Spatiotemporal co-occurrence and overlap of two sympatric mongoose species in an urban environment

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Abstract

Small carnivores are becoming increasingly common in urban areas. What has received less attention is whether and how resource partitioning among sympatric species in urban areas facilitates their coexistence. We examined the spatial, temporal and combined spatiotemporal occurrence and overlap of co-existing yellow mongoose Cynictis penicillata and slender mongoose Galerella sanguinea in an urban estate in South Africa. The reserve comprised two parts, an Eco-Estate where human residential and natural areas are interspersed and wildlife has greater contact with people, and a Nature Estate, where contact is reduced by palisade fencing between people and natural areas. Using photographic data from camera traps collected over 11 consecutive months, we found a moderate level of spatial overlap between the mongoose species. Differences between the species occurred at a finer habitat scale: yellow mongooses were more common in open habitats located near human residents whereas the slender mongooses were more common in covered areas further away from human residents. The detection probability of the yellow mongoose, however, was greater than that of the slender mongoose, and the occupancy probability of the slender mongoose was reduced in the presence of the yellow mongoose. Although both species demonstrated bimodal diurnal peaks in activity, they varied in their active periods, with temporal overlap being greater during colder than warmer months. No complete spatiotemporal overlap (occurrence in the same place at the same time/within a 10-min period) occurred. This may have been as a result of the difference in detection and occupancy probabilities of the two species. Resource availability (food), however, appears to influence the different habitat selection, space use, and activity patterns of yellow and slender mongoose in the study area. Therefore, we conclude that partitioning along the spatial and somewhat on the temporal dimensions aids in the coexistence of these mongoose species in an urban environment.

Key words: camera trap, coexistence, slender mongoose spatiotemporal, urban areas, yellow mongoose

Introduction

Rapid expansion of urban areas poses a number of risks to animals (Newsome et al. 2010; Bateman and Fleming, 2012), and can lead to an increase in habitat fragmentation, which decreases the level of natural habitats available to animals (Duduš et al. 2014; Scott et al. 2014). Nevertheless, the absence of natural predators and an increased availability of natural and alternative food resources makes urban areas attractive to some animals which can thrive in urban habitats (Newsome et al. 2010; Plumer, Daviso, and Saarma 2014; Wong and Candolin 2015).

Carnivores are becoming increasingly prevalent in urban areas by exploiting the opportunities available there (Wong and Candolin 2015; Poessel, Gese, and Young 2017). Those thriving in urban environments tend to be diet generalists, small to medium sized, tolerant and habituate to humans and exploit
anthropogenic resources (Dudu et al. 2014; Scott et al. 2014). For example, the stone marten Martes foina and red fox Vulpes vulpes are perhaps the best adapted for urban life, exhibiting flexibility in their diet (e.g. anthropogenic items) as well as having a considerably high occurrence in, and use of, urban residential areas (Prigioni et al. 2008; Plumer, Daviso, and Saarma 2014; Scott et al. 2014). Other species well adapted to urban areas are the coyote Canis latrans (Murray et al. 2015; Poessel, Gese, and Young 2017), kit fox Vulpes macrotis (Newsome et al. 2010) and Eurasian badger Meles meles (Bateman and Fleming 2012). An increase in the occurrence of carnivores in urban areas presents the opportunity of morphologically and ecologically similar species overlapping in their resource use. Yet, how these species coexist in urban areas has received little attention.

Niche differentiation theory emphasizes that a degree of resource partitioning (spatial, temporal or dietary) between sympatric species must occur in order to avoid niche overlap and the consequent interspecific competition (Pianka 1974; Kylafis and Loreau 2011; Lesmeister et al. 2015; Ribeiro 2016). The food, space and time dimensions, either individually or in combination, are considered the foremost resources partitioned to promote coexistence of sympatric species (Prigioni et al. 2008; Ramesh et al. 2012; Frey et al. 2017). Resource partitioning along the spatial niche, such as in habitat selection, is regarded as the principal dimension of differentiation, while temporal partitioning (after diet) is considered rare (Schoener 1974; Cavallini and Nel 1995).

