RESEARCH ARTICLE

The determinants of mesocarnivore activity patterns in highveld grassland and riparian habitats

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Despite the diversity of mesocarnivores and the broad geographic ranges of these species, our understanding of their behaviour and ecology at multi-species and community levels is limited. Our study was conducted between April and mid-July 2015 and used data collected over 105 days from 39 camera traps to quantify activity patterns of sympatric mesocarnivores in riparian and grassland habitats of Telperion Nature Reserve, South Africa. A total of 13 mesocarnivore species were detected within this relatively small (~7350 ha) reserve. Sufficient records (≥10 records) were obtained for rusty-spotted genet (*Genetta maculata*), black-backed jackal (*Canis mesomelas*), otter species (African clawless otter, *Aonyx capensis*, and spotted-necked otter, *Hydrictis maculicollis*), serval (*Leptailurus serval*), slender mongoose (*Galerella sanguinea*), yellow mongoose (*Cynictis penicillata*) and marsh mongoose (*Atilax paludinosus*). Generalized linear models were used to investigate whether species ID, temperature, vegetation characteristics or moon phase best predicted temporal activity. To assess which species had the highest potential for competitive interaction, we also quantified the coefficient of activity overlap. Our results show that species ID and temperature were the best predictors of mesocarnivore activity. Slender and yellow mongooses displayed the highest coefficient of activity overlap (0.90), followed by marsh mongoose and rusty-spotted genet (0.80), and serval and rusty-spotted genet (0.79). These species are likely to have the highest potential for competitive interactions, but preferences for different vegetation characteristics and variations in the estimated relative abundance may point to coexistence through spatial and fine-scale temporal partitioning. The other species exhibited lower coefficients of activity overlap with each other, suggesting they may coexist through temporal partitioning of resources.

Keywords: carnivore guild, activity patterns, species coexistence, small carnivores, biodioversity.

INTRODUCTION

Understanding coexistence mechanisms between ecologically similar species is necessary to understand ecological communities and their continued persistence (Violle *et al*., 2012). Interspecific competition affects the ability of each species to access limited resources and ultimately shape ecological niches (Chesson, 2000). Species may adapt to interspecific competition by partitioning resources along three main, but not mutually exclusive, dimensions. 1) Spatial partitioning, exploiting the same or similar resources in different areas, 2) temporal partitioning, exploiting the same resources at different times or 3) trophic niche partitioning, exploiting different resources altogether. These strategies ensure that interactions and, therefore, inter-species competition is reduced (Donadio & Buskirk, 2006). Inter-species differences in morphology, behaviour, and physiology can also mediate interspecific competition (Loveridge & Macdonald, 2003). In small nature reserves or urban parks, interspecific competition may intensify when available habitat is limited. Subsequent interspecific contact rates, and the possibility of one or more competitive species impacting the occurrence and activity times of another, may result in some species becoming subordinate (Gehrt *et al*., 2013; Massara *et al*., 2016).

The effects of interspecific interactions are most prominent within the carnivore guild (Palomares & Caro, 1999). Understanding how carnivore–carni-

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vore interactions affect patterns of co-occurrence and the traits that influence interspecific interactions are important components of understanding niche dynamics, coexistence and mesocarnivore release (Monterroso *et al.*, 2020). Compared to large predators, mesocarnivores are habitat and resource generalists, are species-rich and generally more abundant (Roemer, Gompper & Van Valkenburgh, 2009). Mesocarnivores are small to medium sized carnivores weighing ≤15 kg, with a diet of 50–70% meat that occupy a trophic position below the large carnivores (weighing >20 kg) (Ritchie & Johnson, 2009; Bird & Mateke, 2013). A single ecosystem may support several mesocarnivore species; however, a mesocarnivore in one ecosystem may fill the role of an apex predator in another (Roemer, Gompper & Van Valkenburgh, 2009).

Transformed and urbanized environments favour generalist species (Clavel, Julliard & Devictor, 2011). South Africa is a developing country with one of the fastest urbanization rates worldwide (Saghir & Santoro, 2018). It also hosts a large number of protected areas and some of the richest biodiversity in the world (Skowno *et al.*, 2019), including a variety of mammalian mesocarnivore species (Skinner & Chimimba, 2005). Mesocarnivore community composition within protected areas is influenced by various abiotic and biotic factors, including temperature, habitat requirements, interspecific relationships, human pressures and protected area attributes (Tambling *et al.*, 2018). In general, carnivore occurrence within protected areas in southern Africa is influenced by the location of permanent water sources, with higher mesocarnivore occupancy closer to water (Schuette *et al.*, 2013; Rich *et al.*, 2017). Dense vegetation along riparian habitats also attracts mesocarnivores, as it may provide concealment during hunting and refuge from interspecific predation (Boydston *et al.*, 2003; Santos *et al.*, 2011). Increased habitat variability, vegetation and terrain diversity may also support more generalist carnivore species (Roemer, Gompper & Van Valkenburgh, 2009).

Despite the variety of mesocarnivores in South Africa, studies have primarily been on single species, descriptive and focused mainly on diurnal species (Do Linh San *et al.*, 2013). Consequently, we still know little about mesocarnivore behaviour and many aspects related to their ecology and intraguild interactions at multi-species and community levels (González-Maya, Schipper & Benitez, 2009; Do Linh San *et al.*, in press). The overall aim of this study was twofold: 1) to identify which mesocarnivore species were present in a South African nature reserve comprising grassland and riparian habitats, and 2) to determine the activity patterns of each mesocarnivore species as a measure of coexistence mechanisms (spatial or temporal niche partitioning) within this guild. We further evaluated environmental factors that could influence daily activity periods for each mesocarnivore species, predicting that 1) the vegetation characteristics of the landscape would most affect mesocarnivore activity and 2) temperature would affect mesocarnivore species activity times differently.

