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The road less travelled: assessing variation in mammal detection probabilities with camera traps in a semi-arid biodiversity hotspot

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Abstract Camera traps are an increasingly popular tool for monitoring medium to large mammals, but the influence of camera trap placement on the detection probabilities of different species has seldom been investigated. In this study we explore the influence of roads on the detection probability of medium to large mammals in three vegetation types in the Little Karoo, an arid biodiversity hotspot. We placed cameras in nine 100 m-long transects, running perpendicular from roads within a conservation area. The camera traps were spaced at ∼25 m intervals, and were active for an average of 88 days each. Detection probabilities relative to distance from roads showed extensive variation between species and habitat types. There was no clear relationship between distance from the road and the detection probability of most species and guilds, although carnivore detection probability declined significantly as distance from roads increased in all vegetation types. Our results suggest that there is considerable inter-specific variation in detection probability that is significantly influenced by camera trap location relative to roads. Therefore studies that seek to maximise the detection rates of particular species or guilds (e.g. carnivores) by placing cameras on prominent roads and trails are unlikely to provide reliable estimates of the relative abundance of the broader range of sympatric species; a trend observed elsewhere but hitherto untested in arid environments. We recommend that future studies employ a mixed design of cameras located on- and off-roads to provide better estimates of biodiversity in general and predators specifically.

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Introduction

Biodiversity monitoring is largely dependent on our ability to assess both the diversity and
abundance of fauna within a particular area. Over the past two decades, camera traps have
become an increasingly popular means of surveying biodiversity (Rowcliffe and Carbone
2008; O'Connell et al. 2011). Camera traps are non-invasive and cost-effective compared
to other survey methods such as spoor counts or line transects (Balme et al. 2009;
O'Connell et al. 2011; Foster and Harmsen 2012). Furthermore, utility of camera traps is
seldom restricted by topography, substrate or climatic conditions, which can limit the
effectiveness of other survey methods (Funston et al. 2010).

 Camera traps have been used for a number of purposes including development of
biodiversity inventories (de Souza Martins et al. 2007; Tobler et al. 2008; Ahumada et al.
2011), identifying new species (Rovero et al. 2008), studying animal activity patterns
(Azlan and Sharma 2006; Martins and Harris 2013) and performing conservation assess-
ments (Linkie et al. 2006). Arguably the most common application of camera traps is the
use of photographic records within a capture–recapture framework to estimate the abun-
dance and/or density of individually-identifiable species such as tigers (*Panthera tigris*)
(Karanth 1995; Karanth and Nichols 1998), jaguars (*Panthera onca*) (Wallace et al. 2003)
and leopards (*Panthera pardus*) (Balme et al. 2009). Camera trap surveys that target
individually-identifiable species invariably record the presence of other sympatric species,
many of which lack the distinguishing features necessary to identify individuals. These
records may be used to opportunistically estimate relative abundances (O'Brien et al. 2003;
Braczkowski et al. 2012a) and the influence of habitat on overall species abundance (Stein
et al. 2008). Relative abundance indices (RAI) are typically used to measure the com-
parative availability or abundance of prey species, and subsequently to draw inferences
about prey preferences of the focal carnivore species within a study area (Johnson et al.
2006; Braczkowski et al. 2012a).

 However, camera trap-derived RAIs are considered to be flawed due to the implicit and
seldom-tested assumption that all species are equally detectable across time and space
(Williams et al. 2002; Sollmann et al. 2013). While large carnivores are thought to gen-
erally prefer moving along roads and trails (O'Connell et al. 2011), few data have been
collected on the movement preferences of their prey (Weckel et al. 2006). Even sympatric
carnivores with similar life histories [e.g. jaguars and pumas (*Puma concolor*)] may differ
in their use of trails depending on habitat type (Harmsen et al. 2010). However, in at least
one case, prey RAI obtained during capture-recapture sampling of an individually-iden-
tifiable predator (tigers) has been shown to support the results obtained from an inde-
pendent line transect surveys of the same prey species (O'Brien et al. 2003; Kinnaird and
O'Brien 2012).

 Sollmann et al. (2013) used simulations to demonstrate that differences in detection
probabilities, home range sizes, camera trap arrangement and population declines over
time can all influence RAIs derived from camera trap surveys, even under ideal conditions.
Data reveal that RAIs of species such as leopard cats (*Prionailurus bengalensis*), common
palm civets (*Paradoxurus hermaphroditus*) and Sunda clouded leopards (*Neofelis diardi*)

provided misleading abundance estimates when compared to more robust, spatially-explicit capture–recapture density estimates (Sollmann et al. 2013). Bischof et al. (2013) found significant differences in the detectability of sympatric snow leopards (*Panthera uncia*), red foxes (*Vulpes vulpes*) and stone martens (*Martes foina*) linked to site-specific attributes, concluding that this variation rendered multi-species camera trap surveys vulnerable to misinterpretation unless the hierarchical nature of camera trap data is taken into account.

