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Comparing the effectiveness of camera trapping, driven transects and ad hoc records for surveying nocturnal mammals against a known species assemblage.

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Abstract

Management and conservation rely on surveys to determine which species are present but some species, such as nocturnal mammals, can be very difficult to detect. Camera trapping, driven transects, and ad hoc records are well-established nocturnal survey methods, but their detection effectiveness has not been tested against known species presence. We tested the effectiveness of these methods with a known assemblage of nocturnal African mammals. We compared camera traps placed at targeted and random locations, driven transects, and informal ad hoc records against one another and the 20 predominately nocturnal medium- and large-sized mammals known to be on site. Species-specific detection patterns, detection curves for each method, and detection effort required per species, were compared to determine the effectiveness of each method. Each of the methods detected at least 60% of known nocturnal mammal species over a 20-month period: driven transects and ad hoc records were the most successful (16/20 80%), followed by targeted camera traps (15/20 75%) and random camera traps (12/20 60%). Jaccard's Coefficients of Community Similarity peaked at 0.78, showing notable differences in the communities sampled with different methods. There was considerable variation in effort required to detect each species for each method, and the number of species detected with specific levels of effort was also highly variable between methods. We suggest that mixing methods, using different camera placement including use of random locations, and incorporating cost-neutral ad hoc records into formal survey efforts can all greatly increase the overall effectiveness and efficiency of species detection.

Keywords

monitoring; community similarity; casual records; methods comparison; South Africa

Introduction

The management and conservation of species and habitats rely on surveys establishing the presence, and often the abundance, of different species (Spellerberg 2005; Goodenough and Hart 2017). Management decisions, including whether to translocate, introduce or cull certain species, rely on accurate survey data whilst conservation strategies are fundamentally determined by the knowledge of which species are present (Goodenough and Hart 2017). There has been considerable research to develop and refine ecological surveying methods, including consideration of optimal sample sizes (Stockwell and Peterson 2002; Hart et al. 2020), spatial coverage (Rees et al. 2011; Einoder et al. 2018), study duration (Mackenzie and Royle 2005; Halstead et al. 2021) and inter-observer variation (Cherrill and McClean 1999; Kolada et al. 2014; Goodenough et al. 2020).There has also been extensive development of the technology used in ecological surveying, including remote sensing (Pettorelli et al. 2014), tracking movement of animals using GPS (Seidel et al. 2018) or light-logger geolocators (McKinnon et al. 2013), unmanned aerial vehicles (UAVs) (Sun et al. 2017), thermal imaging (Goodenough et al. 2018), passive audio detection (Sugai et al. 2019), and camera trapping (Delisle et el. 2021).

Technological approaches, especially camera traps, are particularly useful in facilitating accurate surveying of species that are elusive, nocturnal, rare or otherwise hard to detect using traditional survey methods (Kelly 2008; Meek et al. 2014; Burton et al. 2015). Camera trapping was initially known as “flashlight trap photography” (Kucera and Barrett 2011), and the first known use of a system was in the 1890s using a camera with a trip wire attached to a flash system. The system was very effective, and could be used to take photographs during both the day and night (Shiras, 1906; 1908; 1913). Subsequent advances have led to the modern camera trap, which typically comprises a battery-powered unit, with a digital memory card, housing a camera triggered by a passive infrared sensor that can record photographic or video footage (Rovero et al. 2013; Apps and McNutt 2018). The resulting images can be used to detect the presence of species, suggest likely absence of species and, where individuals have distinguishing features, the identification of individual animals is also possible (Mendoza et al. 2011). Camera trapping has become a widely used and well-established technique that has proved particularly effective in detecting the presence and activity of nocturnal and crepuscular mammals (Rovero et al. 2013). Depending on the camera set-up, and especially the type of flash used (white, infrared, or black), animals can sometimes be aware of the camera and, if startled, might avoid that location in future (Meek et al. 2014). Avoidance behaviour can be a significant factor for activity studies, or capture-mark-resight studies that rely on frequent observations, but is less problematic for studies where the aim is to determine the presence of specific species or assess baseline community composition (Meek et al. 2014).

Another commonly-used method to survey nocturnal mammals is the walked (e.g. Plumptre 2000) or driven transect (e.g. Ogutu et al. 2006), whereby an observer travels a pre-determined route and records animals seen, often using headlights (driven transects) or spotlights (walked and driven transects) (e.g. Busschots et al. 2020). Driven transects allow considerable ground to be covered, and are often safer to conduct at night, and for these reasons may be preferred over walked transects for nocturnal surveying.

As well as formal data collected via camera trapping and transect sampling, ad hoc records are frequency kept. These records can take the form of casual observations recorded in “sightings books” or “species logs”, rather than being based on formal surveying activities. Although such records are often informal and presence-only, they are cost-neutral and may be useful in local contexts in understanding what species are present and where, and they have been shown to be useful in certain contexts (for example, in cetacean surveying (Higby et al. 2012) and in evaluating extinctions (Solow et al. 2012)). However, ad hoc sightings are often recorded by untrained observers such as visitors or tourists, are unlikely to be validated (a common issue in citizen science approaches in general (Gilfedder et al. 2019)) and are potentially biased towards rare or charismatic species, which are more likely to be deemed “record worthy” by observers. Surprisingly, ad hoc records have very seldom been compared to formal survey methods (an exception being sightings of Cape clawless otters (*Aonyx capensis*) (Okes and O’Riain 2019)), and have not, to date, been empirically tested at sites with known species assemblages to determine their effectiveness.

Different survey methods have fundamental differences in their spatiotemporal coverage. Camera trapping methods, for example, are inherently spatially restricted, being used in a static location and only recording species that move within the detection zone (Apps and McNutt 2018). However, camera traps can be deployed at specific locations for extended periods with minimal maintenance other than replenishing batteries and changing memory cards on a schedule that depends on the number of camera triggers. This means that they not only capture whole night periods (and thus species with different activity patterns) but also multi-night periods. In contrast, driven transects are spatially widespread, covering around 20 km per hour with a survey zone typically at least 10 m either side of the vehicle. Camera traps have relatively low costs whilst in use but have an upfront purchase cost and require time to deploy and also to examine the resultant footage. Driven transects in contrast have higher in-use costs, requiring fuel and time, but typically make use of a vehicle that can be used for other activities. Ad hoc records have more-or-less zero costs since data are collected incidental to other activities, but they are temporally and spatially biased by when and where humans are active. Finally, it is important to note that camera traps are often deployed with the aim of detecting specific species, especially nocturnal or cryptic species that may be thought to frequent certain locations, or at locations that are thought to be regularly used by multiple species (e.g. Jansen et al. 2020), although this is not always true (Meek et al. 2014). In contrast, nocturnal driven methods tend to be less targeted in their approach, although they may preferentially detect species that are more likely to be found on roads at night. The differences between different survey methods potentially result in differences in species-specific detection and therefore differences in the ecological data collected (e.g. Thorn et al. 2010), with subsequent potentially important implications for management and conservation (TEAM Network 2011; Swanson et al. 2015).

