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COMMUNITY ECOLOGY – ORIGINAL RESEARCH

Competition and coexistence in a small carnivore guild

Jacques de Satgé[1] · Kristine Teichman[2,3] · Bogdan Cristescu[3,4]

Abstract The potential for strong competition among small sympatric carnivores results in a need for coexistence strategies whereby competitors partition along spatial, temporal and dietary axes as a means to reduce ecological overlaps. We determined spatial and temporal partitioning patterns of a guild of small African carnivores: the African wildcat *Felis silvestris lybica*, grey mongoose *Galerella pulverulenta*, small-spotted genet *Genetta genetta*, striped polecat *Ictonyx striatus*, and the yellow mongoose *Cynictis penicillata*. We quantified the degree of spatial and temporal co-occurrence of the small carnivores using camera trap data over a year-long period. Carnivores separated into two temporal groups: nocturnal species (wildcat, polecat and genet) and diurnal species (mongooses). In addition, carnivores within the same temporal group had strong patterns of reduced spatial co-occurrence. The smaller bodied carnivores showed lower co-occurrence with the larger bodied African wildcat than expected by chance, supporting the idea of dominant competitor avoidance. Thus, small carnivores likely minimise competitive interactions through spatio-temporal habitat partitioning.

Keywords Biodiversity hotspot · Spatial partitioning · Temporal partitioning · Diel cycle · Succulent Karoo

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Introduction

Interspecific competition shapes the ecological and demographic dynamics of sympatric species through the effects of resource exploitation and interference interactions (Holt and Polis 1997; Grassel et al. 2015). Among carnivores, interference competition is a key driver of morphologies, behaviour and distributions (Donadio and Buskirk 2006). As such, competitive interactions have the potential to change and drive community assemblage patterns, determine niche partitioning and promote the development of coexistence mechanisms among competing species (Davis et al. 2010; Di Bitetti et al. 2010; Chiang et al. 2012; Cristescu et al. 2013). The nature of competition and coexistence in carnivores is further fine-tuned by life history traits such as body size, diet and home range size (Palomares and Caro 1999; Caro and Stoner 2003; Chiang et al. 2012).

Patterns and mechanisms of competition and coexistence are of particular research interest when involving carnivores of the same guild that possess comparable morphologies and overlapping diets. In such situations there is potential for strong competitive interactions (Simberloff and Dayan 1991) and these interactions result in a need for coexistence strategies whereby competitors partition along spatial, temporal and dietary axes as a means to reduce ecological overlaps (Schoener 1974; Di Bitetti et al. 2010).

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Smaller carnivores are arguably under the greatest competitive pressure among all carnivores (Hunter and Caro 2008) given that they face competition on several fronts. First, they are subject to extreme interference competition in the form of interspecific killing within carnivore communities (Polis et al. 1989; Palomares and Caro 1999; Donadio and Buskirk 2006). This threat means that small carnivores live in a landscape of fear (Laundre et al. 2010) and are forced into trade-offs to enable avoidance of dominant predators (Bischof et al. 2014). Second, small carnivores are subject to exploitation competition; they are often "wide-ranging generalist feeders" whose energetic needs overlap those of numerous sympatric competitors (Caro and Stoner 2003, p72). This too reinforces the need for trade-offs in spatial and temporal activities (Schuette et al. 2013), but the extent to which such trade-offs occur in small carnivore guilds is largely undetermined.

Most studies on carnivore assemblages and spatio-temporal partitioning have focused on large and medium-sized carnivores (Davis et al. 2010; Durant et al. 2010; Kamler et al. 2012; Ramesh et al. 2012; Steinmetz et al. 2013; Sunarto et al. 2015). In contrast, small carnivores can be difficult to study in the wild (Bischof et al. 2014), particularly if species are nocturnal, elusive and occurring at low densities (Heilbrun et al. 2006). However, the emergence of camera traps has aided studies collecting data on cryptic species (Cutler and Swann 1999; Carbone et al. 2001) and has made the study of small carnivores more feasible (Chiang et al. 2012).

Here we study competition and coexistence patterns in a guild of small African carnivores as indexed by spatial and temporal occurrence data from camera traps. The African wildcat *Felis silvestris lybica*, small-spotted genet *Genetta genetta*, striped polecat *Ictonyx striatus*, yellow mongoose *Cynictis penicillata*, grey mongoose *Galerella pulverulenta* and meerkat *Suricata suricatta* make up an ecological guild of small carnivores inhabiting many arid areas of the African continent. The wildcat, genet and polecat are typically nocturnal (Lariviere and Calzada 2001; Lariviere 2002; Kok and Nel 2004), while the two mongooses are typically diurnal (Cavallini and Nel 1995). In addition to overlapping distributions, the small carnivores exploit shared resources as befits a guild (Root 1967; Simberloff and Dayan 1991), namely relying on similar items of prey—a combination of rodents and insects—to make up a majority of their diets (Cavallini and Nel 1995; Nowell and Jackson 1996; Apps 2000; Kok and Nel 2004). The guild members also exhibit similar body sizes: grey and yellow mongooses and striped polecats typically weigh just under one kilogram, small-spotted genets weigh just under two kilograms, while wildcats are the heaviest guild member weighing approximately five kilograms. Thus, a combination of traits—sympatric occurrence, overlapping diets and comparable body sizes

(Table 1)—within this small carnivore guild may contribute to an increased chance of competitive overlap (Caro and Stoner 2003; Donadio and Buskirk 2006) and potentially shape patterns of coexistence (Schoener 1974; Jácomo et al. 2004). Given this predisposition to intraguild competition, the spatio-temporal patterns which allow for coexistence among these under-researched carnivores become of particular interest.

