



Location, location, location: Habitat-specific differences of camera trap placement on species detections and capture rates

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ABSTRACT

Species diversity is a fundamental concept in ecology and conservation and camera traps are increasingly used to assess terrestrial mammal communities. While it is well established that camera trap placement can introduce detection biases, how these biases are influenced by habitat type remains unclear. To test this we placed camera traps on trails and off trails in two different habitat types (open and closed) and compared species detections, capture rates and inferences made about species composition and diversity of species > 500 g. We further examined the impact of dietary niche and body size. Using data from 1936 camera trap days, we found that camera trap placement influenced species detection and capture rates, with effects varying per habitat type. In closed habitats, species detection, and therefore species richness and composition, was consistent between on-trail and off-trail placements. However, capture rates were generally higher for on-trail cameras, especially for small mammals (0.5 kg - 20 kg) and omnivores. In open habitats, the type of species that were detected differed between the two placements but the number of species detected and the capture rates were similar, resulting in comparable diversity estimates. These findings suggest that macro-habitat (open vs. closed) influences how animals interact with micro-site features such as trails, affecting both detectability and capture rates. We propose that scale-dependent functional responses may play a key role in shaping detection patterns and should receive more attention in camera trap study design and data analyses.

1. Introduction

Species diversity is a key component in ecology and community-level conservation and management due to its role in ecosystem function, stability and resilience (Loreau et al., 2001, Hooper et al., 2005, Tilman et al., 2006, Naeem et al., 2012). Systems with a high species diversity tend to be more complex and hence more productive (Loreau et al., 2001), more likely to recover from disturbances (MacDougall et al., 2013) and provide more ecosystem services which can be positive for human well-being (Methorst et al., 2021). Species diversity is therefore often used as an indicator of ecosystem health whereby a decline in species diversity can signal

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environmental degradation or the presence of stressors (e.g. Irwin et al., 2010, Górczynski et al., 2021). As such, it is important to obtain robust estimates of species diversity. Estimations of species diversity generally rely on two components: which species are present and their relative abundance. Additionally, diversity in functional traits, such as dietary niche and body size, can provide further insights into community composition and structure (McGill et al., 2006). Obtaining data on species presence and abundance can however be challenging as factors such as sampling bias and detectability can influence inferences made (Roswell et al., 2021).

Camera traps are an increasingly common data collection approach to determine species diversity of terrestrial mammals as they can capture species presence and capture rates can give an indication of species relative abundance (e.g. Tobler et al., 2008, Ahumada et al., 2011, Mugerwa et al., 2013, Broekhuis et al., 2018, Ouya et al., 2024). To minimise detection bias, camera traps are ideally placed at randomly selected locations (Jansen et al., 2014). However, studies that aim to increase species detection and accessibility to camera traps for deployment and servicing, tend to place camera traps non-randomly based on landscape features such as roads or wildlife trails (Burton et al., 2015, Kolowski and Forrester, 2017, Rich et al., 2019). Consequently, detection biases may arise potentially impacting the inferences drawn from the collected data. Indeed, trail use can vary per species (Harmsen et al., 2010) and has been related to factors such as dietary niche and body size (Cusack et al., 2015). For example, some studies found that carnivores have a preference for trail use (Cusack et al., 2015, Tanwar et al., 2021), especially in the dry season, as do larger bodied species in the wet season (Cusack et al., 2015). However, while several studies have investigated the influence of linear features, such as wildlife trails and roads, on species detections and capture probabilities (Di Bitetti et al., 2014, Cusack et al., 2015, Geyle et al., 2020, Fonteyn et al., 2021, Tanwar et al., 2021), results from these studies vary. This could be because these studies were conducted in environs with different habitats. However, little is known about how habitat influences species detection and capture rates in relation to camera trap placement (but see Mann et al., 2015).

Habitat can influence animal movement and space-use patterns (Mason and Fortin, 2017) which in turn influences detection by a camera trap (Kays et al., 2021). While at a broad scale habitat use can be influenced by factors such as resources and risk (Creel et al., 2023), habitat can also play a role in finer scale space use (Jiang et al., 2009, Broekhuis et al., 2013). Fine-scale habitat use can be influenced by the availability and characteristics of habitat at broader spatial scales (William et al., 2018). Trails, for example, can facilitate movement through a landscape (Dickson et al., 2005, Abrahms et al., 2016). However, whether and how trails are used may depend on factors such as the ‘resistance’ of a habitat and may therefore be more pertinent in high resistance habitats. What is experienced as resistance could however depend on intrinsic factors such as body size (Dubost, 1979, Bro-Jørgensen, 2008). As such, species detection and capture rates by camera traps placed on and off trails could differ depending on habitat type and hence influence