METHODS

Study area

The study was conducted at the Telperion Nature Reserve (between the latitudes of 25°38′ and 25°44′S and longitudes of 28°55′E and 29°02′E), from April to mid-July 2015. The property (~7350 ha) lies in the ecotone between the Rand Highveld Grassland biome of Gauteng province near Bronkhorstspruit, and the Loskop Mountain Bushveld Savanna Biome near Emalahleni in Mpumalanga province, South Africa (Mucina & Rutherford, 2006; Coetzee, 2012).

Rhyolite, sandstone and minor shale support predominantly dry and wet degraded grassland (Coetzee, 2012) and the foothills of rocky ridges support a general woodland community, which may extend into grassland. In the lower-lying riparian areas, dense vegetation gives way to rocky ledges and sandy patches along the river (Helm, 2006). Several small tributaries feed into the Wilge River, a perennial water source that flows south to north through the reserve for 19.66 km to form wetlands and reed beds, enhancing water availability in the dry season (Helm, 2006; Coetzee, 2012). Mean temperatures range from 14°C to 27°C in the wet season from September to March, and mean annual rainfall is ~650 mm (Bronkhorstspruit Weather Station). In the dry season, from April to August, mean temperatures range between 4°C and 18°C with frost in the early mornings (Witbank Weather Station).

The property is privately owned, and except for the active management of fire, is managed using a non-intervention approach. Rehabilitation from historical crop and livestock farming for wildlife conservation, eco-tourism, education and research is ongoing. The reserve supports a diversity of herbivores, some of which historically occurred in the province, while others have been introduced (Helm, 2006; Coetzee, 2012).

Study design

We used a random stratified sampling method to deploy 40 Bushnell HD Trophy Cam camera traps (Model 119537, 8 Megapixel sensor with 32 Hyper-night vision LED flash) throughout grassland (n = 29) and riparian (n = 11) areas of the reserve (Fig. 1). However, camera number 7 in the riparian zone went missing within the first week of data collection. Different characteristics within riparian and grassland landscapes were determined visually (Table 1), and active game paths were identified through track and sign interpretation (Liebenberg, 1990). A handheld Global Positioning System (GPS) device (Garmin eTrex 20) was used to record each trap site's longitude and latitude coordinates. Trap sites held one camera, elevated between 50 cm and 1 m above ground depending on natural attachment sites on or near a game path or game path junction to maximize visibility and capture potential for mesocarnivore species (O'Connell, Nicols & Karanth, 2011; Hamel *et al*., 2013). The standardized minimum distance (Karanth & Nichols, 2000; Jackson *et al*., 2005; Kelly, 2008) was maintained between traps at ≥800 m in grassland but were reduced to ≥400 m along only 8.37 km of accessible riverfront in the riparian habitat. All cameras were set to normal sensitivity, synchronized for time and pre-programmed to record the date, temperature, and phase of the moon. The temperatures recorded on the camera traps were consid-

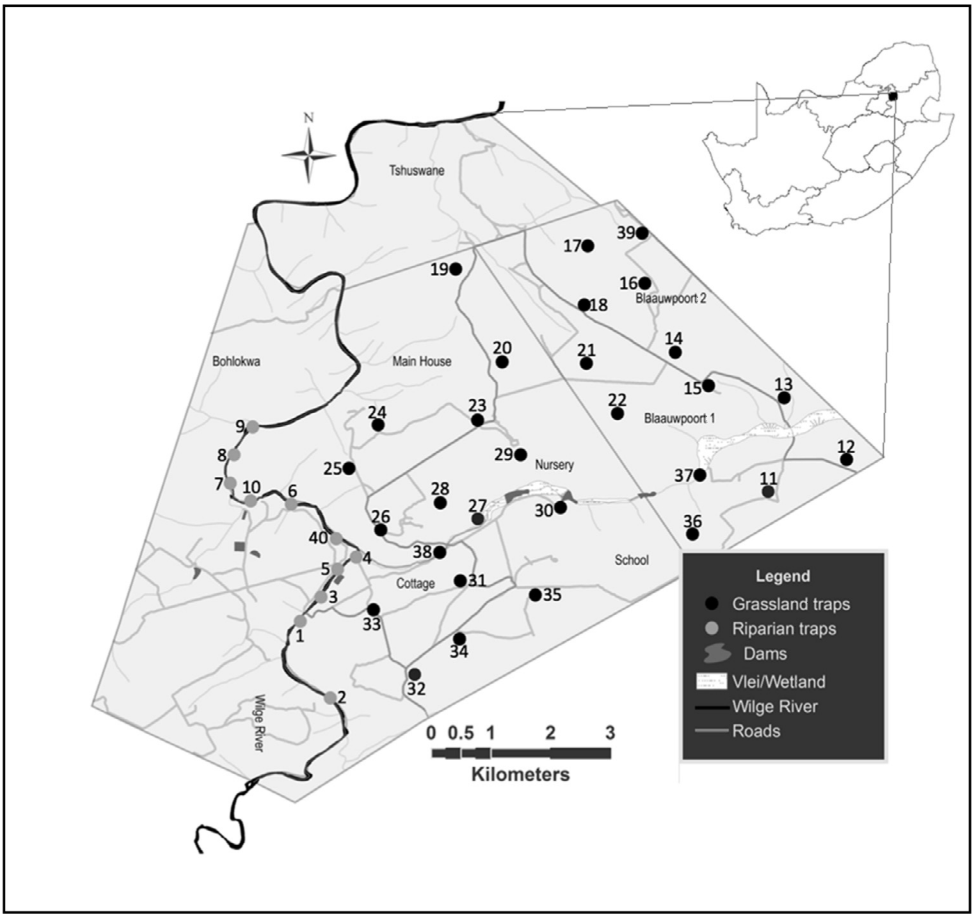

Fig. 1. Random stratified placement of 11 riparian (light grey marker) and 29 grassland (black marker) camera trap stations at Telperion Nature Reserve, on the border between the Gauteng and Mpumalanga province, South Africa, between 1 April and 17 July 2015.