Being the largest member in this guild of small carnivores, the African wildcat may represent a dominant competitor (Donadio and Buskirk 2006). Given this size difference, the theoretical potential for wildcats to kill other carnivores (Kok and Nel 2004), and the potential competition for similar food resources among guild members we expect the carnivores to manipulate spatio-temporal partitioning to reduce overlap. We hypothesised that the guild would separate along a temporal axis, namely forming temporally distinct coexistence groups (temporal partitioning hypothesis). We further hypothesised that species belonging to the same temporal group would spatially organise in a manner that reduced their co-occurrence (spatial partitioning hypothesis). Lastly, we hypothesised that wildcats would be avoided by smaller carnivores (avoidance of dominant competitor hypothesis). These hypotheses reflect our proposition that combinations of spatial, temporal and dietary partitioning allow for coexistence in a guild of small carnivores inherently predisposed to competition.

Materials and methods

Study area

The study area was located in the Succulent Karoo, a shrub-dominated biome internationally recognised as a world biodiversity hotspot (UNESCO 2016). An 810 km² area was delineated in Namaqualand, Northern Cape, South Africa (Fig. 1) where a rectangular grid of camera traps was used to sample occurrence of mammals (mongoose-size and larger) for one year (April 2014–March 2015). The study area falls within Namaqualand's 'hardeveld' biotope (Desmet 2007), a rugged semi-arid landscape with distinct seasonality and a low rainfall of 178–263 mm per year. The region is dominated by low-lying vegetation comprising succulent dwarf shrubs, primarily from the Aizoaceae and Crassulaceae families, while mass flowering of annuals (mainly Asteraceae) occurs during the winter rainfall season. The region is known for its high plant species diversity and endemism, but semi-arid conditions and low-nutrient sandy soils result in a uniform sparse vegetation pattern across much of the study area (Luther-Mosebach et al. 2012). Main land use is free-range livestock production

Table 1 An overview of the literature regarding biological and ecological traits encountered in a guild of small carnivores: the African wildcat, small-spotted genet, striped polecat, yellow mongoose, and grey mongoose

Species	Home range size (ha ± SD)	Body mass (kg) (n, range)	Diet: common prey items (% occurrence in scat)	Distribution and habitat tolerance	Sources
African wildcat *Felis silvestris lybica*	♂ 770 ± 350 (n = 5) ♀ 350 ± 110 (n = 3)	♂ 5.2 (5, 4.2–6.0) ♀ 4.4 (3, 4.0–4.6)	Rodents (48%) Hares and rabbits (26%) Insects (26%) Hyraxes (5%) Arachnids (5%)	Africa (excl. Sahara and tropical west), Arabian peninsula: broad habitat tolerance	Palmer and Fairall (1988), Nowell and Jackson (1996), Kok and Nel (2004), Skinner and Chimimba (2005), Le Roux et al. (2015)
Small-spotted genet *Genetta genetta*	♂ 113 ± 47 (n = 7) ♀ 72 ± 31 (n = 10)	♂ 1.9 (19, 1.5–2.5) ♀ 1.8 (11, 1.4–2.0)	Rodents (55%) Insects (55%) Arachnids (35%) Birds (15%) Reptiles (15%)	Mediterranean Europe, Arabia, Africa (excl. Sahara and tropical west): broad habitat tolerance	(Apps (2000), Lariviere and Calzada (2001), Munuera and Llobet (2004)
Striped polecat *Ictonyx striatus*	Unknown-territorial animals; males have larger home ranges	♂ 0.8 (21, 0.5–1.2) ♀ 0.6 (4, 0.4–0.7)	Insects (62%) Rodents (38%) Arachnids (12%) Birds (10%) Myriapods (5%)	Africa (excl. Sahara and tropical west): broad habitat tolerance	(Apps (2000), Lariviere (2002), Stuart et al. (2015)
Yellow mongoose *Cynictis penicillata*	♂ 102 ± 32 (n = 3) ♀ 27 ± 17 (n = 10)	♂ 0.9 (5, 0.8–1.0) ♀ 0.8 (6, 0.5–0.9)	Insects(70%) Rodents (12%) Arachnids (12%) Birds (10%)	Southern Africa (largely west and central regions): tolerates predominantly grassland, scrub and arid savanna habitats	Cavallini (1993), Cavallini and Nel (1995), Apps (2000), Do Linh San et al. (2015)
Grey mongoose *Galerella pulverulenta*	♂ 68 ± 21 (n = 3) ♀ 31.6 (n = 1)	♂ 0.9 (3, 0.85–1.0) ♀ 0.8 (1)	Insects (66%) Rodents (52%) Birds (9%) Reptiles (9%)	South Africa (excl. northeast), Lesotho and southern Namibia: fairly broad habitat tolerance, largely found in karroid bushveld and sclerophyllous scrub	Cavallini and Nel (1990, 1995), Apps (2000), Do Linh San and Cavallini (2015)