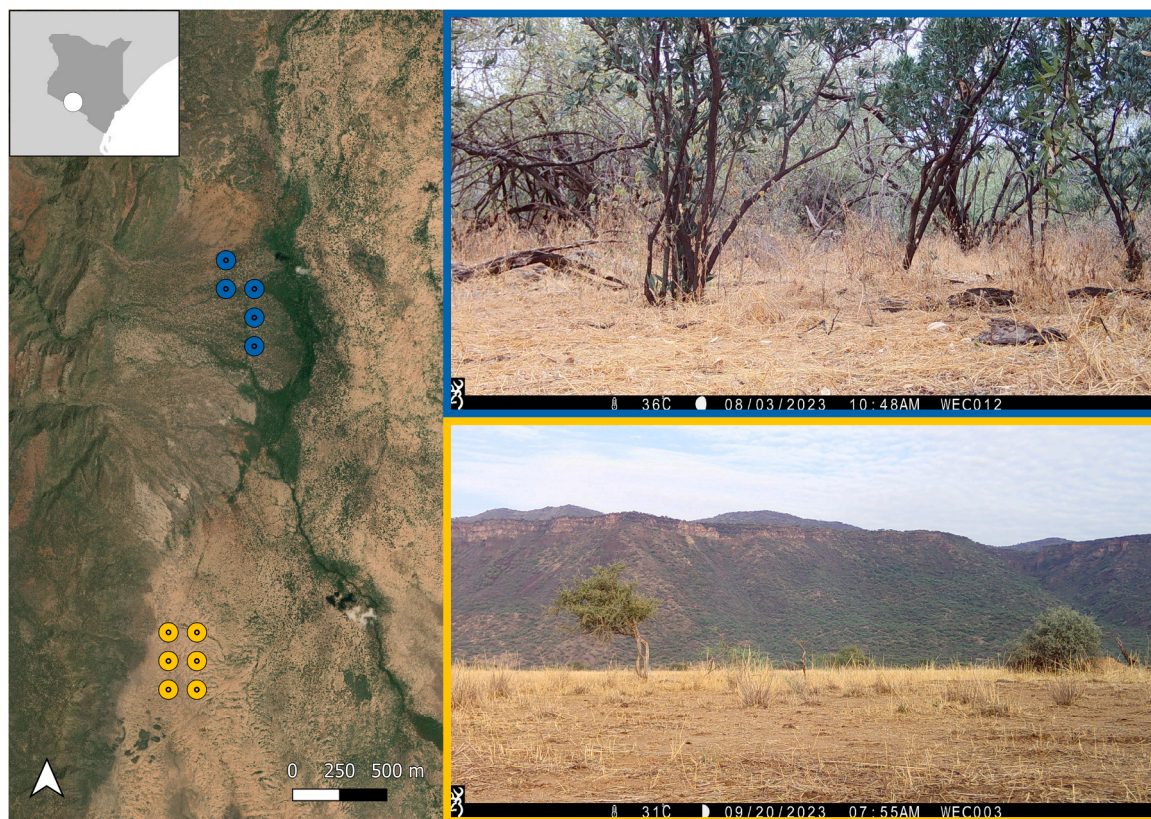


Fig. 1. Map of the study area in Olkiramatian and Shompole conservancies, southern Kenya, showing the locations of the camera trap stations in closed (blue) and open (yellow) habitats. The right panel displays camera trap photographs illustrating differences in habitat structure.

inferences made about species diversity.

In this study, we assess how habitat (open vs. closed) influences species detection and capture rates in relation to camera trap placement (on-trail vs. off-trail). We then investigate how these variations affect inferences about species diversity and whether this could be attributed to dietary niche and body size. We predict that on-trail camera traps would yield higher species detection and capture rates than off-trail traps, with these differences being more pronounced in closed habitats. Additionally, we predict that detection rates would vary by dietary niche and body size, with carnivores and larger-bodied animals being more frequently detected by on-trail camera traps compared to off-trail camera traps.

2. Methods

2.1. Study area

The study was conducted in Shompole and Olkiramatian (1°58 S, 36° 21 E), two communally owned and managed conservation areas in southern Kenya, located on the international border between Kenya and Tanzania (Fig. 1). The area is bordered by the Nguruman Escarpment and the Loita Hills to the west, the alkaline Lake Magadi to the east, and the alkaline Lake Natron to the south (Russell et al., 2018). This region is semi-arid with erratic annual rainfall averaging between 400–600 mm, which varies annually by 33 % (Agnew et al., 2000; Russell et al., 2018). Temperatures range from 18°C at night to 45°C during the day (Russell et al., 2018). The broader landscape can be classified into three primary habitat types: woodland, shrubland and grassland which correspond respectively to map codes 126, 20 and 30 in the Copernicus global landcover layer (version 3.0; Buchhorn et al., 2020). For the purposes of this study, we focused on the two structurally contrasting habitats, woodland and grassland, which we refer to as closed and open habitats, respectively. The closed habitat is characterised by 15–70 %, woody vegetation, with an open canopy cover, that predominantly consists of *Vachellia tortilis*. In contrast, the open habitat is characterised by minimal tree and shrub cover, typically less than 10 %, and is dominated by grass species including *Sporobolus cordufanus*, *Cenchrus* spp. and *Cynodon plectostachyus* (Western, 2018; Buchhorn et al., 2020; Hunter et al., 2020).

2.2. Study design

To place the camera traps, we overlaid a randomly generated 500 × 500 m grid across the study area. For each habitat type (open and closed) we selected six neighbouring grid cells that fell within each habitat type. During camera trap deployment one of the grid cells in the closed habitat was inaccessible so five grid cells were sampled in this habitat type. In each of the 11 grid cells, we placed two camera traps, one off and one on a wildlife trail that showed recent signs of animal activity. As trails have been shown to influence capture rates (e.g. Sollmann et al., 2013), the capture rates obtained from randomly placed camera traps may be a reflection of trail density rather than a proxy for abundance which is needed to calculate diversity indices. For this reason we opted for the on- vs. off-trail setup (e.g. Blake and Mosquera, 2014; Di Bitetti et al., 2014) rather than comparing trail-based camera traps to randomly or systematically placed camera traps as then camera traps may still be placed on trails (e.g. Cusack et al., 2015; Kolowski and Forrester, 2017; Fonteyn et al., 2021). Each camera trap was set up within 50 m of the centroid of the grid cell and the on-trail camera traps were set within 1 m from a trail.