Variation in the temporal niche can include species differing in the timing and level of activity, or in overall diel activity (e.g. diurnal vs. nocturnal). For example, grey foxes Urocyon cinereoargenteus occur at lower densities and are less active in areas at times when coyote activity was greater (Lesmeister et al. 2015). Dholes Cuon alpinus segregated from leopards Panthera pardus and tigers Panthera tigris by being primarily diurnal, possibly to avoid competition with the mainly nocturnal felids (Lesmeister et al. 2017). Similarly, in the spatial niche, species segregate by selecting different habitats, largely influenced by the availability of resources (e.g. food and resting sites; Dudu et al. 2014; Lesmeister et al. 2015). For example, the stone marten and red fox differed in habitat selection in an urban area in Poland: stone martens were located in, and appeared better adapted to, areas closer to city centres where resting sites were almost exclusively in buildings. In contrast, red foxes selected habitats closer to the urban borders, where resting sites are favourable, but still providing access to anthropogenic items (Dudu et al. 2014). In addition, habitat use niche overlap in a peri-urban area in Portugal was high between the Eurasian badger and red fox, but they exhibited different feeding habits which enabled their coexistence (Ribeiro 2016). Despite previous research on resource partitioning, the spatiotemporal co-occurrence of species is poorly understood (Lesmeister et al. 2015).

Here, we present the first study on the spatiotemporal co-occurrence and overlap of two herpestid mongoose species, the yellow Cynictis penicillata and the slender Galerella sanguinea, in a small urban reserve in South Africa. The yellow mongoose is primarily insectivorous and the slender mongoose is an opportunistic carnivore (Nel and Kok 1999; Graw, Lindholm, and Manser 2016; Cronk and Pillay 2018). Both species are diurnal in non-urban habitats (Mbatyi 2012; Graw, Lindholm, and Manser 2016). Yellow mongoose are active during the day between sunrise and sunset (Cavallini and Nel 1995; Mbatyi 2012), while the slender mongoose reportedly exhibits a slight peak in activity before sunset and ceases activity just after sunset (Maddock and Perrin 1993). Yellow mongoose occur in open grassland and scrub habitats (Skinner and Chimimba 2005), and are not common in dense bush and woodland areas (Mbatyi 2012). Conversely, slender mongoose are more prominent in dense covered thicket and woodland/forest areas (Ramesh and Downs 2014), and are not common in open grassland (Rapson, Goldizen, and Seddon 2012). Presently, both species inhabit and coexist in urban areas in South Africa (Cronk and Pillay 2018), but nothing is known about the temporal activity and space use of these species in an urban environment.

We conducted our research in the Meyersdal Nature Area (South Africa) that was divided into two parts: an Eco-Estate where wildlife utilize household gardens and corridors between houses, and a Nature Estate, where houses are separated from wildlife by fences, reducing contact with humans and homes. Within the Meyersdal Nature Area, we investigated the spatial and temporal occurrence and overlap of yellow and slender mongooses through camera trap surveillance. In addition, we specifically investigated whether or not both species were utilizing the same spaces at the same time (spatiotemporal overlap). Furthermore, camera traps aided in assessing broad habitat use and the distance from, and utilization of, the human residential areas within these estates for both species. We had four predictions:

1. Mongoose species would segregate in the spatial niche: (i) both species would utilize distinct micro-habitat types, in accordance with the niche differentiation theory—yellow mongoose would occur more commonly in open areas and slender mongoose in dense covered areas; (ii) yellow mongoose would occur more frequently near human residences compared with slender mongoose, since yellow mongoose are more habituated to humans (pers. obs.); slender mongoose would occur more frequently in the natural areas further from human residents. 2. Mongoose species would overlap in the temporal niche: (i) since both mongoose species are diurnal, we predicted both species will have similar activity patterns and therefore show temporal overlap in activity. 3. Seasonal variation in the spatial and/or temporal niche: the less favourable conditions during the colder season may lead to both species utilizing larger areas and adjusting their activity to differing environmental conditions in search of resources, and thus may show greater overlap in activity and/or space use in the colder compared with the warmer season. 4. No combined spatiotemporal overlap: the occurrence of both species in the same place at the same time was not expected since the two species were predicted to segregate along either the spatial or the temporal niche, thereby facilitating coexistence (Karanth et al. 2017) in the Meyersdal Nature Area.

**Methods**

**Study site**

Field work took place from May 2015 to March 2016 in the Meyersdal Nature Area (composed of ecological residential estates) in Johannesburg, South Africa. The climate in the area is warm and temperate, with an average annual temperature of 16°C, and average precipitation of 723 mm. The warmest temperatures occur in December-February (average min. of 14°C and average max. of 26°C) and the coldest in July (average min. of 3°C and average max. of 19°C). We sampled two adjacent study areas, namely the Meyersdal Eco-Estate (26°17’10.4”S 28°05’14.7”E; 480 ha) and the Meyersdal Nature Estate (26°17’32.1”S 28°05’23.2”E; 300 ha). Wildlife occur on both estates but more frequently come into contact with people in
Camera trap surveillance