Table 1. Classifications assigned to the vegetation characteristics, timing of activity, moon phase and other environmental variables used for classifying explanitory variables in the statistical models of mesocarnivore activity in the Telperion Nature Reserve, South Africa. Numbers in brackets in the vegetation category indicate number of camera traps deployed.

		Category	Rationale
Habitat	Grassland	Dry Open (10)	Relatively homogenous, dry open grassland, various elevations
		Rocky Outcrops (11)	Rocky outcrops in dry grassland, little vegetation cover, various elevations
		Wet near tributaries (5)	Vleis, marsh, or in close proximity to tributary in open grassland – cannot be characterized as true riparian
		Wooded areas (3)	Concentrated clusters of trees surrounded by open dry grassland
	Riparian	Dense vegetation (4)	Little sky visible – dense vegetation along game paths
		Rocky ledges adjacent to river (2)	Rocky ledges adjacent to the river
		Drainage line pathway (2)	Open areas along game paths in Riparian vegetation – patches of little cover
		Sandy patches adjacent to the river (3)	Sand predominates, minimal grass and little tall vegetation
Time of activity		Midnight to dawn	00:01 to 06:00
		Dawn to midday	06:01 to 12:00
		Midday to dusk	12:01 to 18:00
		Dusk to midnight	18:01 to 24:00
Moon phase		New moon and waning crescent	0–25% illumination
		First quarter and waxing gibbous	50–75% illumination
		Full moon and waning gibbous	100–75% illumination
		Last quarter and waning crescent	50–25% illumination
Temperature			°C

ered to be correlated with ambient air temperature (Hofmann *et al*., 2016). A 30-second time delay was used between capture events, and a single photograph was produced in response to motion detection (Karanth & Nicols, 2000; Kelly, 2008; O'Connell *et al*., 2011). Camera trap data were collected over six weeks, with cameras recording data continuously over 24 hours for a total of 105 days. Cameras, batteries and secure digital (SD) card capacity were checked every two weeks from 1 April to 17 July 2015. Data from SD cards were downloaded to a laptop computer in the field. SD cards were re-formatted, and camera settings checked and corrected after each survey. Batteries were replaced as necessary.

Detection rates and mesocarnivore activity

We calculated trap detection rates by summing the total number of detections that yielded mesocarnivore data for each trap within each habitat type (grassland or riparian) and divided this by the number of traps deployed in each area. Using photo-detections from all 13 mesocarnivore species detected (Table 2), we determined species composition on the property. The proportion (%) of time each mesocarnivore species was detected in each landscape was determined by dividing the number of detections per species per landscape type (riparian or grassland), and the times at which each mesocarnivore species was active were recorded and plotted. Detections of the same species recorded at 60-second intervals or less were removed to minimize autocorrelation (Sollmann, 2018; Havmøller *et al*., 2021; Kays *et al*., 2021). In all cases, this removed successive detections of the same individual at a specific trap site. Rather than identifying individuals, our focus was on identifying the mesocarnivore species present and comparing detection rates between species and areas. Therefore, we did not expect the time between independent photographs to introduce a bias toward either one of these factors (Jenks *et al*., 2011). Two large carnivore species, leopards (*Panthera pardus*) and brown hyaenas (*Parahyaena brunnea*), were also detected from photographs but were not included in the analy-

Table 2. Complete list of carnivores and mesocarnivores identified at the study site. The number of detections per species (*n*), proportion of detections in each habitat type for seven species of mesocarnivores in the grassland and riparian landscapes and the overall relative abundance index (RAI) and the characteristics of detection locations in the Telperion Nature Reserve from April–July 2015.

	Family	Scientific name	Common name	Body mass (kg)	(*n*)	Detections (%) in each habitat type		Relative abundance index (RAI)	Vegetation characteristic
						Riparian	Grassland		
1	Felidae	*Felis nigripes*	Black-footed cat	1.6–2.45	1	–	100%		Dry open grassland
2		*Leptailurus serval*	Serval	9–18	15	1%	99%	0.53	Wet grassland, Dry open grassland, Riparian sandy patches
3		*Caracal caracal*	Caracal	7–19	6	–	100%		Dry open grassland, Rocky outcrop, Wet grassland
4	Canidae	*Canis mesomelas*	Black-backed jackal	6–13	505	9%	91%	12.47	All characteristics of grassland, all characteristics of Riparian except rocky ledges
5	Hyaenidae	*Proteles cristatus*	Aardwolf	10–14	6	50%	50%		Dry open grassland, wet grassland, riparian rocky ledges
6	Viveridae	*Genetta maculata*	Rusty spotted genet	1.3–3	136	77%	23%	3.32	Woodland and rocky outcrops in grassland, All characteristics of Riparian
7	Herpestidae	*Galerella sanguinea*	Slender mongoose	0.46–0.57	118	56%	44%	2.88	Rocky outcrops, wet grassland, All characteristics of Riparian
8		*Cynictis penicillata*	Yellow mongoose	0.6–3	85	–	100%	2.08	Dry open grassland
9		*Atilax paludinosus*	Marsh mongoose	2.5–2.9	82	44%	56%	2.00	Wet grassland, All characteristics of Riparian
10		*Suricata suricatta*	Meerkat	0.62–0.97	5	–	100%		Dry open grassland
11	Mustelidae	*Aonyx capensis* *Lutra maculicollis*	African clawless otter Spotted-necked otter	3–6.5	41	12%	88%	1.22	Wet grassland (fast-flowing shallow tributaries), Riparian dense vegetation
12		*Mellivora capensis*	Honey badger	9–16	1	–	100%		Grassland rocky outcrops
13		*Ictonyx striatus*	Striped polecat	0.6–1.3	8	–	100%		Dry open grassland, Rocky outcrops