Comparison of camera trapping with other surveying methods has been undertaken previously, but with comparisons usually being between camera traps and indirect signs (e.g. scat, tracks or hair) of single species rather than other direct survey methods (e.g. wildcat (*Felis silvestris silvestris*) scat on Etna Volcano, Italy (Anile et al. 2014); hair tubes and scat for pine martens in central Italy (*Martes martes*) (Bartolommei et al. 2013); and sightings, fresh diggings and scat for numbats (*Myrmecobius fasciatus*) in Western Australia (Seidlitz 2021)). Other studies have compared assemblages of species, such as medium-sized ground-dwelling mammals using hair tubes in Australia (Paull et al. 2012) and carnivore communities using track plates, scats and tracking in New York forests (Gompper et al. 2006). There have also been studies comparing camera trapping with transect surveys (e.g. Silveira et al. (2003), with live trapping (De Bondi et al 2010), or comparing sign surveys with spotlighting methods (Thorn et al. 2010). However, these studies compared survey methods with each other rather than against well-established ecological data on species community composition. Ideally, comparing different methods of detecting species requires the actual species assemblage to be previously well documented using methods that provide a solid baseline for comparison.

In this study, for a reserve with a known assemblage of nocturnal mammal species, we compared four commonly-used methods for determining nocturnal species presence: (1) camera traps placed at targeted locations (water holes); (2) camera traps placed randomly; (3) formal driven transects; and (4) informal ad hoc records. Species-specific detection patterns were compared and detection curves for each method, and the effort required to detect individual species, allowed the effectiveness and associated sample effort (as trapping nights/distance driven) of each method to be determined.

Methods

Study site

All fieldwork was undertaken over a 20-month period between March 2019 and November 2020 at a wildlife reserve in Northwest Province, South Africa. The site is centred on 25°15’S 27°17’E and covers an area of 4,750 hectares surrounded by a 30 km game-proof fence. The reserve is divided into 20 unequally-sized blocks, which are burned in rotation on a 4-6 year cycle to encourage palatable and nutritious grasses (Brockett, *et* al. 2001). This rotational block-burning has resulted in a mosaic of grassland and acacia scrub, thereby preventing localised overgrazing and reducing parasite load (Goodenough et al. 2017).

The reserve supports a diverse resident mammal community, including 20 species of medium-to-large mammal that are predominantly nocturnal or crepuscular. This includes carnivores such as brown hyaena (*Hyaena brunnea*), black-backed jackal (*Canis mesomelas*) and caracal (*Caracal caracal*); insectivores such as aardvark (*Orycteropus afer*); omnivores such as honey badger (*Mellivora capensis*) and white-tailed mongoose (*Ichneumia albicauda*); and herbivores such as cape bushbuck (*Tragelaphus sylvaticus*) and mountain reedbuck (*Redunca fulvorufula*). The reserve has been operational for more than 25 years with an annual aerial game count conducted by helicopter, but also has continuous anti-poaching foot and driven patrols, and hosts a rolling series of groups undertaking conservation education programs that give a near constant presence on the ground, day and night throughout the year. Collectively, these activities mean that the medium-to-large mammal assemblage is well-characterised and well-known. All the species listed have been confirmed as present during the research period itself or within a few weeks either side the research period. Although it is possible that the list is incomplete (i.e. species being present without having been detected), particularly in the case of rare transient individuals of species such as young leopards, we are confident that the baseline is as robust as ecologically possible especially for resident species.

Camera trapping: targeted and random

We used Bushnell™ Trophy Aggressor cameras, which have a passive infrared sensor and a field of view of 38°. In nocturnal mode an infrared flash allowed the capture of monochrome images, which provided sufficient detail to identify species at distances of up to 30 m without the disturbance associated with a white (visible light) flash. After pilot testing multiple units side-by-side to compare settings in field conditions, the sensor level was set to low, which avoided multiple false triggers without decreasing detection of actual animals in this environment. To maximise identification potential, camera traps were set to record up to six photographs per triggering event: the first rapid-sequence of three images was taken immediately (0.2 second lag after detection); the second rapid-sequence of three images was taken 3 seconds later if the animal was still in the detection zone. The shutter speed was determined automatically. Images were written to 32GB SanDisk Ultra SD cards and the units were powered by 8x AA batteries. The cameras were mounted on 1 m metal angle-iron posts hammered into the ground using a sledgehammer. For consistency, cameras were mounted at a height of approximately 40 cm, as per the recommendation of Meek *et al.* (2014) and references therein for optimal detection of medium-to-large nocturnal mammals, and were oriented away from sunrise and sunset directions to minimise lens flare at these times. To reduce the likelihood of false triggers caused by vegetation moving in the wind, vegetation around the field of view was cleared to a distance of 3m (Meek et al. 2014).

Camera traps were deployed to both targeted and random locations (Meek *et al.* 2014) and were active from sunset to sunrise (approximately 17:30 – 06:30); each trapping location had a camera trap set up

Table 1 Key information for camera trapping and driven survey methods used in this study.

