Investigating the effects of management practice on mammalian co-occurrence along the West Coast of South Africa (#40171)

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Investigating the effects of management practice on mammalian co-occurrence along the West Coast of South Africa

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~~Substantial knowledge gaps related to the local effects of global environmental change drivers persist, particularly those that do not manifest in obvious ways.~~ The more subtle and cascading effects (e.g. altered interspecific interactions) that anthropogenic stressors have on local ecological assemblages are particularly concerning given their importance in ecosystem function. The abundance of small antelope in the contractual Postberg section of the West Coast National Park (the park) has been an ongoing management concern. The perception of a lower small antelope abundance has been attributed to predation by a mesopredator (caracal, *Caracal caracal*). However there are potential other factors, such as interspecific competition, which are also known to influence species abundance. Since Postberg has been influenced by the overstocking, and consequent overgrazing, of larger-bodied managed ungulates, we aimed to assess the influence of different ungulate management practices on interspecific interactions. Using camera traps, we investigated species co-occurrence and temporal activity between small antelope, managed ungulates and caracals in Postberg as well as another part of the park and a farm outside of the park. Data were analysed in R, using the *unmarked* and *overlap* packages to assess occurrence and temporal activity respectively. Results suggest that small antelope and managed ungulates have a high degree of spatial and temporal overlap, while temporal partitioning between small antelope and caracal is apparent. Further, small antelope and managed ungulates appear to occur independently of one another. Higher detection of managed ungulates within the park on fallow lands when compared to the more vegetated sites suggests that segregated food resources play a role ~~in this~~. Small antelope had a much higher probability of occurrence outside of the protected area. While the driver for this is uncertain, less variable (more intact) habitat outside of the protected area is likely the

reason. Ecological systems are complex with multiple interacting factors which makes elucidating patterns from a small sample size difficult. This problem is exacerbated in protected areas that attempt to replicate patterns and processes that would historically have taken place over larger areas. Our inability to detect clear cause and effect has negative implications for adaptive management. We recommend continued monitoring over multiple seasons and a wider area to determine the spatial information requirements to inform management of small protected areas.

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Abstract

Substantial knowledge gaps related to the local effects of global environmental change drivers persist, particularly those that do not manifest in obvious ways. The more subtle and cascading effects (e.g. altered interspecific interactions) that anthropogenic stressors have on local ecological assemblages are particularly concerning given their importance in ecosystem function. The abundance of small antelope in the contractual Postberg section of the West Coast National Park (the park) has been an ongoing management concern. The perception of a lower small antelope abundance has been attributed to predation by a mesopredator (caracal, *Caracal caracal*). However there are potential other factors, such as interspecific competition, which are also known to influence species abundance. Since Postberg has been influenced by the overstocking, and consequent overgrazing, of larger-bodied managed ungulates, we aimed to assess the influence of different ungulate management practices on interspecific interactions. Using camera traps, we investigated species co-occurrence and temporal activity between small antelope, managed ungulates and caracals in Postberg as well as another part of the park and a farm outside of the park. Data were analysed in R, using the *unmarked* and *overlap* packages to assess occurrence and temporal activity respectively. Results suggest that small antelope and managed ungulates have a high degree of spatial and temporal overlap, while temporal partitioning between small antelope and caracal is apparent. Further, small antelope and managed ungulates appear to occur independently of one another. Higher detection of managed ungulates within the park on fallow lands when compared to the more vegetated sites suggests that segregated food resources play a role in this. Small antelope had a much higher probability of occurrence outside of the protected area. While the driver for this is uncertain, less variable (more intact) habitat outside of the protected area is likely the reason. Ecological systems are complex with multiple interacting factors which makes elucidating patterns from a small sample size difficult. This problem is exacerbated in protected areas that attempt to replicate patterns and processes that would historically have taken place over larger areas. Our inability to detect clear cause and effect has negative implications for adaptive management. We recommend continued monitoring over multiple seasons and a wider area to determine the spatial information requirements to inform management of small protected areas.

Keywords: steenbok, common duiker, caracal, resource partitioning, over~~s~~-stocking, ungulates, land-use, habitat, vegetation structure

Introduction

Land use results in habitat conversion, degradation and fragmentation which have, along with climate change, altered the biodiversity and ecosystems of the earth (Chapin *et al.* 2000; Newbold *et al.* 2015). Importantly, human activities also impact top-down and bottom-up ecosystem processes at the landscape level (Burgi *et al.* 2017). Substantial knowledge gaps related to the local effects of global environmental change drivers persist, particularly those that do not manifest in obvious ways (Newbold *et al.* 2015). It is the more subtle and cascading effects (e.g. altered interspecific interactions or behaviour) that anthropogenic stressors have on local ecological assemblages that are particularly concerning given their importance in ecosystem function (Erb *et al.* 2017; Frey *et al.* 2017). Niche partitioning between species at the same trophic level is an important facilitator of coexistence (Frey *et al.* 2017; Herfindal *et al.* 2017). Understanding how environmental stressors influence niche partitioning between species is critical for informing management decisions as well as for improving our understanding of how local assemblages respond to anthropogenic changes (Frey *et al.* 2017).

Since species have evolved traits in response to variation within their environment, the environment essentially determines species distribution and abundance, which shapes populations (Molles 1999) and social organisation (Jarman 1974). Resource partitioning is commonly observed in diet segregation, habitat use, spatial aggregation or timing of peak activity, which is needed for sympatric species to co-exist (Herfindal *et al.* 2017; Marti *et al.* 1993). Resource partitioning amongst ungulates is usually driven by body size (Cromsigt and Olff 2006), competition and resource availability (Gordon and Illius 1989). For example, smaller antelope have higher per-mass metabolic rates, thus requiring higher quality forage compared to larger ungulates, with lower relative metabolic rates, who rely on consuming larger quantities of forage (Cromsigt and Olff 2006). As such, resources are partitioned along a niche axis of quantity versus quality (Cromsigt and Olff 2006). Forage quantity varies vertically (accessible plant height), as well as horizontally (heterogeneity of vegetation and patch size), as such influencing behaviour (Cromsigt and Olff 2006; Venter *et al.* 2014). Time can also be considered a resource (Frey *et al.* 2017), where time spent on one activity is a lost opportunity for gains of another activity (e.g. forage intake, predation risk and thermoregulation (Owen-Smith and Goodall 2014; Rowcliffe *et al.* 2014), which has associated energetic trade-offs. Animal activity level (time spent active) is, therefore, a good indicator of species energetics, foraging effort and risk exposure, albeit poorly understood due to the challenges of quantifying activity in the field (Rowcliffe *et al.* 2014). Relative timing of species' activity levels may also be an indication of dominance (Lazenby and Dickman 2013) or risk avoidance (Díaz-Ruiz *et al.* 2016; Tambling *et al.* 2015).

Land use and management practices affect habitat, with ~~knock-on~~ effects on species interactions, thus playing an important role in determining species distribution and abundance patterns (Lazenby and Dickman 2013). Furthermore, direct alteration of species abundance and composition (e.g. through introduction, culling or species removal) could influence free-ranging species through facilitative or competitive interactions. A common example in Africa is farming of livestock in the presence of wild ungulates. While low abundance of domestic ungulates may improve foraging for wild ungulates (Charles *et al.* 2017)~~.~~, the effect becomes negative as densities increase (Herfindal *et al.* 2017). The majority of studies indicate that wild ungulates are negatively impacted by livestock, with the greatest negative responses being due to competition and a change in forage quantity and quality (Schieltz and Rubenstein 2016).

The apparent low abundance of small antelope (common duiker, *Sylvicapra grimmia*, and steenbok, *Raphicerus campestris*) in the contractual Postberg section of the West Coast National Park (hereafter referred to as the park) has been a management concern since the early 1990s (Avenant 1993 and Heydenrych 1995). There is a perception that these two species have lower abundance in the contractual section of the park, compared to other sections, which landowners have attributed to predation by a mesopredator (caracal) (Postberg owners consortium, pers. comm.). Caracals (*Caracal caracal*) are the largest predator in the system following the historical extirpation of apex predators. The caracal's "release" from the top down competition that would have occurred in the presence of large predators prior to extirpation (Cruz-Uribe and Schrire 1991) may have enhanced its impact on small antelope populations in the area. However, while the predation threat may be realistic, it is not the only process that could result in low abundance of small antelope. Historical land use and management practice within Postberg includes agriculture (livestock and crop cultivation) and more recently the overstocking of large ungulates which has resulted in extensive habitat degradation and potentially competition.