All sourced home range sizes (ha) were estimated using 95–100% minimum convex polygons. Dietary information derived from studies undertaken in South Africa
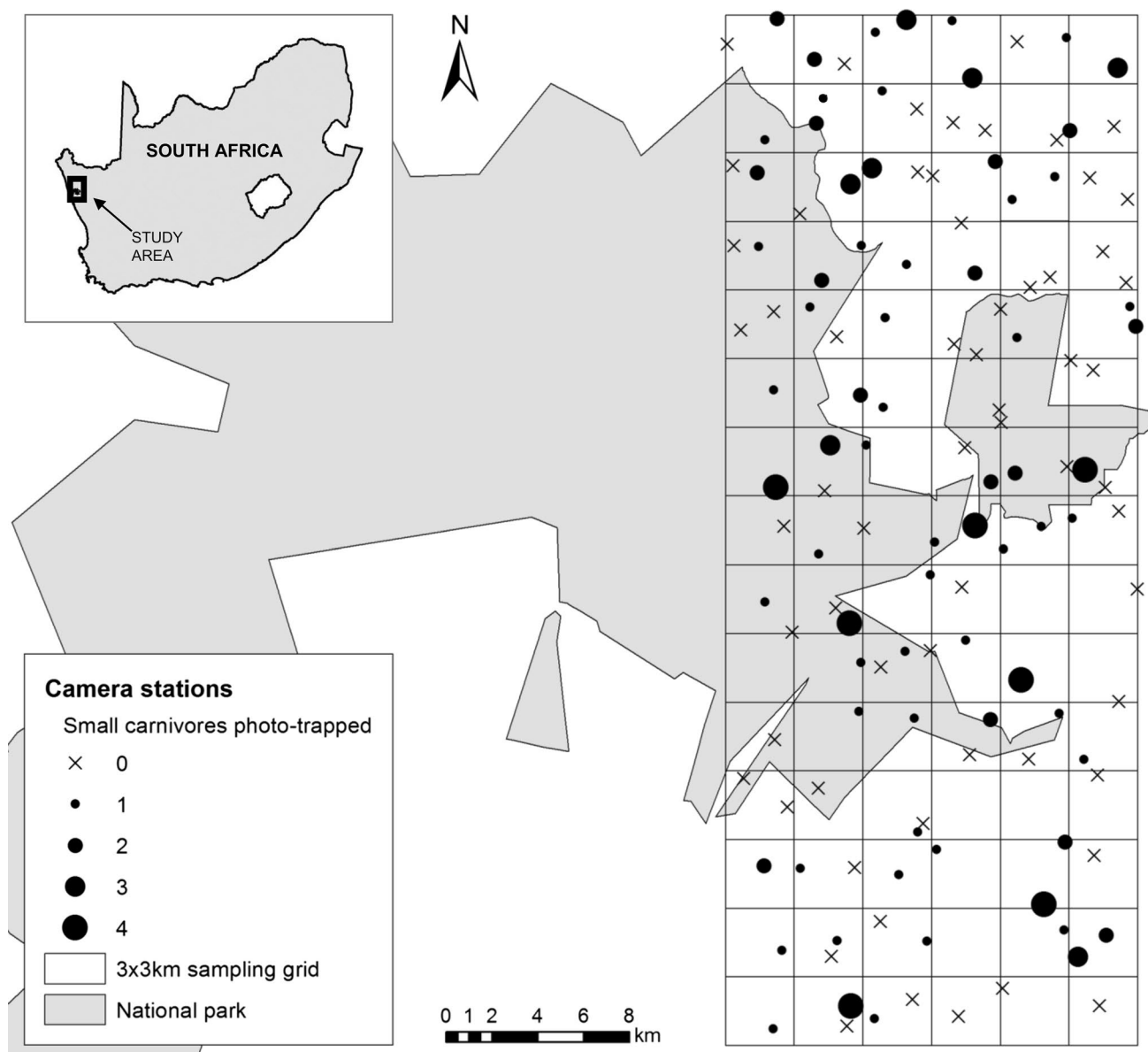
Fig. 1 Locations of camera trap stations distributed in a 3 × 3 km grid system in Namaqua National Park and neighbouring farmland. *Camera trap* symbols illustrate the degree of carnivore co-occurrence. *Inset* map shows study area location in South Africa

with some of the area recently protected (1994) as Namaqua National Park.

Camera trapping

Two camera trap stations were set in rotation in each of the ninety 3 km × 3 km grid cells. The study was part of a larger project investigating mammalian carnivore biodiversity, hence grid cell size was set to reflect mesocarnivore home range [caracal (*Caracal caracal*)], which was of intermediate size between the home ranges of the smallest (grey mongoose) and the largest [leopard (*Panthera pardus*)] carnivores in the study area. A single camera was

rotated in each cell once between stations to maximise spatial coverage of the cell and survey more than one season. We enforced a minimum distance between stations of 500 m and we aimed to have each station active for minimum 45 days. Each station consisted of a single unbaited motion-activated camera placed on a metal post and facing a 4WD track. Cameras were set at a standardised lens height of 40 cm and at 1 m from the nearest track. Camera make and model were identical across stations (Cuddeback Ambush Black Flash 1194, year 2013). The black flash option minimised visual disturbance to passing animals.