The few studies that have empirically tested the assumption of equal detectability across species have typically been done on captive, enclosed populations (Rowcliffe et al. 2008) in tropical forests in South America (Weckel et al. 2006; Harmsen et al. 2010), Asia (Sollmann et al. 2013, Bischof et al. 2013) or in the savannah regions of Africa (Kinnaird and O'Brien 2012). While these studies have concluded that detection probabilities vary between species, no similar study has documented variation in detection probabilities in African mammals in arid and semi-arid environments where animal densities are likely to be low.

In this study, we assess variation in road usage and the detection probabilities of African mammals in three different habitat types in the Little Karoo; an approximately 27,000 km^2 semi-arid area in South Africa that contains elements of three global biodiversity hotspots; Cape Floristic Region, succulent karoo and Maputoland-Pondoland-Albany thicket (Myers et al. 2000; Mittermeier et al. 2005). Our study aims to test the null hypothesis that photographic capture frequencies observed on roads are representative of capture frequencies observed across the broader area. The results will inform future survey designs for biodiversity monitoring. We predict that predator species will generally prefer roads, which will be avoided by prey species, and that all species will use roads more in habitat types where dense vegetation impedes movement away from roads.

Methods

Our study site was Groenefontein Nature Reserve (5,200 ha, co-ordinates S:33.64625, E:21.65100) and an adjoining, privately-owned property (1,100 ha). Both properties form part of the Rooiberg Conservancy, a 69,200 ha contiguous area with minimal human disturbance. Neither property was open to the public (apart from a single public road that was not sampled in our study), and at the time of our study only had a single permanent resident. We sampled biodiversity with camera traps in three vegetation types: fynbos, subtropical thicket, and riverine vegetation (Vlok and Schutte-Vlok 2010—see Fig. 1). These vegetation types differ markedly in structure and composition. Within the sample areas, fynbos vegetation was heather-like, approximately one to 1.5 m high, and occurred at a uniform density, with few discernible patches or game trails. Fynbos forms part of the Cape Floral Region biodiversity hotspot, and within our study area, is typically found at altitudes exceeding 600 m where annual precipitation is greater than in the low-lying areas. Riverine vegetation occurs in low-lying drainage lines, where trees such as *Acacia karroo* grow in relatively deep, sandy soils. Riverine vegetation typically comprises patches of trees and bushes, separated by open areas. Subtropical thicket vegetation (part of the Pondoland-Maputaland-Albany Thicket biodiversity hotspot) occurs on slopes at intermediate altitudes, forming dense clumps of bush separated by open areas. These vegetation types form a complex mosaic in the study area (Fig. 1), with the type of vegetation in a
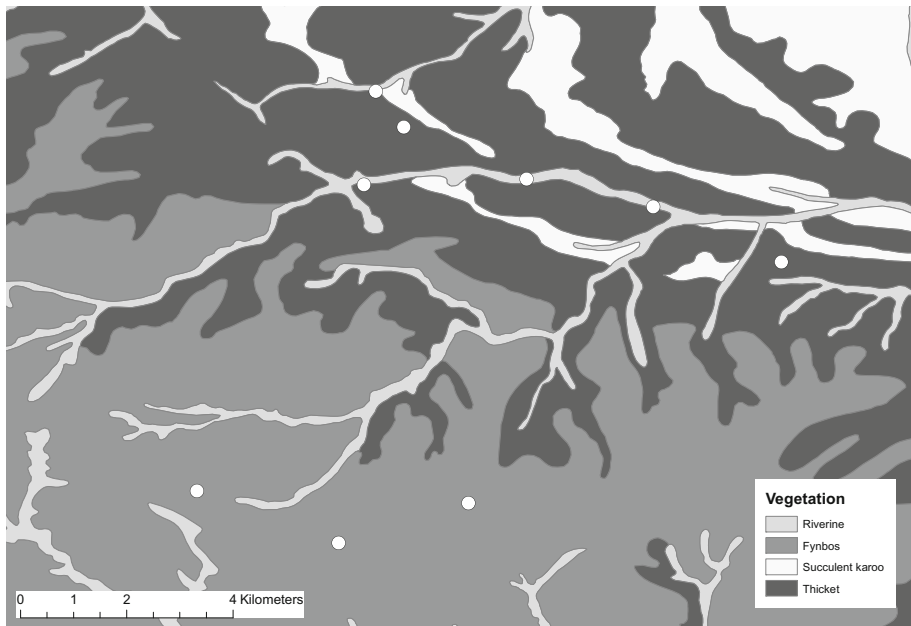
Fig. 1 Map of the study area showing the location of the Little Karoo in South Africa (*inset*) and the location of the transects within the study area (*white circles*), relative to the different vegetation types

given area strongly influenced by altitude and rainfall, soil type, and temperature regimes (Vlok and Schutte-Vlok 2010).