	Camera trapping survey methods		Driven survey methods	
	Targeted	**Random**	**Transect**	**Ad hoc**
Sample size	276 nights 46 locations 21,040 nocturnal images	380 nights 50 locations 2,115 nocturnal images	357 nights Total distance 8,383 km Total time 427 hours	221 night drives where an ad hoc sighting was made
Data type	Presence-absence: failure to detect = assumed absence			Presence-only: could be biased towards rare or flagship species
Effort known?	Yes: number of trapping nights		Yes: kilometres travelled; one observer	Partly: number of drives known but not distance nor number of observers
Spatial and temporal distribution	Spatially-restricted but excellent temporal coverage (sunset-sunrise; multiple nights)		Temporally-restricted but excellent (whole site) spatial coverage	Influenced by spatiotemporal patterns of human activity
Species identification accuracy	High: experienced observer studying photographic evidence that was usually good quality		Medium: experienced observer but sightings often fleeting	Unknown: multiple observers with varying levels of experience

for 6-10 nights (mean = 6.83 nights). There were 656 trapping nights (cameras X nights) in total, over a 20-month period, which produced over 23,000 nocturnal images (see Table 1 for further information). Targeted camera traps were set up by permanent water holes (Figure 1a). These included natural water sources, concrete-lined artificial pumped pans (refilled by pumping water from nearby bore holes every 2-4 weeks), and hybrid continual flow pans (concrete-lined pans on trickle flow from a municipal water source, which usually had an adjacent natural mud wallow). For randomly-located camera traps, open-source software QGIS 3.12.3 was used to generate georeferenced locations on the reserve. To ensure that there was good coverage of the reserve, both spatially and in relation to burning regime, a stratified random approach was used with at least four trapping locations per burn age and at least one trapping location in each of the 20 blocks. To reduce edge effects and avoid overlap with areas along roads covered by driven methods, all trapping locations were ≥ 150 m from the edge of the reserve or any roads; 150 m was also set as the minimum distance between trapping locations. In the field, locations were found using a Garmin GPSMAP 62 Global Positioning System unit. The camera was then set up within a 30 m radius of that location, oriented towards a game trail if one was present or alternatively facing the direction with the longest open vista.

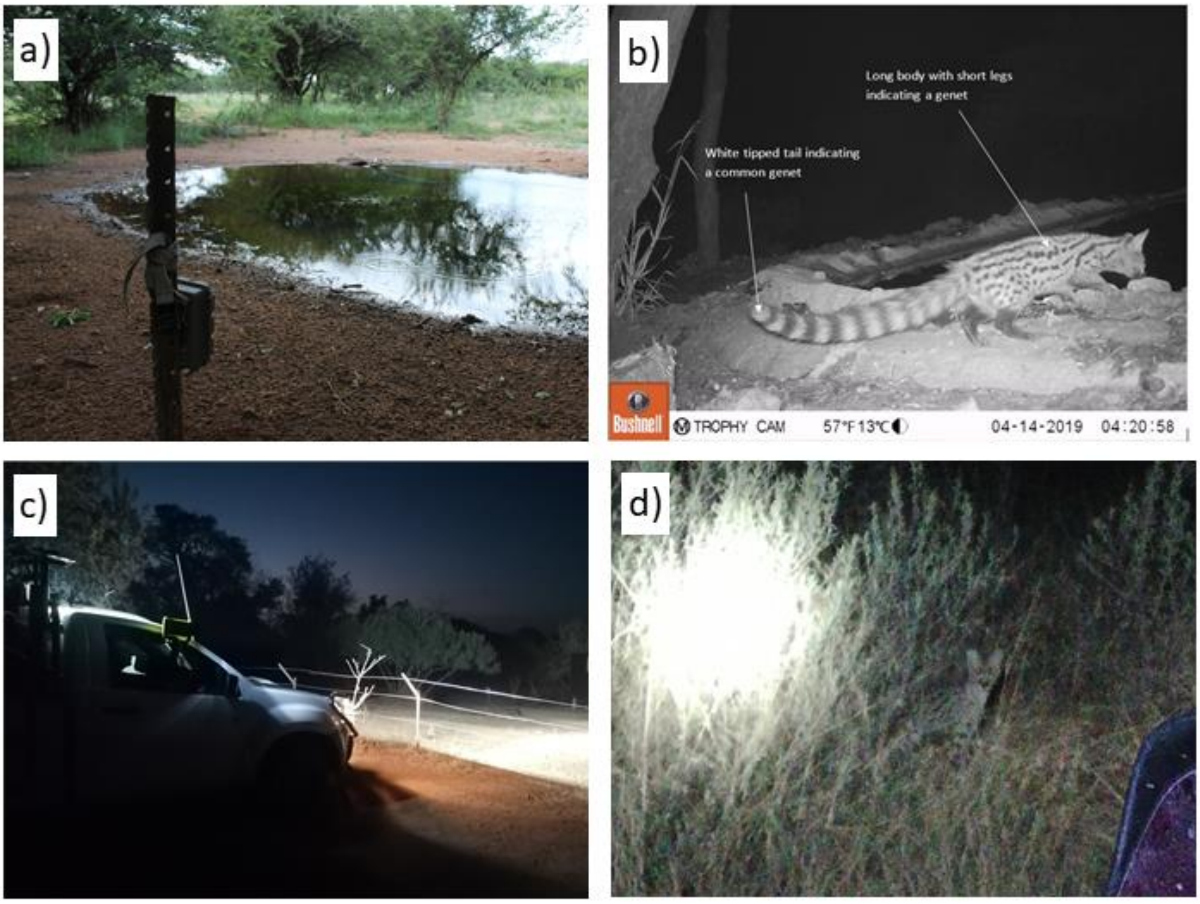

Figure 1 Survey methods used during this study: (a) targeted camera trap deployed at a pan; (b) image from a camera trap showing a common genet (Genetta genetta) with key identifying features highlighted; (c) one of the vehicles used for driven transects and driven ad hoc records showing forward-facing lights; (d) serval (Leptailurus serval) found on a driven transect illuminated using a hand-held spotlight.

Once images were downloaded, species identification was undertaken based on key identifying features (Figure 1b). Because the focus was on species that were predominantly nocturnal or crepuscular, footage of predominantly diurnal species (e.g. white rhino (*Ceratotherium simum*), Burchell's zebra (*Equus quagga burchellii*), and impala (*Aepyceros melampus*)) captured at night was disregarded. Nights with no target species were documented. It was assumed that all animals at the camera trapping locations would have been recorded, such that the data were regarded as presence-absence data rather than presence-only data.

Driven surveys: transects and ad hoc

All driven surveys were conducted from an Isuzu Fleetside pick-up truck or a Kia K2700. Each vehicle was equipped with standard headlights (illumination range 120 m; narrow field of view) and an overhead forward-facing bar light with 60 LEDs across 80 cm (illumination range 60 m; wide field of view) (Figure 1c). A handheld LED 1000-lumen spotlight, powered from a car battery, was also carried that could be used to scan either side of the vehicle and provide additional directional illumination of detected animals to assist identification.