We minimised the likelihood of non-detection of target species by calculating the average first detection time of

each species across all camera stations. The longest time to first detection was 44.96 days recorded for polecats. We used this value as a threshold by which the data were trimmed wherein camera stations active for <45 days were excluded from the data set. To ensure independence of photographic capture events any consecutive photographs of the same species within one hour were recorded as a single occurrence event (Tobler et al. 2008; Treves et al. 2010; Chiang et al. 2012).

Temporal partitioning

Using a date-adjusted sunlight-hours calendar (http://www.cmpsolv.com/los/sunset.html, accessed October 2014) we sorted each independent photographic capture event into one of three temporal categories: 'nocturnal', 'crepuscular' or 'diurnal'. Using these categories we determined broad temporal groupings by generating a contingency table of the temporal data. Pearson's Chi-square test was used to evaluate if the observed temporal patterns deviated significantly from the pattern expected under a Chi-square distribution. A Fischer post hoc test using Bonferroni correction to adjust for multiple comparisons was performed to determine differences between species pairs. To explore temporal partitioning in further detail we analysed species' diel cycles. We created an index of the relative activity level for each species by dividing the hourly number of occurrence events of a species by the total number of occurrence events for all species (Chiang et al. 2012). These activity levels were expressed as percentages across 24 h and reflect both the activity pattern of each species, and their relative contribution to all recorded occurrence events. For the analyses of these circadian activity patterns, we used the R (version 3.3.3) package 'circular' (version 0.4-7) (Lund and Agostinelli 2013; R Core Team 2017). Activity data of each species were transformed from hours to degrees and Whatson–Wheeler non-parametric tests were used to test for significant differences in active hours between species pairings.

Spatial partitioning

Based on the temporal analysis we constructed three presence–absence matrices ('nocturnal', 'diurnal' and 'global') recording the occurrences of the five small carnivores in question. For example, the presences and absences of nocturnal species were recorded in a 3×68 block matrix, whereby three rows were defined for each nocturnal species (genet, polecat and wildcat) and 68 columns for the camera sites where ≥ 1 of the nocturnal species were recorded. Similar matrices were created for the diurnal and global species groupings, but no presence–absence matrix was built for the 'crepuscular'

period because of small sample sizes for this temporal category. To evaluate spatial patterns of co-occurrence in each observed matrix we created corresponding null matrices for comparison. Each null matrix was generated using the 'SIM2 fixed-equiprobable' randomisation algorithm defined by Gotelli (2000) using the R package 'EcoSimR' (version 0.1.0). This generated a randomly structured presence–absence matrix (the 'null matrix') based on the marginal row and column totals of the observed matrix. The null matrix column sums were 'fixed' and identical to those in the observed matrix, thus preserving differences in species incidence (Gotelli 2000). The row sums of the null matrix were allowed to vary randomly and with equal probability, thus assuming that all camera sites are 'equiprobable' as befits relatively homogenous environments (Zhang et al. 2009). Both the null and observed matrices were assessed for the average degree of species co-occurrence, expressed as the 'c-score' or 'checkerboard score' test statistic (Stone and Roberts 1990). Species c-scores significantly higher than expected by chance suggest a lack of species overlaps within the matrix and imply a negative pattern of species co-occurrence (Stone and Roberts 1990; Zhang et al. 2009). Each of the three null matrices (nocturnal, diurnal and global) were simulated ten thousand times, thereby allowing a comparison of the degree of difference between the distribution of null matrix c-scores and the observed matrix c-score which was expressed as a standardised effect size (SES) classified as 'small' (>0.2), 'medium' (>0.5) or 'large' (>0.8) (Cohen 1988). Gotelli (2000) found that the fixed-equiprobable null model is most appropriate for quadrat censuses in relatively homogenous environments whereby sites are of similar size and quality, factors we deemed in accordance with our study area and sampling methodology.

Dominant competitor avoidance

In addition to spatial and temporal tests, we calculated the degree to which wildcats exhibited site sharing and the proportions of species overlaps at shared sites. To test for spatial avoidance of African wildcat (the potentially dominant competitor) by the other small carnivores of the study we simulated two further occurrence-based tests: a test incorporating the occurrences of wildcat and the pooled occurrences of the respective species with which wildcats did not share a temporal niche; and a test incorporating the wildcat's occurrences and the pooled occurrences of the species which shared the wildcat's temporal niche. The tests were designed using the same fixed-equiprobable null model comparisons (EcoSimR package) as the three tests detailed under "Spatial partitioning".

Results

Of 141 camera stations in total, 129 stations were active for >45 days of which 75 recorded at least one small carnivore. The total number of camera trap nights (24 h periods) for the 129 stations was 15,450 (mean ± SD: 119.77 ± 65.88), with 8830 nights (mean ± SD: 117.2 ± 51.81) for the 75 stations where target species were recorded. Of the camera stations which recorded small carnivores, 45 (60%) recorded only one species of small carnivore. Sixteen stations (21.3%) photo-captured two species of small carnivore, 7 (9.3%) stations recorded three species, and a further 7 (9.3%) stations recorded four species. In total we obtained 269 distinct photos of small carnivores: 134 (49.8%) of the African Wildcat, 38 (14.1%) of the small grey mongoose, 33 (12.3%) of the striped polecat, 32 (11.9%) of the small-spotted genet, 22 (8.2%) of the yellow mongoose, and 10 (3.7%) of the meerkat. The low total number of meerkat photos resulted in exclusion of this species from analyses.