ses. Insufficient data (<10 detections) were recorded for caracal (*Caracal caracal*), honey badger (*Mellivora capensis*), black-footed cat (*Felis nigripes*), striped polecat (*Ictonyx striatus*), aardwolf (*Proteles cristatus*), and meerkat (*Suricata suricatta*) and were removed from the dataset before statistical modelling. Data were pooled for African clawless otter (*Aonyx capensis)* and spotted-necked otter (*Hydrictis maculicollis*), as it was not always possible to identify individuals to species level. In addition to pooled data from 'otter sp.', rusty-spotted genet (*Genetta maculata)*, black-backed jackal (*Canis mesomelas*), serval (*Leptailurus serval*), slender mongoose (*Galerella sanguinea*), marsh mongoose (*Atilax paludinosus*) and yellow mongoose (*Cynictis penicillata*) were detected and used for statistical analyses and mesocarnivore activity plots. We calculated the relative abundance index (RAI) for each of the seven species to evaluate differences in the detection rates by taking the sum of all detections for each species multiplied by 100 and divided by the total sampling effort (39 × 105) (Karanth & Nichols, 1998; Jenks *et al*., 2011). We acknowledge that care must be taken when interpreting RAIs, since they are influenced by the behaviour and movement patterns of study species, camera trap setup and the size of the study area (Sollmann *et al*., 2013).

Statistical analysis and predictors of mesocarnivore activity

To test whether the predictor variables; species ID (categorical), temperature (°C, numeric), vegetation characteristic (Rocky Grassland, Wet Grassland, Wooded Grassland, Dense Riparian, Open Riparian, Rocky Riparian, and Sandy Riparian or moon phase (Full, Last Quarter, New Moon, Waning Crescent, Waning Gibbous, Waxing Crescent and Waxing Gibbous) predicted mesocarnivore time of detection (numeric response variable), generalized linear models (GLMs) with Gaussian error distributions were constructed in the software R (version 1.1.463: 2013) (The R Foundation for Statistical Computing 2013). The time of detection was converted from hh:mm:ss to decimal hours (hh:mm:ss × 24) and used for the GLM modelling. We tested for multi-colinearity using Variance Inflation Factors (VIF) using the R *car* package (Fox & Weisberg, 2011). All VIFs were <5, indicating low co-linearity between covariates (Sheather, 2009) and all covariates were subsequently retained in the global model.

Thirteen separate stepwise GLM models were then constructed. To select the most suitable GLM model, we performed a multi-model selection using the Akaike Information Criterion (AIC), the difference between the best model in each set (lowest AIC value) and all other models (Δ_i) and Akaike weights (W_i) (Bartoń, 2019). Models where $\Delta_i < 3$ were deemed the most informative (Burnham, Anderson & Huyvaert, 2011). To assess the goodness-of-fit of the various models, we plotted the sample and theoretical quantiles of the model residuals (Kery & Royle 2015). The relative importance of each predictor variable (x_i) was then calculated as the sum of the AIC weights of each informative model that included the predictor (Burnham & Anderson, 2002). Because analyses yielded multiple parsimonious models, we used model averaging for all models where $\Delta_i < 3$ (Burnham & Anderson, 2002). We calculated the model-averaged parameter estimates (average model coefficients), adjusted standard errors (S.E.) and associated *z*-values for variables for the top-ranked generalized linear models and compared the direction and magnitude of effects of the various levels within factors (*e.g.* species ID within the species factor). To investigate the overlap of the activity patterns between the seven mesocarnivore species, the time of detection was converted to radians following the requirements of the *overlap* package (Ridout & Linkie, 2009). The coefficient of overlapping (Δ_1 for small sample sizes $n < 50$) and 95% confidence interval was calculated, generating 1000 bootstrap estimates per species (Ridout & Linkie, 2009). The overlap coefficient ranges from 0, indicating no overlap, to 1, indicating complete overlap. All graphing was conducted using the package *ggplot2* (Wickham, 2009).

RESULTS

Detection rates

The total sampling effort using 39 traps over 105 days yielded 420 783 total detections, of these only 802 contained identifiable mesocarnivores. Camera trap detections of mesocarnivores differed between the landscapes, with riparian traps having 150% higher detection rate (mean ± standard deviation = 38 ± 27.86 detections per trap) than grassland traps (16 ± 21.31 detections). Community composition differed between the landscapes; six (46.15%) mesocarnivore species (yellow mongoose, black-footed cat, caracal, meerkat, honey badger and striped polecat) were detected only in grassland, while seven (53.84%) mesocarnivore species (otter spp., serval, black-backed jackal, aardwolf, rusty-spotted genet, slender mongoose and marsh mongoose) were detected in both landscape types (Table 2). None of the species were exclusively detected in riparian habitat. Black-backed jackals were the most abundant species detected in the study area (RAI = 12.47), with detections of servals being the least abundant (RAI = 0.53). Black-backed jackals also had the highest overall detection rate, with the most detections recorded in the grassland landscape (10.65), whilst servals had the lowest detection rate (0.48) (Fig. 2). The rusty-spotted genet was the most frequently detected species in riparian areas (8.54). The different mesocarnivores were also detected in different vegetation types throughout the study site (Table 2). Although slender mongooses were detected in both riparian and grassland landscapes, they were not detected in dry open grassland; areas occupied predominantly by yellow mongooses. Instead, when utilizing grassland, slender mongooses confined their activities to the rocky outcrops in grassland where the other two mongoose species were not detected. When using the riparian areas, slender mongooses were detected mostly in densely vegetated areas.

Mesocarnivore activity patterns

Black-backed jackals, rusty-spotted genets and marsh mongooses showed crepuscular peaks of activity, with low to zero activity detected during the day (Fig. 3A,B,D). Servals also showed crepuscular peaks in activity but were most active two hours after dusk (Fig. 3E). Slender and yellow mongooses showed diurnal peaks in activity (Fig. 3F,G). The otter species were most active in the four hours following dawn, with low activity around dawn and dusk (Fig. 3C).