We sampled each of the three vegetation types with three 100 m transects a minimum of 1 km apart. We attempted to account for variation in detection probability through our study design, rather than post hoc development of detection probabilities (Banks-Leite et al. 2014). All transect locations were carefully selected to reduce the influence of topographic factors, such as steep slopes. The heterogenous nature of the study site effectively restricted the maximum length of transects to 100 m. Camera traps were placed at 25 m intervals with the first camera on the road and the remaining four in a perpendicular straight line leading away from the edge of the road. All roads sampled in our study were seldom used, unpaved, and consisted of two parallel ∼50 cm-wide tracks separated by low scrub. The small interval between cameras (25 m) was selected to maximise the probability of detecting an animal walking through transects within a given habitat type. Distances between cameras were measured using a tape-measure, and cameras were set within 5 m of the desired point if dense vegetation prohibited optimal camera placement. This was typically only necessary in the riverine and thicket vegetation types, both of which comprise thick stands of bush in a matrix of short, shrubby vegetation (Vlok and Schutte-Vlok 2010). We did not actively seek to locate cameras along game paths or trails, although cameras were set in relatively open areas to prevent brush from obscuring or repeatedly triggering the camera. Sampling was done with Cuddeback Capture™ cameras (Non-Typical, Inc. Green Bay, Wisconsin), set ∼40 cm above ground level. All transects were run simultaneously for a period of approximately 90 days during the period from late August to early December 2012 to control for seasonal variation in animal presence.

We entered the data into a database using the program Camerabase v1.4 (Tobler et al. 2008). All animals were identified to species level and the date, time, vegetation type and distance from the road recorded. Birds were not included in the analysis, as these are unlikely to be reliably detected by camera traps set to record medium to large mammals (O'Brien and Kinnaird 2008). Photographs of the same species recorded less than 1 hour apart at the same camera were treated as non-independent and excluded from the analysis (Tobler et al. 2008). Unless otherwise stated, data from transects within each vegetation type were pooled for statistical analysis. However, data from different vegetation types were analysed separately due to the distinct structural variation between the three vegetation types sampled, which may have influenced detection probability. Animals were analysed both at the species level and when grouped into one of four feeding guilds (carnivores, herbivores, omnivores and insectivores).

We conducted all statistical tests in R (R Development Core Team, 2013) using the package lme4. We analysed the data in a generalised mixed model framework, where the number of photographs of each species within a vegetation type were treated as a Poisson random variable depending on distance from the road. Our null hypothesis was that the regression coefficient for this variable was zero, which would indicate equal catchability of the species across a transect, regardless of distance from the road. Conversely, a significant coefficient would indicate that the probability of detecting a species was influenced by distance from the road. We pooled data across all transects to avoid underestimating between-transect variance, and used the number of trap nights that each camera was active as an offset to account for uneven sampling due to camera or battery failure.

Results

In total, all cameras recorded 802 independent photographs of mammal species over 3,419 trap nights. Camera failure was low in fynbos vegetation (two cameras failed, 26 trap nights lost), but higher in riverine (three cameras failed, 133 trap nights lost), and thicket vegetation (five cameras failed, 172 trap nights lost). All other cameras remained operational for the duration of the study. A total of 96 vehicle photographs and 10 human photographs were recorded at the nine roadside cameras, suggesting relatively low levels of human activity. Sampling effort was relatively even across the fynbos (1,174 trap nights, 274 photographs), riverine (1,097 trap nights, 457 photographs) and subtropical thicket (1,148 trap nights, 308 photographs) vegetation types. The final data set included a total of 23 mammal species; nine in fynbos, 18 in riverine, and 13 in subtropical thicket.

