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RESEARCH ARTICLE

Estimating mesocarnivore abundance on commercial farmland using distance sampling with camera traps

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Abstract

1. Mesocarnivores are of particular interest in wildlife management. Their adaptability makes them a focus of public attention globally, as negative interactions with people occur regularly, but their importance to wider ecosystem function is increasingly apparent. Robust methods for estimating mesocarnivore densities are essential for long-term management strategies. Estimating densities of unmarked populations remains challenging, but new methods, based on camera trapping, have recently become available and require field testing.
2. We conducted two camera trap surveys over two 200 km^2 areas of commercial farmland in South Africa. One survey sampled 25 locations, while the second used a migrating grid to sample 59 locations; total sampling effort was similar across the two surveys. We applied distance sampling with camera traps (CTDS), developing a method to estimate animal distances by applying a distance measurement overlay grid to camera trap images.
3. We aimed to establish meaningful density estimates of the mesocarnivore guild and evaluate CTDS's suitability for broader use with these types of species. We obtained density estimates for four carnivores, African civet *Civettictis civetta*, black-backed jackal *Canis mesomelas*, brown hyena *Hyaena brunnea* and caracal *Caracal caracal*, providing valuable insight into their status in commercial farmland. Imprecision in the estimates was almost exclusively due to encounter rate variance, which was not reduced with the migrating camera grid.
4. We explored the sensitivity of our results to assumptions determining the value of the 'snapshot interval', demonstrating that careful selection of this parameter is vital to ensuring reliable estimates when using rapid-fire photo burst modes.
5. CTDS can provide useful density estimates for mesocarnivores, but future studies should aim to maximize precision and reliability by increasing sampling locations. More studies are required in areas with known densities to promote confidence in accuracy.

KEYWORDS
density estimation, human wildlife interactions, snapshot interval, wildlife management

1 | INTRODUCTION

Knowledge of population abundance is a fundamental concept in ecology, influencing almost all aspects of species biology and conservation (Burton et al., 2015; Royle et al., 2009). Accordingly, reliable estimation of population abundance and density is essential for effective conservation and management planning (Keiter et al., 2017). Despite mesocarnivores far outnumbering large carnivores (Prugh et al., 2009; Roemer et al., 2009), their ecological role and population abundance have received relatively little research attention. Insufficient data hinders the management of carnivores (Williams et al., 2017) and their relationships with human populations (Ray, 2000). This is particularly true for mesocarnivores.

Ecologically, mesocarnivores are defined as any midranking carnivore in a food web, irrespective of their taxonomy or size (Prugh et al., 2009). Globally, mesocarnivores play a vital role in complex food webs; changes in their abundance have important impacts on ecosystems (Henke & Bryant, 1999; Jones et al., 2008; Ripple & Beschta, 2004; Roemer et al., 2002). Despite low research effort, mesocarnivores attract a lot of public attention (Ray, 2000) owing to negative interactions with humans (Roemer et al., 2009). Mesocarnivores are often highly adaptable species, frequently thriving where other carnivores cannot. Many human-modified environments are, accordingly, identified as strongholds for these species (Loock et al., 2018; Yarnell et al., 2016); in agricultural areas, in particular, this increases human-mesocarnivore interactions, invariably resulting in conflict (Nowell & Jackson, 1996).

Understanding the population dynamics and abundance of mesocarnivores is globally important (Golding et al., 2018; Recio et al., 2015), but many are difficult or impossible to census via traditional methods (Ray, 2000). In North America, harvest records and trapping have been used as proxies for mesocarnivore abundance (Ray, 2000), while, as in other locations, occupancy modelling has also been used (Golding et al., 2018). Other methods include genetic techniques (Burgar et al., 2018) and indirect or index-based methods, such as track counts (Read & Eldridge, 2010) or scat surveys (Moriarty et al., 2018; Recio et al., 2015). Although indices can produce useful proxies of abundance, they are context dependent and often controversial, because they seldom account for probability of detection (Hayward et al., 2015). To improve our understanding of the role and impact of mesocarnivores worldwide, robust density estimation methods are a fundamental requirement (Golding et al., 2018; Hayward et al., 2015; Minnie et al., 2016; Minnie, Avenant, et al., 2018; Roemer et al., 2009).

Camera trapping has significantly enhanced the potential to obtain accurate density estimates of many carnivore species, but the methods have generally been applied to species with uniquely marked individuals (Cutler & Swann, 1999). Many mesocarnivores lack natural, individually unique markings and so camera trapping methods for these species have been limited to questionable relative abundance indices (Anderson, 2001; Burton et al., 2015) and unreliable capture-recapture models for unmarked species (Augustine et al., 2019; Chandler & Andrew Royle, 2013; Le Saout et al., 2014). Distance sampling with camera traps (CTDS; Howe et al., 2017) is one recent, though relatively untested, method proposed to overcome this problem.