Using camera traps, we aimed to assess co-occurrence and temporal activity overlap between small antelope and managed ungulates (competition) and caracal (predation) with a view to establish how land management influences species interactions. Camera traps are especially useful tools for observing animal interactions as they provide 24 hour surveillance that can record multiple species over space with time-of-detection (Lazenby and Dickman 2013; Rowcliffe *et al.* 2014), which is important for assessing interactions between co-occurring species. Furthermore, camera traps are instrumental in estimating species distribution and abundances in relation to anthropogenic change and stressors (Frey *et al.* 2017) as they are very effective at detecting medium to large sized terrestrial mammals (Reilly *et al.* 2017). We used data from cameras in three areas with different management practices and managed ungulate abundances (two within the park, Postberg and Langebaan, and one on a research livestock farm) to assess how the presence or absence of managed ungulates and caracal affects the occupancy of small antelope (steenbok and common duiker) and whether there is a difference in temporal activity patterns between the species groups. We expected the presence of managed ungulates to negatively influence occurrence probabilities of small antelope in Postberg due to direct competition for resources with, or habitat modification by, the more abundant larger managed ungulates (Fritz *et al.* 2002). We also predicted a greater temporal overlap between managed ungulates and small antelope in Postberg when compared to more natural areas within the park due to the higher abundance of managed ungulates, thus forcing the small antelope to spend more time looking for appropriate resources. To add scope to the comparisons and influence of managed ungulates on small antelope we also investigated co-occurrence and temporal overlap between managed ungulates on a research farm where livestock are restricted to fenced camps. Here, as with Postberg, we expected the presence of livestock to have a negative influence on the occupancy of small antelope as well as to have higher temporal activity overlap when compared to the larger more natural area in the park where ungulates are free ranging. Finally, we expected a significant temporal niche partitioning between small antelope and caracal, to lower their predation risk (Tambling *et al.* 2015).

Materials and methods

Study area

This study took place in the largely nutrient-poor Fynbos Biome (Mucina and Rutherford 2012), along the west coast of South Africa, where annual average rainfall varies between 152 mm in the north and 265 mm in the south. The predominant vegetation type of the region is Strandveld which is dominated by sclerophyllous, broad-leaved shrubs that form communities of medium density to closed shrublands (Mucina and Rutherford 2012).

We defined three study areas (scenarios) by their different management practices where the 'stocking rate' and species of managed ungulates at each scenario acted as a proxy for 'management practice'. Managed ungulates were defined as those species that require the intervention of people to manage the populations e.g. removals, introductions, feed supplementation and census. Ungulates were classified into different size classes according to weight (Table 1), based on the natural segregation of weight ranges between the managed ungulates, where animals <25 kg were classified as small, between 26 – 200 kg were classified as medium and anything >201 kg was classified as a large. No managed ungulate was classified in the small class. Two scenarios were within a protected area (Postberg and Langebaan sections of the West Coast National Park) and the third was on a research farm (Lamberts Bay, hereafter referred to as the farm). The park is located approximately 100 km north-west of Cape Town, South Africa, was proclaimed in 1985 and since then it has expanded to its current size of approximately 47 000 ha (SANParks 2013). The farm is located outside of the town Lamberts Bay which is approximately 100 km north of the park (Fig. 1). The farm was selected due to its being of comparable size (the majority of commercial farms along the west coast are used for crop production with little livestock and are therefore not of a comparable size to the two areas within the park) while still being within the bioregion and having comparable vegetation types.

Postberg

Postberg has historically been characterised by intensive management of large and medium-sized herbivores in a small area (1 800 ha). The land was originally acquired in the early 1800s by a group of farmers and was used primarily for winter grazing, but the land was also ploughed. Postberg was proclaimed as a private nature reserve in the 1960s, after which it was contractually included into the park in 1987. Many indigenous and extra-limital large and medium-sized ungulate species were introduced to Postberg since the 1960s which resulted in overgrazing of the small, fenced area. Managed ungulates at this site were estimated to occur at ± 11.3 animals/km^2 (SANParks unpublished data) and included bontebok (*Damaliscus pygargus pygargus*), Cape mountain zebra (*Equus zebra zebra*), red hartebeest (*Alcelaphus* *buselaphus caama*), eland (*Taurotragus oryx*), blue wildebeest (*Connochaetes taurinus*), kudu (*Tragelaphus strepsiceros*), springbok (*Antidorcas marsupialis*) and gemsbok (*Oryx gazelle*). Although there have been consistent removal efforts of extra-limital and other ungulates since Postberg's inclusion into the park, November 2016 (6 months prior to the study) saw a significant removal of these species from the area, resulting in slightly lower densities during this study. Due to slow reproduction rates of ungulates and recovery of vegetation, the past overabundance of large herbivores in the Postberg section was nonetheless expected to have a legacy effect of potential disturbance on vegetation and small antelope that would extend through the duration of this research.

Langebaan

In the Langebaan scenario, large herbivores occur at lower densities and are not confined to a small area. Historically this area was also used for agriculture, which included livestock and crop production and different portions were proclaimed as part of the park in 1989 and 1996. Managed ungulates within the Langebaan scenario were eland, bontebok, and red hartebeest and occurred at around 7.6 animals/km^2 (SANParks unpublished data).

Lamberts Bay (the farm)

The farm scenario made use of the Nortier research farm that falls under the management of the Department of Agriculture (Elsenburg), Western Cape Government and is 2780 ha in size. Several resource flocks and herds are kept on the farm for the Directorate: Animal Sciences, while it is also the site of veld rehabilitation projects run by the Directorate: Plant Sciences. The livestock present include sheep (*Ovis airies*), comprising three breeds (Namaqua Afrikaner, Dorper, and SA Mutton Merino), Bonsmara beef cattle (*Bos taurus*) and ostriches (*Struthio camelus*). The ostrich flock was restricted to camps that were not surveyed. In addition to the livestock, Impala (*Aepyceros melampus*) and Nyala (*Tragelaphus angasii*) are also present on the farm and were considered as managed ungulates, which were collectively estimated to occur at around 7.6 animals/km^2 (C. Rheeder, research farm manager, pers comms). The research farm is located in a matrix of other farms where predator control is known to take place.

Survey design and in-field methods

The three scenarios were surveyed over the winter of 2017 using 18 Cuddeback®, model C3 blackflash (Non-Typical, De Pere, WI) camera traps. Postberg was surveyed between May and July, followed by Langebaan between July and August and the farm from August to October 2017. We overlaid each area with a grid of 1 km^2 cells in ArcGIS (ESRI 2012). The centroid of each of the 18 resultant cells served as the camera location. Once in the field, we used a handheld GPS to navigate to the centroid, after which we walked outward in a spiral fashion for up to 120 m from the centroid, seeking the first location where two or more signs of animal activity were detected (Colyn 2017). The camera was set at this point. Cameras were mounted approximately 40 – 50 cm above ground level, onto a wooden stake and faced in a southerly direction, away from the sun, to prevent false triggers and overexposure (Glen *et al.* 2014). The cameras were programmed to capture three burst photographs when triggered, with a 30-second delay between photographs.

Vegetation height and cover were measured at each site according to the protocol described in Colyn (2016), i.e. by taking a measurement at one and two-meter distances from the camera trap location in a North, South, East and West direction (eight measurements in total). Vegetation height was recorded at the prescribed 1 m and 2 m distances with a measuring tape and percentage cover were also measured at these points using a densitometer (Li *et al.* 2000). Height and cover were averaged across the eight measurements for use in analyses. Elevation was extracted at site level from the CGIAR-CSI SRTM 90m Digital Elevation Data (Jarvis *et al.* 2008) using the spatial analyst tool within ArcGIS (ESRI 2012). Similarly, slope was calculated using a digital slope model from the same DEM using the spatial analyst tool within ArcGIS (ESRI 2012).