Model outputs for all species are summarised in Fig. 2 and detailed results of the generalized linear models are provided in Appendix Tables 1, 2, and 3. We found that distance from the road produced significant declines in detection probability for leopards in fynbos vegetation ($Z = -3.14$, df $= 13$, $p = 0.002$), caracals (*Caracal caracal*) in thicket ($Z = -2.37$, df $= 13$, $p = 0.018$) and riverine ($Z = -9.21$, df $= 13$, $p < 0.001$) vegetation and African wild cats (*Felis sylvestris*) in fynbos ($Z = -3.14$, df $= 13$, $p = 0.002$). Considered as a guild, carnivore detection probability was significantly influenced by the distance from the road in all three habitat types, with detection probabilities declining sharply as distance from the road increased (fynbos: $Z = -4.61$, df $= 13$, $p < 0.001$; riverine: $Z = -9.75$, df $= 13$, $p < 0.001$; thicket: $Z = -2.37$, df $= 13$, $p = 0.018$). In all
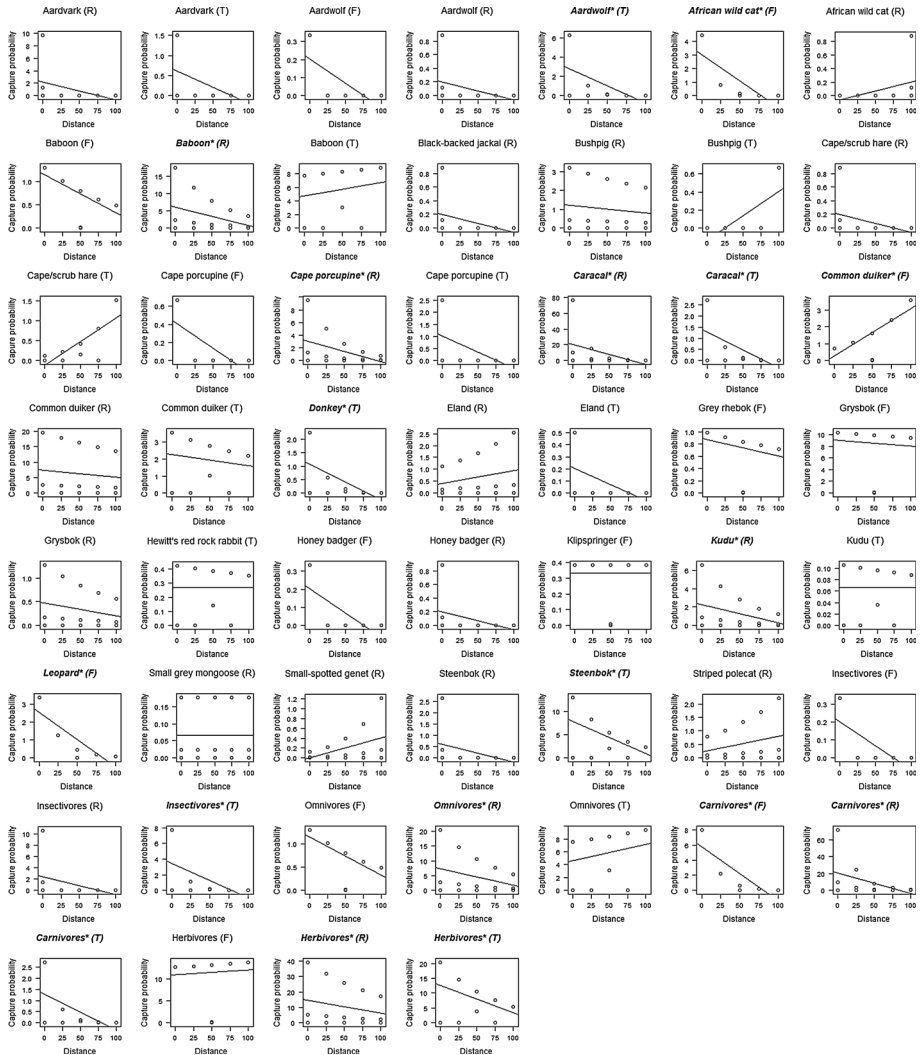
Fig. 2 Capture probabilities of mammals recorded in fynbos, riverine and subtropical thicket habitat. The y-axis is analogous to capture probability, as it shows the expected rates of photographs of each species recorded at each camera on any given trap night. This is plotted against distance from the road (x-axis) to show trends in detection probability as distance from the road increases. Species for which a significant trend was observed are labelled in *bold italics* and denoted with an *asterisk* (*). The vegetation type is shown in *brackets* after the species name, with 'F' representing fynbos, 'R' representing riverine, and 'T' representing thicket vegetation respectively

habitat types, the largest recorded carnivore species (leopards in fynbos and caracals in riverine and thicket vegetation) showed a significant preference for roads.