We used motion triggered infrared Bushnell Essential® camera traps equipped with high powered batteries and 32GB memory cards, ensuring a minimum of 1-week uninterrupted data collection. The use of camera traps is advantageous since it incurs very minimal environmental disturbance and is a non-invasive method of data collection (Rovero et al. 2014). Three camera traps were placed at various locations (hereafter referred to as camera sites) in both the Eco-Estate and Nature Estate (total of six cameras). Camera traps were attached to rigid surfaces (rocks/trees) ~0.5 – 1.0 m off the ground, and positioned so the field of view included an active wildlife trail (Jenks et al. 2011; Rovero et al. 2014). The understory plant growth was cleared at camera sites to avoid impeding the camera view.

The cameras were set to capture two consecutive photographs at each trigger, and a delay period of 1 s was set between triggers to ensure multiple captures of any rapid movement of a mongoose. All cameras were active 24 h a day, and no bait was used to lure the mongooses. Camera traps were checked once a week to change memory cards, ensuring a minimum of 1-week uninterrupted data collection. The use of camera traps is advantageous since it incurs very minimal environmental disturbance and is a non-invasive method of data collection (Rovero et al. 2014). Three camera traps were placed at various locations (hereafter referred to as camera sites) in both the Eco-Estate and Nature Estate (total of six cameras). Camera traps were attached to rigid surfaces (rocks/trees) ~0.5 – 1.0 m off the ground, and positioned so the field of view included an active wildlife trail (Jenks et al. 2011; Rovero et al. 2014). The understory plant growth was cleared at camera sites to avoid impeding the camera view.

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Data analysis

Two-species occupancy modelling

We used two-species occupancy modelling using the programme PRESENCE version 12.39 (MacKenzie, Bailey, and Nichols 2004) to estimate the occupancy and detection probabilities of the yellow and slender mongoose in the two estates. The intention was solely to ascertain whether the presence or detection of one species influences the presence or detection of the other species. The two-species occupancy models were used to investigate the spatial co-occurrence between the two mongoose species while accounting for imperfect detection (MacKenzie, Bailey, and Nichols 2004). Taking all camera trap capture histories for the entire study period, we followed the methods for a single season-two-species occupancy model (no separation of cold/warm sampling periods), with no categorical or continuous covariates included in the analysis. We created two species capture histories (1 per estate) organized in a matrix with 66 sites (rows) by 14 periods (columns; camera trap replicate days per site) in the Eco-Estate and Nature Estate, respectively. A recording of 0 represented neither species were present, 1 represented when only the yellow mongoose was present, 2 represented when only the slender mongoose was present and 3 when both species were detected (MacKenzie, Bailey, and Nichols 2004). We drew inference about the two species’ patterns of occupancy from the species interaction factor (SIF; Φ). Values of Φ < 1 suggested the two species occur together less often than chance (i.e. potential avoidance), and Φ > 1 suggested the two species occur together more often than chance. When Φ ≈ 1 the two species were considered to be spatially independent (Richmond, Hines, and Beissinger 2010; Chen et al. 2019).

Spatial occurrence and spatial overlap

Statistical analyses were conducted using R Statistical Software (www.r-project.org, R version 3.4.3). Because of differences in duration of sampling per season, we categorized sampling periods as colder (autumn/winter; March to August) and warmer (spring/summer; September to February) months to reflect South Africa’s seasons in all analyses. A t-test was used to analyse the number of independent captures to establish which species occurred more frequently in both estates. Photographic rate (number of captures per number of trap days) can be used to estimate species abundance (Bowkett, Rovero, and Marshall 2008; Jenks et al. 2011; Rovero et al. 2014). We calculated the relative abundance index (RAI) for each species in the study area to evaluate differences in the abundance of the two species, which may affect the number of photographs captured. RAI was calculated by taking the sum of all independent captures for each species multiplied by 100 and divided by the total number of camera trap days (occurrence per species per 100 trap days; Jenks et al. 2011).