Temporal partitioning

Small carnivores were active at varying times of day as delineated by broad temporal classes (Table 2: $\chi^2 = 174.1$, $df = 8$, $P < 0.001$). Pairwise Fischer post hoc tests (Table 3) indicated that African wildcat, striped polecat and small-spotted genet showed no significant pairwise differences, and neither did the two mongoose species. Based on these results we pooled the first three species as nocturnal and the latter two species as diurnal. Pairwise analyses of active hours in species circadian activity indicated the same temporal groupings as Fischer tests; African wildcat circadian activity did not significantly differ from that of other nocturnal small carnivores (wildcat–genet: $W = 1.4159$, $df = 2$, $P = 0.49$; wildcat-polecat: $W = 3.044$, $df = 2$, $P = 0.22$) despite the fact that wildcats were sometimes active during daylight and crepuscular hours (Fig. 2). The nocturnal polecat and genet did not differ in their circadian activity levels ($W = 1.4575$, $df = 2$, $P = 0.48$) and neither did the two diurnal mongooses ($W = 0.31879$, $df = 2$, $P = 0.85$). However, each diurnal–nocturnal species pairing showed

Table 3 Differences in broad temporal activity (nocturnal, diurnal, crepuscular) of small carnivore pairs as determined by post hoc Fischer exact tests on the Chi-square contingency table (Table 2: $\chi^2 = 174.1$, $df = 8$, $P < 0.001$)

Pairwise comparison	P value
Genet–grey mongoose	**<0.001**
Genet–yellow mongoose	**<0.001**
Genet–polecat	1
Genet–wildcat	1
Grey mongoose–yellow mongoose	1
Grey mongoose–polecat	**<0.001**
Grey mongoose–wildcat	**<0.001**
Polecat–wildcat	0.24
Polecat–yellow mongoose	**<0.001**
Wildcat–yellow mongoose	**<0.001**

Bold numbers indicate significant difference (P value <0.05)

significant differences in circadian activities: yellow mongoose–wildcat ($W = 8.31$, $df = 2$, $P = 0.016$), grey mongoose–wildcat ($W = 6.95$, $df = 2$, $P = 0.031$), yellow mongoose–genet ($W = 10.51$, $df = 2$, $P = 0.0051$), grey mongoose–genet ($W = 12.04$, $df = 2$, $P = 0.0024$), yellow mongoose–polecat ($W = 16.23$, $df = 2$, $P = 0.0003$) and grey mongoose–polecat ($W = 18.56$, $df = 2$, $P = 0.00009$).

Spatial partitioning

More than one small carnivore species were photographed at 41.7% of camera sites, although no single camera site ever recorded all five small carnivores at the same location over the year-long study (Fig. 3). The nocturnal group of small carnivores was spatially structured in a significantly non-random manner with limited co-occurrences of the different species [large effect: c-score (observed) = 253.3, mean c-score (simulated) = 127.0; $P < 0.0001$, SES = 4.51] (Fig. 3). Similarly, the diurnal group (mongooses) was found to be strongly spatially structured with highly limited co-occurrences [large effect: c-score (observed) = 108.0, mean c-score (simulated) = 31.4; $P < 0.0001$, SES = 4.44] (Fig. 3). The global model of species spatial structuring

Table 2 Small carnivore photo-captures divided into three temporal classes as recorded by 75 camera stations in the Namaqualand region during 2014–2015

Species	Temporal class		
	Crepuscular	Day	Night
Genet	0 (0)	2 (6.3)	30 (93.8)
Grey mongoose	0 (0)	38 (100)	0 (0)
Polecat	1 (3.0)	0 (0)	32 (97.0)
Wildcat	6 (4.5)	20 (14.9)	108 (80.6)
Yellow mongoose	0 (0)	22 (100)	0 (0)