Two driven survey methods were undertaken. The first was formal driven transects, which were conducted by one person (co-author RF) and where effort was quantified by recording kilometres travelled. Transects covered an average of 23.5 km (± 11.36 SD) with a mean duration of 1 hr 13 mins (± 38 mins SD; max = 3 hrs 47 mins, min = 6 mins); the typical speed (allowing for stops when animals were detected) was 20 km/h as per (Silveira et al. 2003). Across the survey period, 357 transects were undertaken covering a combined distance of 8,383 km. Care was taken that transects were driven throughout the night, rather than being biased towards dusk or dawn, and to ensure that there was good spatial coverage both in relation to the geography of the reserve and the burning regime. The second method was ad hoc recording making use of a "sightings book" in which multiple casual observers (with varying levels of experience and knowledge) recorded when they had seen a nocturnal animal whilst driving around the reserve at night. Drives on which ad hoc sightings were recorded were entirely separate from those in which formal driven transect data were collected. Ad hoc records for this study were only ever collected from vehicles. Observers included students, long-term volunteers, and members of reserve staff and data were recorded for 221 nights. These ad hoc records were presence-only (i.e. no absence data were recorded) and without quantification of survey effort by distance travelled. No location or time data were recorded, but sightings were likely biased spatially towards the southeast quadrant of the reserve where the two permanent camps were located and temporally to between sunset (ca 17:30) and mid-evening (ca 21:00) due to the timing of human activity.

In both types of driven survey – driven transects and driven ad hoc – animals were often detected by observing eyeshine caused by the tapetum lucidum, a layer of tissue located behind the retina acting as a retroreflector. When eyeshine was observed, the vehicle moved slowly or stopped to allow the spotlight to be used to track and identify the animal (Figure 1d). As with camera trapping, sightings of diurnal species were ignored. Summary information about the driven survey methods, including samples size, and how key parameters compare to the camera trap survey method, are given in Table 1.

Data manipulation and analysis

The species communities detected using the four survey methods were compared in several different ways. To give a baseline understanding of differences, all species detected using each survey method at any time during the 20 months of fieldwork were summarised based on presence (and assumed absence). The relative similarity of communities was then compared numerically using Jaccard's Coefficient of Community Similarity (CCj) (Jaccard 1912; Staudhammer et al. 2018). This approach has been used previously to compare species detections arising from different camera trap protocols (Cusack et al. 2015).

To extend analysis beyond presence-absence, we examined differences in the communities quantified by each survey method based on the relative frequency of detection of each species. For this analysis, detection events for each species were defined thus: camera traps = the number of nights when at least one individual of that species was sighted; driven transects = the number of nights when at least one individual of that species was sighted. In other words, for each method, for each night, if a species was recorded once, or more than once, this was coded as 1 (present), otherwise the species coded as 0 (absent). This way of defining detection, whereby the trapping night or night transect became the "sampling event", allowed comparison between methods where the unit of measurement of sampling effort (time *versus* distance) was fundamentally different. The number of encounters per night was not included since there was usually no way of knowing whether or not repeated sightings were of the same individual, especially on static camera traps. Although it is possible, indeed likely, that the same animals were encountered on several different nights, this is not problematic given that we are quantifying frequency of detection (on a nightly basis) rather than abundance (Meek et al. 2014). To quantify the frequency of detection we calculated the number of nights on which each species was detected in the overall dataset and summed these to give Unique Species Detections (USDs), effectively this gives the cumulative number of detection nights for each species. For driven ad hoc records, we simply summed the number of occasions where a species was reported as being encountered regardless of the number of individuals sighted. In all cases, count data were transformed into percentages to allow for the fact that sample sizes were unequal between methods (Table 1). A chi square test for association was used on the raw data to test for statistical difference in the frequency of species detections between the survey methods.

Species detection curves were used to show, cumulatively, how much effort was needed to detect the species of nocturnal mammals known to be present on the reserve. Effort was quantified using number of nights when targeted or random camera traps were deployed, kilometres travelled (driven transects), and number of presence-only records (driven ad hoc). Since it was impossible to produce replicates within this long-term study of a single site, another way of generating replicates was needed to give averages and confidence intervals for species detection curves. This was achieved through a permutation process (bootstrapping-without-replacement), whereby 25 pseudo-replicates were created for each method by randomised reordering of the original data (Wilcox 2003). For driven transects, the original data from each of the 357 nights, ordered chronologically, was permuted (randomly reordered) to create 25 separate datasets with nights in a different random order in each case. The same process was used for the 221 ad hoc records. For targeted camera traps and random camera traps, the process was essentially the same but rather than trapping nights being reordered *completely* randomly, which would have de-coupled nights from trapping locations, we retained the ordering of the nights on which cameras were deployed at each specific location (6-10 nights per location) and instead randomly reordered the locations themselves. Again, this resulted in 25 datasets for each method location. Using these randomised datasets, mean species detection curves were created for each survey method, with range and 95% confidence intervals calculated to understand the role of variability – and thus the role of chance – in species detection rates for each method. This allowed generalisations and inferences to be made in a way simply not possible for a single dataset, and a single detection curve, per method (Lunneborg 1999). This concept has been discussed previously for detection curves of bird data (Xuan Mao et al. 2005) and a similar approach, using bootstrapping with replacement, has been used previously to generate confidence intervals on species detection curves (e.g. Cusack, et al. 2015).

Finally, to consider which specific species required more or less effort to detect – and whether or not this was consistent between the survey methods – the previous bootstrapping approach was used to quantify the amount of effort needed to detect each specific species; sampling effort was quantified in the same way as detection curves. This also allowed consideration of what might be influencing variation in detection patterns between methods, including species rarity, home range size, and behaviour.

Results

At least one nocturnal species was detected on 114 of 276 trapping nights at targeted locations (41%) and 58 of 380 trapping nights at random locations (15%). For targeted camera traps, there were 189 unique species detections (USDs, see Methods for definition) over 276 nights, equating to 0.68 USDs per night (range 0-6); for random camera traps, there were 68 USDs across 380 nights equating to 0.18 unique species detections per night (range 0-2). At least one nocturnal species was detected on 266 of the 357 driven transects (75%) and there were 477 USDs, which equates to 1.34 USDs per night (range 0-8). Because ad hoc data were presence only, calculation of percentage detection rates was not possible but 245 USDs were recorded across 221 submitted presence-only records.