Data analysis

Camera trap images were downloaded and image data were processed and captured using the TimeLapse2 Image Analyzer software (Saul Greenberg, University of Calgary, Calgary, Alberta) and then exported to excel per camera station. Image databases of camera stations were merged for each management scenario. Non-animal photographs were removed from the database and when more than one species was captured in a single photograph, entries were duplicated and edited to capture the number of individuals of each species as separate records. If a photographed animal was not recognisable at species level but could be classified as either a small antelope or managed ungulate, then it was captured as such. Image data were binned into independent capture events using a loop in R (R Development Core Team, 2015) which grouped all captures of a particular species, at a particular location. It then calculated the time difference between each picture and partitioned photographs of the same species at the same location into 30 minute interval groups. The photograph with the highest number of individuals of that species was selected from each group and appended to the analysis database as an independent capture. We used the *tidyverse* and *ggplot2* packages (Wickham 2016, 2017) in R to manipulate databases and produce plots and summaries where necessary.

Occupancy

To assess how the presence of managed ungulates influenced the occurrence of small antelope, we conducted single season, two-species occupancy analyses in PRESENCE (Hines 2006) and ran single season, single-species occupancy models in R (R Development Core Team, 2015) using the *unmarked* package (Fiske and Chandler 2011). Since Postberg had the shortest survey duration (32 days), the data from the farm and Langebaan were partitioned so that only the data collected in the first 32 days were used for all occupancy analyses. Postberg however also had one camera failure which resulted in 542 trap nights for Postberg, compared to 582 for Langebaan and 579 for the farm.

Single-species occupancy

Site-specific covariates (Table 2) were captured in a separate site database and correlations assessed for those variables with numeric/continuous values. There was a strong positive correlation between vegetation height and cover (0.75) and therefore we only used vegetation height in models as a proxy for vegetation structure.

We used the *camtrapR* package (Niedballa et al. 2016) in R to create a camera operation matrix and a detection history for individual species / or suites of species of interest (e.g. managed species). Temporal replication was defined per species by dividing the camera survey into sampling occasions which can range from 1- 15 days (Kok 2016). Occasion length varied for different species depending on their detectability. Shorter occasion lengths are better for assessing occupancy of species that are frequently detected, while longer occasion lengths are better for assessing occupancy of species that are less abundant and that have low detection probabilities. We experimented with different occasion lengths and settled on 5 days for caracal detection, 2 days for managed ungulate abundance and 7 days for steenbok and duiker occupancy.

Occupancy and abundance were analysed using the *unmarked* package in R (R Development Core Team, 2015) using the detection history of the species of interest, observation level, and site-specific covariates. Large and medium ungulate abundance per site was estimated using the abundance-induced heterogeneity model, *occuRN* function, (Royle and Nichols 2003) in the *unmarked* package in R (R Development Core Team, 2015). Data were pooled for all three scenarios; effort was used to explain detection probability and scenario to explain occupancy. Small antelope occupancy and caracal detection were estimated using the single season, single species occupancy model implemented by the *occu* function (MacKenzie et al. 2002). Data across scenarios were pooled to estimate small antelope occurrence and scenario was included to explain occupancy, while effort was included to explain detection for all species. The managed ungulate species' abundance estimates along with other site-specific covariates were used as predictors of small antelope occupancy. The best models were selected using the *modsel* and *fitlist* functions which produce a table of AIC and R^2 values. Models were assessed for relative goodness of fit by scrutinizing the AIC, delta and R^2 values in the model summaries.

The "best" model is considered the model which produces the lowest AIC value. We also considered the delta value, which is the difference in AIC value between a model and the model with the lowest AIC. Earlier literature suggested that models with a delta value of >2 were poor, however recent evidence suggests that models with a delta value in the range of 2 – 7 should also be considered (Burnham et al. 2011). We made predictions based on the top models and inspected the 95% confidence intervals of the predictions (Table 3). Models that had no predictive power (i.e. produced lower and upper occupancy confidence estimates ranging between 0, i.e. complete absence, and 1, i.e. 100% occupancy) were not considered to be informative. If there were no covariates that provided strong predictive power, we made predictions based on either the null model or a model that used effort to explain detection and scenario to explain occupancy, depending on comparative AIC values.

Because many of the occupancy models did not have sufficient data or data variation to converge, we also tested particular hypotheses directly. We compared abundance, occupancy, vegetation height, detections and slope between each scenario. All these data were non-parametric (tested using the Shapiro-Wilk test of normality) and thus we used a Dunn's Test that accounts for tied ranks. We hypothesised that managed ungulates would show a preference for fallow lands and as such would be detected more often, with a shorter time between captures than recorded elsewhere. Conversely, we expected small antelope to avoid these areas, and thus their time between captures on fallow lands would be higher (fewer detections). To assess this we calculated the number of detections for small, medium and large ungulates at each vegetated site and compared the number of detections on fallow versus natural lands across areas for an equal number of days (32). We also compared the average time between independent captures for species from each group (small/medium/large) between fallow and natural lands in Postberg and Langebaan. These analyses were not conducted for the farm as no fallow lands are present there.

Temporal activity and overlap

Activity level and overlap of small antelope and managed ungulates were assessed using the *overlap* (Ridout and Linkie 2009) and *activity* (Rowcliffe 2016) packages in R (R Development Core Team, 2015). Prior to activity and overlap analyses, time was converted to decimal numbers. The time of sunrise and sunset was calculated using the *StreamMetabolism* package (Sefick 2016) and stored for each record based on the date and GPS location of the record. To increase the available sample size for the temporal activity and overlap analyses, we lumped the data generated by the systematic survey described above with camera trap data that was opportunistically collected in the Postberg and Langebaan sections of the park between June 2016 and February 2017, where cameras were set on management tracks using the same camera settings as above as well as data generated from the full 60 days for which the farm was surveyed. This resulted in 1150, 1159 and 1213 trap nights for the Postberg, Langebaan and the farm respectively. We did not have enough time-of-day observations for caracal at the farm and Postberg to assess temporal activity and overlap with small antelope, so this analysis was restricted to the Langebaan site.

The analysis of circular data is specialised, and standard statistical measures such as mean and variance, or regression are not appropriate (Ridout and Linkie 2009). Time was converted to radians, a requirement of the *overlap* package. Activity was broadly depicted by non-parametrically estimating activity patterns using kernel density estimation with the bandwidth concentration parameter set at a maximum of 3 (Ridout and Linkie 2009). This was further multiplied and adjusted by 1.5 as per Rowcliffe *et al.* (2014) who noted that bandwidth adjustment of 1.5 gave the most robust and minimally biased activity level estimations. The degree of overlap in temporal use of different species groups was estimated using the coefficient of overlap, Δ, where 0 = complete separation and 1 = complete overlap. If there were less than 75 observations for one of the species, the *Dhat1* overlap estimator was applied whereas if the sample size was greater than 75 for both species, *Dhat4* was used (Ridout and Linkie 2009). We compared the activity overlap of the species of interest across scenarios first to assess whether they displayed any difference in activity patterns in the different areas. Following this, we compared the overlap between managed ungulates and small antelope at each scenario to determine if there is any evidence of temporal niche partitioning between species groups. Data were bootstrapped and resampled 500 times for each overlap estimate to generate 95% confidence intervals. To test whether activity patterns differed between species, we applied the Watson-Wheeler test of homogeneity for circular data to non-bootstrapped data using the *circular* package in R (Agostinelli and Lund 2017, Tasdan and Yeniay 2013). Activity levels and overlap were plotted using the *overlap* package.

Results

There was no significant difference in vegetation height between the sites (ρ0.1627), however, vegetation height on the farm was significantly less variable than in the park (ρ0.002, using an asymptotic test in the *cvequality* package in R (Marwick & Krishnamoorthy 2018). This was driven by the very high variation in vegetation height within Postberg and Langebaan, both of which included sites with no vegetation (former fallow lands) and well-vegetated sites with high vegetation height, whereas sites on the farm were more evenly vegetated.

