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RESEARCH ARTICLE

Combining detection dogs and camera traps improves minimally invasive population monitoring for the cheetah, an elusive and rare large carnivore

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Abstract

1. Monitoring large carnivores is imperative for conservation planning, but is difficult due to their elusive behaviour and natural rarity. Some carnivores such as the cheetah (*Acinonyx jubatus*) are particularly wide ranging and often go undetected despite being present, or are detected at rates too low to make meaningful quantitative inferences. The combination of minimally invasive survey techniques, such as detection dog surveys and camera traps, holds promise for improving monitoring efforts of large carnivores.
2. We surveyed a cheetah population within the Acacia savanna biome of central east Namibia, employing various search strategies and camera trap configurations. We analysed detection data in an occupancy framework and estimated the effort required to confirm cheetah presence with 95% certainty.
3. We found that sign surveys required intensive field effort when walked as road transects, but detections of scat by the detection dogs were twice that of tracks (5/100 and 2.5/100 km, respectively, 7.5/100 km combined). Vehicular searches to identify cheetah marking sites appear to be an efficient alternative or complementary approach (3.8/100 km), if a road network is available and marking sites are visually distinguishable. The detection probability (p) of cheetahs with one camera trap station per sampling unit placed at roads was low ($p = 0.167$), but increased for camera traps placed at marking sites that were identified through the detection dog survey ($p = 0.244$), and in particular when multiple camera trap stations were placed per sampling unit and detections were pooled across stations

Stijn Verschueren and Tim Hofmann contributed equally to this manuscript.

($p = 0.348$–0.750). The minimum survey effort required to reliably detect cheetahs in each 256 km^2 sampling unit was estimated to be 45 km or 10 h of walking, 123 km or 5 h of driving or 150 nights of camera trapping.

4. *Practical implications*. We showed that complementing detection dog surveys with camera trapping can comprehensively and efficiently inform occurrence patterns for an exceptionally wide-ranging terrestrial carnivore. Our findings provide practical guidance for designing effective minimally invasive monitoring programmes, which are important for empirically deriving distribution maps of cheetahs and other carnivores in data-poor regions.

KEYWORDS

Acinonyx jubatus, detection, non-invasive sampling, occupancy, predator monitoring, scat detection, species distribution

1 | INTRODUCTION

Species distribution patterns are fundamental for conservation assessments, in particular for keystone species such as large carnivores that impart important trophic functions (Ripple et al., 2014). Monitoring large carnivores poses challenges, due to their elusive and wide-ranging nature, making them difficult to detect (Long et al., 2008). Consequently, distribution maps may lack accuracy, and for many species, comprehensive information on their conservation status remains unknown across a substantial portion of their range (Strampelli, Campbell, et al., 2022).

Various minimally invasive survey techniques have emerged in carnivore research programmes, which can substantially improve species detections and monitoring efficiency (Kelly et al., 2012). These methods include the use of passive detectors such as motion and heat-triggered cameras (Burton et al., 2015), and the search for indirect signs of presence, such as tracks, scat, hair and kill, remains (Karanth et al., 2011). In addition, the genetic verification of signs such as scat or hair to confirm species of interest is becoming increasingly accessible and minimizes false-positive detections (Palomares et al., 2002). Presence data can be used to infer on carnivore distributions using quantitative modelling approaches (Cristescu et al., 2019) and analytical advancements have enabled accounting for imperfect detection (or false negatives/non-detections), often within an occupancy framework with various adaptations tailored to different species, methods and habitats (MacKenzie et al., 2006).

Among large carnivores, cheetahs (*Acinonyx jubatus*) present a particularly challenging case for population monitoring, given their low population densities and extensive home ranges, which are thought to be related to their avoidance strategy of dominant carnivores (Durant, 1998; Marker, Cristescu, et al., 2018). Despite methodological and analytical developments, many surveys targeting African large carnivores often fail to detect cheetahs, or at rates too low to be used in a reliable modelling framework (Strampelli, Henschel, et al., 2022; Van der Weyde et al., 2018; Verschueren et al., 2021; Williams et al., 2016). One study estimated that a minimum of 193 camera trap nights are needed, or 16 km to be walked on transects to confirm cheetah presence in a given 100 km^2 area (Andresen et al., 2014), while in arid and low cheetah density areas of Algeria, even >1000 camera trap nights are required across a 2500-km^2 study area (Belbachir et al., 2015). Furthermore, the sociospatial organization of cheetahs, where territorial males occupy substantially smaller home ranges compared to non-territorial males and females (Melzheimer et al., 2020), challenge density estimation methods such as spatial capture–recapture (Edwards et al., 2018; Linden et al., 2020). In addition, estimating population density from the frequency and abundance of track counts encountered during sign surveys may be too imprecise to be meaningful (Dröge et al., 2020), although various efforts have attempted to do so for cheetah (Henschel et al., 2020; Houser et al., 2009; Williams et al., 2016). As such, vast gaps remain in our knowledge of cheetah population status and distribution (Verschueren et al., 2024), while the species is facing severe population declines (Durant et al., 2017).