Method comparisons: presence and absence data

In total, 18 of 20 predominantly nocturnal or crepuscular mammal species known to be present were detected overall: the exceptions were aardwolf and brown hyena, which were not detected despite there being known populations on the reserve (Table 2). All detected species were found using at least two of the methods and 10 of 18 detected species were found using all four methods. More species were detected using targeted camera traps than random camera traps (15 of 20 (75%) *versus* 12 of 20 (60%)). An important point to note is that random camera traps also missed species that were inherently scarce and elusive relative to targeted camera traps. For example, caracal, African wildcat, Cape bushbuck and bushpig were only detected using targeted camera traps (Table 2). Steenbok were

Table 2 Presence and (assumed) absence of nocturnal and crepuscular species as recorded by four different survey methods over a 20-month period at a reserve with a well-characterised mammal species list.

			Survey methods			
Family	Species common name	Species scientific name	Targeted camera	Random camera	Driven transect	Driven ad hoc
Felidae	Caracal	*Caracal caracal*	✓	X	X	✓
Felidae	Serval	*Leptailurus serval*	✓	✓	✓	✓
Felidae	African wildcat	*Felis lybica*	✓	X	✓	X
Canidae	Black-backed jackal	*Lupulella mesomelas*	✓	✓	✓	✓
Hyaenidae	Aardwolf	*Proteles cristata*	X	X	X	X
Hyaenidae	Brown hyena	*Hyaena brunnea*	X	X	X	X
Viverridae	African civet	*Civettictis civetta*	X	X	✓	✓
Viverridae	Common genet	*Genetta genetta*	✓	✓	✓	✓
Viverridae	Large-spotted genet	*Genetta maculata*	✓	✓	✓	✓
Herpestidae	White-tailed mongoose	*Ichneumia albicauda*	✓	✓	✓	✓
Mustelidae	Honey badger	*Mellivora capensis*	✓	✓	X	✓
Orycteropodidae	Aardvark	*Orycteropus afer*	✓	✓	✓	✓
Bovidae	Cape bushbuck	*Tragelaphus sylvaticus*	✓	X	✓	✓
Bovidae	Common duiker	*Sylvicapra grimmia*	✓	✓	✓	✓
Bovidae	Mountain reedbuck	*Redunca fulvorufula*	✓	✓	✓	✓

Bovidae	Steenbok	*Raphicerus campestris*	X	✓	✓	✓
Suidae	Bushpig	*Potamochoerus larvatus*	✓	X	✓	X
Leporidae	Scrub hare	*Lepus saxatilis*	✓	✓	✓	✓
Hystricidae	Cape porcupine	*Hystrix africaeaustralis*	✓	✓	✓	✓
Pedetidae	South African springhare	*Pedetes capensis*	X	X	✓	✓

detected using random camera traps alone. Driven transects and driven ad hoc methods both detected 16 of 20 species (80%), but there were several differences in species composition (Table 2). African civet and South African spring hare were detected using both driven methods, but neither camera method. Jaccard's Coefficient of Community Similarity (CCj) indicated a relatively high level of similarity between all methods (0.65-0.78), with the greatest levels of similarity between ad hoc records and all three formal survey methods (0.72-0.78; Figure 2). It was notable, though, that all CCj values were <1, such that the species communities did not converge for any of the four methods despite considerable survey effort.

Figure 2 Community similarity between the survey methods calculated using Jaccard's Coefficient of Community Similarity, which runs between 0 (no species in common) to 1 (all species in common).

Method comparisons: frequency of observation

There were substantial differences in the relative frequency of detection of different taxa between the methods, such that the species list was fundamentally dependent upon the survey method used (Figure 3); this was statistically significant (chi square test for association, $\chi^2 = 131$, d.f. = 24, $p < 0.0001$). Particularly notable is the high frequency of detection of scrub hares (Leporidae) on driven transects and in the driven ad hoc records compared to both camera trap methods, the low frequency of detection of the four antelope species (Bovidae) in driven ad hoc surveys compared to the three formal methods, and the high frequency of detection of genets, civets, and mongoose (Viverridae/Herpestidae) using random camera traps compared to the other methods.