The 22 infrared camera traps (Browning 2021 Recon Force Elite HP4) were placed in protective metal cases which were welded onto sturdy 120 cm angle iron poles. Each pole was hammered into the ground so that the camera lens was 30 cm from the ground allowing for the detection of small to large mammal species (Cusack et al., 2015). The camera traps were deployed for 99 days from the 15th of July to the 21st of October 2023 and no baits or lures were used. The camera traps were set to be active 24 h a day with a delay of 1 s and a trigger frequency of eight pictures. To minimise data loss, the camera traps were serviced once every four days. During each servicing, battery levels were checked and batteries were replaced if the battery level was > 50 %. During each servicing the 64GB SD cards were replaced.

2.3. Data processing

Camera trap images were managed and species were manually annotated and validated in the Agouti software (Casaer et al., 2019). Only identifiable species were retained for the analysis. Additionally, any images of vehicles, people and domestic animals were excluded from the analyses. We categorised species into three dietary niche classes (carnivore, herbivore and omnivore) based on Kissling et al. (2014) whereby carnivores predominantly eat animals, herbivores predominantly eat plant material and omnivores feed on both animals and plants. We also categorised species according to size (0.5 kg < small ≤ 20 kg, 20 kg < medium ≤ 85 kg and 85 kg < large ≤ 4000 kg) using body mass information derived from PanTHERIA database (Jones et al., 2009). All records of species with a body mass of 500 g or less were removed prior to analyses (Cusack et al., 2015). The data were then resampled into unique detections based on a 30 min interval between sequences (Ridout and Linkie, 2009).

2.4. Analyses

Our aim was to assess whether camera trap placement affects detection and capture rates within each habitat type, as species presence and detection distances can vary across habitats (Gorczyński et al., 2023; Snider et al., 2024). Analyses were therefore conducted separately for each habitat, across all species, as well as by dietary niche and size class, using R version 4.3.2 (R Core Team,

2023).

We first determined species composition, based on which species were detected. To determine whether the species composition differed depending on camera trap placement, we calculated the Sørensen index of similarity. The Sørensen index of similarity (SS) provides values between 0, indicating no similarity, and 1, complete similarity. We also determined species richness by quantifying the number of species that were captured per camera trap placement. Next we tested whether species capture rates differed between the two camera trap placements. Species-specific capture rates for each placement were calculated by dividing the number of independent detections by the number of camera trap days and multiplying the output by 100. We then tested for differences between species capture rates using either a paired *t*-test or a Wilcoxon signed-rank test, based on normality which was assessed using a Shapiro-Wilk test.

We further determined differences in species diversity through sampling-unit-based accumulation curves, using the *iNext* package, which accounts for potential biases caused by sampling effort (Chao et al., 2014, Hsieh et al., 2016). Species diversity indices were calculated using Hill numbers, a unified approach that incorporates different orders of diversity (q) to quantify species richness ($q = 0$), the Shannon diversity ($q = 1$), and the Simpson diversity ($q = 2$; Chao et al., 2014). For the species richness ($q = 0$) each species is treated the same regardless of their abundance. The Shannon and Simpson's indices, on the other hand, incorporate species abundance, giving more weight to common species as q increases (Chao et al., 2014). Here we used the capture rates as an index of abundance.

3. Results

In total we had 1936 camera traps days, with 875 camera trap days in closed habitat and 1061 in open habitat. During this time we captured 39 species of wild animals over 500 g of which 32 were captured in the closed habitat and 26 in the open habitat (Appendix A).

3.1. Closed habitat

3.1.1. All species

In the closed habitat, a total of 32 species were detected, of which 30 and 29 were captured by the on-trail and off-trail camera traps, respectively, resulting in similar species richness and composition between the two placements (SS = 0.90, Fig. 2A). Three species were unique to the on-trail camera traps and two to the off-trail camera traps (species specific details can be found in Appendix A). Species capture rates were significantly higher for the on-trail camera traps (median = 2.52) compared to the off-trail camera traps (median = 1.30; Table 1) suggesting that the on-trail camera traps recorded a greater evenness of species, which is also reflected in the higher Shannon and Simpson's indices (Fig. 3A). Species with the highest difference in capture rates (CR) were the Kirk's dik-dik *Madoqua kirkii* (CR = 44.48), crested porcupine *Hystrix cristata* (CR = 18.54), Masai giraffe *Giraffa tippelskirchi* (CR = 14.34) and white-tailed mongoose *Ichneumia albicauda* (CR = 14.24; Appendix A).

3.1.2. Dietary niche

We detected 10 carnivore, 14 herbivore and eight omnivore species. For the omnivores, the same species were captured by both

