0.0667	
		R	−14.3	7.41				
		D	71.2	35.89				
Grey duiker	1	H	−71.3	32.24				
		Constant	1.29	0.204	(Intercept)	28.13	11.62	
					F	−3.45	1.51	
	2				R	−7.19	2.83	
		(Intercept)	15.08	3.39	H	−66.45	27.47	
		J	−56.8	12.88	Constant	−0.741	0.149	
Red duiker	1	H	−6.81	3.27				
		(Intercept)	4.619	1.723	(Intercept)	−0.927	0.957	
		F	−0.893	0.375	D	9.547	3.308	
	2	D	−22.449	6.644	H	−4.869	3.098	
		(Intercept)	−9.11	5.95	(Intercept)	0.74	0.3	
		C	−15.77	7.83	F	0.295	0.188	
2	H	32.99	21.66					
	(Intercept)	3.59	2.81	Constant	0.877	0.196		
	F	−1.5	1.05					
			C	−12.47	6.67			

Abbreviations: F = % farmland; R = nature reserve; C = caracal occupancy; D = domestic dog occupancy; H = human occupancy; J = jackal occupancy.

antelope's lowest daytime activity corresponded with human activity peak; however, human activity peaked at mid-day, corresponding to the highest day-time temperatures, which may be masking the effect on temporal activity patterns. Moreover, we could not quantify the influence of poaching within the study area, which could directly be influencing the activity patterns.

4.3. Carnivore influences on activity patterns and temporal overlap

Black-backed jackal and caracal selected specific diel activity phases, which may be to avoid competition or persecution by humans and dogs (Humphries et al., 2015). The literature describes both caracal and black-backed jackal as nocturnal species; however, our pooled results showed a greater percentage day-time activity and active selection of dawn and dusk diel activity phases, respectively. Black-backed jackals also selected dawn diel phases in both farmland and nature reserves, whereas caracal selected the nocturnal diel phase within nature reserves. Farris et al. (2015) found evidence of native carnivores shifting their temporal activity patterns in the presence of exotic carnivores. It appeared that a peak in carnivore activity corresponded with reduced human and domestic dog activity. As both carnivore species are persecuted throughout their range (Humphries et al., 2015), this activity pattern may be to avoid contact with humans and dogs, which were more active from mid-morning. The population density and ranging behaviour of domestic dogs are fundamental predictors of ecological impact on native carnivores (Vanak and Gompper, 2009). Based on the number of unique observations, domestic dogs currently outnumber the native predators encountered. Therefore, they have a large potential as interference competitors, especially for small and medium-sized carnivores (Vanak and Gompper, 2009).

Caracals had the highest coefficient of temporal overlap with each antelope species with nature reserves. Caracals and bushbucks actively

selected the dawn diel activity phase, were active the earliest of all the species and had the highest coefficient of overlap (86%) between guilds. Within residential areas domestic dogs had the highest coefficient of overlap with each species. Similarly, dogs within farmland had the highest overlap with southern bushbuck and grey duiker. Humans had a 74% overlap with red duiker. Within farmland it may be that the presence of humans and domestic dogs that negatively influence the presence of black-backed jackals that corresponded with red duiker activity peaks and overlapped in activity periods with southern bushbuck and grey duiker. The activity pattern (activity peaks or lulls) and selection of the dusk diel phase of black-backed jackal corresponded with patterns of all three-duiker species. However, within farmland blue duiker and black-backed jackal had the highest coefficient of overlap and both species selected the dusk diel phase. Ferguson et al. (1988) found that jackal activities were closely paralleled by the activity levels of some of their most important prey. Our results suggested a shift from nocturnal to crepuscular activity patterns, but also analogous activity peaks with potential prey species.

4.4. Spatial distribution

Each of the duiker species was influenced by both biotic (predators) and abiotic (land use and anthropogenic disturbances) factors which varied across survey cycles. Previously, we highlighted the importance of seasonality and how seasons influence land-use intensity and anthropogenic disturbance (Ehlers Smith et al., 2018). Each species in turn responded differently to individual factors. Black-backed jackals had the largest negative effect on blue and grey duiker occupancy. This, in combination with high coefficients of overlap and the selection of dusk diel activity phases indicated that jackals may be considered the most active predator for these species, particularly on farmland.

Caracal also had a negative influence on blue duiker, in addition to

influencing red duiker occupancy. Yet, despite selecting the same diel phase as bushbuck and the large temporal overlap with grey duiker, it did not influence the occupancies of these species directly. Caracals had the highest occupancy within nature reserves, and black-backed jackal occupancy was higher on farmland. Caracals are thought to predominantly occupy habitats within rural areas with lower human density and thus their spatial patterns are more affected by land-use intensity. There appears to be a human-density threshold for their persistence in an area; once exceeded they may relocate to establish a new territory in less disturbed areas (Kauffman et al., 2007). The decline of blue duiker at the southernmost limit of its distribution has been attributed to the arrival of caracal within the region, but despite a reduction in caracal numbers the blue duiker population remained relatively low (Hanekom and Wilson, 1991).