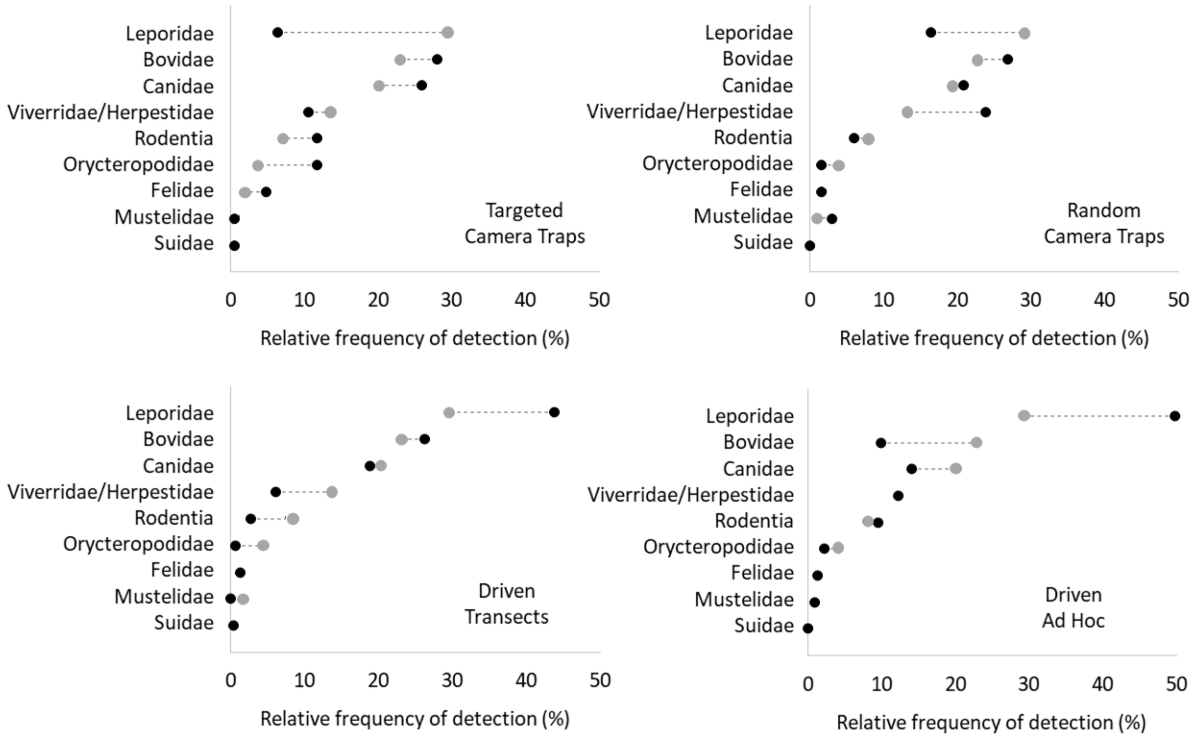

Figure 3 Frequency of detection of each Family or Order using the different survey methods based on number of nights where taxa were detected, listed in descending order based on overall detection by all methods combined. In each panel, frequency of detection using that method is shown by a black dot. Where there is a substantial deviation between the method-specific mean and the all-method mean, the all-method mean is shown using a grey dot with the dashed line indicating the magnitude of the deviation. In cases where method-specific means and the all-method mean were within one percentage point, the all-method mean is omitted for clarity. The Family or Order grouping is thus: Felidae = caracal, serval, African wildcat; Canidae = Black-backed jackal; Viverridae/Herpestidae = African civet, common genet, large-spotted genet, white-tailed mongoose; Mustelidae = honey badger; Orycteropodidae = aardvark; Bovidae = Cape bushbuck, common duiker, mountain reedbuck, steenbok; Suidae = bushpig; Leporidae = scrub hare; Rodentia = Cape porcupine, South African springhare.

Survey comparisons: detection curves

For all methods, and as expected, cumulative species detection was positively correlated with effort and species detection curves showed characteristic logarithmic growth (Fig 4). Error bars were smallest near the start of the species detection curve and increased considerably as new species became more difficult to detect.

The effort required to detect 50% of the species known to be present was: 64 trapping nights for targeted camera traps; 198 trapping nights for random camera traps; 879 km for driven transects; and 39 presence-only records for driven ad hoc. To detect the maximum number of species for each method required: 228 trapping nights for targeted camera traps (permutated data range 164-276 trapping nights; N = 15 species); 314 trapping nights for random camera traps (permutated data range 185-374 trapping nights; N = 12 species); 5,864 km for driven transects (permutated data range 2,357 – 8,348 km; N = 16 species); and 163 presence-only records for driven ad hoc (permutated data range 99-220; N = 16 species).

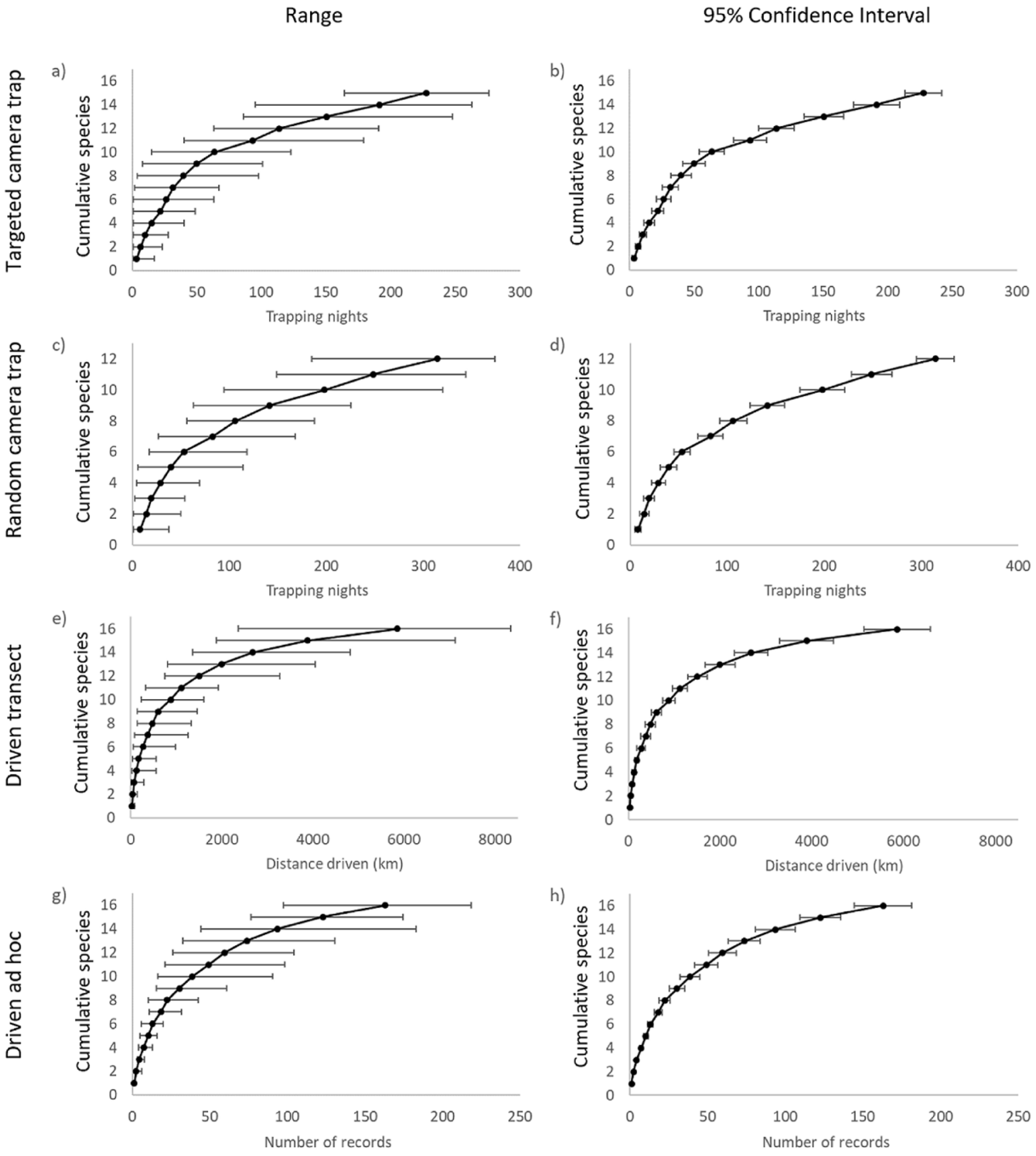

Figure 4 Species discovery curve for camera trapping and driven survey methods relative to effort (trapping nights, kilometres travelled or number of presence-only records). Y-axis shows cumulative species in all cases. Error bars show range (left) and 95% confidence intervals (right). Note that x- and y-axes differ for different methods.