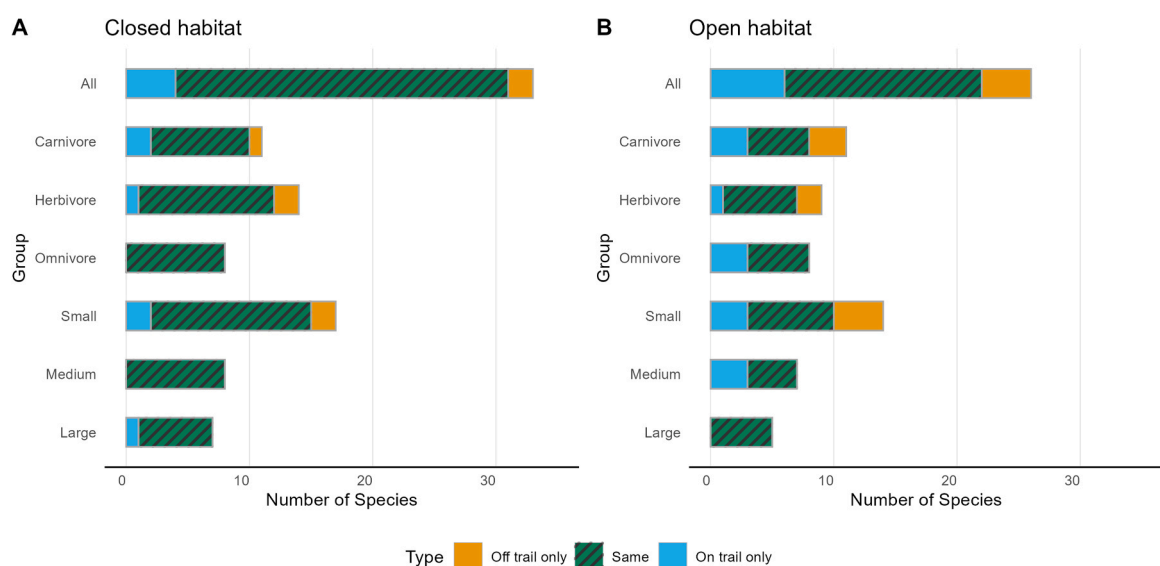


Fig. 2. Similarity in species composition between the on-trail and off-trail camera traps for A) closed and B) open habitat. This was calculated for all species combined and per dietary niche (carnivore, herbivore and omnivore) and size class category (small, medium and large).

Table 1

Results of paired statistical tests comparing species capture rates between on-trail and off-trail camera traps in closed and open habitats. Analyses were conducted for all species combined and by ecological group (diet and body size). Significant results ($p < 0.05$) are shown in bold.

	Closed			Open		
	Test	Test statistic	p-value	Test	Test statistic	p-value
All species	Wilcoxon	V = 447	> 0.001	Wilcoxon	V = 173	0.956
Carnivore	t-test	t = 3.134	0.012	Wilcoxon	V = 31	0.343
Herbivore	Wilcoxon	V = 81	0.079	Wilcoxon	V = 15	0.407
Omnivore	t-test	t = 1.999	0.086	Wilcoxon	V = 16	0.834
Small	Wilcoxon	V = 132	0.009	Wilcoxon	V = 63	0.529
Medium	Wilcoxon	V = 27	0.234	Wilcoxon	V = 11	0.673
Large	Wilcoxon	V = 25	0.076	t-test	t = -0.355	0.741

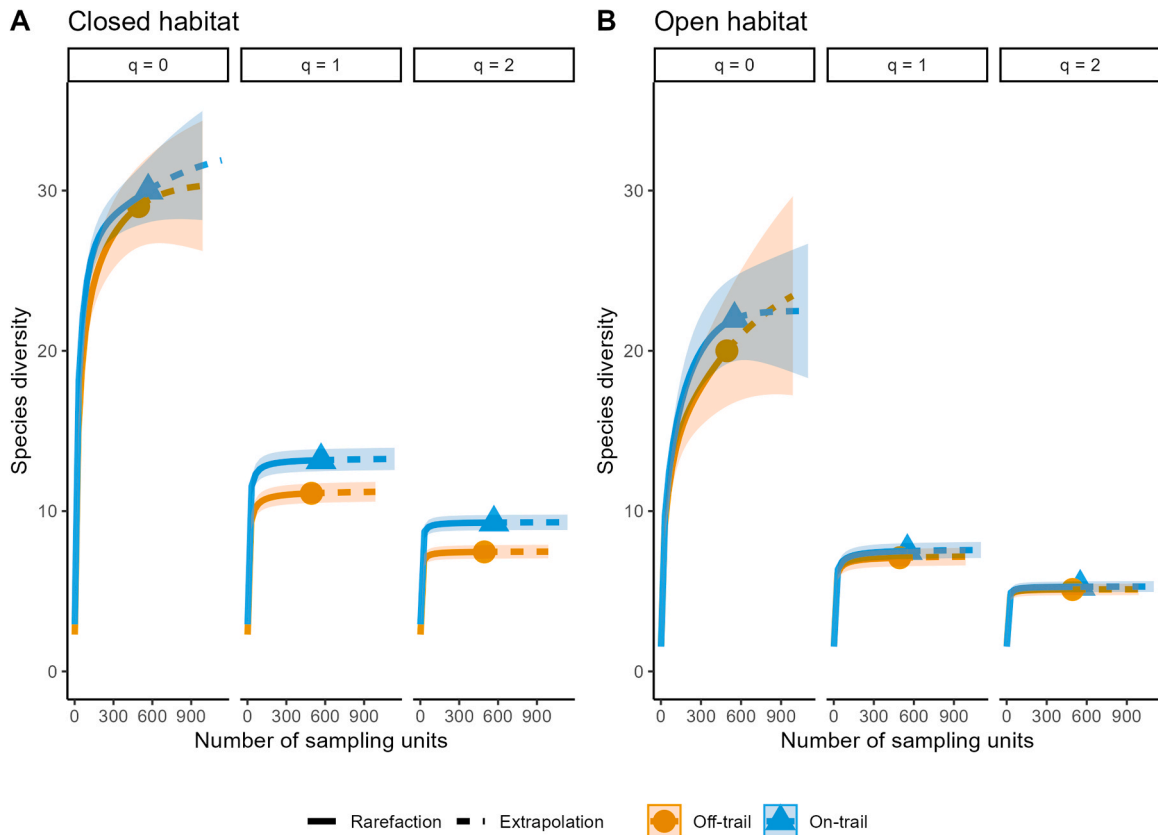


Fig. 3. Species accumulation curves for species richness ($q = 0$), the Shannon diversity ($q = 1$) and the Simpson diversity ($q = 2$) for A) closed and B) open habitat.