We used two approaches to analyse spatial occurrence of the mongooses. Firstly, a logistic regression model (glm in R) using absence/presence data was used to analyse occurrence of each species at each camera site in order to determine whether they are using the same areas and which factors (estate, species, habitat and distance) influenced their occurrence. Secondly, we assessed the number of occurrences of each species per camera site (dependent variable) in order to compare the extent of use of each camera site between species. We used the bestNormalize package in R (Peterson and Cavanaugh 2019) to transform the dependent variable. A linear mixed effects model (lmer in R) was used to assess significant predictors of the number of occurrences of the two mongoose species on camera trap footage. The analyses comprised first order and interaction effects of the following predictor variables: species; season (colder/warmer months); habitat category (open/covered vegetation type); and distance to human residents (continuous
covariate); estate was included as a random factor. We derived several candidate models from the global model (Grueber et al. 2011), including all of the abovementioned independent variables. Using model averaging, we ranked the models based on the Akaike’s Information Criterion with small sample adjustment (AICc) using the R package MuMin (Barton 2009). We selected the model with the lowest AICc value as the best fit model (Burnham and Anderson 1998; Grueber et al. 2011), which included species, distance to human residents, habitat category and the species × distance and species × habitat interactions. The best fit model did not include season or interactions with season, and these are hence not described. We used emmeans (Lenth and Herve 2019) for post hoc analysis of significant predictors, and the significant interactions involving fixed effects, and emtrends to analyse the significant interaction involving the distance covariate.

We used Pianka’s Index (Krebs 1989) of overlap to assess the overall spatial overlap between species at camera trap sites (Ribeiro 2016), as well as whether spatial overlap varied between cold and warm months. The index ranges from 0 (no overlap) to 1 (complete overlap).

Activity patterns and temporal overlap
We used the R package ‘overlap’ to obtain pair-wise temporal overlap coefficients (A; Meredith and Ridout 2014) to assess the activity profiles and temporal overlap between the two mongoose species, using the time stamp data from camera trap footage. In this analysis, we compared the activity of the yellow and slender mongoose for the entire study duration (both estates) and compared activity between colder and warmer months. Temporal overlap of activity patterns was estimated using the kernel density estimation following the methods proposed by Ridout and Linkie (2009). We selected a smoothing parameter of 1.0 since the size of the smallest sample size was >75 (Meredith and Ridout 2014). The overlap coefficient (A) ranges from 0, indicating no overlap, to 1, indicating complete overlap (Frey et al. 2017).

Results
We sampled 66 sites with differing vegetation and distances to human residents in both the Eco-Estate and Nature Estate (n = 122 in total; Fig. 1). A total of 1494 photographs of mongoose were obtained in the Eco-Estate and 1374 in the Nature Estate (Table 1). Yellow mongooses occurred significantly more frequently in photographs than slender mongooses in both the Eco-Estate (mean ± SE: yellow 19.53 ± 2.96; slender 3.11 ± 0.99; t130 = 5.26, P < 0.001) and Nature Estate (yellow 19.18 ± 2.39; slender 1.64 ± 0.39; t130 = 7.23, P < 0.001). For relative abundance for the entire study area, yellow mongooses were detected 138.25 times and slender mongoose 17.05 times (per 100 trap days; Jenks et al. 2011). Detection was slightly lower during the warmer months (133.06 and 16.67 times) than during the colder months (145.77 and 17.33 times) for both yellow and slender mongoose, respectively.

Detection and occupancy probability
Generally, the detection and occupancy probabilities were greater for yellow mongoose than slender mongoose (Table 2). In the Eco-Estate, the detection probability of yellow mongoose (PA = 0.935 ± 0.018) was greater when the slender mongoose was absent, and vice versa for the detection probability of the slender mongoose when the yellow mongoose was absent (PA = 0.717 ± 0.138). At sites where both species were present, detection probability was considerably lower (PA = 0.344 ± 0.022). The probability of slender mongoose occupancy was greater when the yellow mongoose was absent (psiBA = 0.971 ± 0.041) than when the yellow mongoose was present (psiBA = 0.666 ± 0.061) at a site. Overall, individual species detection probabilities were lower in the Nature Estate (PA = 0.930 ± 0.008; PA = 0.378 ± 0.035) compared with the Eco-Estate. However, at sites where both species were present (PA = 0.577 ± 0.031), detection probability was greater in the Eco-Estate (Table 2). Like the Eco-Estate, the occupancy probability of slender mongoose was also greater when the yellow mongoose was absent (psiBA = 0.666 ± 0.061) than when the yellow mongoose was present (psiBA = 0.666 ± 0.061) at a site. SEM denotes the estimates standard error. Conf. int. denotes the upper and lower 95% confidence interval range. psiA denotes occupancy probability of the dominant species (yellow mongoose). psiBA denotes occupancy probability of the subordinate species (slender mongoose) when the dominant is present. psiBA denotes occupancy probability of the subordinate species in the absence of the dominant species. PA denotes the probability of detecting the dominant species, given the absence of the subordinate. PA denotes the probability of detecting the subordinate, given the absence of the dominant. PA denotes the probability of detecting the dominant, given both are present. PA denotes the probability of detecting the subordinate, given both are present and the dominant is detected. ϑ denotes the SIF.