Significant differences were detected in managed species abundance across sites. Medium sized ungulate abundance was significantly higher at the farm when compared to Postberg (ρ< 0.0017) and Langebaan (ρ<0.001) with a mean site abundance of 1.62 individuals per site. There was no difference in site abundance of managed medium-sized ungulates between Postberg and Langebaan (ρ = 0.054) with a mean of 0.511 and 0.371 individuals per site respectively. Large managed ungulates had a mean abundance of 0.074, 2.69, and 3.30 individuals per site for the farm, Langebaan, and Postberg respectively. As such, abundance was significantly lower at the farm compared to both park scenarios (ρ = <0.001), while there was no difference between Langebaan and Postberg (ρ = 0.19). However, when large and medium-sized ungulates were pooled as 'managed ungulates' Postberg was estimated to have higher abundance than the farm (0.0461) areas (Fig. 2).

Differences in detection probability were also detected across areas and between the focal species groups (ρ<0.001, Fig. 3). Caracal detection was highest at Langebaan (0.0520), followed by Postberg (0.0398) and was lowest at the farm (0.0253). Common duiker, steenbok and small antelope (common duiker and steenbok lumped) detection differed significantly between all scenarios (ρ<0.001). Detections were highest at the farm (0.778, 0.416, 0.867 respectively) followed by Langebaan (0.671, 0.384, 0.761 respectively) and Postberg (0.194, 0.0974, 0.256 respectively). Conversely, large managed ungulates were detected most frequently at Postberg (0.275) followed by Langebaan (0.202) and were detected least frequently at the farm (ρ<0.001). While large ungulates had the lowest detection probability at the farm, medium and managed (medium and large lumped) ungulates had higher detection probabilities there (0.324, 0.328 respectively) compared to Postberg (0.261, 0.317 respectively) and Langebaan (0.113, 0.231 respectively).

Occupancy

We found that when detection probability was <0.1, occupancy could not be estimated, and therefore we could not make confident predictions for caracal occupancy for Postberg or the farm (Lamberts Bay).

The results from the two species occupancy models were not particularly informative. Data were insufficient to run two-species occupancy models in Postberg, but models from the other scenarios suggest that ungulate species in different size classes occur independently of one another (see supplementary material).

Common duiker occupancy (ψ) differed significantly (ρ<0.001) across scenarios with the farm having the highest occupancy of 1 (± 0 SE), followed by Langebaan (ψ = 0.889 ± 0.052 SE) and Postberg (ψ = 0.473 ± 0.098 SE). Steenbok occupancy was significantly different (ρ<0.001) across all scenarios with the farm having the highest probability of occurrence (ψ = 0.841 ± 0.222 SE) followed by Langebaan (ψ = 0.486 ± 0.013 SE) and then Postberg (ψ = 0.192 ± 0.012 SE) (Fig. 4). Models for small antelope (common duiker and steenbok lumped) produced similar results to that of common duiker. Vegetation height was the strongest predictive variable for common duiker occurrence. While medium ungulate abundance produced the most reliable predictions for steenbok occurrence (Table 3), slope appeared to have a weak influence as it appeared in two of the top ten models. Estimates for the farm, however, remained uninformative due to 100% occupancy across sites.

Large herbivores were captured significantly more often on fallow lands (ρ = 0.02, Wilcox test), which were visited on average every 2.8 days, while natural lands were visited every 8.2 days across areas. This pattern was particularly prevalent in Langebaan, where most detections took place on or near fallow sites (Fig. 5). Overall, there was no difference in small antelope detections between fallow and non-fallow lands however, the sample size of fallow sites was small and 32 detections at one fallow land site in Langebaan obscured potential patterns (Fig. 5). There were no fallow land detections for small antelope at any of the five other fallow sites, inclusive of all fallow sites at Postberg.

Temporal activity and overlap

Activity patterns were typical for the species of interest. Managed ungulates were primarily diurnal, small antelope crepuscular (Fig. 6) and caracals mostly nocturnal (Supp. Fig. 1). We assessed temporal overlap between caracal and small antelope independently as well as pooled (common duiker and steenbok) at the Langebaan site. The overall trend across the overlap analyses was for small antelope activity to peak at periods of low caracal activity (Supp. Fig. 1). Activity overlap between managed ungulates and small antelope was also assessed separately for each scenario (Fig. 6). As hypothesised, activity overlap was highest at Postberg (86%, CI: 0.77 - 0.93) followed by Langebaan (79%, CI: 0.73 – 0.84) and the farm (74%, CI: 0.68 – 0.79). At the latter two sites temporal activity was deemed to be significantly different (ρ<0.001).

Discussion

Co-existence between sympatric species requires segregation of resources such as food, habitat use, spatial distribution and temporal activity to facilitate niche partitioning (Frey *et al.* 2017; Herfindal *et al.* 2017). Adjusting temporal activity is also a way for prey species to avoid predation and escape risk (Owen-Smith 2015). In this study, we explored the influence of different management practices on interspecific interactions by investigating species co-occurrence and temporal activity overlap between small and managed ungulates as well as a potential predator, the caracal. Results suggest that small antelope and managed ungulates have a high degree of spatial and temporal overlap, while temporal partitioning between small antelope and caracal is apparent. A surprising finding was the much higher occurrence of small antelope outside of the park.

Small antelope occurrence

Management practice had an obvious impact on the occurrence of both steenbok and common duiker with Postberg consistently having the lowest probability of occurrence, with a much higher occupancy outside of the protected area at the farm (Fig. 4). Although few of our measured covariates had strong predictive power, vegetation structure was a good predictor for common duiker occurrence (Supp. Fig. 2), while medium ungulate abundance and slope had a weak effect on steenbok occurrence (Table 3). This suggests that habitat and interactions with managed ungulates may be important drivers for the occurrence of small antelope within our study area. Therefore, we specifically explored interactions (i.e. competition and facilitation, habitat and predation) as possible mechanisms driving small antelope occurrence.

Competition versus facilitation

The lower occurrence of small antelope at Postberg is unlikely to be due to medium ungulates since medium ungulate abundance was comparatively lower at Postberg than the farm. However, managed ungulates at the farm were primarily livestock restricted to camps, therefore, the potential influence on small antelope would be restricted within and not widespread across the area. We also considered the potential of managed ungulates facilitating forage opportunities for small antelope. However, facilitation is considered unlikely due to the nutrient-poor soils and slow growth rates of the vegetation which encourages competition between ungulates (Fritz *et al.* 2002). In addition, small antelope occurrence is lowest in the areas with the highest densities of managed ungulates, which may indicate competition (Fig. 5). For example, elimination of buffalo (*Syncerus caffer*) from the Serengeti National Park is suggested to have driven increased abundance of small antelope as a result of competition release (Arsenault and Owen-Smith 2002). While there seems to be little interspecific competition at the local level, this might not be the case at a larger scale. For example, roe deer and wild boar have been seen to occur independently of cattle at the habitat level in China but displayed segregation at the landscape level (Wang *et al.* 2018). Further, research in the Kruger National Park suggests that interspecific interactions may have effects on the distribution of African megafauna, but that this may not be evident at the local scale (Ryan and Ladau 2017). The two-species occupancy results (Supplementary Material) as well as the high overlap in activity (Fig. 6) suggest that small antelope and managed ungulates occur independently of one another at the local scale. However, given that the small area assessed in this study represents the full area under management (for Postberg at least), larger landscape level analyses are not possible in this context.

Habitat, forage and cover availability

Ecological theory suggests that for sympatric species to co-exist, subordinate species need to be able to exploit a resource which is not available to dominant species (Gordon and Illius 1989). It is therefore likely that small antelope and managed ungulates have segregated food resources at our study site. This segregation may be due to the difference in body size that dictates forage requirements and forage availability on the vertical and horizontal planes (Cromsigt and Olff 2006). Small antelope would be able to access new growth that is located at a low level or within the shrub itself, whereas the large ungulates are likely utilising the outer and higher parts of the shrub component. Larger ungulates naturally have more access along the horizontal plane as they are not restricted to home ranges (Jarman 1974) and therefore can move greater distances between suitable foraging patches (Venter *et al.* 2015). Additionally, common duiker and steenbok are both known to prefer habitats where shrubs provide adequate cover (Heydenrych 1995).