placements ($SS_{\text{omnivores}} = 1.00$; Fig. 2A). For carnivores and herbivores the similarity between the two placements was high ($SS_{\text{carnivore}} = 0.84$, $SS_{\text{herbivore}} = 0.96$) with only a few species unique to either placement (Appendix A). Capture rates for carnivores were significantly higher for the on-trail camera traps (median = 1.37) compared to the off-trail camera traps (median = 0.38) but no significant differences were detected for herbivores nor omnivores (Table 1). However, for omnivores both the Shannon and Simpson indices were higher for the on-trail camera traps compared to off-trail camera traps (Fig. 4A). This was largely due to the higher capture rates of the African civet *Civettictis civetta*, the common genet *Genetta genetta* and the white-tailed mongoose. The same was the case for Simpson's index for the herbivores, which was due to the large differences in capture rates of crested porcupine, Masai giraffe and Kirk's dik-dik which had higher capture rates at the on-trail camera traps compared to off-trail camera traps. For the carnivores, the asymptote was not reached indicating that more sampling units were needed.

3.1.3. Body size

Of the 32 species, 17 were small, eight medium and seven large. The species composition for the on-trail and off-trail camera traps was similar for the large ($SS_{\text{large}} = 0.92$) and medium sized animals ($SS_{\text{medium}} = 1.00$; Fig. 2A) and no significant differences in capture

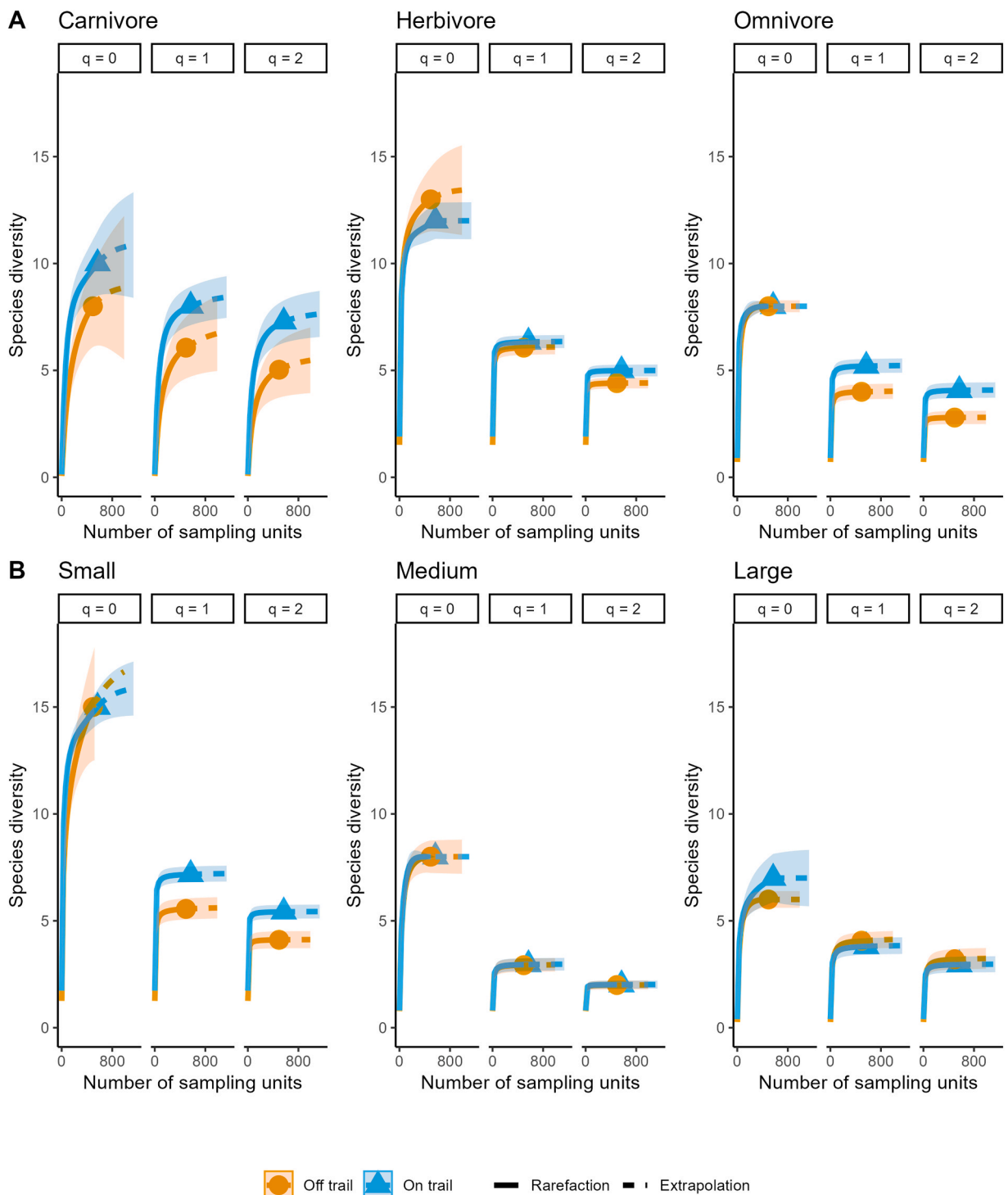


Fig. 4. Closed habitat species accumulation curves for species richness ($q = 0$), the Shannon diversity ($q = 1$) and the Simpson diversity ($q = 2$) per A) dietary niche (carnivore, herbivore, omnivore) and B) size (small, medium, large).