The SIF was lower than 1 in both the Eco-Estate (ϑ = 0.977) and Nature Estate (ϑ = 0.748) indicating potential segregation or avoidance rather than spatial co-occurrence. SIF was, however,
considerably close to 1 (as well as having an upper confidence interval going beyond 1) in the Eco-Estate in particular, potentially indicating that the two species are more than likely occurring spatially independently of one another (i.e. there is a possibility the two species may not exhibiting avoidance or aggregation).

**Spatial occurrence and spatial overlap**

A logistic regression analysis testing the likelihood that a mongoose was present at a camera site (Table 3) showed a significant effect of species ($\beta = 1.911, z = 6.102, P < 0.001$) and distance ($\beta = 0.002, z = 3.443, P < 0.001$). The remaining variables had no significant effect on the presence or absence of mongoose (Table 3). According to the model (predicted logit of presence = $-0.821 + 1.912 \times$ species + $0.002 \times$ distance), the log of the odds of a mongoose being present at a camera site was positively related to both species and distance. The odds of a yellow mongoose being present were 6.740 ($=e^{1.908}$; Table 3) times greater than the odds of a slender mongoose being present. The regression coefficient was especially low for the distance variable, with an almost negligible odds ratio, showing that as distance from residents increased, the likelihood of mongoose presence also increased by only 1.002 times ($=e^{0.002}$, Table 3).

![Table 1: Number of independent photographs of yellow and slender mongooses in open and closed cover categories during different seasonal periods in the two Meyersdal estates](https://academic.oup.com/jue/article-abstract/6/1/juaa013/5857627)

| Habitat category | Months | Eco-Estate | Nature Estate |
|------------------|--------|------------|---------------|
|                  |        | Yellow mongoose | Slender mongoose | Yellow mongoose | Slender mongoose |
| Open             | Cold   | 453        | 5              | 563            | 3              |
|                  | Warm   | 576        | 9              | 453            | 11             |
| Covered          | Cold   | 113        | 117             | 63             | 47             |
|                  | Warm   | 147        | 74              | 187            | 47             |
| Total            |        | 1289       | 205             | 1266           | 108            |

![Table 2: Co-occurrence model estimates and beta estimates of occupancy (psi) and detection probabilities ($P$ and $r$) of the yellow and slender mongoose in the two Meyersdal estates](https://academic.oup.com/jue/article-abstract/6/1/juaa013/5857627)

| Parameters          | Estimate (SEM) | 95% CI | $\beta$ Estimate (SEM) |
|---------------------|----------------|-------|------------------------|
| Co-occurrence in the eco-estate | psi$_{A}$ | 0.953 (0.029) | 0.848–0.986 | 2.998 (0.653) |
|                     | psi$_{BA}$    | 0.666 (0.061) | 0.538–0.774 | 0.692 (0.275) |
|                     | psi$_{Y}$     | 0.971 (0.041) | 0.892–1.000 | 19.801 (3.362) |
|                     | $P_{A}$       | 0.935 (0.018) | 0.889–0.962 | 2.660 (0.294) |
|                     | $P_{B}$       | 0.717 (0.138) | 0.395–0.906 | 0.927 (0.681) |
|                     | $r_{A}$       | 0.344 (0.022) | 0.301–0.389 | 0.647 (0.099) |
|                     | $r_{BA}$      | 0.029 (0.012) | 0.013–0.065 | 3.484 (0.416) |
|                     | $r_{BA}$      | 0.170 (0.019) | 0.135–0.213 | 1.584 (0.140) |
|                     | $\phi$        | 0.977 (0.016) | 0.946–1.007 | – |
| Co-occurrence in the nature estate | psi$_{A}$ | 0.788 (0.050) | 0.673–0.870 | 1.312 (0.301) |
|                     | psi$_{BA}$    | 0.387 (0.069) | 0.263–0.528 | –0.461 (0.292) |
|                     | psi$_{Y}$     | 0.856 (0.091) | 0.779–0.938 | 23.232 (4.142) |
|                     | $P_{A}$       | 0.990 (0.008) | 0.956–0.989 | 3.775 (0.358) |
|                     | $P_{B}$       | 0.378 (0.035) | 0.312–0.447 | –0.499 (0.147) |
|                     | $r_{A}$       | 0.577 (0.031) | 0.516–0.637 | 0.312 (0.127) |
|                     | $r_{BA}$      | 0.055 (0.018) | 0.029–0.104 | –2.837 (0.348) |
|                     | $r_{BA}$      | 0.143 (0.032) | 0.091–0.218 | –1.791 (0.263) |
|                     | $\phi$        | 0.748 (0.071) | 0.609–0.887 | – |