Although managed ungulates were detected at a high proportion of sites, they may be transient at many of them and merely passing through. This is supported by the much higher detection of managed ungulates at sites that were classified as fallow lands when compared to the more vegetated sites within the park. Research has also suggested that habitat heterogeneity, such as observed in Postberg and Langebaan, may drive movement scales of larger herbivores as they move between suitable foraging patches (Venter *et al.* 2015).

Predation risk

Large managed ungulates were less active at night indicating that they were likely meeting their foraging requirements during the day since there is no predation risk for them. In contrast small antelope were more active at night. This likely stems from trade-offs between foraging and vigilance for predators (not required at the current site for larger species) that results in small antelope not meeting their foraging requirements during the day (Owen-Smith and Goodall 2014; Rowcliffe *et al.* 2014). Caracal activity in the park is typical of that observed in other felids (Ramesh and Downs 2015; Reilly *et al.* 2017), being predominantly nocturnal, with a distinct drop in activity between sunrise and midday after which activity picked up again. Small antelope showed a largely inverse, crepuscular pattern. This is indicative of anti-predator behavior portrayed by small antelope. However, there is a degree of temporal overlap between the species (delta ~0.5) and this might suggest that caracals do not present a significant risk as a predator, which is corroborated by previous research which found that caracal diet within the park consists primarily of rodents (84% occurrence in scat), while small antelope were less important with a 6.5% occurrence in scat (Avenant & Nell 2002).

Caveats

Ecological systems are complex and interactions can be influenced by multiple biotic and abiotic characteristics. The capability of our models was limited due to low variation in the data, such as detection of small antelope at all sites on the farm, which made elucidating patterns of interest difficult. Although camera traps are excellent tools for monitoring animal communities, they still have some limitations as they only monitor a fixed point in the landscape. For example, dense vegetation restricts the detection zone, which could have influenced detection of species at vegetated sites. Therefore detection probability is a particularly important consideration when conducting camera surveys, especially surveys that focus on communities rather than an individual species as different species often have specific habitat requirements and are thus detected more frequently in areas where other species might not be detected.

Conclusions and recommendations

Although this study had certain limitations, the results suggest a high level of spatial and temporal overlap between managed ungulates and small antelope. Further, there is an indication that the two groups of species likely occur independently of one another, which is substantiated by the results from the two-species occupancy models (see Supplementary Material). This suggests that competition and facilitation are unlikely drivers of small antelope occurrence, but rather that these sympatric species co-exist due to segregation of food resources. While the low occurrence of small antelope in Postberg might be ascribed to competitive exclusion by managed ungulates, this may rather be a legacy effect of disturbance. Although, we were unable to estimate this due to data limitations, further investigation over the long term will be valuable in assessing how small antelope populations recover after the removal of managed ungulates. Additionally, Postberg is significantly smaller than Langebaan and the farm with significantly steeper slope which may suggest that there is simply less suitable habitat for small antelope within Postberg.

While managed ungulates were detected at a high proportion of sites at Postberg and Langebaan we postulate that it is due to them moving between areas of suitable forage. This is supported by the fact that they spent significantly more time on the fallow lands, with lower residence at other sites (Fig. 5). Radloff (2008) concluded that eland and bontebok avoided sandstone and limestone Fynbos, and when they did occur there they mainly utilised grassy microhabitats, much like the fallow lands in this study. The managed ungulates are water dependent, whereas the small antelope are not (Valeix *et al.* 2009), and thus would need to travel between water points and forage patches regularly. This made it challenging to assess their influence on small antelope occurrence, relative to movements required to meet their own metabolic needs and resource partitioning. Deploying GPS collars on managed ungulates and small antelope in the Langebaan and Postberg sections would provide a finer scale understanding of resource partitioning and co-occurrence of these sympatric species.

Overall we found some effects of inter-specific interactions at the local scale but there was a lack of reliable pattern across areas. This is consistent with literature that suggests large-scale ecological trends are difficult to detect at fine scales (Ryan and Ladau 2017; Wang et al. 2018). Inability to determine cause and effect has implications for the adaptive management of protected areas since many of South Africa's protected areas are small, fenced and stock ungulate species that have large spatial requirements. The resultant restriction of natural movement patterns within these protected areas, therefore, confounds our ability to detect ecological processes. Considering the financial and human resource capacity of most small protected areas, this study represents a realistic (if not more so) level of ecological monitoring. This begs the question, can we realistically monitor and understand the impacts of management practices in small protected areas? In addition, replication of historical ecological processes in the small land parcels remaining for protection is uncertain, especially considering species that were transient and whose home ranges exceed the size of the protected area. We recommend replicating the experiment in an area that allows greater spatial representation to better understand requirements for existence of individual species as well as co-existence, which will benefit the management of small protected areas.

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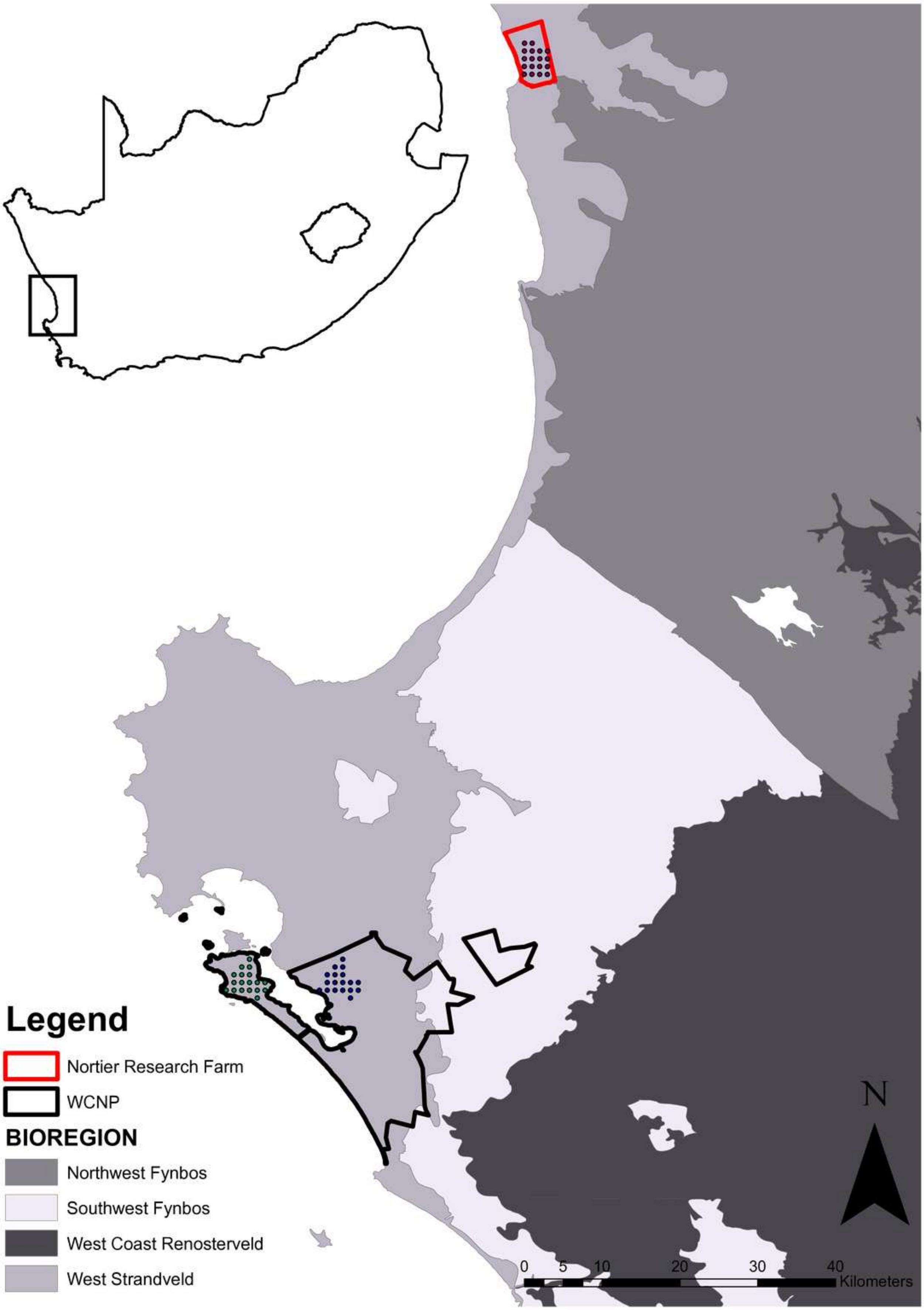
Figure 1

Map of the study area.