rates or diversity indices were found between placements (Table 1; Fig. 4B). For the small species, the similarity between the two placements was lower ($SS_{\text{small}} = 0.87$) with two unique species at each placement (Appendix A). Capture rates were significantly higher at the on-trail camera traps compared to the off-trail camera which was also reflected in the Shannon and Simpson's indices (Table 1; Fig. 4B). This was again due to the higher capture rate of Kirk's dik-dik, crested porcupine and white-tailed mongoose.

3.2. Open habitat

3.2.1. All species

In open habitat, 26 species were detected, 22 by the on-trail and 20 by the off-trail camera traps. Whilst the number of species, and

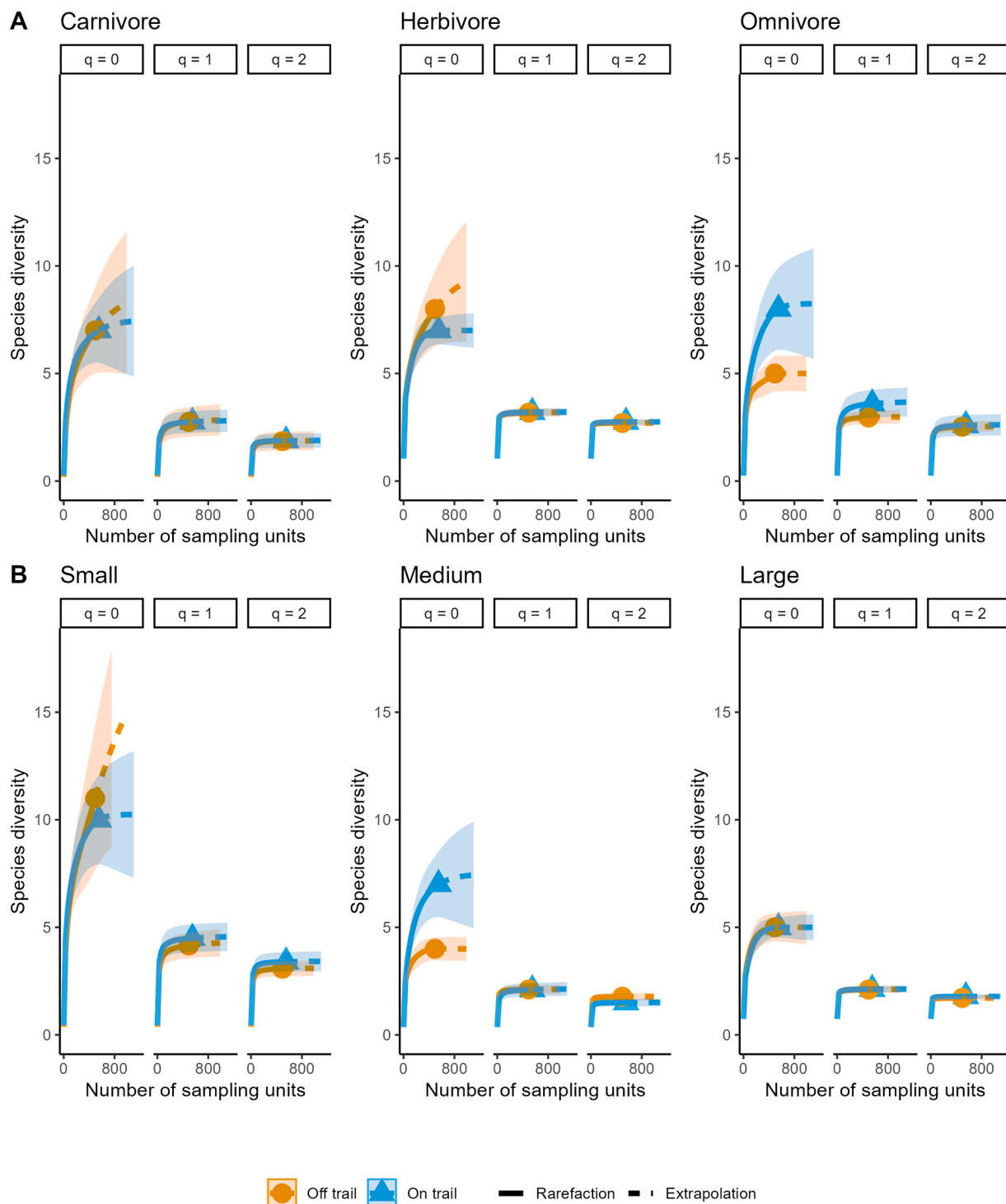


Fig. 5. Open habitat species accumulation curves for species richness ($q = 0$), the Shannon diversity ($q = 1$) and the Simpson diversity ($q = 2$) per A) dietary niche (carnivore, herbivore, omnivore) and B) size (small, medium, large).S.

hence the species richness was similar, the species identity between the two placements differed; six species were unique to the on-trail and four to the off-trails camera traps with 16 species in common ($SS = 0.76$; Fig. 2B). The species capture rates between the two camera trap placements did not differ significantly nor did the species richness and evenness (Table 1; Fig. 3B). However, for the off-trail camera traps, more sampling units were needed to reach an asymptote.