Not only was there considerable variation in effort required to detect each new species for each method, the number of species detected with specific levels of effort was also highly variable. For example, undertaking targeted camera traps for 10 nights could, depending on stochastic variation and the effect of chance, detect 1-9 species (Fig 4a), while undertaking 25 trapping nights could detect 3-10 species; 50 trapping nights could detect 6-11 species; and 100 trapping nights could detect 9-14 species. The equivalent values for random camera trapping were 1-5, 1-5 2-7, and 5-10, respectively (Fig 4c). For driven transects, driving 500 km could result in the detection of 4-11 species; 1000 km could detect 7-13 species; 2000 km could detect 12-15 species; and 4000 km could detect 13-16 species (Fig 4e). For driven ad hoc, data were presence-only and thus only drives where target species had been detected were recorded. However, there was still considerable variation in the number of species recorded cumulatively over time: 10 records could detect 4-8 species; 25 drives could detect 7-11 species; 50 drives could detect 9-14 species; and 100 drives could detect 12-16 species (Fig 4g).

The amount of survey effort required to detect each specific species also differed between methods. For example, mountain reedbuck was a species detected using all methods but required relatively little effort to detect using driven transects (4th out 16) compared to considerable effort (9th of 15 species) to detect using camera trapping (targeted: 9th of 15; random 12th of 12) and driven ad hoc (12th of 16) (Fig 5). A notable exception to this variation between methods was the detection of black-backed jackal, which required very little survey effort in all cases (Fig 5).

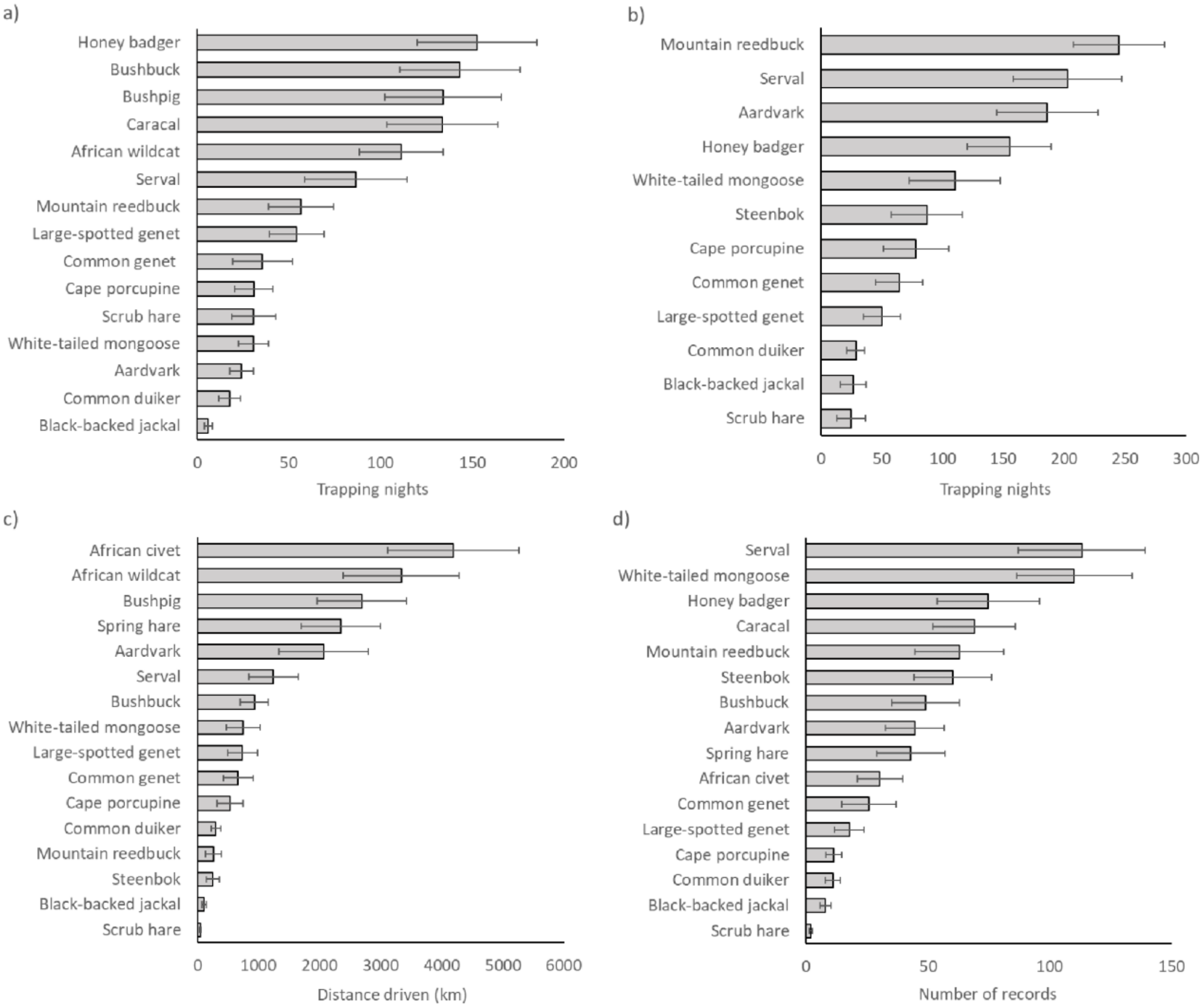

Figure 5 Average effort needed for discovery of specific species for: (a) targeted camera traps against trapping nights; (b) random camera traps against trapping nights; (c) driven transects against kilometres travelled; and (d) driven ad hoc records. Error bars show 95% confidence intervals.

Discussion

Each of the four methods considered here (targeted camera traps; random camera traps; driven transects; ad hoc records) were successful in detecting at least 60% of known nocturnal mammal species over a 20-month period. Driven transects and driven ad hoc records were the most successful techniques in terms of the overall number of species detected, but only outperformed targeted camera traps by one species and random camera traps by four species. Despite this relative similarity in total diversity, Jaccard's Coefficients of Community similarity peaked at 0.78, showing notable differences in the communities sampled with the different methods despite a large sample effort and all species discovery curves starting to plateau.