All fixed predictors and their interactions included in the best fit linear mixed effects model had a significant effect on the number of occurrences of each species at camera sites (Table 4). The estate random variable had minimal effect on occurrence (variance contribution=0.016). The number of occurrences in photographs was significantly greater for yellow mongooses than slender mongooses (estimate=SE= 3.398 ± 0.155; $P < 0.001$), and the number of photographs captured was notably fewer in areas classified as covered habitat versus areas classified as open ($-0.256 ± 0.144; P = 0.046$). There was a negative trend with distance which showed that as distance from human residences increased, the number of photographs of mongoose decreased (number of occurrences= 17.436 – 0.020 × distance).

The interaction between species and habitat (Fig. 2) showed that yellow mongooses occurred significantly less in covered areas compared with open areas ($-1.145 ± 0.110; P < 0.001$), and the slender mongoose occurred significantly more in covered than in open areas (0.685 ± 0.110; $P < 0.001$). The post hoc analysis of the interaction between species and distance (from emtrends; Fig. 3) showed that at the averages, increasing distance had a decreasing effect on the number of occurrences of yellow mongooses while increasing the number of occurrences of slender mongooses (estimate=SE= –0.061 ± 0.004; $P < 0.001$). The distance trend for yellow mongooses showed a negative
mongoose was in the overall activity patterns between yellow and slender de-
crease in activity at these times generally. Temporal overlap the day (midday), slender mongooses showed no measurable
tivity was greater during the colder period (0.66) than during the warmer period (0.37).
Overall, yellow mongooses had a higher detection probability than slender mongoose, and the occupancy of slender mongoose at sites was greater when the yellow mongoose was as-
sent. Yellow mongooses were more common in open habitats located near human residents, and slender mongooses were more common in covered areas further away from residents, and consequently these differences account for the moderate level of overlap measured (Pianka’s index = 0.55). Temporal

Activity patterns and temporal overlap
The diurnal start and end activity times (based on the occurrence on camera trap photographs) of yellow mongooses were 06:29 ± 00:28, 18:19 ± 00:37 (mean ± SE) and that of slender mo-
gooses were 05:48 ± 00:45, 18:01 ± 01:11 (Fig. 4a). Yellow mongooses demonstrated a typical bimodal peak activity pattern, one peak between 10:00 and 11:00 and another between 16:00 and 17:00. Slender mongooses exhibited similar bimodal activity patterns but their activity was greater closer to sunrise (~6:00) with the first peak occurring later in the morning, and their activity decreased later in the evenings compared with yellow mongooses. Interestingly, while yellow mongooses showed greatly reduced activity during the hottest periods of the day (midday), slender mongooses showed no measurable decrease in activity at these times generally. Temporal overlap in the overall activity patterns between yellow and slender mongoose was Δ=0.74 (CI=0.71 – 0.79).

Spatiotemporal overlap
There were no instances of co-occurrence of yellow and slender mongooses in the same image at the same time. We then con-
sidered images captured within a 0 – 10 min time frame (i.e. one species in an image, followed by the other species in a consecu-
tive image captured within 10 min), and found 21 such occu-
rences overall (19 in the Eco-Estate and 2 in the Nature Estate), constituting a total of only 1.41% of all photographs captured over the entire study period; all of these taken during winter/au-
tumn months.

Discussion
We investigated the spatial and temporal occurrence and overlap of yellow and slender mongooses in an urban setting. Overall, yellow mongoose had a higher detection probability than slender mongoose, and the occupancy of slender mongoose at sites was greater when the yellow mongoose was absent. Yellow mongooses were more common in open habitats located near human residents, and slender mongooses were more common in covered areas further away from residents, and consequently these differences account for the moderate level of overlap measured (Pianka’s index = 0.55). Temporal

During the colder months, activity for both species appeared to start slightly later in the morning, and concluded earlier in the evening in comparison to the warmer months. Bimodal peaks in activity were present in both species during the colder months, with the first peak being later in the morning in slender mongooses compared with yellow mongooses and a second similar peak in activity later in the afternoon in both species (Fig. 4b). During the warmer months, slender mongoose activity peaked earlier in the morning and then again later in the morn-
ing, but the overall peak in activity in the morning was greater in the yellow mongooses (Fig. 4c). The activity of both species peaked again in the later afternoon, being greater and earlier in the yellow mongoose. Overall, yellow mongooses had reduced activity around midday, noticeably more so during the warmer months than during the colder months. Slender mongooses were comparatively more active at these times, particularly dur-
ing the colder months. During the warmer months, however, the slender mongooses first showed a decrease in activity around midday, and then an increase earlier in the afternoon compared with the yellow mongooses. Temporal overlap in ac-
tivity was greater during the colder period (Δ=0.80, CI = 0.79 – 0.87) compared with the warmer period (Δ=0.66, CI = 0.63 – 0.74).