3.2.2. Dietary niche

We detected nine carnivore, nine herbivore and eight omnivore species. Of these, carnivores had the lowest similarity in species composition ($SS_{\text{carnivore}} = 0.63$), with only five species in common and three species unique to each placement (Fig. 2B, Appendix A). Omnivores had a slightly higher similarity in species composition ($SS_{\text{omnivore}} = 0.77$), with five species captured at both placements and three species uniquely captured by the on-trail camera traps resulting in some difference in the species richness between the two placements (Fig. 5A). The similarity in herbivore composition between the two placements was relatively high ($SS_{\text{herbivore}} = 0.80$), six species were captured at both placements, one species unique to the on-trail camera traps and two species unique to the off-trail camera traps. Despite these differences, capture rates and diversity indices did not differ significantly between the two placements (Table 1; Fig. 5A).

3.2.3. Body size

Of the 26 mammal species, 14 were small, seven medium and five large. All large-bodied species were captured at both camera trap placements ($SS_{\text{large}} = 1.00$). The similarity for the medium-bodied species was lower ($SS_{\text{medium}} = 0.70$) with three more species captured by the on-trail camera traps. The small-bodied species had the largest difference in composition with three species unique to the on-trail and four to the off-trail camera traps (Appendix A). However, because the overall number of small-bodied species were captured at both placements, there were no differences observed in species richness and the diversity indices. For the medium-bodied species, there were more species captured at the on-trail camera traps influencing the species richness. The capture rates for all size categories did not differ significantly as a result of camera trap placement. For the medium-bodied species the Shannon's index was slightly lower for the on-trail camera traps compared to the off-trail camera traps (Fig. 5B). This was largely because the capture rates of Grant's gazelle *Nanger granti* and striped hyaena *Hyaena hyaena* which were higher for the off-trail camera traps compared to the on-trail camera traps (Appendix A).

4. Discussion

Our results indicate that camera trap placement influences species detection and capture rates, with effects varying according to habitat type. More specifically, in closed habitat the species detected are comparable between placements but capture rates showed significant differences. In open habitat the opposite was the case, species detection differed between placements, but capture rates showed no significant differences. This subsequently influenced inferences about species diversity.

In closed habitat, inferences made about species composition and richness were not influenced by placement due to similarities in the number and type of species that were detected, particularly for omnivores and medium-sized mammals. This is similar to previous findings of camera trap studies in forested environs (Fonteyn et al., 2021). In contrast, results differed for the open habitat. While the number of species detected, and thus inferences about species richness, remained consistent across placements, the type of species varied influencing inferences made about species composition. Species-specific differences in trail or road use have been found in other studies (Trolle and Kéry, 2005, Srbek-Araujo and Chiarello, 2013, Mann et al., 2015). For example, tapirs *Tapirus terrestris* avoid roads, possibly to minimise encounters with their predators who prefer using roads (Trolle and Kéry, 2005). Indeed, how animals respond spatially to risks, such as predation and competition, can be more pronounced in open habitats (Broekhuis et al., 2013). However, we did not find a clear pattern of opposing trail use by carnivores and herbivores in open habitat. Interestingly, cheetahs *Acinonyx jubatus* were solely captured on trails as were impalas *Aepyceros melampus*, their main prey (Broekhuis et al., 2018). A similar pattern was found in the (semi-)arid Karoo region in South Africa where roads were frequently used by carnivores but were not avoided by herbivores (Mann et al., 2015). It is therefore possible that the observed differences in species composition between placements in open habitat is due to insufficient data.

In open habitat, the accumulation curves for the overall species richness did not reach a saturation point indicating that detections were low. Indeed, species that were captured only once were captured either on or off trail. As such, more trapping days might be necessary in open habitat types to strengthen inferences on placement impact (Colyn et al., 2018). That more camera trap days are needed in open habitat compared to closed habitat could be due to factors such as increased animal space use in open habitats (Ofstad et al., 2016). More camera trap days could be achieved by either increasing the length of the survey or increasing the number of camera traps (Hofmeester et al., 2021). Despite more data being needed, our results, especially regarding omnivores and medium-sized mammals, do indicate that there are some species that may only use trails in the open habitat. Possible species-specific differences could be investigated further but this could be challenging, particularly in complex habitats where species diversity tends to be high (Gorczynski et al., 2023).

We used capture rates as a proxy for relative index of abundance to calculate the Shannon and Simpson diversity indices. While in the open habitat capture rates did not differ between placements, in closed habitat species capture rates were higher for the on-trail cameras compared to the off-trail camera traps. This aligns with findings from forested environments (Harmsen et al., 2010, Tanwar et al., 2021). If based solely on placements, different inferences could be drawn regarding species abundance and diversity indices. However, as the on-trail and off-trail camera traps at each station were set within 50 m of one another, we can assume that mammal abundances were comparable between the two placements and therefore the capture rates are a reflection of fine-scale habitat use

rather than broader scale abundances. Indeed, caution should be taken when using capture rates as a relative abundance index (Sollmann et al., 2013; Burton et al., 2015) as capture rates can be influenced by a suite of factors that affect detectability (Srbek-Araujo and Chiarello, 2013; Kolowski et al., 2021), including habitat and placement as illustrated in our study.