The scent-marking behaviour of cheetahs presents an opportunity for minimally invasive population monitoring (Brassine & Parker, 2015; Marnewick et al., 2008). Marking sites are concentrated in core territories of males that are sparsely distributed throughout the landscape (Melzheimer et al., 2020). These marking sites are often prominent landscape features such as large trees, termite mounds or rocky outcrops (Caro, 1994; Walker et al., 2016), yet previous efforts to identify these sites have either relied on long-term monitoring efforts or invasive methods such as GPS satellite trackers (Fabiano et al., 2020; Melzheimer et al., 2020). Notably, detections at marking sites are biased towards territorial males and detecting females remains challenging (Cornhill & Kerley, 2020).

Pooling detections from multiple camera trap stations deployed within the same sampling unit presents a promising way to achieve the minimal required number of camera trap nights to meet statistical modelling assumptions within a feasible and demographically closed study period (Evans et al., 2019). In addition, the use of trained detection dogs for wildlife surveys is becoming increasingly popular and could substantially increase detections of target species signs, especially

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compared to traditional searches with human observers (Becker et al., 2017; Grimm-Seyfarth et al., 2021; Hofmann et al., 2021). Complementing multiple detection methods may improve estimates of occupancy and detection probabilities (Miller et al., 2019). While some efforts have focused on comparing and combining camera trapping and detection dog surveys (Clare et al., 2015; Cozzi et al., 2021; Harrison, 2006; Long et al., 2007), no such comparison has been conducted for an extremely wide-ranging African carnivore such as the cheetah to our knowledge.

Here, we present the complementarity of two minimally invasive methods, camera trapping and scat detection dog surveys to confirm the presence of an elusive and rare large carnivore, the cheetah. By empirically testing different field methods and their possible combinations, we aim to improve the detection of the species. The two techniques have the potential to be easily expanded and replicated in other parts of the cheetah's range and we further provide practical recommendations for an optimal study design and minimal survey effort required for the detection of wide-ranging carnivores.

2 | MATERIALS AND METHODS

2.1 | Study area

The study area covered 2048 km^2 of farmland in the Omaheke region of central east Namibia (21.83511° S, 18.68592° E). The area experiences an annual rainfall of approximately 350–400 mm, primarily occurring from November to April (Atlas of Namibia Team, 2022). Our survey was conducted during the dry season (May–October) in 2021, to maximize the chances of finding scat (Reed et al., 2011). In addition, the lower grass cover outside the wet season may improve camera trap detection probability (Moll et al., 2020). The study area consists of private farms with an average size of 45 km^2. The area is characterized as Acacia tree-and-shrub savanna with deep sandy soils providing limited water and nutrient retention. The predominant land use activity is cattle farming, while there is some small stock farming, irrigated crop cultivation, hunting, tourism and game breeding (Atlas of Namibia Team, 2022). Most farms are stock-fenced, allowing unrestricted wildlife movement while limiting livestock. A smaller number of farms are game-fenced, which restricts movement of larger game but permits movement of smaller game, including predators (Cozzi et al., 2013).

The area is situated within a global stronghold for the cheetah (Weise et al., 2017). Larger predators such as lions (*Panthera leo*), African wild dogs (*Lycaon pictus*) and spotted hyaenas (*Crocuta crocuta*) are absent, while brown hyaenas (*Parahyaena brunnea*) and leopards (*Panthera pardus*) are present but in low numbers (NCE et al., 2022). The area is rich in potential cheetah prey species, including eland (*Taurotragus oryx*), greater kudu (*Tragelaphus strepsiceros*), gemsbok (*Oryx gazella*), red hartebeest (*Alcelaphus buselaphus*), warthog (*Phacochoerus africanus*), springbok (*Antidorcas marsupialis*), common duiker (*Sylvicapra grimmia*), steenbok (*Raphicerus campestris*) and scrub hare (*Lepus saxatilis*). Throughout the study area, cheetahs are assumed to be resident and present in higher densities than in other parts of their range (Weise et al., 2017); hence, this provided an ideal scenario to estimate detection successes of various search strategies and camera trap configurations without conflating non-detections with species absence.

We overlaid the study area with a rectangular grid consisting of eight cells or sampling units, each measuring 16 km × 16 km (Figure 1). One sampling unit (256 km^2) approximated the minimal home range of cheetahs in comparable ecosystems (Marker et al., 2008; Melzheimer et al., 2018). Each sampling unit was further divided into four quadrants, each measuring 8 km × 8 km. This design ensured an optimized spatial representation for both methods within the study area.

2.2 | Detection dog-based sign survey

We define detection dog-based sign survey (hereafter named 'detection dog survey') as the combination of scat detection dog transects (T), executed on foot to find cheetah scats and tracks and vehicular searches (V) aiming to detect conspicuous marking sites which were then investigated by the detection dog (Figure 2; Table 1). These differed from traditional sign surveys as the main focus was on detecting scat rather than other signs of cheetah presence (kills or tracks).

The 'dog-team' consisted of a trained scat detection dog (spayed female Belgian Malinois), a dog handler and a field technician. The detection dog was trained to alert to cheetah scat by sitting next to it. The training and handling of the dog adhered to general principles in this field of work (Smith et al., 2003; Wasser et al., 2004). At the commencement of the survey, the dog had approximately 2 years of field experience and was evaluated as performing adequately for field work (T. Hofmann, submitted). The dog handler was an experienced field ecologist familiar with identifying carnivore tracks in the study system.