Predictors of mesocarnivore activity

Species ID and temperature (relative importance x_1 and x_2 = 100% across two informative models) were predictors of variation in the activity time between the seven mesocarnivore species used for statistical modelling (Table 3). Vegetation characteristics (relative importance x_3 = 20% for one model) and moon phase (relative importance x_4 = 14% for one model) predicted variation in times of activity for mesocarnivores to a lesser extent.

Parameter estimates for the parsimonious model differed in direction (+/–) and magnitude across the four predictor variables used to explain the variation observed in mesocarnivore activity (Fig. 5). Serval and marsh mongoose activity times were not significantly different when compared to

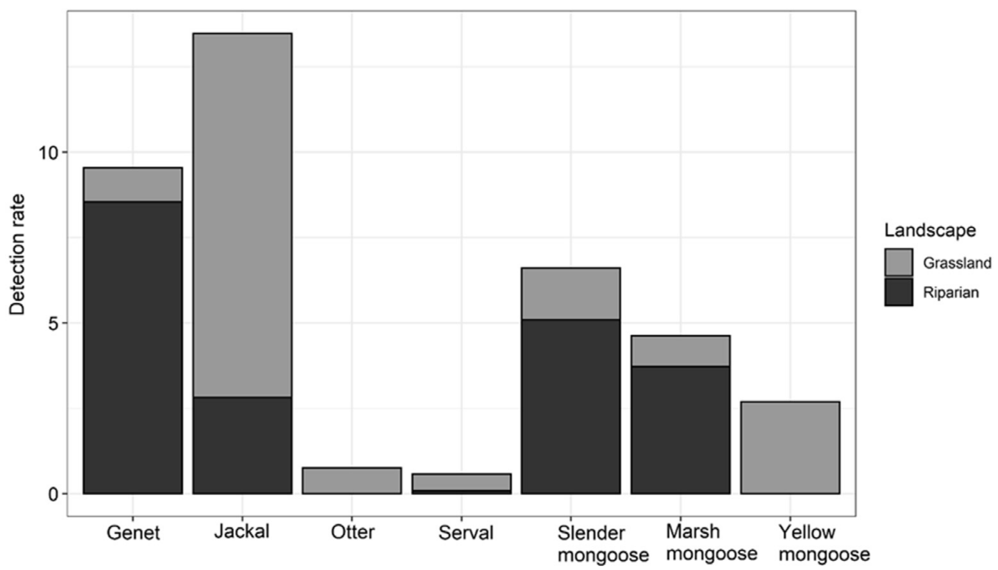

Fig. 2. Detection rate (number of detections/total number of camera traps) for the grassland (light grey, n = 29 traps) and riparian (dark grey, n = 11 traps) for rusty-spotted genet (Genet, *Genetta maculata*), black-backed jackal (Jackal, *Canis mesomelas*), otter (*Lutra maculicollis and Aonyx capensis*), marsh mongoose (*Atilax paludinosus*), serval (*Leptailurus serval*), slender mongoose (*Galerella sanguinea*) and yellow mongoose (*Cynictis penicillata*) in the Telperion Nature Reserve, South Africa, from April–July 2015.

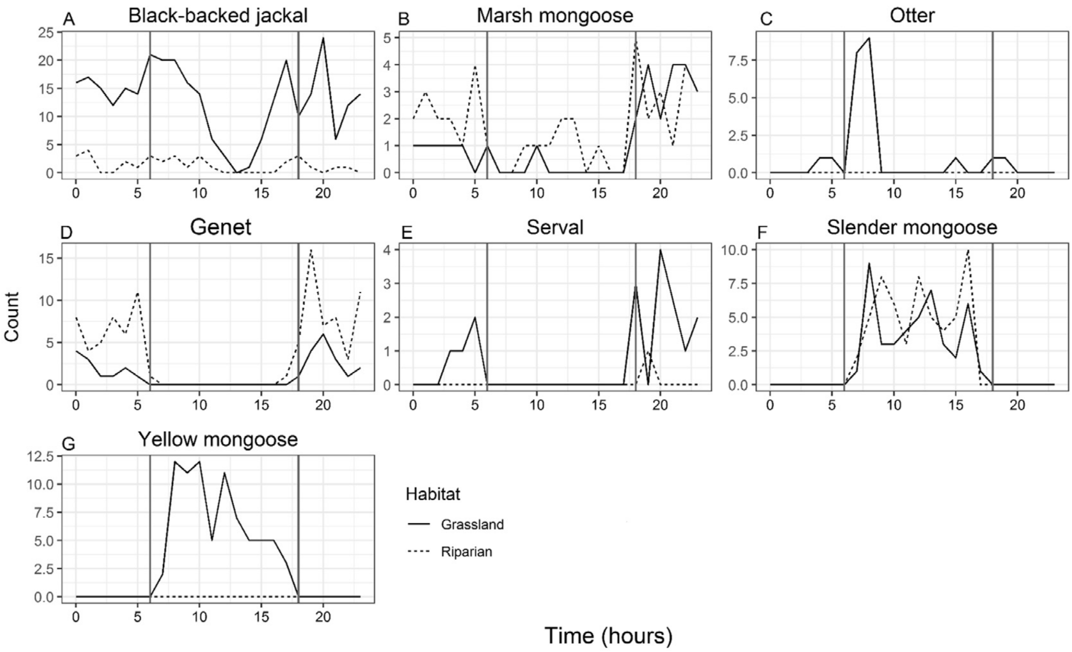

Fig. 3. Detection counts across 24-hour periods (0:00 to 23:00) for (**A**) Black-backed jackal (*Canis mesomelas*), (**B**) marsh mongoose (*Atilax paludinosus*), (**C**) otter (*Lutra maculicollis and Aonyx capensis*), (**D**) rusty-spotted genet (*Genetta maculata*), (**E**) serval (*Leptailurus serval*), (**F**) slender mongoose (*Galerella sanguinea*) and (**G**) yellow mongoose (*Cynictis penicillata*) in riparian (dashed black line) and grassland (solid black line) landscapes in the Telperion Nature Reserve, South Africa, from April–July 2015. Solid grey vertical lines denote dawn (6:00) and dusk (18:00). Note differences in *y*-axis scales.