Accounting for habitat-related biases may not be necessary in studies that are carried out in habitat patches that are spatially and temporally homogenous (e.g. Colyn et al., 2018). However, in studies where the habitat is heterogenous (e.g. Tanwar et al., 2021), explicitly accounting for habitat-specific placement could potentially yield more robust results. Indeed, our results corroborate other studies that micro-site, or 4th order space use, should be taken into consideration when using camera traps (Hofmeester et al., 2019; Kays et al., 2021; Kolowski et al., 2021). Biases associated with camera trap placement can be accounted for either in the study design or data analyses (Hofmeester et al., 2019). For example, hierarchical approaches where features that influence detection probability, such as on- vs. off-trail, are explicitly included as a detection covariate can be used to obtain more robust estimates of species richness (Tobler et al., 2015). However, our findings suggest that micro-site use could be more nuanced as it can be conditional on broader scale factors, such as macrohabitat (Myrsterud and Ims, 1998; Holbrook et al., 2019). Therefore, a species functional response in habitat selection (Holbrook et al., 2019) should be considered as only accounting for microhabitat, such as trails, may not be sufficient to account for biases. Similarly, while here we focused on trails as a landscape feature, or micro-site, that may be preferred or avoided we believe that the same could apply to other features, including those that are used to place camera traps. For example, it is common practice to place camera traps on trees (e.g. Cusack et al., 2015; Palmer et al., 2018; Swanson et al., 2015; Tanwar et al., 2021). However, a tree in an open grassland or savanna that provides shade could, due to its relative abundance, have a different function to a tree in a woodland or forest (Myrsterud and Ims, 1998). This interaction between micro- and macrohabitats should also be accounted for in studies comparing multiple sites and/or across seasons (Ahumada et al., 2011; Rich et al., 2017). We only conducted this study in one dry season, but it has been shown that season can influence species detection and capture rates (Cusack et al., 2015; Kolowski et al., 2021). Since habitat structure can vary seasonally, it is possible that this may influence micro-site use.

Generally, it was difficult to compare our findings to other studies, especially as results can be conflicting (Di Bitetti et al., 2014; Cusack et al., 2015; Geyle et al., 2020; Fonteyn et al., 2021; Tanwar et al., 2021). While there have been studies on camera trap placement in other African savannah and grassland landscapes (Cordier et al., 2022), the details on the finer scale habitat of where camera traps are placed is often lacking (e.g. Cusack et al., 2015) making comparisons difficult. In addition to standardising reporting of information on camera trap makes, their settings and the overall study design (Meek et al., 2014), perhaps information on habitat structure at camera trap locations should also be provided. This could be challenging because landscapes can be very heterogenous, but based on our findings, this heterogeneity should be considered when designing and interpreting results from camera trap studies.

Another factor contributing to the variability in results across studies involving on-trail camera traps could be the study design. Studies that have examined species detections by on-trail camera traps have generally compared these to detections from systematically placed camera traps (e.g. Cusack et al., 2015; Fonteyn et al., 2021; Tanwar et al., 2021). These systematically placed, or random, camera traps are typically positioned at predetermined locations to sample habitats in proportion to their availability. However, this systematic deployment might still result in some camera traps being placed along roads or wildlife trails (Fonteyn et al., 2021). For example, Cusack et al. (2015) reported that 16.7 % of the random cameras were positioned on trails. Consequently, the observed effect of species detections on trail placement relative to random placement could be confounded by trail density. Specifically, in studies with high trail densities, the impact of trails on species detections and capture rates, particularly for carnivores that tend to favour trails (Harmsen et al., 2010; Srbek-Araujo and Chiarello, 2013; Cusack et al., 2015), may be challenging to disentangle. Given our interest in determining whether camera trap placement influences species detection and capture rates, we opted for a direct comparison between camera traps placed on and off trails. Furthermore, since we wanted to determine if this varied depending on habitat type, we aimed to ensure a direct comparison of trail use, considering that wildlife trail densities may be higher in more open habitats (Newmark and Rickart, 2012).

Camera traps are a useful tool for non-invasive monitoring of terrestrial mammals especially for detecting rare and elusive species. However, when using such data to estimate species diversity, care should be taken to minimise biases in species detection and capture rates. Here we add to the growing body of research that camera trap placement can influence species detection and capture rates and hence inferences made (e.g. Cusack et al., 2015; Mann et al., 2015; Hofmeester et al., 2019; Kolowski et al., 2021). More specifically, the interaction between micro and macro-habitat use may require more attention in camera trap study design and data analyses.

Authors' contributions statement

All authors contributed to the conceptualization and methodology. FB and YL validated the data, while FB conducted the formal analysis. PS and PM carried out the investigation. FB, SN, YL, and GW provided resources, and YL and MT curated the data. FB wrote the original draft, with SN, YL, and GW reviewing and editing. FB and GW managed the project and secured funding. All authors contributed critically to this study and approved the final version for publication.

CRediT authorship contribution statement

Femke Broekhuis: Writing – original draft, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Guy Western:** Writing – review & editing, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Moses Tenke:** Writing – review & editing, Methodology, Data curation, Conceptualization. **Peter Meiponyi:** Methodology, Investigation, Conceptualization. **Peter Sankale:** Writing – review & editing, Methodology, Conceptualization. **Yorick Liefing:** Writing – review & editing, Visualization, Validation, Resources,

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Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the author(s) used ChatGPT (GPT-5) to assist with spelling and grammar improvements. All content generated with the aid of this tool was subsequently reviewed and edited by the author(s), who take full responsibility for the final version of the publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2025.e03819](https://doi.org/10.1016/j.gecco.2025.e03819).

Data Availability

Data will be made available on request.

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