Temporal use as percentage indicated in brackets
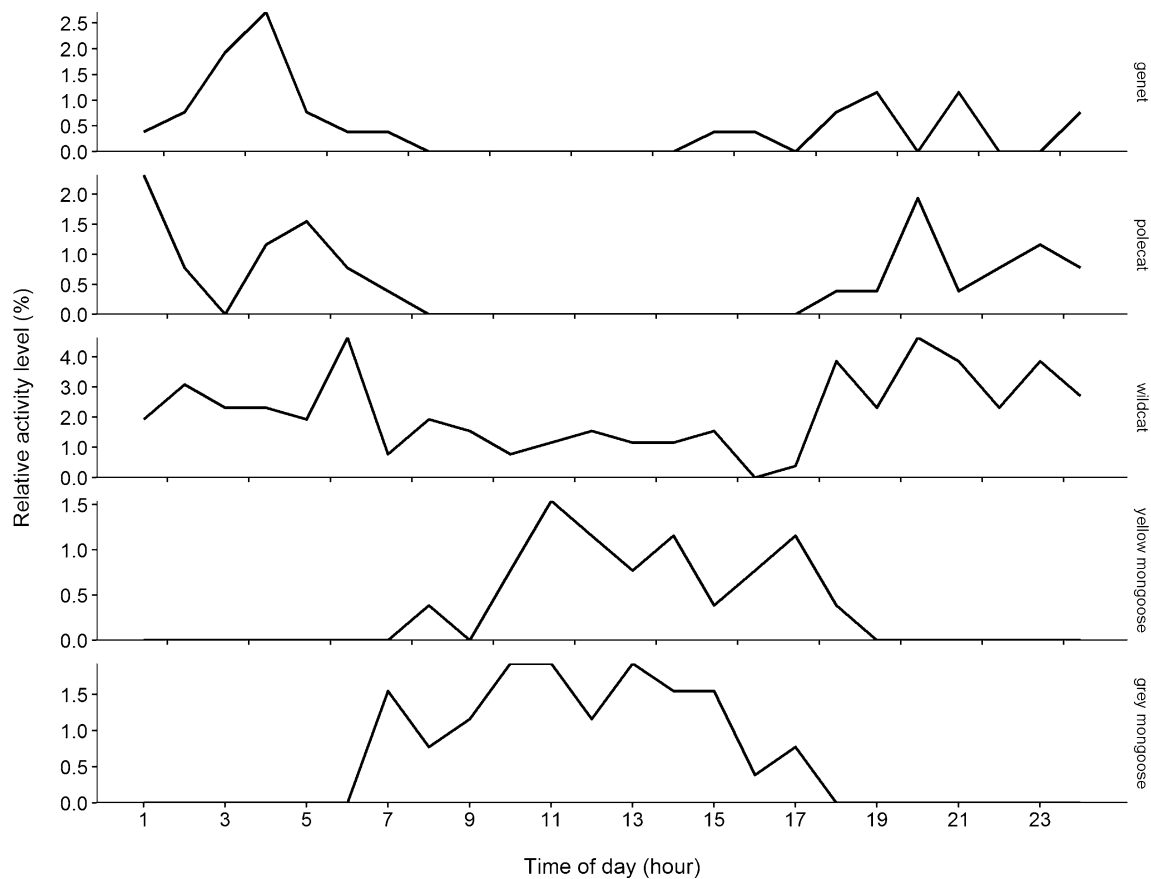
Fig. 2 Activity patterns of the African wildcat *Felis silvestris lybica* (*n* = 134), grey mongoose *Galerella pulverulenta* (*n* = 38), small-spotted genet *Genetta genetta* (*n* = 32), striped polecat *Ictonyx stria-* *tus* (*n* = 33), and yellow mongoose *Cynictis penicillata* (*n* = 22) in the Namaqualand study area based on year-long camera trapping data from 2014 to 2015

also revealed a negative species co-occurrence pattern [large effect: c-score (observed) = 177.8, c-score (simulated) = 150.2; *P* = 0.044, SES = 1.68].

Dominant competitor avoidance

Wildcats were the most frequently photographed small carnivore but were also seen to proportionally share the least sites with the other small carnivores (Fig. 4), whereby 54% of wildcat photographs were captured at a station where no other small carnivore was recorded. At stations which were shared by the African wildcat and other small carnivores (46%), the wildcat spatially co-occurred most often with grey mongoose (39.5%), followed by polecat (23.7%), genet (21.1%) and yellow mongoose (15.7%). The African wildcat showed a detectable but non-significant pattern of negative co-occurrence with the pooled occurrences of the two diurnal mongooses (large effect: c-score (observed) = 324.0, c-score (simulated) = 225.3; *P* = 0.14, SES = 1.37). In addition, the African wildcat showed highly limited co-occurrence with the pooled occurrences of the

polecat and genet (large effect: c-score (observed) = 480.0, c-score (simulated) = 223.4; *P* = 0.0016, SES = 3.60).