rusty-spotted genet activity times (Table 4). Temperature had a significant positive effect on activity times of modelled mesocarnivore species, with overall activity increasing as ambient temperatures increased (Table 4). Rusty-spotted genets and marsh mongooses were active above 5°C, while black-backed jackals were active over the full range of ambient temperatures recorded on traps from –10°C to 40°C. Servals were active within a narrow range of temperatures between

Table 3. Ranked Akaike Information Criterion (AIC), difference between the top-ranked model and the *i*th model (Δ_i) with AIC weight (W_i) from generalized linear models investigating if species, temperature (Temp), moon phase (Moon) or vegetation characteristics (Vegetation) explain the variation in the activity time of seven mesocarnivore species in the Telperion Nature Reserve.

Model	d.f.	AIC	Δ_i	W_i
Species + Temp	9	4953.7	0	0.611
Species + Temp + Vegetation	18	4954.8	1.07	0.209
Species + Temp + Moon	19	4955.9	2.96	0.139
Species + Temp + Moon + Vegetation	28	4990.6	5.40	0.041
Temp	3	4991.6	36.90	0
Temp + Moon	13	4994.4	40.69	0
Species + Vegetation	15	4994.4	40.68	0
Temp + Vegetation	12	4995.3	41.61	0
Species	8	4997.8	44.11	0
Species + Moon	15	4998.3	44.62	0
1 (null)	2	5011.7	57.99	0
Moon	9	5012.7	59.01	0
Vegetation	9	5017.9	64.24	0

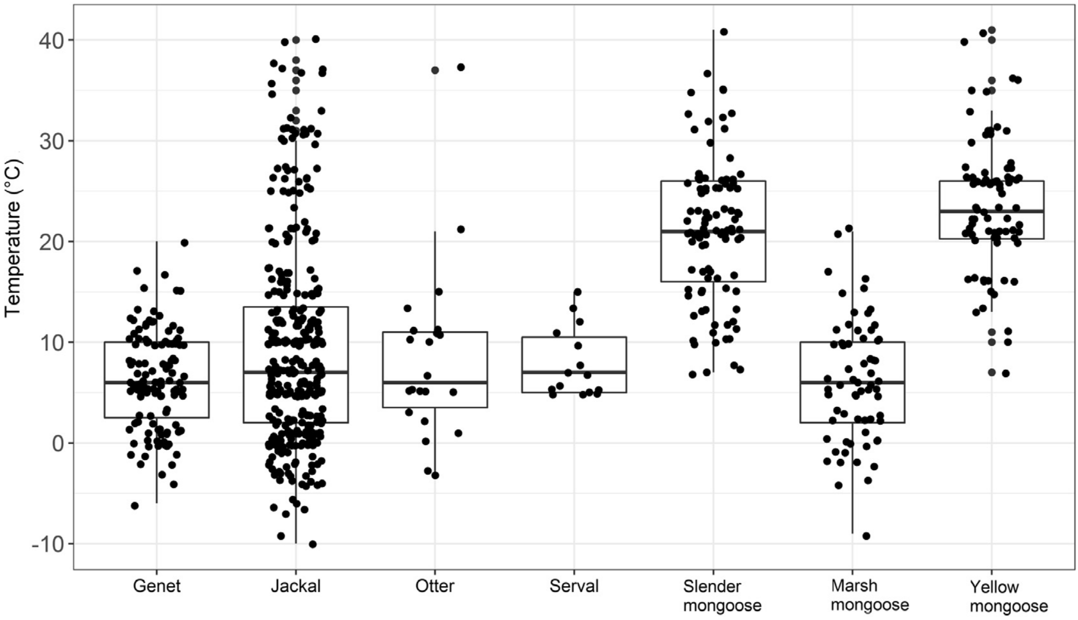

Fig. 4. Boxplot showing medians and interquartile ranges (Tukey-style whiskers extend to 1.5 × IQR) of the temperature ranges during which rusty-spotted genet (*Genetta. maculata*), black-backed jackal (Jackal, *Canis mesomelas*), otter (*Lutra maculicollis* and *Aonyx capensis*), marsh mongoose (*Atilax paludinosus*), serval (*Leptailurus serval*), slender mongoose (*Galerella sanguinea*) and yellow mongoose (*Cynictis penicillata*) were active at the Telperion Nature Reserve, South Africa, from April to July 2015.

5°C and 15°C, while slender and yellow mongooses were active during the hottest part of the day (Fig. 4). Activity times of modelled mesocarnivore species were influenced positively or negatively by moon phase and vegetation characteristic. The magnitude of these variables could also be seen across species; however, neither of these effects were statistically significant.

Slender and yellow mongooses had the highest coefficient of activity overlap ($\Delta_1 = 0.905$), followed by marsh mongooses and rusty-spotted genets ($\Delta_1 = 0.804$) and servals and rusty-spotted genets ($\Delta_1 = 0.798$; Table 5). The lowest coefficient of activity overlap was observed between yellow and slender mongooses with servals ($\Delta_1 = 0.071$).