Within each 64 km^2 quadrant, the dog team conducted two transects (T) of 2 km length leading to eight transects per sampling unit and 16 km transect length. The starting points of the eight transects were selected based on accessibility from a pool of 24 random locations generated using GIS software (QGIS 3.24.2 Tisler), ensuring a minimum distance of 2 km between locations and random coverage of the sampling unit. Whenever feasible, the transects were walked into the wind to enhance the chances of detecting scat samples (T. Hofmann, submitted). Transects were walked during the cooler hours of the day in the early mornings and late afternoons to enhance dog performance, with a maximum of 10 km walked per day.

The vehicular surveys (V) were executed in each 256 km^2 sampling unit according to the existing road network, and thus differed in length between sampling units (see Section 3). Potential marking sites, predominantly distinct trees in this area, were investigated by the dog team after initial identification from the vehicle. If scat was detected, the marking site was used as candidate for camera trap placement (see Section 2.4; Table 1). If no scat was detected but the site had the presumably right environmental characteristics (Walker et al., 2016), it was recorded as potential marking site and used as a camera trap location if no confirmed marking site was available in a quadrant.

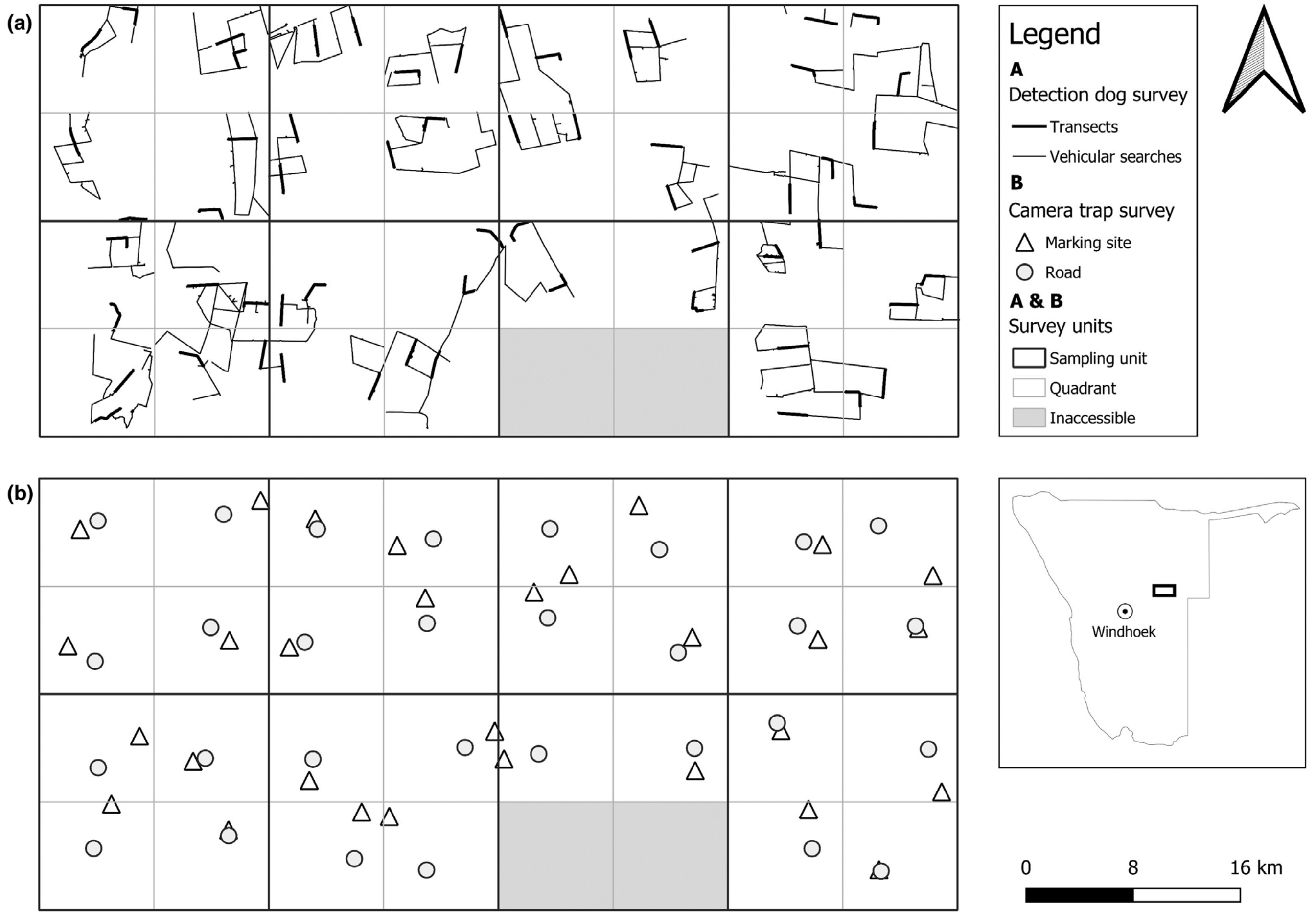

FIGURE 1 Schematic study area map of survey effort conducted for the detection dog survey (a) and the camera trap survey (b) targeting cheetah detection in central east Namibia.

We estimated survey effort in time (h), based on the following speed estimates: 4.5 km/h for walking transects (T), which we inferred from the time taken to complete 2 km transects, and 25 km/h for vehicular searches (V), which allowed for careful scanning of the surroundings and identifying potential marking sites.