Detection probabilities of small carnivores such as small grey mongooses (*Galerella pulverulenta*), small-spotted genets (*Genetta genetta*) and striped polecats (*Ictonyx striata*) tended to increase or remain constant as distance from the road increased (Fig. 2), although

these trends were not significant. Insectivore detection probabilities tended to decrease further from the road, although this trend was only significant in thicket vegetation (Z = − 3.65, df = 13, p < 0.001). Similarly, omnivore detection probabilities were only significantly influenced by distance from roads in riverine vegetation (Z = −3.46, df = 13, p < 0.001), largely due to the significant negative result observed for baboons (*Papio ursinus*, Z = −3.70, df = 13, p < 0.001) in this habitat (Fig. 2).

Common duikers (*Sylvicapria grimmia*) were the only species to exhibit a significant increase in detection probability further from roads, and this trend was only observed in fynbos vegetation (Z = 2.65, df = 13, p = 0.008). Herbivores as a guild showed negative significant trends with distance from the road in both riverine (Z = −3.51, df = 13, p < 0.001) and thicket vegetation (Z = −4.90, df = 13, p < 0.001). In riverine vegetation, both Cape porcupines (*Hystrix africaeaustralis*, Z = −3.34, df = 13, p < 0.001) and kudus (*Tragelaphus strepsiceros*, Z = −2.34, df = 13, p = 0.019) showed a significant decline in detection probability as distance from road increased. A similar, significant trend was observed for both donkeys (*Equus* asinus, Z = −2.20, df = 13, p = 0.028) and steenbok (*Raphicerus campestris*, Z = −4.62, df = 13, p < 0.001) in thicket vegetation (Fig. 2).

Discussion

Our results suggest that RAIs derived solely from camera traps placed on roads were unlikely to be representative of the medium to large-bodied mammalian community in the sample area. This was largely due to species, and feeding guilds, differing in their probability of road usage. Carnivores and insectivores were generally more likely to be detected on roads, whereas herbivores and omnivores seemed largely indifferent to roads, with detection patterns varying between species and vegetation types.

Individually identifiable medium and large carnivores are often the focal species of capture–recapture studies, and our results confirm previous findings that roads and prominent trails increase the detection probability of such species (Karanth 1995; Soisalo and Cavalcanti 2006; Balme et al. 2009; O'Connell et al. 2011). Leopards and caracals were the two largest predators present in our study area, and both showed a strong preference for roads, but in different habitat types. All leopard photographs recorded away from roads were the result of a single individual which walked the length of one transect and was recorded by all five cameras in short succession.

Our results therefore do not support the opportunistic use of photographs, obtained from camera traps placed on roads and trails to detect carnivores, for estimating prey abundance or density. Herbivores and omnivores in our study were generally less likely to use roads than either carnivores or insectivores and would thus have lower detectability. Our assumption that all mammals passing through the transects were detected may be open to debate but we maintain that the transect as a whole is likely to have provided a far more representative sample of animal movement in the area than that based on a single roadside camera.

While leopard and caracal prey species were less likely to be recorded on roads in our study, capture probabilities of most species (with the exception of common duiker) did not increase with distance from the road. It is possible that the relatively short total length of our transect influenced this result, as both leopards and caracals have been shown to stalk prey from a distance of well over 100 m in arid environments, although mean stalking distance for both species is approximately 50 m (Stander et al. 1997; Melville 2004). This

would imply that there is insufficient reduction in predation risk to influence prey species distribution within 100 m of a road. Jaguar show a similar preference for roads but in contrast to our findings detection probabilities for jaguar prey species increased with distance from roads (Weckel et al. 2006). Importantly the study by Weckel et al. (2006) positioned cameras 275, 525, 775 and 1,025 m from roads, but in our study area such distances would have included major changes in topography and vegetation that would have had a potentially greater influence on predation risk than distance to roads. An additional factor which may explain the apparent lack of avoidance of roads by prey in this study is that predators typically occur at lower densities in arid environments (Hayward et al. 2007), and prey species may be less inclined to avoid hazardous areas close to roads due to the low probability of encountering a predator. In this regard it is notable that no herbivore or omnivore species showed a significant preference for roads when in the vegetation type in which leopards were detected (i.e. fynbos, Fig. 2). These same prey species did however use roads when in habitat in riverine and thicket vegetation where caracal were detected. Caracal are much smaller than leopards and pose little threat to herbivores such as kudus and donkeys, or animals with strong defence mechanisms such as baboons and porcupines (Grobler 1981, Braczkowski et al. 2012b), all of which showed a significant preference for roads in these habitats. Interestingly, steenbok (a much smaller ungulate) also showed a preference for roads in thicket vegetation, but these appear to be seldom predated by either leopards (Hayward et al. 2006) or caracal (Grobler 1981, Braczkowski et al. 2012b).