Discussion

Small carnivores have a potentially strong predisposition to intraguild competition (Caro and Stoner 2003; Donadio and Buskirk 2006; Di Bitetti et al. 2010). We showed that temporal and spatial partitioning patterns allow for intraguild carnivore coexistence in a homogenous semi-arid environment, a finding in alignment with Hardin's (1960) competitive exclusion principle. Results supported our temporal, spatial and dominant competitor hypotheses. First, we hypothesised that the small carnivore guild comprising the African wildcat, small-spotted genet, striped polecat, grey mongoose and yellow mongoose would separate along a temporal axis and form distinct temporal groups. Temporal partitioning results supported this hypothesis, indicating that the small carnivores exploited different temporal niches, dividing into nocturnal (African wildcat,
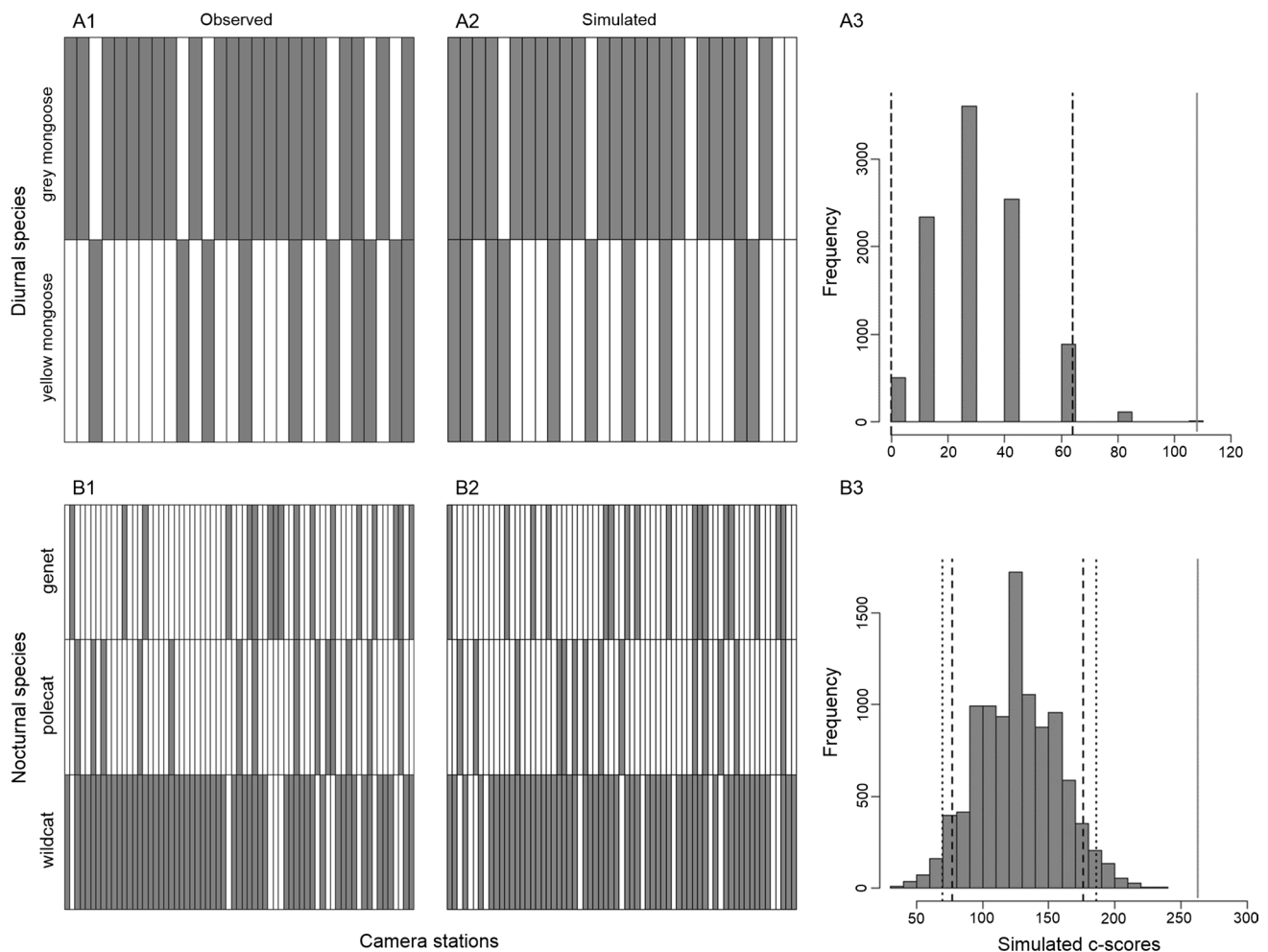
Fig. 3 Spatial partitioning in **a** diurnal and **b** nocturnal species groups. *A1/B1* Presence–absence matrices for observed (diurnal: c-score = 108.0; nocturnal: mean c-score = 127.0) and *A2/B2* simulated (diurnal: mean c-score = 31.4; nocturnal: mean c-score = 127.0) occurrences of small carnivores across 28 (diurnal) and 67 (nocturnal) camera stations where at least one species was recorded. *Filled cells* represent species presences and *empty cells* species absences. *A3* Diurnal species c-score comparisons. Histogram represents simulated c-scores (10 000 reps; mean c-score = 31.4) while the *solid grey line* indicates the observed c-score (108.0) of the species' presence–absence matrix. *Vertical long-dash lines* indicate the 95% one-tailed cut-points, and the *short-dash lines* indicate the 95% two-tailed cut-points. *B3* Nocturnal species c-score comparisons; histogram as described for A3, simulated mean c-score = 127.0 and observed c-score = 253.3

spotted genet and striped polecat) and diurnal (grey mongoose and yellow mongoose) groups. Second, we hypothesised that species belonging to the same temporal group would spatially organise in a manner that reduced their co-occurrence. Spatial partitioning results found spatial avoidance within both nocturnal and diurnal groups, as carnivores within both groups illustrated strong negative co-occurrence patterns. Finally, we hypothesised that wildcats would be avoided by smaller guild members more than expected by chance. Results supported this hypothesis indicating that smaller competitors exhibited lower spatial co-occurrence than expected by chance with the larger and, therefore, potentially more dominant (Palomares and Caro 1999), African wildcat. Thus, results supported our

proposition that spatial and temporal partitioning may allow for coexistence within this guild of small African carnivores.