When a sign (track, kill or scat) of cheetah presence was detected, its location was recorded using a handheld GPS device (Garmin Alpha 100). Multiple samples found at one marking site were considered as one detection. In the case of scat detections, dry samples were placed in sealable plastic zip-lock bags, while wet samples were stored in plastic tubes containing approximately 22 g of silica gel beads to ensure the preservation of DNA. All samples were frozen upon arrival at the Cheetah Conservation Fund (CCF) and maintained at −20°C until extraction.

2.3 | Genetic species verification

We verified the species identity of samples indicated as cheetah by the detection dog at CCF's Namibia-based conservation genetics laboratory. We used a mitochondrial mini-barcode (primers ATP6-DF3 and ATP6-DR1; Chaves et al., 2012; Haag et al., 2009), shown to successfully amplify and differentiate Namibian carnivores (Wong et al., 2024), to match one sample per individual to a species reference sequence database.

We extracted the scat samples with the QIAamp® Fast DNA Stool Mini Kit (QIAGEN) following manufacturer's recommendation, with the following modifications: We varied the amounts of scat, starting with 100 mg for the first extraction, and we reduced the elution volume to 100 μl to improve DNA concentration. We attempted up to three extractions per sample and up to six PCR amplifications per extraction, and sequenced successful amplicons using the ATP6-DR1 primer. We verified species identity based on alignment to reference sequences in Geneious Prime 2022.1 (https://www.geneious.com).

2.4 | Camera trap survey

Within each 256 km^2 sampling unit, we placed eight camera trap stations, targeting two location types per quadrant (Figure 2; Table 1). We deployed one station alongside roads intersecting with a wildlife trail, within a 2-km radius of each quadrant's centre (Road cameras, R). The second station was placed at confirmed marking sites

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identified through the detection dog survey if possible (Marking site cameras, M; see Section 2.2). Each station consisted of two camera traps that aimed to photograph both sides of the target animal and no bait or lure was used. Camera trap stations remained active for at least 60 days and were serviced halfway through the study period.

We used Browning Strike Force Pro XD cameras with infrared flash. Road cameras were set to take a burst of five images with a 5-min delay between triggers, while marking site cameras were configured to take a burst of three images with a 1-min delay between triggers. The difference in camera trap settings was based on the differential behaviours of cheetahs at roads and at marking sites. Camera trap images were sorted to species-level using TrapTagger, an open-source web application that uses artificial intelligence along with a manual annotation interface for processing camera trap data (WildEye, 2023). We relied on MegaDetector built into TrapTagger for the detection of animals and the removal of empty images. We manually annotated all detections using the TrapTagger interface and subsequently verified these with AI-generated annotations based on a southern African species classifier.

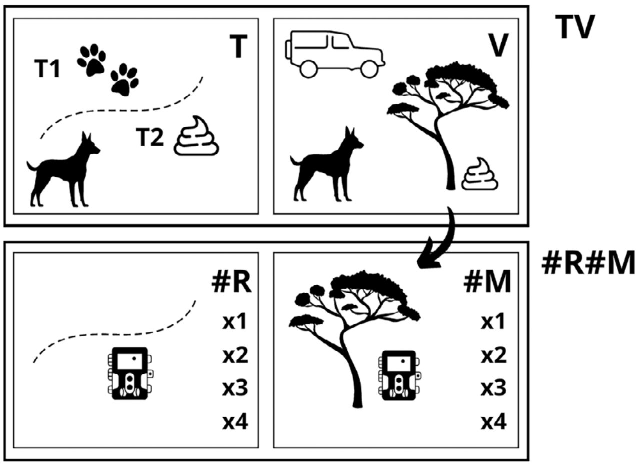

FIGURE 2 Diagram visualizing the various search strategies of the detection dog-based surveys (top) and the camera trap configurations (bottom). The various combinations used to confirm cheetah presence in one sampling unit are represented to the right of the figure. The dashed line represents a road, the paws represent cheetah tracks, and the scat pile cheetah scat which was either found at a marking site or randomly on or near a road. The tree represents a cheetah marking site the arrow symbolizes that the trees found by the detection dogs are then used as camera trap station. T = Transect, V = Vehicular survey, R = Camera trap at road, M = Camera trap at marking site. The letter codes are further described in Table 1.

2.5 | Data analysis

We summarized our detection data descriptively by presenting the number of detections per survey method. For the detection dog survey, we calculated detection frequency as the number of signs encountered per 100 km covered. For the camera trapping survey, we calculated the capture rate as the number of independent (i.e. >30 min between captures) cheetah captures per 100 camera trap nights.

We analysed our data in an occupancy modelling framework, where we kept occupancy constant, while including detection

TABLE 1 Methodological overview of the different search strategies and camera trap configurations to detect the presence of cheetahs.