Rowcliffe et al. (2008) suggested a means of estimating the densities of non-individually identifiable species using a model based on gas particle physics. One frequently-cited drawback of this model is that it requires random positioning of camera traps (Rowcliffe et al. 2008; Foster and Harmsen 2012; Sollmann et al. 2013). Our results suggest that roads cannot be considered as random sites, as they are likely to be preferred by carnivores and insectivores, while herbivore species may vary in their road usage according to habitat type and the probability of predator presence. However, the lack of a clear relationship between distance from roads and capture probabilities of most species suggests that cameras can be located at any distance in excess of 25 m from roads and be treated as being randomly-positioned relative to roads.

The substantial differences in structure between the vegetation types in this study appeared to have some influence on the degree of road usage by different mammals. We expected road-usage to be greater in the riverine and thicket vegetation types, where the dense and often thorny vegetation imposes a greater cost on animal movement across the landscape. In contrast, we anticipated that roads would have less influence on animal movement in heathery fynbos vegetation, which is more open and easily traversed. Our results provided limited evidence for these predictions, based on trends observed for the four species that were present in all habitat types. Aardwolf (*Proteles cristatus*) generally preferred roads, but only in thicket vegetation was this trend significant, although this result may be due to the low number of captures (n = 1) observed in riverine and fynbos vegetation as opposed to thicket (n = 15). Similarly, porcupines only showed a significant, negative relationship to increasing distance from roads in riverine vegetation (22 captures), but the non-significant trends reported for fynbos and thicket may be due to the low number of photos recorded in these vegetation types (two captures in each). Baboons and common duiker were relatively common across all vegetation types, and their detection probabilities relative to roads varied across all three. Common duiker appeared to avoid roads in fynbos vegetation, but showed a weak, non-significant decline in detection probability away from roads in other vegetation types. Baboons, in contrast,

showed a general preference for roads in riverine (significant) and fynbos (non-significant) vegetation, and a weak, non-significant trend of increasing detection probability away from roads in thicket vegetation. This suggests that some species and feeding guilds will move along roads more readily than others, regardless of habitat type, a similar trend to that observed by Weckel et al. (2006) in tropical forest.

We were careful to select transect sites at which topographic influences on transects would be minimal in order to isolate the effect of roads. However, camera trap surveys often take advantage of topographical features such as drainage lines and gorges, where animal movement is likely to be channelled through a small area that can be effectively covered by a single camera (O'Connell et al. 2011; Gutierrez-Gonzalez et al. 2012). It is possible that topographical channels are more effective than roads in funnelling all passing animals through a camera traps detection zone, and this would be an interesting avenue for future research. However, it is also possible that many prey species avoid these areas entirely due to the potential presence of predators and their reduced ability to escape a predator in a more confined area. We thus recommend that RAIs drawn from such studies be interpreted with similar caution to those derived from cameras placed on roads or trails. Differences in the detection probabilities of different species should thus be explicitly taken into account when analysing camera trap data (sensu Bischof et al. 2013)

Our study provides clear evidence that species were not equally detectable across space and time at camera traps positioned on and off roads in a semi-arid habitat. This suggests that data from predator surveys in which effort is typically higher on roads and other topographical channels should not be used to estimate prey RAIs in a semi-arid environment. This finding has implications both for the derivation of the relative abundances of the prey species, and for the use of camera traps as tools for conducting biodiversity surveys and inventories. We suggest that future studies which use camera traps to survey biodiversity employ a mixed design of cameras located on and off roads to ensure a more representative sample of local mammal diversity.

Appendix

See Tables 1, 2, and 3.

Table 1 Results of the generalized linear model of detection probability against distance from the road in fynbos vegetation