The nocturnal and crepuscular mammal species detected by the different methods likely differed for a number of reasons, all of which link to the likelihood of encountering a species at a given location and time and/or the likelihood of actually detecting that species. Driven transects are more likely to encounter species that are close to, and in some cases positively associated with, roads (di Bitetti et al. 2014; Cooke et al. 2020). This includes species such as black-backed jackal, which use roads for travel and as good areas either to hunt or scavenge (van de Ven et al. 2013), or species that make use of use roads for thermoregulation (Wagner et al. 2021). Conversely, species that are deterred by vehicles, avoid open ground, or are suspectable to habitat edge effects are less likely to be encountered using driven methods (Thorn et al. 2010). Moreover, because of the use of headlights and spotlights on nocturnal driven transects, this method is more likely to detect species that have notable eyeshine. Eyeshine is found in felids, canids and many ungulates, as well as viverrids (genets in this study) but it absent from some primates (including humans), bushpigs, aardvarks and also pangolin (Manidae), where its absence often leads to an under-recording of presence (Wilcox et al. 2019). Indeed, eyeshine is such a prominent and distinctive phenomenon that it is often, in practice, the dominant cue used to detect and subsequently identify mammal species in methods relying on artificial light (Thorn et al. 2010). Despite this, we found only weak evidence to suggest that absence of eyeshine influenced detection. Aardvarks, lacking eyeshine, were detected with less effort in targeted camera traps (where eyeshine is irrelevant; only duiker and jackal requiring fewer trapping nights) than in either driven method, but bushpigs were equally hard to find in the two methods (targeted camera traps and driven transects) that detected them. Species detectability is also influenced by behaviour (whether individuals are disturbance sensitive and move quickly away from approaching vehicles, possibly before they are even sighted), size and camouflage, as well as whether individuals are at ground level in open habitat (i.e. on the road itself) or whether they are arboreal or semi-arboreal, such as galagoes (Galagidae) and, in this study, genets (*Genetta*); as well as non-mammal species such as chameleons (Chamaeleonidae) and owls (Strigiformes).

Targeted camera traps were, unsurprisingly, more effective than random camera traps but traps at random locations still yielded 12 species (versus 15 for targeted): both were inferior to driven transects where 16 species were detected. Although random camera traps were successful at generating presence data for nocturnal mammals, the method did miss 8 species and it was notable that it was species more likely to be scared and/or elusive that were missed (for example, random camera traps missed two of the three felids detected by other methods, cape bushbuck and bushpig). Moreover, there were considerably fewer overall triggers, and thus fewer images, for random camera traps relative to targeted camera traps and thus fewer replicates and a larger number of nights with no-captures. Overall, though, random camera placement still seems more effective than might be commonly assumed. Although this could be strongly influenced by habitat, it is notable that our results echo the findings of Gray (2018) in tropical forest in southwest Cambodia, where randomly-deployed cameras where highly successful in monitoring forest ungulates and also detected elusive predators such as clouded leopard (*Neofelis nebulosa*), and Asiatic black bears (*Ursus thibetanus*). Indeed, in another study in Eastern African, Cusack et al. (2015) showed that random and targeted camera traps, in this case with targeted cameras being positioned on game trails, had caused little difference in overall community structure detected, although, as in our study, there were some species-specific differences with African wild dogs (*Lycaon pictus*) being detected only by targeted cameras and ground pangolins (*Smutsia temminckii*) only by random cameras. Cusack et al. (2015) went as far as suggesting that if extensive surveys could be conducted (> 1400 trapping nights) randomly-placed cameras may even yield a more complete list of species, whilst also suggesting that researchers with less time or not many camera traps available, trail-based cameras would produce more detections more rapidly. Where random placement will likely fail is for species that are strongly associated with specific targets (water in the case of our study) and occur at very low density, where chance encounters at any given random location will occur with a low probability. Randomly placed traps may have a greater probability of detecting species that do not frequent water sources or other target locations (such as well-used game trails) and in this study, randomly placed camera traps detected steenbok which were not detected by targeted traps. Detectability will, of course, be highly dependent on habitat and species composition but nonetheless we suggest that more consideration should be given to randomly placed traps, and that for some species such an approach may be far better than traditional targeting camera traps at, for example, water sources.

Notably, and unexpectedly, we found that driven ad hoc records converged with the species detected by all of the more formal methods better (CCj = 0.72-0.78) than those formal methods converged with each other (CCj = 0.65-0.68). Furthermore, ad hoc records tied with driven transects in terms of total species detected, failing only to detect African wildcat and bushpig to the sum of the species detected across all three formal methods. The fact that driven ad hoc records were so successful in detection, and so efficient in terms of effort, whilst being gathered incidentally served to highlight how valuable such records can be. Sightings books, and mobile applications that record visitor sightings, are widely-used (Blenkinsop et al. 2018), and this study strongly suggests that they can be highly effective for nocturnal mammal presence surveys. Given how widespread their use is, serious attention should be given to ways that these records can be formally integrated into wider surveying and related management activities.

Data permutation revealed the importance that chance has in the success of all methods of mammal detection. For example, if a targeted camera trap was left out for 10 nights, a realistic deployment duration in this habitat, the range of species detected varied from just one to nine (half the total detected species in this study). Driven transects were similarly variable, with 500 km of driving yielding a detection range of four to 11 species. The high variability in detection revealed by this bootstrapping-without-replacement method shows how difficult it is in practice to recommend minimum survey effort for the survey methods used, and that caution is necessary to avoid over-interpreting differences between methods, especially for scarce species that are, de facto, likely to be infrequently recorded. It also shows that considerable effort can be required, especially if there is little prior knowledge on which, and how many, species are present. Interestingly, the species detection curves were similar for both random and targeted camera traps despite the considerably higher number of overall detections for the later. This was because the large number of nights where no species were sighted at random locations was matched by a large number of same-species (and possibly same-individual) repeats at targeted locations and suggests that number of triggers is not a good indicator of species richness.

Overall, our findings highlight the large amount of effort that is required to survey nocturnal mammals, even with targeted camera trap placement and formal, regular driven transects. Given the importance of determining species presence for management and conservation decisions, we suggest that mixing methods, using different camera placement including use of random locations, and especially incorporating cost-neutral ad hoc records into survey efforts can all greatly increase the overall effectiveness and efficiency of species detection. This is especially true for scarce species, where records from any method will likely be infrequent and influenced by chance. If resources prohibit a robust mixed-method approach then we suggest making full of cost-neutral ad hoc sampling, including implementing vehicle sightings books, visitor log books in accommodation, viewing areas and hides, and mobile-phone based sightings groups using social media or messaging applications.

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Statements and Declarations

Competing Interests

The authors have no competing interests to declare that are relevant to the content of this article.

Data Availability Statement

The datasets generated during and/or analysed during the current study are available from the author on request.

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