Detection covariate	Detection method	Sampling occasion	Detection	Effort per sampling occasion
1. Search strategy	Transect (T1)	1 quadrant; 4 occasions	Track on transect	4 km transect walked by dog team
	Transect (T2)		Scat on transect	
	Transect (T)		Track or scat	
	Vehicular surveys (V)		Marking site (with scat)	16.67 km (6.1–31.7 km) driven by dog team
	Combination (TV)		All signs on transects and vehicular surveys	Combined effort transects and vehicular surveys
2. Camera trap configuration	Road cameras (#R)	14-day period; 4 occasions	Detection at ≥1 station in the configuration. Detections in the same configuration for the same sampling unit are pooled across camera trap stations.	Station placed at road locations in the centroids of quadrants, ranging from 1 to 4 stations per sampling unit with a 60-day activity time
	Marking site cameras (#M)			Station placed at marking site locations identified by sign transects and vehicular surveys, ranging from 1 to 4 stations per sampling unit with a 60-day activity time
	Combination (#R#M)			Combination of stations placed at road and marking site locations, ranging from 2 to 8 stations per sampling unit with a 60-day activity time

covariates to account for different search strategies related to the detection dog survey and different configurations of camera trap stations related to the camera trap survey (Figure 2; Table 1). Two independent occupancy models were constructed: one model incorporated various combinations of search strategies as detection covariates for the detection dog survey, where sampling occasions reflected spatial replicates (i.e. quadrants; 4 occasions); and a second model included various camera trap configurations, where sampling occasions reflected temporal replicates (i.e. 14-day sampling period; 4 occasions). We selected subsets and resampled our data to allow the various combinations of search strategies ($n_{dog}=5$; Table 1) and camera trap configurations ($n_{camera}=24$; Table 1); hence, the number of sampling units considered in the occupancy models was a multiple of the actual sampling units covered during the survey ($n=8$) and the number of combinations considered for the detection dog survey and camera trap survey, respectively. Our analysis considered variation in detection among sampling units, while detection probability among sampling occasions was assumed constant as sampling occurred within the same season. We used the R package *unmarked* (Fiske & Chandler, 2011) in R version 4.2.2 (R Core Team, 2022) to construct the occupancy models.

The cumulative probability p_k of detecting cheetahs at least once at a given sampling unit after k repeat sampling occasions was calculated using the formula $p_k=1-(1-p)^k$ where p is the per-survey detection probability of the detection method used. Following this, the minimum number of sampling occasions required (N_{min}) to reach a cumulative detection probability of 0.95 within a given sampling unit was calculated as: $N_{min}=\log(0.05)/\log(1-p)$ (Andresen et al., 2014). This was interpreted as confirming cheetah absence with 95% certainty if cheetahs remained undetected for the effort conducted over N_{min}. Hence, minimal survey effort required to either confirm cheetah presence or absence with 95% certainty was calculated as the effort per sampling occasion multiplied by N_{min}, although the realized effort for detecting cheetahs was most likely be lower when cheetahs are present.

The optimal camera trap configuration was identified based on the configuration that resulted in the lowest sum of field days (the number of days during which camera traps were active) and camera trapping days (field days multiplied by the number of camera trap stations). This allowed us to determine the configuration that required the fewest camera trap stations for the shortest period of time while achieving a 95% certainty in inferring cheetah presence. We considered 90 days as an upper threshold to satisfy assumptions of demographic population closure for large carnivores (Karanth et al., 2004); hence, only camera trap configurations that required fewer than 90 field days were considered suitable.

2.6 | Permits and ethical standards

The research was authorized by the Namibian National Commission on Research Science & Technology under Section 21 of the Research Science and Technology Act No. 23 of 2004. The execution of data and sample collection was performed under the research permit number AN202101032 of the Cheetah Conservation Fund (Namibian-based Institute RCIV00122018). Fieldwork took place with consent of the landowners. We followed the ethical code of conduct for the use of camera traps in wildlife research (Sharma et al., 2020). The training and handling of the detection dog was endorsed by the animal welfare officer of the University of Goettingen.

3 | RESULTS

We obtained data from all quadrants of seven sampling units. For the eight sampling unit, two quadrants were omitted due to limited access on private land (Figure 1). Based on each detection method independently (detection dog survey vs. camera traps), we confirmed cheetah presence in all 256 km^2 sampling units, resulting in a naïve occupancy of 1.

Across 60 transects (120 km total) walked, our dog team detected cheetah scat at six locations, of which three were marking sites and three were randomly placed on or near roads, and three cheetah tracks. We derived a detection frequency of 5.0/100 km for scats on transects and 2.5/100 km for tracks on transects, leading to a total detection frequency for signs of presence (scat and tracks) of 7.5/100 km. Furthermore, we identified 19 marking sites and 1 cheetah kill (cattle calf) on 500 km of vehicular searches (averaging 62.51 km ± 20.30 per sampling unit), leading to a detection frequency of 3.8/100 km and 0.2/100 km, respectively. The combined detection frequency for vehicular searches was 4.0/100 km. The detection of the cheetah kill was omitted from the occupancy analysis because we only had one detection.

The probability of detecting cheetah presence through signs was lowest when we only considered cheetah tracks found during transects ($p_{T1}=0.067$) (Figure 3; Table S1). It increased when we only considered scats found on transects ($p_{T2}=0.167$) or incorporating of all signs of cheetah presence identified while walking transects ($p_T=0.233$), and was highest for marking sites found during vehicular surveys ($p_V=0.333$). The combination of transects and vehicular searches lead to a detection probability of $p_{TV}=0.469$. The minimal survey effort required to detect cheetah presence with 95% certainty was 173 km or 38 h when only considering cheetah tracks found on transects, 66 km or 15 h when only considering scats found on transects, 45 km or 10 h when considering both tracks and scats found on transects, and 123 km or 5 h when conducting vehicular searches to identify marking sites (Table S1).