Fynbos vegetation Species	Captures	Distance to road				Intercept				Null deviance (df = 14)	Residual deviance (df = 13)
		Estimate	Std error	Z	p	Estimate	Std error	Z	p		
Aardwolf (*Proteles cristatus*)	1	−0.793	486.402	−0.002	0.999	−81.099	1.00	−81.099	<0.001	5.133	2.197
African wild cat (*Felis sylvestris*)	16	−0.068	0.021	−3.144	0.002	−78.507	0.270	−290.740	<0.001	49.045	18.144
Baboon (*Papio hamadryas*)	11	−0.010	0.008	−1.171	0.241	−79.747	0.428	−186.210	<0.001	9.251	7.807
Cape porcupine (*Hystrix africaeaustralis*)	2	−0.819	480.692	−0.002	0.999	−80.406	0.707	−113.710	<0.001	7.493	1.622
Common duiker (*Sylvicapria grimmia*)	25	0.016	0.006	2.647	0.008	−80.316	0.471	−170.624	<0.001	54.517	46.536
Grey rhebok (*Pelea capreolus*)	11	−0.003	0.008	−0.397	0.692	−80.017	0.472	−169.541	<0.001	29.070	28.912
Grysbok (*Raphicerus melanotis*)	128	−9.496 × 10⁻⁴	0.002	−0.408	0.684	−77.767	0.144	−540.421	<0.001	196.40	196.23
Honey badger (*Mellivora capensis*)	1	−0.793	486.402	−0.002	0.999	−81.099	1.000	−81.099	<0.001	5.133	2.197
Klipspringer (*Oreotragus oreotragus*)	5	−4.409 × 10⁻¹⁶	0.012	0.000	1	−0.810	0.740	−109.400	<0.001	23.114	23.114
Leopard (*Panthera pardus*)	15	−0.040	0.013	−3.144	0.002	−78.788	0.297	−265.160	<0.001	42.082	23.849
Insectivores	1	−0.793	486.401	−0.002	0.999	−81.099	1.000	−81.099	<0.001	5.133	2.197
Omnivores	11	−0.010	0.008	−1.171	0.241	−79.747	0.428	−186.210	<0.001	9.251	7.807
Carnivores	32	−0.051	0.011	−4.611	<0.001	−77.918	0.197	−395.384	<0.001	84.365	34.364
Herbivores	171	8.123 × 10⁻⁴	0.002	0.403	0.687	−0.775	0.128	−603.327	<0.001	202.38	202.22

For each species recorded in fynbos vegetation, the number of photographic records, or 'captures' is shown, together with the estimate, standard error, Z and p values for both the 'distance to road' variable and the intercept. The null and residual deviances of the models are also shown

Table 2 Results of the generalized linear model of detection probability against distance from the road in riverine vegetation

Riverine vegetation / Species	Captures	Distance to road				Intercept				Null deviance (df = 14)	Residual deviance (df = 13)
		Estimate	Std error	Z	p	Estimate	Std error	Z	p		
Aardvark (*Orycteropus afer*)	11	−0.755	92.162	−0.008	0.993	−85.7290	0.302	−284.331	<0.001	90.234	54.827
Aardwolf (*Proteles cristatus*)	1	−0.740	253.067	−0.003	0.998	−88.127	1.000	−88.127	<0.001	7.473	4.254
African wild cat (*Felis sylvestris*)	1	0.840	880.114	0.001	0.999	−172.118	88,011.36	−0.002	0.998	3.473	0.254
Baboon (*Papio hamadryas*)	52	−0.016	0.004	−3.699	<0.001	−85.139	0.193	−439.436	<0.001	446.20	432.07
Black-backed jackal (*Canis mesomelas*)	1	0.843	913.725	−0.001	0.999	−88.127	1.000	−88.127	<0.001	3.473	0.253
Bushpig (*Potamochoerus larvatus*)	15	−0.004	0.007	−0.547	0.585	−86.838	0.420	−206.944	<0.001	86.624	86.324
Cape porcupine (*Hystrix africaeaustralis*)	22	−0.025	0.008	−3.344	<0.001	−85.748	0.274	−312.553	<0.001	62.810	48.731
Cape hare (*Lepus capensis*)	1	−0.679	118.258	−0.006	0.995	−88.127	1.000	−88.127	<0.001	35.473	32.254
Caracal (*Caracal caracal*)	108	−0.065	0.007	−9.209	<0.001	−83.661	0.105	−794.575	<0.001	288.974	73.135
Common duiker (*Sylvicapria grimmia*)	93	−0.004	0.003	−1.244	0.213	−85.029	0.169	−501.898	<0.001	384.83	383.27
Eland (*Tragelaphus oryx*)	10	0.008	0.009	0.887	0.375	−87.882	0.635	−138.313	<0.001	95.766	94.959
Grysbok (*Raphicerus melanotis*)	5	−0.008	0.013	−0.627	0.531	−87.761	0.685	−128.018	<0.001	172.36	171.96
Honey badger (*Mellivora capensis*)	1	−0.843	913.725	−0.001	0.999	−88.127	1.000	−88.127	<0.001	3.473	0.254
Kudu (*Tragelaphus strepsiceros*)	19	−0.017	0.007	−2.344	0.019	−86.116	0.317	−271.335	<0.001	18.098	11.961
Small grey mongoose (*Galerella pulverulenta*)	1	8.62×10^{10}	0.028	0.000	1.000	−89.74	1.732	−51.81	<0.001	3.473	3.473
Small-spotted genet (*Genetta genetta*)	3	0.022	0.020	1.149	0.251	−90.071	1.587	−56.763	<0.001	11.827	10.234
Steenbok (*Raphicerus campestris*)	3	−0.659	52.690	−0.012	0.990	−87.028	0.577	−150.737	<0.001	106.418	96.762
Striped polecat (*Ictonyx striatus*)	8	0.010	0.010	0.986	0.324	−88.236	0.741	−119.008	<0.001	44.012	42.998