Figure 2. The mean number of photographs (±SE) recorded for yellow and slen-
der mongoose in the open and closed habitat categories in the Meyersdal estates.

Figure 3. The number of photographs recorded for yellow and slender mongoose at various distances (in metres) from human residents in the Meyersdal estates.

Figure 4. Temporal overlap of yellow (solid line) and slender (dashed line) mon-
goose activity patterns within the Meyersdal area for the (a) entire study period, (b) colder and (c) and warmer months. The overlap coefficient (Δ) is the area un-
der the minimum of two density estimates indicated by the grey area below curves.
overlap was relatively high, but the two species varied in peak activity periods. There were no occurrences of complete spatio-temporal overlap. We discuss below how food resources mainly may influence these observed differences in habitat selection, space use, and activity patterns of the two sympatric mongoose species.

While several studies have failed to identify strict habitat use differences among co-existing carnivores (Gompper et al. 2016), our study does suggest that both mongoose species utilize different habitat types. Habitat use by carnivores is strongly affected by the availability and abundance of food resources (Pedrini, Prigioni, and Volcan 1995). While yellow mongooses occur in a wide range of habitats (Mbatyoti 2012), it prefers open and short grassland vegetation habitats (Skinner and Chimimba 2005), which was also evident in our study, as predicted. With increasing shrub cover, there was a consequent reduction in the abundance of insects, the main food sources of yellow mongoose (Nel and Kok 1999; Blaum and Rossmannith 2010). The greater occurrence of yellow mongoose in open habitat types may be due to the favourable conditions for obtaining prey, since previous research in this study area showed that insects form the main part of their diet (Cronk and Pillay 2019). The open habitats dominated by grassland type vegetation might also provide conditions conducive for underground denning (Le Roux et al. 2016); these underground dens were frequently occurring in the study area (personal observation).

As predicted, slender mongoose occurrence was greater in covered areas. While several biotic factors limit the distribution and space use of species, slender mongooses are reportedly not limited by rainfall and vegetation type and also have a tolerance for a range of habitat types (Smithers 1983; Maddock 1988). Nonetheless, other studies indicate that slender mongooses prefer covered areas with rocky outcrops and associated tree cover, which also supports high densities of their rodent prey (Rood and Waser 1978; Smithers 1983; Ramesh and Downs 2014), which was also a main component in their diets in the study area (Cronk and Pillay 2019). The use of cover might also provide protection from aerial predators, as reported in other small viverrids (Taylor 1975). However, while a pair of resident black eagles occurred at Meyersdal, other large birds of prey were not common here, and incidents of mongoose predation by raptors were not known in the study area. Another reason for the differences in habitat use could be competitive exclusion. The larger of two competing carnivore species is typically superior (Lesmeister et al. 2015) and subordinate carnivores may shift their habitat use to avoid competition (Mattison et al. 2011). Maddock (1988) showed that slender mongooses generally avoided open habitats, occurring in covered areas to avoid interactions with the larger Egyptian mongoose Herpestes ichneumon, since both species compete for the same food source. Slender mongooses are only slightly smaller than yellow mongoose, so body size alone cannot adequately explain the differences in habitat use.

Yellow mongooses actively exploit anthropogenic resources and are more habituated to humans (Cronk and Pillay 2018), which may account for their greater presence near human residents in comparison to slender mongooses. The majority of slender mongoose occurrences were located at sites furthest away from residents, despite relative ease of access to anthropogenic food and other resources. This is possibly due to sites near residents being more open than covered, consequently being more regularly used by yellow mongoose. Contrary to our prediction, habitat selection and the number of occurrences of these mongoose species at differing distances from human residents did not differ between seasons.