From the camera trap survey, we detected cheetahs independently 13 times at 10 of the 30 road locations, and 55 times at 13 of the 30 marking site locations over 3720 camera trap nights, leading to a capture rate of 0.27/100 days and 1.48/100 days, respectively. The probability of detecting cheetahs was lowest when we only considered one road station placed per sampling unit ($p_{1R}=0.167$; Figure 4; Table S2). The detection probability increased when we considered camera trap stations placed at marking sites ($p_{1M}=0.244$) and, in particular, when we considered multiple camera trap stations

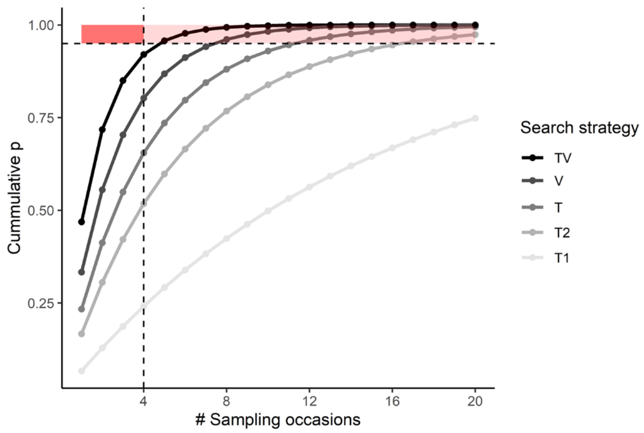

FIGURE 3 Cumulative probability of detecting cheetah signs with detection dog surveys at least once at a 256-km^2 sampling unit in relation to the number of sampling occasions using different search strategies. Effort of one sampling occasion corresponds to 4 km walked, or 16 km driven. The red box indicates the survey effort required to confirm cheetah presence with 95% certainty. The area left of the dashed line (dark red box) indicates the number of sampling occasions achieved in this survey, while the area on the right (light red box) represents the estimated required effort. The greyscale reflects the number of sampling occasions (spatial replicates) required for various search strategies, with darker colours requiring fewer occasions. V = Vehicular survey, T# = Transect variations, TV = Combination of transects and vehicular survey.

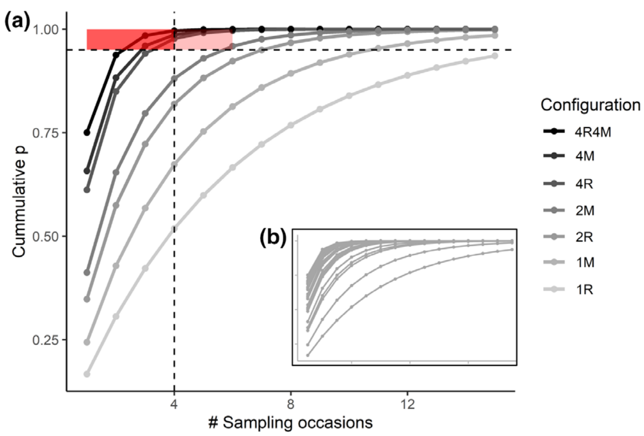

FIGURE 4 Cumulative probability of detecting cheetahs at least once in a 256-km^2 sampling unit in relation to the number of sampling occasions for specific camera trap configurations of interest (a) and all camera trap configurations (b; see Table S2). Effort of one sampling occasion corresponds to a 14-day activity period. The red box indicates the survey effort required to confirm cheetah presence with 95% certainty within a demographically closed population (i.e. 90-day period or six sampling occasions). The area left from the dashed line (dark red box) indicates the number of sampling occasions achieved in this survey, while the area on the right (light red box) represents the estimated required effort. The greyscale reflects the number of sampling occasions (temporal replicates) required for various configurations, with darker colours requiring fewer occasions. R = camera at road, M = camera at marking site, #R#M = Configuration of cameras placed at roads and marking sites.

with pooled detections per sampling unit (e.g. $p_{4R4M}=0.750$). The increments in detection probability were greatest when shifting from one to two stations and then gradually reduced (Figure 4; Table S2). The minimal survey effort required to detect cheetah presence with 95% certainty ranged from 30 to 230 field days and 150–242 camera trap days depending on the configuration (Table S2). The optimal configuration was the placement of camera trap stations at four marking sites ($p_{4M}=0.657$; 39 field days, 156 camera trap days), while the configuration with four road camera trap stations was also among the better configurations ($p_{4R}=0.612$; 44 field days, 177 camera trap days; Figure 5). Configurations where the estimated number of field days exceeded 90 days to reliably infer cheetah absence violated the demographic closure assumption, as was the case for traditional configurations with only one station placed per sampling unit, even if the station was deployed at a marking site.