Table 2 continued

Riverine vegetation / Species	Captures	Distance to road				Intercept				Null deviance (df = 14)	Residual deviance (df = 13)
		Estimate	Std error	Z	p	Estimate	Std error	Z	p		
Insectivores	12	−0.758	90.752	−0.008	0.993	−85.642	0.289	−296.673	<0.001	94.642	56.016
Omnivores	67	−0.013	0.004	−3.547	<0.001	−84.981	0.176	−482.461	<0.001	516.56	503.99
Carnivores	123	−0.043	0.004	−9.754	<0.001	−83.728	0.105	−794.408	<0.001	272.68	109.47
Herbivores	153	−0.008	0.002	−3.512	<0.001	−84.335	0.124	−681.516	<0.001	710.24	697.57

For each species recorded in riverine vegetation, the number of photographic records, or 'captures' is shown, together with the estimate, standard error, Z and p values for both the 'distance to road' variable and the intercept. The null and residual deviances of the models are also shown

Table 3 Results of the generalized linear model of detection probability against distance from the road in subtropical thicket vegetation

Thicket vegetation / Species	Captures	Distance to road				Intercept				Null deviance (df = 14)	Residual deviance (df = 13)
		Estimate	Std error	Z	p	Estimate	Std error	Z	p		
Aardvark (Orycteropus afer)	3	−0.6862	74.36	−0.009	0.993	−87.595	0.577	−151.718	<0.001	58.213	48.340
Aardwolf (Proteles cristatus)	15	−0.0723	0.0213	−3.392	<0.001	−86.167	0.279	−308.569	<0.001	642.35	607.25
Baboon (Papio hamadryas)	86	0.001	0.003	0.486	0.627	−85.960	0.191	−449.634	<0.001	1,412.2	1,412.7
Bushpig (Potamochoerus larvatus)	2	0.711	216.113	0.003	0.997	−159.541	21,611.26	−0.007	0.994	9.355	4.394
Cape porcupine (Hystrix africaeaustralis)	5	−0.647	35.392	−0.018	0.985	−87.084	0.4472	−194.725	<0.001	210.38	193.93
Cape hare (Lepus capensis)	7	0.026	0.014	1.913	0.056	−90.166	1.172	−76.965	<0.001	144.37	139.49
Caracal (Caracal caracal)	7	−0.060	0.025	−2.370	0.018	−87.001	0.419	−207.49	<0.001	164.68	151.22
Common duiker (Sylvicapria grimmia)	29	−0.005	0.005	−0.970	0.332	−86.731	0.297	−292.51	<0.001	284.35	283.40
Donkey (Equus asinus)	6	−0.055	0.025	−2.201	0.028	−87.193	0.459	−189.990	<0.001	17.654	6.943
Eland (Tragelaphus oryx)	1	−0.785	418.609	−0.002	0.999	−88.693	1.000	−88.693	<0.001	4.677	1.386
Hewitt's red rock rabbit (Pronolagus saundersiae)	4	−0.002	0.013	−0.130	0.897	−88.863	0.839	−105.890	<0.001	18.710	18.69
Kudu (Tragelaphus strepsiceros)	1	−0.002	0.027	−0.065	0.948	−90.249	1.678	−53.769	<0.001	6.677	6.673
Steenbok (Raphicerus campestris)	66	−0.018	0.004	−4.622	<0.001	−85.431	0.169	−506.780	<0.001	1,478.2	1,460.40
Insectivores	18	−0.078	0.021	−3.648	<0.001	−85.957	0.252	−340.907	<0.001	691.72	646.97
Omnivores	88	0.002	0.003	0.753	0.451	−85.978	0.192	−448.714	<0.001	1,408.7	1,407.60
Carnivores	7	−0.0603	0.025	−2.370	0.018	−87.001	0.419	−207.490	<0.001	164.68	151.22
Herbivores	119	−0.013	0.003	−4.897	<0.001	−84.989	0.132	−646.212	<0.001	2,030.1	2,010.00

For each species recorded in thicket vegetation, the number of photographic records, or 'captures' is shown, together with the estimate, standard error, Z and p values for both the 'distance to road' variable and the intercept. The null and residual deviances of the models are also shown

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