Legend
Nortier Research Farm
WCNP
BIOREGION
Northwest Fynbos
Southwest Fynbos
West Coast Renosterveld
West Strandveld
N
0 5 10 20 30 40
Kilometers

Figure 2

Estimated managed ungulate abundance per site across the three scenarios.

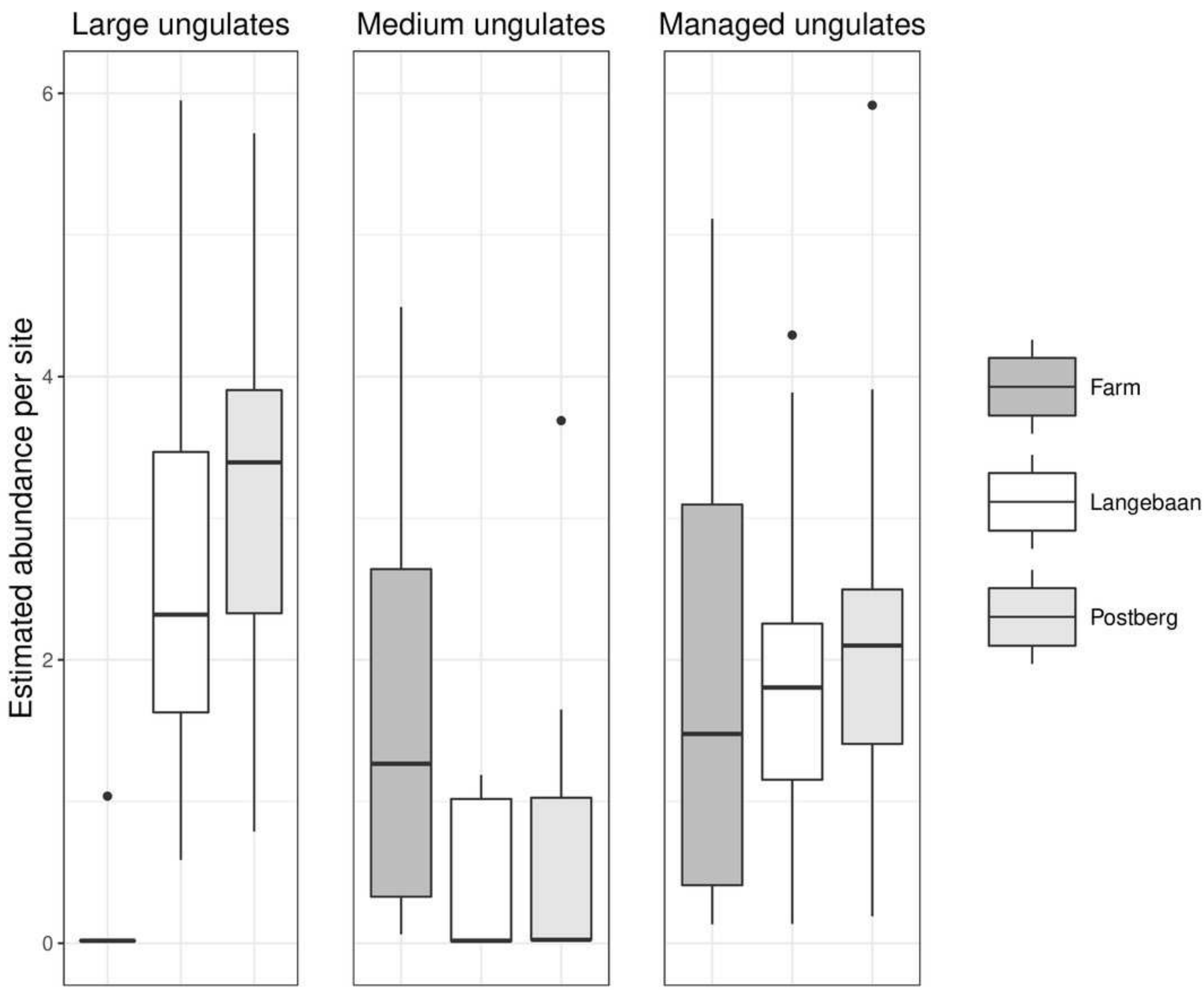


Figure 3

Detection probability ± standard error of focal species across the scenarios.

Note that the scales differ between the first and second rows of graphs.

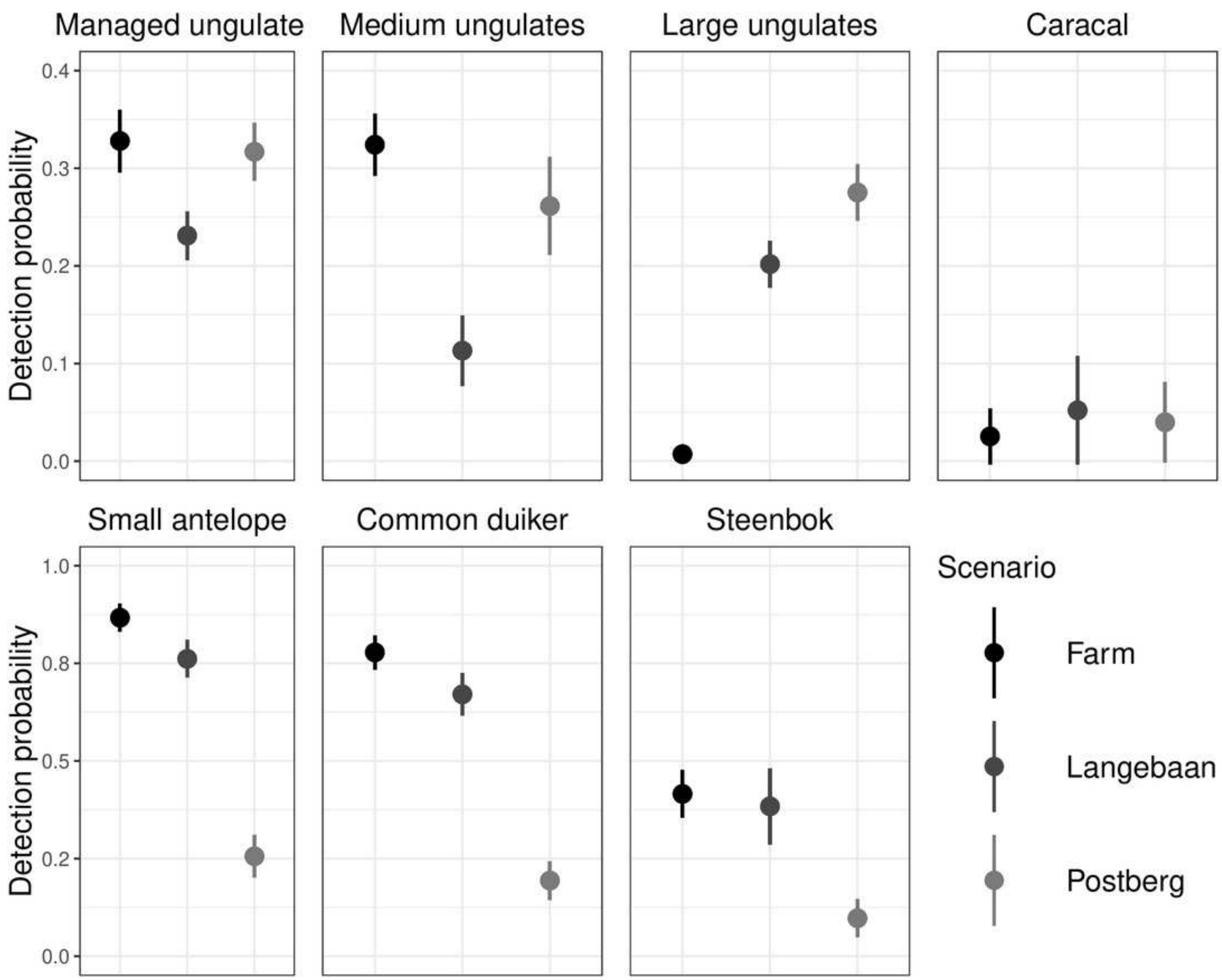


Figure 4

Probability of occurrence for common duiker and steenbok across the scenarios.