4 | DISCUSSION

Identifying marking sites during the detection dog survey substantially improved the probability of cheetah detection compared to only considering tracks and scats detected away from marking sites. Similarly, including these marking sites in camera trap configurations with multiple stations per sampling unit yielded higher detection rates compared to camera traps placed at roads. Traditional monitoring strategies deploying a single camera trap station per sampling unit, or relying solely on track detection from transects, may thus fail to detect some of the widest ranging species, such as

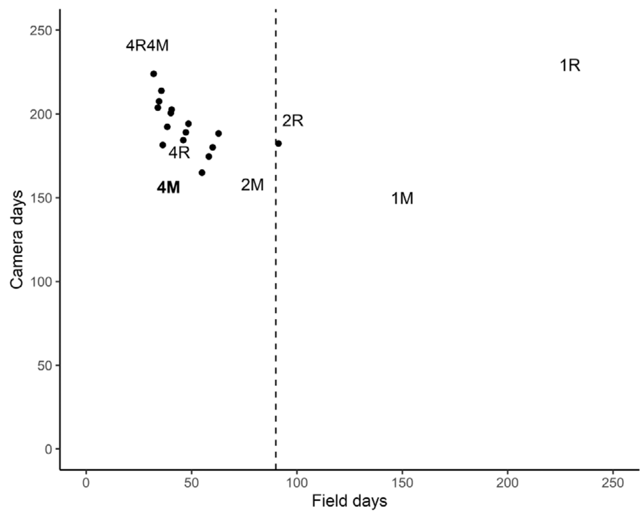

FIGURE 5 Relationship between field days and camera trap days required to confirm cheetah presence with 95% certainty based on different camera trap configurations and with labels representing the points of specific configurations of interest. The dashed line indicates the available window of 90 field days to assume demographic closure. R = camera at road, M = camera at marking site #R#M = Configuration of cameras placed at marking sites and roads. The configuration in bold (4M) was the optimal configuration.

the cheetah. This is supported by the low detection rates in earlier studies (Strampelli, Henschel, et al., 2022; Verschueren et al., 2021; Williams et al., 2016) and underscores the importance of marking sites for cheetah population monitoring (Brassine & Parker, 2015; Marnewick et al., 2008). Unlike previous efforts that relied on long-term and/or invasive monitoring programmes, our systematic approach identified marking sites without prior knowledge of the study area in a minimally invasive way. This method therefore offers potential for easy replication and expansion into understudied regions. We acknowledge that detection probability is ultimately dependent on population density and the environment of the study area. However, the methodological comparison of various search strategies and camera trap configurations remains broadly relevant to inform the study design of population monitoring programmes targeting cheetahs and other species with localized areas of frequent use (Campbell-Palmer & Rosell, 2011).

The combination of all signs of presence from transects (track + scat frequency) led to a detection frequency of 7.5/100 km, showcasing the complementary strength of detection dogs in sign surveys. Notably, our frequency of track detection was towards the upper range of previous efforts, even though our focus was on scat detection [Track frequency in our study: 2.5/100 km vs. 0.49/100 km (Strampelli, Henschel, et al., 2022), 0.97/100 km (Williams et al., 2016), 2.32/100 km (Houser et al., 2009), 2.4/100 km (Henschel et al., 2020), 7.26/100 km (Andresen et al., 2014)]. This relatively high detection rate may be explained by the higher cheetah density in our study area. Our frequency of scat detections was comparable to previously reported frequency of confirmed scat detections [5/100 km vs. 4.95/100 km (Becker et al., 2017)]. Their study assumed smaller minimum home ranges as sampling sites and searched mainly off road, while we conducted transects solely along roads. Cheetahs may minimize the use of roads to avoid larger predators such as leopards (Rafiq et al., 2020) or humans (Van der Weyde et al., 2017), although territorial males in the Kruger National Park, South Africa, concentrated marking activities along roads (Broomhall et al., 2003). Investigating road use by cheetahs and walking transects on game trails away from roads may provide additional insights. Additionally, variations in detection frequencies can also be explained by different working characteristics of the individual dog teams (Long et al., 2008).

Restricting survey efforts to walking transects would demand an intensive effort to reliably infer the absence of cheetahs, even with the support of a detection dog. Our estimated effort required (45 km or 10 h for 256 km^2) was considerably higher than our current effort of 16 km or 4 h per sampling unit, and also our vehicular searches for marking sites required larger distances per sampling unit (123 km or 5 h for 256 km^2) relative to our current effort (62 km or 3 h for 256 km^2). Vehicular searches appeared to be a time-efficient alternative to walking transects requiring only about half the time per sampling unit if cheetah absence was to be reliably inferred, as long as roads are available and marking sites are conspicuous. On the other hand, our dog also detected cheetah scat at sites that did not match the typical characteristics described for marking sites (Walker et al., 2016) and those would have remained undetected by human observers during vehicular searches. Therefore, choosing the appropriate sampling approach will depend on the circumstances in the study area. Since much of the cheetah's range may have poor road network, walking transects may be the only possible approach if sign detection, in particular scat collection, is a primary study objective, and specifically from females and non-territorial males as only territorial males frequently defecate at marking sites (Cornhill & Kerley, 2020). Vehicular searches may be suitable to monitor populations where cheetahs consistently visit conspicuous marking sites (Caro, 1994; Melzheimer et al., 2020).

We identified a similar pattern from our camera trap survey, where camera trap stations placed at roads yielded lower probabilities of detecting cheetahs compared to camera trap stations placed at marking sites, concordant to earlier studies (Brassine & Parker, 2015; Fabiano et al., 2020). In addition, targeted camera trap placement at marking sites may not only increase the probability of detecting territorial males, but likely also improve chances of capturing individuals of different sex and life-history stages that may only inspect marking sites (Melzheimer et al., 2020). In areas where marking sites are absent or remain undetected, the placement of multiple camera trap stations within the same sampling unit could be an alternative strategy as this approach substantially increased the probability of detecting cheetahs regardless of whether camera trap stations were placed alongside roads, at marking sites or included both features.