DISCUSSION

Our study aimed to identify mesocarnivore species within the Telperion Nature Reserve, South Africa, and investigate their activity patterns. A diverse group of 13 mesocarnivore species was identified within this relatively small area. All species broadly followed similar activity patterns to those found previously throughout Africa (reviewed in Skinner & Chimimba (2005) and Kingdon & Hoffman (2013)) except for servals, which in our study were detected only at night. The type of mesocarnivore species and ambient temperature best explained overall variation in times of activity for the seven modelled species, namely the otter sp., rusty-spotted genet, black-backed jackal, serval, slender mongoose, marsh mongoose and yellow mongoose. The various species detected differed in their estimated relative abundances, with black-backed jackals detected most often, and servals detected the least, although these results may relate to behaviour and movement patterns of the different study species (Sollmann *et al*., 2013). We also acknowledge that the relatively short sampling period may have affected the rate at which species were detected on the camera traps and that more longitudinal monitoring would be needed to investigate activity patterns across multiple seasons.

Black-backed jackals are highly mobile and wide-ranging when foraging for a wide variety of food (Kaunda, 2001), which may contribute to higher detection rates. In comparison, servals are more cryptic with a preference for rodent prey and dense grassland habitats (Ramesh *et al*., 2016), which may lead to lower detection rates. The highest coefficient of activity overlap was observed between slender and yellow mongooses, followed by marsh mongooses and rusty-spotted genets,

Table 4. Model-averaged parameter estimates (average model coefficients), adjusted standard error (S.E.) and associated *z*-values for variables for the top-ranked generalized linear models testing the effects of species, temperature (Temp), moon phase or vegetation characteristics on the variation of seven mesocarnivore species' activity time. For each factor, the category used as the intercept is indicated in brackets. Parameter estimates not overlapping zero (showing statically significant effects) are highlighted in bold.

Factor		Estimate ± S.E.	*z*-value	Pr (>|*t*|)
	(Intercept)	12.74 ± 1.46	8.704	<0.001
Species (Genet)	**Jackal**	**–3.52 ± 1.17**	**3.00**	**<0.01**
	Otter	**–5.00 ± 1.87**	**2.66**	**<0.01**
	Serval	2.03 ± 2.09	0.97	0.33
	Slender mongoose	**–3.94 ± 1.04**	**3.78**	**<0.001**
	Marsh mongoose	0.94 ± 1.12	0.84	0.40
	Yellow mongoose	**–5.72 ± 1.45**	**3.92**	**<0.001**
Temperature	**Temp**	**0.20 ± 0.03**	**6.60**	**<0.001**
Moon phase (First quarter)	Full	–0.84 ± 1.16	0.73	0.46
	Last quarter	1.34 ±1.40	0.96	0.33
	New moon	–0.24 ± 0.87	0.28	0.77
	Waning crescent	0.23 ± 0.86	0.27	0.78
	Waning gibbous	–0.75 ± 1.09	0.69	0.49
	Waxing crescent	–0.49 ± 1.04	0.48	0.63
	Waxing gibbous	0.54 ± 1.07	0.51	0.61
Vegetation (Grassland: Open)	Grassland: Rocky	–0.94 ± 1.25	0.75	0.45
	Grassland: Wet	0.03 ± 0.56	0.06	0.95
	Grassland: Wooded	–1.22 ± 1.57	0.77	0.43
	Riparian: Dense	–0.84 ± 1.10	0.77	0.44
	Riparian: Open	–087 ± 1.28	0.68	0.49
	Riparian: Rocky	–1.77 ± 1.66	1.06	0.28
	Riparian: Sandy	1.01 ± 1.26	0.80	0.42

and servals and rusty-spotted genets, indicating that these species are likely to have the highest potential for competitive interaction in this study area.

Slender and yellow mongooses are diurnal and have comparable omnivorous diets (Wilson & Reeder, 2005). However, yellow mongooses were exclusively detected in the grassland landscape, whilst slender mongooses were detected more often in the riparian landscape. Similar to our findings, other studies have demonstrated differences in fine-scale habitat selection; yellow mongooses select open habitats with short grassland vegetation, whereas slender mongooses prefer covered areas with rocky outcrops (Cronk & Pillay, 2020). Additionally, whilst both yellow and slender mongoose species are diurnal, they have several peaks in their activity throughout the day. Our study was conducted during autumn–early winter, and temporal overlap between yellow and slender mongooses may be greater during colder months when day length is shorter and resources are scarcer than in warmer months (Cronk & Pillay, 2020). This finding suggests that yellow and slender mongoose species use a combination of spatial and fine-scale temporal partitioning as coexistence mechanisms (Donadio & Buskirk, 2006).

Rusty-spotted genets, servals and marsh mongooses all showed crepuscular peaks of activity. Rusty-spotted genets and servals favour mammalian (mainly rodent) prey, which can comprise more than 80% of the diet of both species (Ramesh & Downs, 2015; Zemouche, 2018). Considering their similar activity patterns, it seems probable that there may be competition between rusty-spotted genets and servals for similar food resources in the reserve. The low detection rates of servals and the predominant use of grassland habitat by this species compared to rusty-spotted genets detected mainly in riparian habitat suggest that encounter rates between these two species may be low. This result may indicate spatial partitioning and aid in predation risk avoidance (Ramesh & Downs, 2015) or is simply due to generally low serval densities in nature reserves (Taylor, 2020). Insects (28%) and crabs (26%) form substantial components of

Table 5. Activity overlap coefficients (Δ_1, in bold) and 95% confidence intervals (in brackets) for each species pair among seven mesocarnivores at the Telperion Nature Reserve, South Africa, from April to July 2015.