Temporal divides in activity patterns facilitate coexistence for mesopredators (Monterroso et al. 2014). The emergence of a diurnal group (mongooses) and a nocturnal group (African wildcat, polecat and genet) of small African carnivores, a finding reflected at both broad and fine temporal scales, is a reflection of such a partitioning strategy. Furthermore, each temporal grouping exhibited strong within-group patterns of negative spatial co-occurrence. This pattern may have emerged as members within each group did not exhibit significant differences in their fine-scale temporal use. While wildcats were active during

Fig. 4 The degree to which different small carnivore species exhibited site sharing, whereby camera traps recorded ≥1 of the five small carnivores at the same station
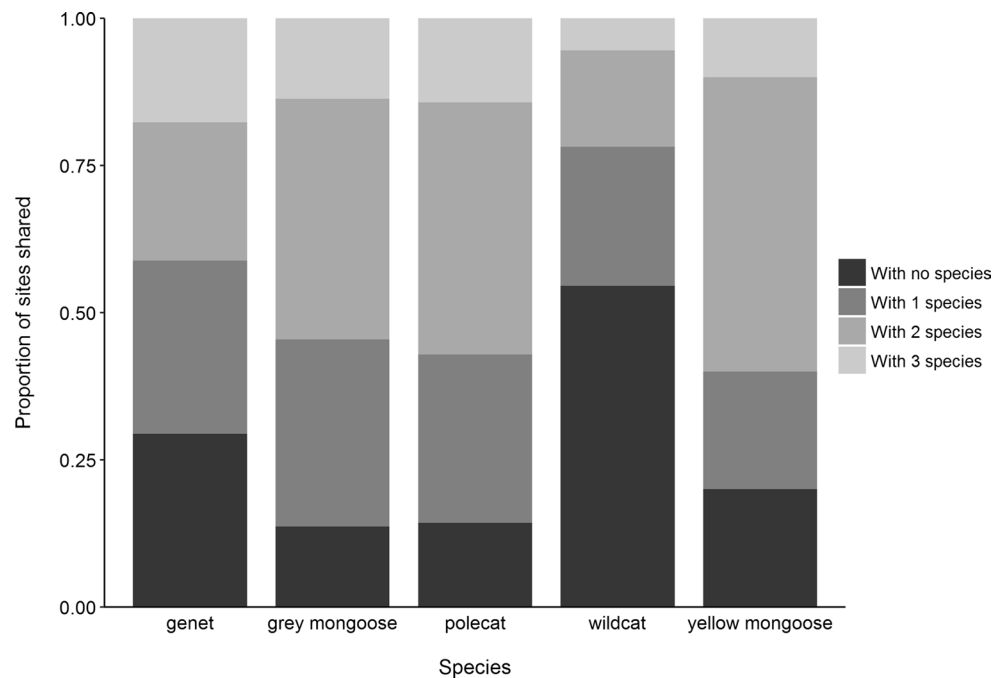
daylight hours, their diel cycle was not significantly different to the nocturnal one (Fig. 2). The fact that the genet, polecat and wildcat exhibited strong levels of spatial segregation suggests a level of avoidance, whereby the two smaller nocturnal competitors partition space to potentially avoid the larger dominant wildcat (Schuette et al. 2013).

A similar pattern was observed for the yellow and grey mongooses whereby analogous diurnal activity patterns were compensated for by limited spatial co-occurrence. While mongoose habitat use patterns have not been studied in the Namaqualand environment, micro-habitat preferences found by Cavallini and Nel (1995), in a study in South Africa's West Coast National Park, may partially explain the limited mongoose co-occurrence we observed. Cavallini and Nel's (1995) study found yellow mongooses to show a strong preference for open areas such as short-grass plains, while grey mongooses favoured habitats with thicker vegetation, preferring refuge areas such as dense bushes and rocky outcrops. While the Namaqua landscape consists mostly of open scrubland, the scarce presence of patches of thicket vegetation and rocky outcrops (Luther-Mosebach et al. 2012) could potentially facilitate similar mongoose micro-habitat use and coexistence in small sections of our study site. A further axis of separation between the mongooses may be their limited degree of dietary overlap (Kitchen et al. 1999), as yellow mongooses are primarily insectivorous (Cavallini and Nel 1995).

Wildcats were the most photographed small carnivore (n = 134) and were recorded at the greatest number of camera trap stations (n = 55). Besides strong dominance being

the underlying reason for this pattern, it may in part be attributable to the site selection for camera trap placement (Edwards et al. 2016). It is possible that some small carnivores wary of larger dominant predators may have avoided 4WD tracks potentially decreasing photographic rates (Hayward and Marlow 2014). Such potential effects cannot be excluded as our design involved the consistent use of a specific type of linear feature to minimise variability in inferences associated with camera placement. In addition, male African wildcats potentially exhibit home-range sizes (Table 1) large enough to overlap two camera stations within a singular sampling grid cell (900 ha), thereby potentially marginally inflating their photo-captures. However, this is unlikely to noticeably increase the likelihood of their photographic capture compared to smaller carnivores (Sollmann et al. 2013) given the expected lower density of larger bodied carnivores compared to smaller bodied ones (Carbone and Gittleman 2002).

Across all camera sites, African wildcats shared the lowest proportion of camera sites with other members of the guild. African wildcats can average twice the weight of a small-spotted genet and are nearly five times the weight of a mongoose or polecat (Table 1). The pooled occurrences of the smaller genet and polecat showed a significant negative pattern of co-occurrence with the African wildcat, a pattern which strongly suggests spatial avoidance. Among competitors this body size difference is likely to trigger avoidance behaviour in subordinate species to avoid interspecific or exploitative competition (Linnell and Strand 2000; Lucherini et al. 2009). While

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