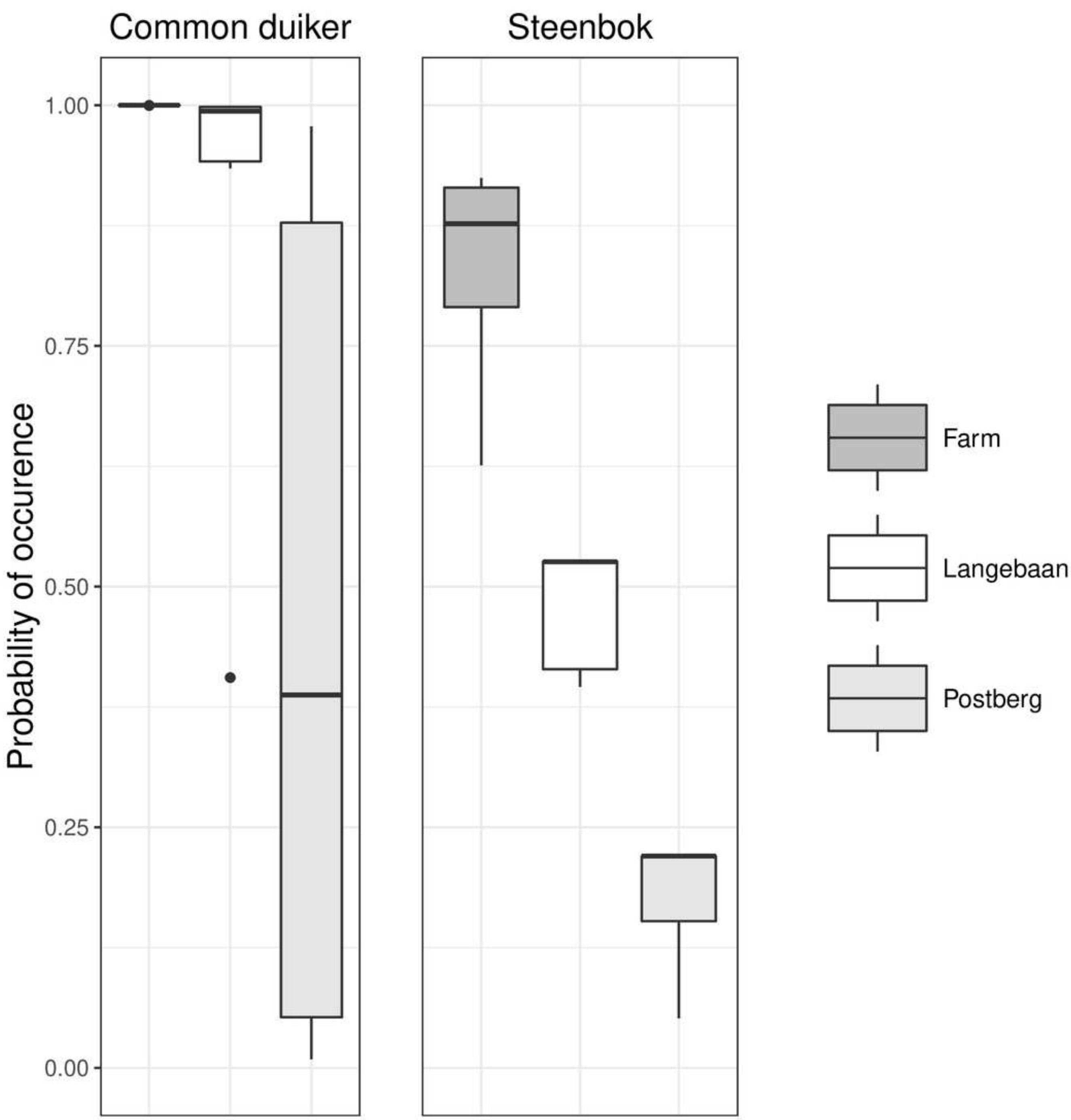


Figure 5

Detection maps of small antelope and managed ungulates within the park.

Points represent camera sites and the size of the dots represents the frequency of detections at each site. Red dots indicate sites which were fallow lands.

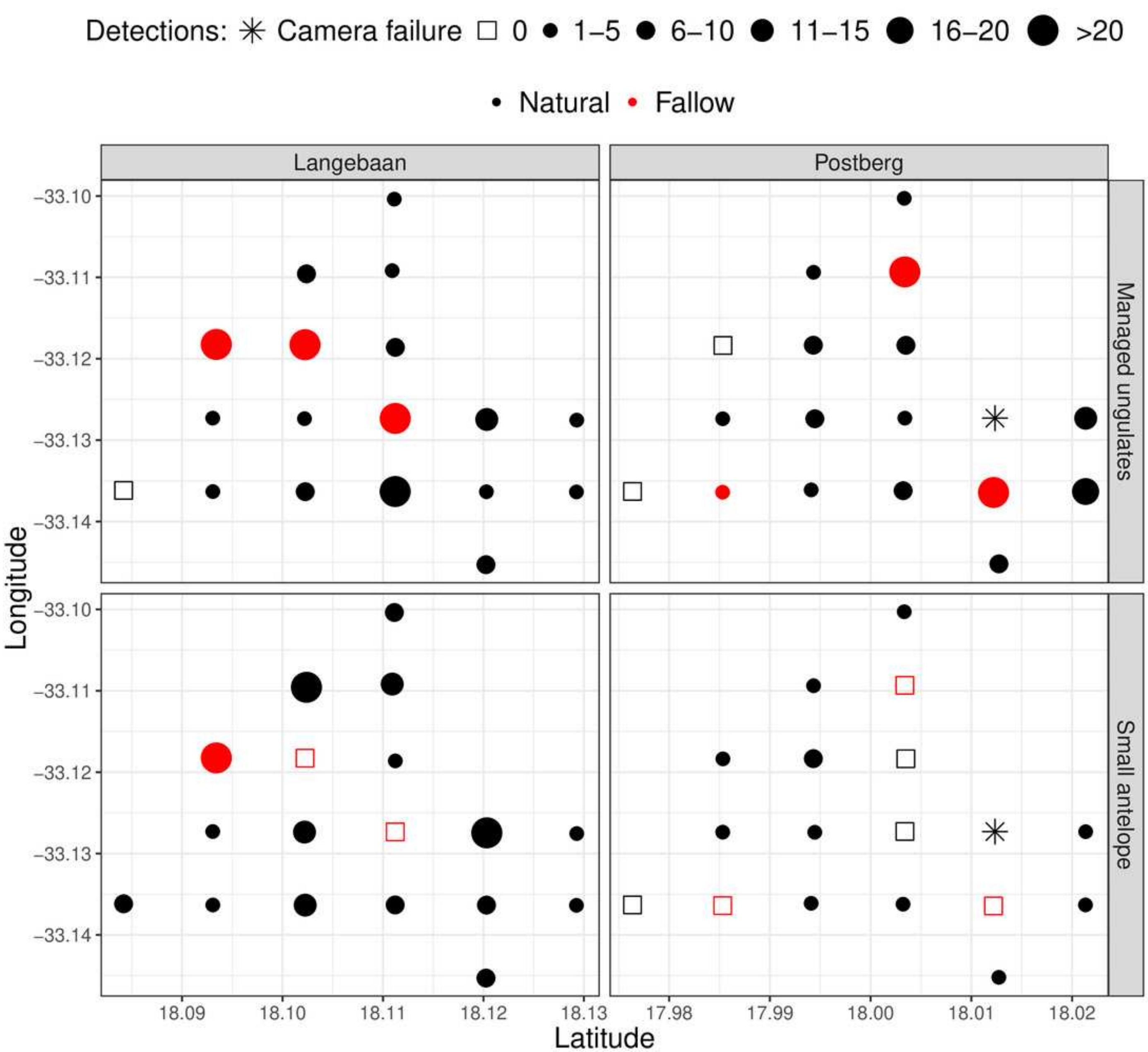


Figure 6

Temporal overlap estimates between small antelope and managed ungulates at the three scenarios.