	Genet	Jackal	Otter	Serval	Slender mongoose	Marsh mongoose	Yellow mongoose
Genet	1						
Jackal	**0.605** (0.54–0.66)	1					
Otter	**0.194** (0.07–0.33)	**0.442** (0.29–0.58)	1				
Serval	**0.798** (0.61–0.94)	**0.516** (0.34–0.67)	**0.197** (0.03–0.36)	1			
Slender mongoose	**0.051** (0.01–0.09)	**0.383** (0.32–0.44)	**0.325** (0.18–0.46)	**0.071** (−0.02–0.17)	1		
Marsh mongoose	**0.804** (0.70–0.88)	**0.711** (0.61–0.80)	**0.257** (0.11–0.40)	**0.711** (0.52–0.88)	**0.214** (0.12–0.32)	1	
Yellow mongoose	**0.055** (0.01–0.10)	**0.382** (0.31–0.44)	**0.366** (0.22–0.50)	**0.071** (−0.01–0.17)	**0.905** (0.80–0.98)	**0.216** (0.12–0.31)	1

marsh mongoose diet (Somers & Purves, 1996). Although marsh mongoose activity overlap with rusty-spotted genets was high, coexistence between these species is likely facilitated by resource partitioning (*e.g.* food) and different foraging strategies (Mills *et al.*, 2019).

Temperature was the other important factor affecting the behaviour of mesocarnivores in the Telperion Nature Reserve. Behavioural strategies are affected by various intrinsic and external factors, including ambient temperature (Caraco *et al.*, 1990). Given that midday ambient temperatures for this region can peak above 40°C during summer, the risk of thermoregulatory stress may inhibit the activity of most mesocarnivores around midday (Monterroso, Alves & Ferreras, 2014). Of the seven species compared, only slender and yellow mongooses were active during the hottest parts of the day. This behaviour suggests that these species may take advantage of food resources not utilized by other species because of a narrow thermal tolerance range, although further studies would be required to investigate diurnal activity for all seasons for these two species

Vegetation characteristics predicted variation in times of activity to a lesser extent when compared to temperature. Vegetation characteristics within the landscape may affect mesocarnivore activity by influencing the distribution and availability of prey species (Schuette *et al.*, 2013). Rodents, for example, may be associated with denser vegetation and taller grass (Thompson & Gese, 2007), which provides suitable habitat for hiding or resting (Krofel, 2008; Pretorius, 2019). The selection of different microhabitats within a landscape causes differences in species distributions, allowing for the coexistence of species with seemingly similar activities and diets (Noor *et al.*, 2017). Animals modify their spatial territory when faced with increased interspecific competition, resulting in successful coexistence (Yang *et al.*, 2018; Zhao *et al.*, 2020). Habitat heterogeneity, particularly in small nature reserves, may be crucial to supporting the coexistence of a diverse set of mesocarnivores (Moreira-Arce *et al.*, 2016; Carricondo-Sanchez *et al.*, 2019), like those that inhabit the Telperion Nature Reserve.

Moon phase somewhat predicted variation in times of activity of the mesocarnivores, with no clear pattern of effect for our analysis on times of activity between the modelled species. This result may be influenced by the fact that three of the modelled species were exclusively diurnal (otter, slender mongoose and yellow mongoose), three species exhibited crepuscular activity (black-backed jackal, marsh mongoose and rusty-spotted genet), whilst only servals exhibited a nocturnal peak in activity two hours after dusk. Visually orientated hunters experience increased detectability under moonlit conditions, which increases predation risk for nocturnal mammals and may result in suppressed activity (Prugh & Golden, 2014). In large African carnivores, African wild dogs (*Lycaon pictus*) and cheetahs (*Acinonyx jubatus*) show heightened nocturnal activity and better hunting opportunities during moonlit nights despite the increased mortality risk from lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*) (Cozzi *et al.*, 2012). To our knowledge, the effects of moon phase on nocturnal South African mesocarnivores have not yet been examined and would warrant further investigation.

Mesocarnivores are important components of healthy ecosystems (Roemer *et al.*, 2009). However, major overlaps in diet and activity times, in addition to limited space within small nature reserves, may heighten competition between members of this guild (Massara *et al.*, 2016), particularly in South Africa with its rich mesocarnivore diversity (Skinner & Chimimba, 2005). Our study detected several mesocarnivore species that showed comparable patterns of temporal activity and probably shared similar diets, indicating possible competition for resources (food and space) between these species. Our results also provide a useful first description of mesocarnivore diversity and activity patterns for this small reserve for future studies to build on.

Variable detection rates for various species in the riparian and grassland landscapes suggest that most mesocarnivore species in the Telperion Nature Reserve employ spatial partitioning rather than temporal or trophic niche partitioning as a coexistence mechanism (Donadio & Buskirk, 2006). With its mixture of riparian and grassland vegetation types, the heterogeneity of the nature reserve, and the related diversity of available prey species (Afonso *et al.*, 2021), was likely the main contributor to the rate of species detected, despite its relatively small size. Landscape heterogeneity has been shown to facilitate niche partitioning and enable coexistence (Fisher *et al.*, 2013) and is particularly important in increasingly human-dominated landscapes (Manlick *et al.*, 2020). Therefore, maintaining heterogeneity in enclosed nature reserves in South Africa is one important consideration to promote mesocarnivore biodiversity, as demonstrated in other parts of the world (Moreira-Arce *et al.*, 2016; Curveira-Santos *et al.*, 2017).

CONCLUSION

Interspecific competition may intensify when available habitat is limited, such as in small nature reserves like Telperion Nature Reserve. Our results show that Telperion hosts a variety of mesocarnivore species that follow diverse activity patterns across grassland and riparian landscapes. Species ID and temperature were shown to be the best predictors of activity patterns, likely related to the different behavioural strategies and different tolerances to thermal stress. Several species-pairs showed high degrees of activity overlap, which included slender and yellow mongooses, followed by marsh mongooses and rusty-spotted genets, and servals and rusty-spotted genets. These species pairs likely utilized different spatial, temporal and resource (in the case of marsh mongoose and rusty-spotted genet) partitioning strategies to facilitate coexistence in this relatively small nature reserve. This shows that preserving habitat heterogeneity in small nature reserves is likely essential to the continued persistence of the diverse mesocarnivore guild observed in this study.

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