The higher detection probability in the yellow mongoose may have accounted for why the frequency of the number of photographs recorded for the yellow mongoose was far greater than that of the slender mongoose. The demonstration of a negative association of occupancy in both estates (i.e. occupancy of slender mongoose being far greater when yellow mongoose was absent) may be indicative of spatial avoidance (or segregation), and suggests different site preferences (therefore inferring differing habitat preferences the likelihood of occurring at the different distances from human residents) between the two species (Richmond, Hines, and Beissinger 2010). Since the SIs were lower than 1 in the Meyersdal area (and in conjunction with the supporting results from our spatial occurrence analyses), we assume that the yellow and slender mongoose are exhibiting some sort of spatial avoidance or segregation (Richmond, Hines, and Beissinger 2010; Chen et al. 2019).

Studies assessing temporal overlap have largely focussed on species which vary in their diel cycles, such as being either diurnal or nocturnal (Gerber, Karpanty, and Randrianantenaina 2012; Ramesh et al. 2012; Lesmeister et al. 2015; Frey et al. 2017; Karanth et al. 2017), and some report shifts or subtle changes in activity as an adaptation to competition avoidance, habitat disturbances or resource availability (Norris, Michalski, and Peres 2010; Lesmeister et al. 2015; Frey et al. 2017). For example, ring-tailed mongoose Galidae elegans and broad-striped mongoose Galidictis fasciata, which share a similar diet, segregate temporally by being primarily active during dusk/day and night, respectively (Gerber, Karpanty, and Randrianantenaina 2012). However, in the same study, in the presence of a larger competitor, the small Indian civet Viverricula indica, ring-tailed mongoose avoided dusk activity, the preferred activity period of the civet, and the activity of the ring-tailed mongoose was vastly greater at dusk in sites where the civet did not occur (Gerber, Karpanty, and Randrianantenaina 2012).

In contrast to the species above, the activity patterns of yellow and slender mongoose were strictly diurnal in our study. Complete overlap between the two species was potentially reduced by species differences in activity peaks, possibly due to differing foraging times. Maddock (1988) suggested that differences in the activity of prey consumed by similar species should also be considered in the timing of activities, which may also facilitate coexistence. The activity of the main prey of the mongoose in our study area needs to be confirmed to test whether prey activity drives mongoose activity. In addition, since slender mongoose activity was significantly greater in covered areas, and the lack of reduced activity during the warmest times of the midday period (compared with the considerable decrease in activity in yellow mongooses during this time period) may be due to their occurrence in covered areas that provide shade. Temporal overlap was slightly higher during the colder months than the warmer months, and this may be due to adjusting activity times to obtain favourable prey.

Niche partitioning appears evident by the lower spatial overlap between species in the Meyersdal area, thereby permitting greater temporal overlap. Taylor (1986) suggested that species overlap is reduced by differences in activity patterns, where foraging at different times may segregate species, which may be evident in our study too; an additional assessment of activity profiles of both species in this study area, noting timing of foraging, may provide further evidence of this.

We specifically investigated spatiotemporal overlap by assessing instances of yellow and slender mongoose occurring
in the same place at the same time (or within 10 min of each other). As expected, this was not common. The fact that there were no instances of occurrence in the same place at the same time, and only few instances of occurrences within a 10-min period (1.41% of all occurrences, all of these during colder months), suggests that resource partitioning, either along the spatial and/or temporal niche, is evident. In contrast, in a previous study in the same population, individuals of both species fed on a reed-buck Redunca arundinum carcass at the same time in winter (Cronk and Pillay 2018). Even so, the majority of these joint feeding occurrences resulted in slender mongooses aggressively vocalizing and lunging towards yellow mongooses, chasing them away after a short period. This suggests that under certain conditions, e.g. an abundance of food resources at a large carcass during winter, spatiotemporal overlap is possible for short periods. In addition, from our occupancy modelling, however, we could infer that the lower detection probability of the slender mongoose, as well as the effect of yellow mongoose presence on slender mongoose occupancy may also account for why this combined spatiotemporal overlap is not common.

In conclusion, we showed that in an urban estate, the spatiotemporal ecology of small co-existing carnivores is potentially influenced by food resources. While combined spatiotemporal overlap has not been widely assessed in coexistence studies, it has been reported that segregation or overlap along the combined spatiotemporal niche does not necessarily emulat the findings of spatial and temporal overlap separately (Karanth et al. 2017), which was also observed in this study. The likelihood of access to and the potential to exploit anthropogenic items appears to influence whether resource partitioning along the spatial (including differing habitat and site use) or temporal niche is more apparent in yellow and slender mongooses in this urban setting, but with low combined spatiotemporal overlap. Future studies should conduct an assessment of prey availability and distribution in conjunction with spatial and temporal occurrence of yellow and slender mongooses.

Data availability
The datasets generated and/or analysed during the current study are available from the corresponding author upon request.

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