The optimal camera trap configuration required 39 field days with camera trap stations placed at four marking sites per 256 km^2 sampling unit. Little additional effort (i.e. 5 field days) was required when detections were pooled across camera trap stations placed at four road locations. However, with conservation programmes notoriously underfunded (Brooks et al., 2006), this camera trap-intensive design may not always be scalable across large study extents to accommodate for the cheetah's low density and wide-ranging behaviour. Configurations with fewer camera trap stations, and in particular when including marking sites, achieved comparable detection estimates while falling within the 90-day period to assume demographic closure. Across all configurations, the estimated number of camera trap nights required to infer cheetah absence averaged 192 camera trap nights per 256 km^2 sampling unit. Our data further show that using a single camera trap station per sampling unit to reliably detect cheetahs is failing to meet the closure assumption. Pooling detections across multiple camera trap stations within each sampling unit is recommended to improve monitoring efforts (Evans et al., 2019). However, this also suggests that obtaining enough spatial recaptures of individuals is difficult and may challenge density estimation methods such as spatially explicit capture–recapture models (Edwards et al., 2018).

While scat detection at marking sites generally resulted in subsequent camera trap observations of cheetahs at these sites, we also noticed several events where we failed to detect cheetahs with camera traps afterwards. Vice versa, we also detected cheetahs with camera traps at potential marking sites, that is, sites with the environmental characteristics of a marking site but where we failed to detect scat. Both observations could be attributed to infrequent visits of cheetahs to marking sites outside of core territories (Kusler et al., 2019). In addition, a few of these sites may have been located within a vacant territory at the time of the detection dog survey which was conducted earlier in the dry season than the camera trap survey.

While we presented a species-specific case study, our findings are broadly relevant for other species with challenging monitoring conditions. Sound ecological knowledge of the study species is key to designing practical monitoring programmes (Nichols & Williams, 2006). Hence, we built on the extensive insights developed on cheetah socio-spatial organizations over the past decades (Caro, 1994; Marker, Boast, & Schmidt-Küntzel, 2018; Melzheimer et al., 2020). We tailored two minimally invasive survey techniques to the monitoring challenges and needs of this wide-ranging species. Through identifying sites of concentrated use, we substantially increased the probability of detecting cheetahs using both survey methods. Localized areas of frequent use are not unique to cheetahs, with marking sites, latrines and leks commonly described for other species and greatly helping in monitoring programmes (Campbell-Palmer & Rosell, 2011). In the absence of such areas, our data suggest the placement of multiple camera trap stations within the same sampling unit as an alternative approach. The use of a detection dog tripled the frequency of detections when added to track counts and holds promise for expanded implementation if resources are available. In addition, the recent development of integrated occupancy models allows the combination of different data sources, which could substantially improve model estimates for surveys implementing multiple field methods simultaneously (Miller et al., 2019), and would allow covering larger landscapes with one study while adopting different methods based on what best suits the local conditions. We conclude that integrating camera trap surveys with insights gained from scat detection dog surveys holds potential for increasing detections, and the methodology outlined in our study provides guidance for monitoring efforts targeting wide-ranging carnivores.

AUTHOR CONTRIBUTIONS

Bogdan Cristescu, Tim Hofmann, Laurie Marker, Anne Schmidt-Küntzel and Stijn Verschueren conceptualized the study; Tim Hofmann, Benny Munyandi, Anne Schmidt-Küntzel and Stijn Verschueren curated the data; Tim Hofmann and Stijn Verschueren conducted the formal analysis; Niko Balkenhol, Bogdan Cristescu, Tim Hofmann, Laurie Marker and Anne Schmidt-Küntzel acquired the funding; Tim Hofmann, Mikael Kakove and Stijn Verschueren carried out the investigation; Bogdan Cristescu, Laurie Marker and Anne Schmidt-Küntzel administered the project; Niko Balkenhol, Hans Bauer, Bogdan Cristescu, Herwig Leirs, Laurie Marker, Stephan Neumann and Anne Schmidt-Küntzel supervised the work; Tim Hofmann and Stijn Verschueren drafted the original manuscript; all authors reviewed and edited the manuscript, contributed critically to the drafts and gave final approval for publication. Stijn Verschueren and Tim Hofmann contributed equally to the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data available from the Zenodo open data repository: https://doi.org/10.5281/zenodo.14524055 (Verschueren & Hofmann, 2024).

RELEVANT GREY LITERATURE

You can find related grey literature on the topics below on Applied Ecology Resources: Detection, Predator monitoring, Species distribution.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: Summary table of detection probability, minimum number of sampling occasions (N_{min}) and minimal effort required to infer cheetah absence with 95% certainty based on various search strategies for sign surveys (T1 = track on transect, T2 = scat on transect, T = track or scat on transect, V = vehicular survey, TV = combination of transects and vehicular survey).

Table S2: Summary table of detection probability, minimum number of sampling occasions (N_{min}) and minimal effort required to infer cheetah absence with 95% certainty based on various camera trap configurations (R = camera at road, M = camera at marking site, #R#M = Configuration of cameras placed at roads and marking sites).

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