Time of day starts and ends at midnight on the x-axes and the fitted kernel-density is on y-axes. The grey shaded area indicates overlap and is described by the coefficient of overlap (Δ) and the associated estimator used (number in subscript) along with the 95% confidence intervals in parentheses. The vertical dotted lines represent the earliest and latest sunrise and sunset times across the study period. ρ is derived based on a Watson-Wheeler test of homogeneity for circular data. Dashed lines along the x-axes indicate the sample size of time-of-day observations.

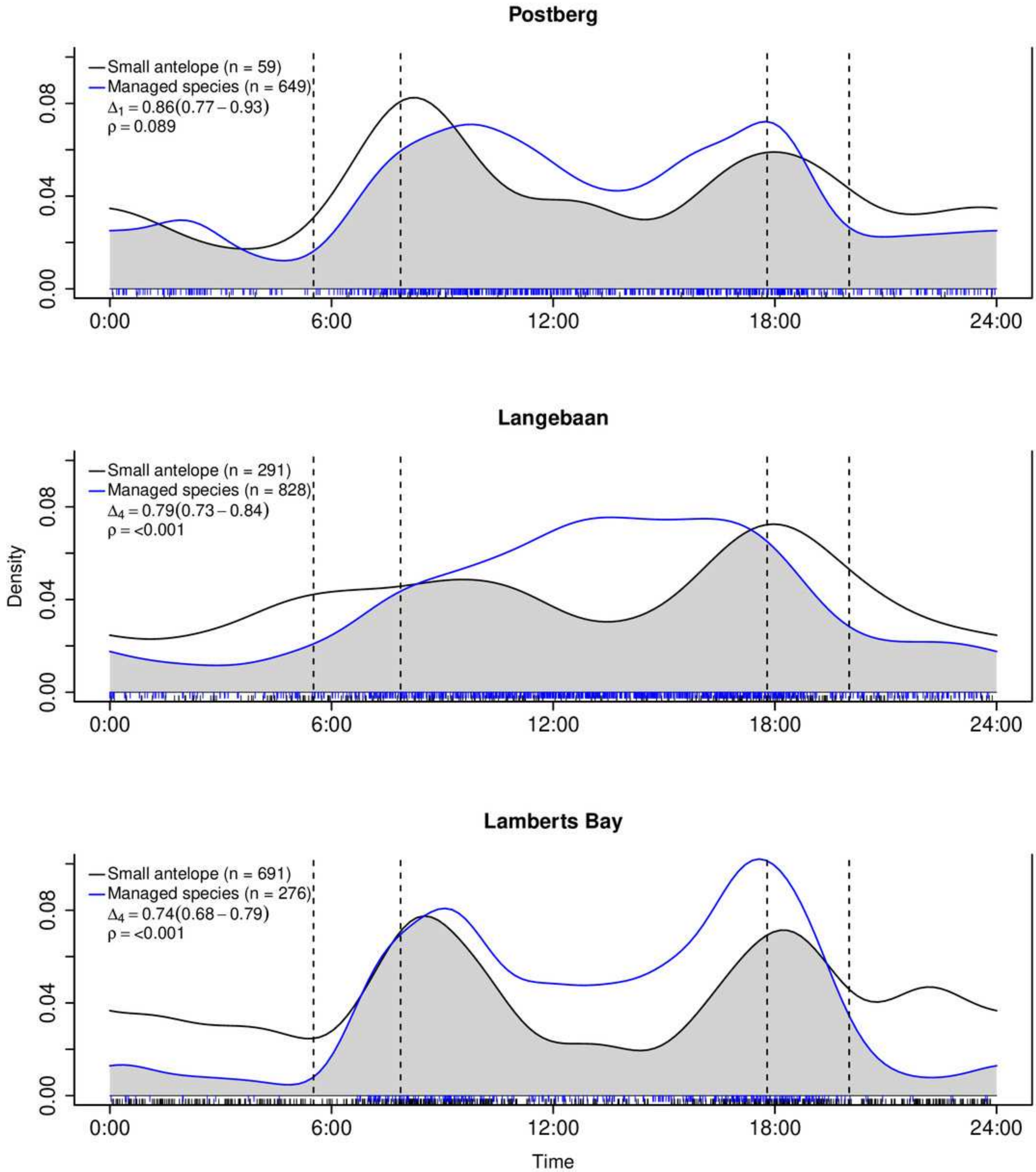

Postberg
Small antelope (n = 59)
Managed species (n = 649)
$\Delta_1 = 0.86(0.77 - 0.93)$
$\rho = 0.089$
Langebaan
Small antelope (n = 291)
Managed species (n = 828)
$\Delta_4 = 0.79(0.73 - 0.84)$
$\rho = <0.001$
Lamberts Bay
Small antelope (n = 691)
Managed species (n = 276)
$\Delta_4 = 0.74(0.68 - 0.79)$
$\rho = <0.001$
Density
Time
0:00
6:00
12:00
18:00
24:00
0.00
0.04
0.08

Table 1(on next page)

Classification of ungulates by weight (ordered alphabetically per class). No managed ungulates were classified within the “Small” class.

Small ungulates (<25 kg)	Medium ungulates (26-200kg)	Large ungulates (>200kg)
Common duiker Steenbok	Bontebok Impala Nyala Red hartebeest Sheep Springbok	Blue wildebeest Cape mountain zebra Cattle Eland Gemsbok Kudu

Table 2(on next page)

Site- and observation-level co-variates.

These data were used to model detection (ρ) and occupancy (ψ) per species as well as the source of the data. Effort was the only observation level co-variate considered.

Co-variate	Variable type	Response variable	Source of data
Management scenario	3-level factor: Postberg, Langebaan, Lamberts Bay	ρ & ψ	Component of study design
Effort	Continuous variable, starting at 0	ρ	Camera traps
Vegetation height	Continuous variable, starting at 0	ψ	Field data collection
Fallow land	2 level factor: 1 – yes, 0 - no	ψ	Field data collection
Elevation	Continuous variable	ψ	Digital Elevation Model (DEM) depicting elevation (m) at 90m resolution (Jarvis *et al.* 2008)
Slope	Continuous variable	ψ	Digital slope model depicting slope (°) at 90m resolution (Jarvis *et al.* 2008)
Trail type	2-level factor: road & game trail	ρ	Field data collection
Large managed ungulate abundance	Continuous variable, starting at 0	ψ	Royle-Nichols Occupancy model output, based on data from camera traps
Medium managed ungulate abundance	Continuous variable, starting at 0	ψ	Royle-Nichols Occupancy model output, based on data from camera traps

Table 3(on next page)

Top models for managed ungulate abundance and small antelope occupancy.

ρ = detection probability and ψ = probability of occurrence. Co-variates used in the model are indicated in brackets while (.) indicates no co-variates were used. Modelled managed ungulate abundance outputs per site were used as co-variates in common duiker and steenbok occupancy models.

	nPars	AIC	delta	AICwt	cumltvWt	Rsq
Large ungulate abundance						
ρ (effort), ψ (scenario)	5	614.62	0	1.0000	1	0.63
ρ (.), ψ (.)	2	661.02	46.4	0.0000	1	0
Medium ungulate abundance						
ρ (effort), ψ (scenario)	5	488.95	0	0.99982	1	0.36
ρ (.), ψ (.)	2	506.23	17.29	0.00018	1	0
Managed ungulate abundance						
ρ (effort), ψ (scenario)	5	898.47	0	0.9959	1	0.27
ρ (.), ψ (.)	2	909.43	10.96	0.0041	1	0
Common duiker occupancy						
ρ (effort), ψ (scenario, veg height)	6	292.48	4.08	0.0280	0.69	0.55
Steenbok occupancy						
ρ (effort), ψ (scenario, medium ungulate abundance)	6	236.82	0.66	0.04284	0.1	0.25

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