Although some degree of spatial and temporal overlap between the carnivores and antelope existed, we cannot conclusively state that carnivore behaviour patterns shifted according to prey species patterns, or how they were directly influenced by the presence of humans and dogs or land-use intensity. However, this potential effect would be hard to decouple from the direct influence that dogs as predators have on ungulates, i.e., does the presence of dogs deter meso-carnivores and alter their behaviour and therefore benefit antelope? Further, there is an additive interaction between the presence of humans and their dogs that subsequently influences carnivore abundance negatively (Reed and Merenlender, 2011). In relative terms, caracal and jackal have only recently been recorded within the area and at present their numbers are relatively low. Nevertheless, the influx of novel predators may impact both blue and red duiker metapopulations, the abundance of which are considered to be declining because of habitat loss, land-use change and illegal hunting pressures (Ehlers Smith et al., 2016; Venter et al., 2016).

Southern bushbuck was the only species influenced by land use, specifically nature reserves. Nature reserves within our study region protect the largest mature forest habitat patches, which are their preferred habitat (Ehlers Smith et al., 2017). However, when purely assessing the impacts of land-use classification on the occupancy of bushbuck, we found previously that nature reserves had a positive influence on the species occupancy (Ehlers Smith et al., 2018). Our results also showed that southern bushbuck and grey duiker occupancy were negatively influenced by humans, which was the highest within nature reserves where hiking trails were present. This also corresponded with the higher degree of nocturnal behaviour present within nature reserves, indicating that the direct effects of human disturbance on spatio-temporal distributions may be counter-influencing the positive impact of nature reserves as ‘safe havens’ on these species’ persistence, and highlighting the need to include disturbance levels when assessing the impacts of different land-use types. Taylor and Knight (2003) showed that mule deer *Odocoileus hemionus* within Antelope Island State Park, Utah presented a 70% probability of flushing within 100 m of recreationists either side of a trail and stated that the park may be potentially unsuitable for diurnal wildlife use due to human disturbance. This highlights how visitation rates to nature reserves can influence the spatio-temporal behaviour patterns of ungulates.

4.5. Niche separation

The degree of ecological flexibility within an ecosystem is determined by the biology of a species (Cardillo et al., 2004), and how it responds to different levels of disturbance (Estrada et al., 1994; Martinoli et al., 2006). The antelope species within our study region exhibited a large degree of similarity in temporal overlap and activity peaks. The larger of the two antelope, southern bushbuck and grey duiker, had the largest coefficient of overlap (i.e. the greatest similarity in activity) and exhibited similar temporal activity patterns. Thus, the differentiation between their sympatric niches was not based on segregation of activities or avoidance, but related to habitat selection (Ehlers Smith et al., 2017), body size and degree of feeding

specialisation, where the grey duiker (smaller of the two) is a concentrate browser, and the southern bushbuck a selective browser (Hofmann, 1973; Allen-Rowlandson, 1986; Hofmann, 1989; Skinner and Chimimba, 2005). Previously, we showed that grey and blue duiker exhibit a preference for denser habitats such as regenerating forest patches, whereas southern bushbuck preferred microhabitat structures relating to mature indigenous forest patches (Ehlers Smith et al., 2017).

Of the three duiker species, blue and red duikers (the true forest duikers) had the highest coefficient of overlap, indicating that they were active at similar times and did not have times during which they avoided each other. Blue and red duiker activity patterns both peaked at dusk, but blue duikers exhibited comparatively more nocturnal activities. Niche separation may be in relation to dietary preference. Although both species are considered concentrate selector browsers (Bowland and Perrin, 1998), blue duiker are capable of processing a lower quality diet (Shiple and Felicetti, 2002), utilising food items with high tannin content, making them specialised high Carbon:Nutrient dietary selectors (Seydack and Huisamen, 1999), whereas red duiker are less capable of digesting fibres (Bowland and Perrin, 1998).

Spatial segregation was apparent when considering differences in species occupancy levels across the survey region. We previously highlighted differences in occupancy between these sympatric species based on habitat associations and land-use types (Ehlers Smith et al., 2017, 2018). Competitive release presents itself in relation to individual species-specific habitat preferences (Ehlers Smith et al., 2017), which would be dictated by nutritional requirement (availability of preferred food items), but also tolerance to anthropogenic landscapes (Ehlers Smith et al., 2018). Furthermore, a larger-bodied species, such as southern bushbuck, has a larger home-range size, but a decrease in dietary specialisation, therefore relaxing inter-specific competitive pressures. Consequently, the ecological adaptations of antelope species allow species of different body sizes to avoid competition with each other (Whelan, 2004).

5. Conclusion

Our results supported our hypothesis that both abiotic and biotic would influence the spatial and temporal patterns of antelope species. With the exception of red duiker, we found no seasonal influence on activity patterns, but noted variation in occupancy between survey cycles (years). Furthermore, we found shifts in what could be considered ‘normal’ activity periods described in the literature (e.g. change from diurnal to crepuscular activity patterns or selection of specific diel phases), based on land-use type. Overall, we highlighted the complex interactions among predators, land-use intensity and anthropogenic disturbance and how these factors exerted different influences on each of the sympatric species.

We found partial support for our second hypothesis that niche separation between forest antelope would be facultative, through spatial and temporal segregation of activities. We found a large degree of temporal overlap; however, the level of spatial overlap varied between species, and was influenced by differing biotic and abiotic factors, highlighting the multiple facets driving niche separation. Niche separation in these sympatric forest antelope was driven in combination by spatio-temporal segregation of activities and with ecological and physiological traits to avoid competitive exclusion. This study demonstrates how camera trapping methods may be used to describe the seasonal spatio-temporal patterns of cryptic forest mammals, but also highlights the importance of incorporating predation effects and disturbance factors when assessing the influence of landscape scale factors.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.beproc.2018.12.005>.

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