CTDS combines the unobtrusive nature of camera trapping with the proven theoretical framework and software of distance sampling (Howe et al., 2017; Sanderson & Trolle, 2013). The majority of CTDS studies have collected data using videos (Bessone et al., 2020; Cappelle et al., 2019, 2021; Howe et al., 2017), although a small number have used photos (Corlatti et al., 2020; Mason et al., 2022). Distance sampling is considered a snapshot method, where the snapshot interval value (t) for a study is predefined (e.g., 1 s or 1 min). In these snapshot moments, animals are deemed frozen, preventing their movement biasing the distribution of detection distances (Thomas et al., 2010). At each snapshot moment, the horizontal radial distance and angle to the midpoint of the animal from the camera are recorded. The probability of an animal being observed by a camera within its angle of view, at a snapshot moment, and within a pre-set maximum distance, defines the probability of detection for the animal (Howe et al., 2017). Ensuring an appropriate value for t—or an 'effective t'—is vitally important, since published camera specifications may cause bias in density estimates, such that performance must be tested empirically (Corlatti et al., 2020). We evaluate how different methods to define the snapshot moment value influence density estimates when using photo burst settings for data collection.

For distance sampling, it is vital that distance measurements are precise to avoid biasing density estimates (Buckland et al., 2001). Previous CTDS studies have used video recordings of researchers holding distance markers (Cappelle et al., 2019; Howe et al., 2017) and still photos with ground markers (Corlatti et al., 2020) at several distance intervals at each camera location to assign distance measures to observations. These approaches might not be feasible or robust in all environments and also require constant comparison to reference images, which could reduce accuracy and increase data processing time (Palencia et al., 2021).

Here, we use CTDS to estimate the density of an African mesocarnivore guild (African civet *Civettictis civetta*, black-backed jackal *Canis mesomelas*, brown hyena *Hyaena brunnea* and caracal *Caracal caracal*) in the Alldays area of South Africa, across two survey areas. Caracal and black-backed jackal are considered two main predators of both livestock and high-value wildlife species in southern Africa (Minnie, Zalewski, et al., 2018), while there is minimal data on the African civet despite it being directly and indirectly impacted by human interactions (Swanepoel et al., 2016). Many local farmers deem brown hyena responsible for livestock fatalities and believe that they are highly abundant in the Alldays area. More data on mesocarnivores are needed for key landscapes, such as agricultural land that continues to grow across southern Africa (van der Waal & Dekker, 2001). CTDS might provide a practical method to facilitate monitoring of these often elusive, nocturnal, low density and wide-ranging animals. Past CTDS studies have observed considerable encounter rate variance and recommend increasing survey locations to improve precision (e.g., Cappelle et al., 2019), so we migrated cameras within our second survey to explore the effects on variance. Migrating the grid not only increases survey locations, but also reduces survey effort at each location, reducing the accumulation of observations from any one site. We developed a new approach to obtain distance measures for animal observations from camera trap images, examined the impact of migrating camera traps on estimate precision, and explored the implications of snapshot moment values by testing three different approaches. In evaluating the applicability of CTDS as an efficient and viable density estimation method for mesocarnivores, we highlight considerations for applying the method more generally.

2 | MATERIALS AND METHODS

2.1 | Study site

The study was conducted in the multi-use landscape surrounding Alldays in the Blouberg Municipality of Limpopo Province, South Africa (Figure 1; central coordinates: S −22.674960, E 29.020938). Survey 1 cameras were spread across mixed-use farms dominated by game and livestock farming, with several also having crop fields; two cameras were placed on a private nature reserve. Survey 2 cameras were placed across two large game farms and one game and livestock farm. The area has a semi-arid climate (Findlay & Hill, 2020); mean annual rainfall was 650 mm per year, most of which falls in the summer months (October–March). The dryer winters (April–September) have an average daily minimum temperature of 13°C in June and July, with an average maximum temperature of 33°C in November (Findlay & Hill, 2020). Alldays falls within the Limpopo Sweet Bushveld vegetation type that provides a high grazing capacity, making it a good area for game and cattle farming (Mucina & Rutherford, 2006).

2.2 | Field setup and data collection

All research had approval from the Department of Anthropology Ethics and Data Protection Committee at Durham University and was conducted in consultation with the Limpopo Economic Development, Environment and Tourism, South Africa and with landowner permission. Survey 1 (study site: 192 km^2) used 25 cameras in fixed locations for 90 days between June 2019 and August 2019, while Survey 2 (200 km^2) used a migrating grid, with three deployments of approximately 20 cameras that moved 1.5 km south-east every 30 days, totalling 59 locations between December 2019

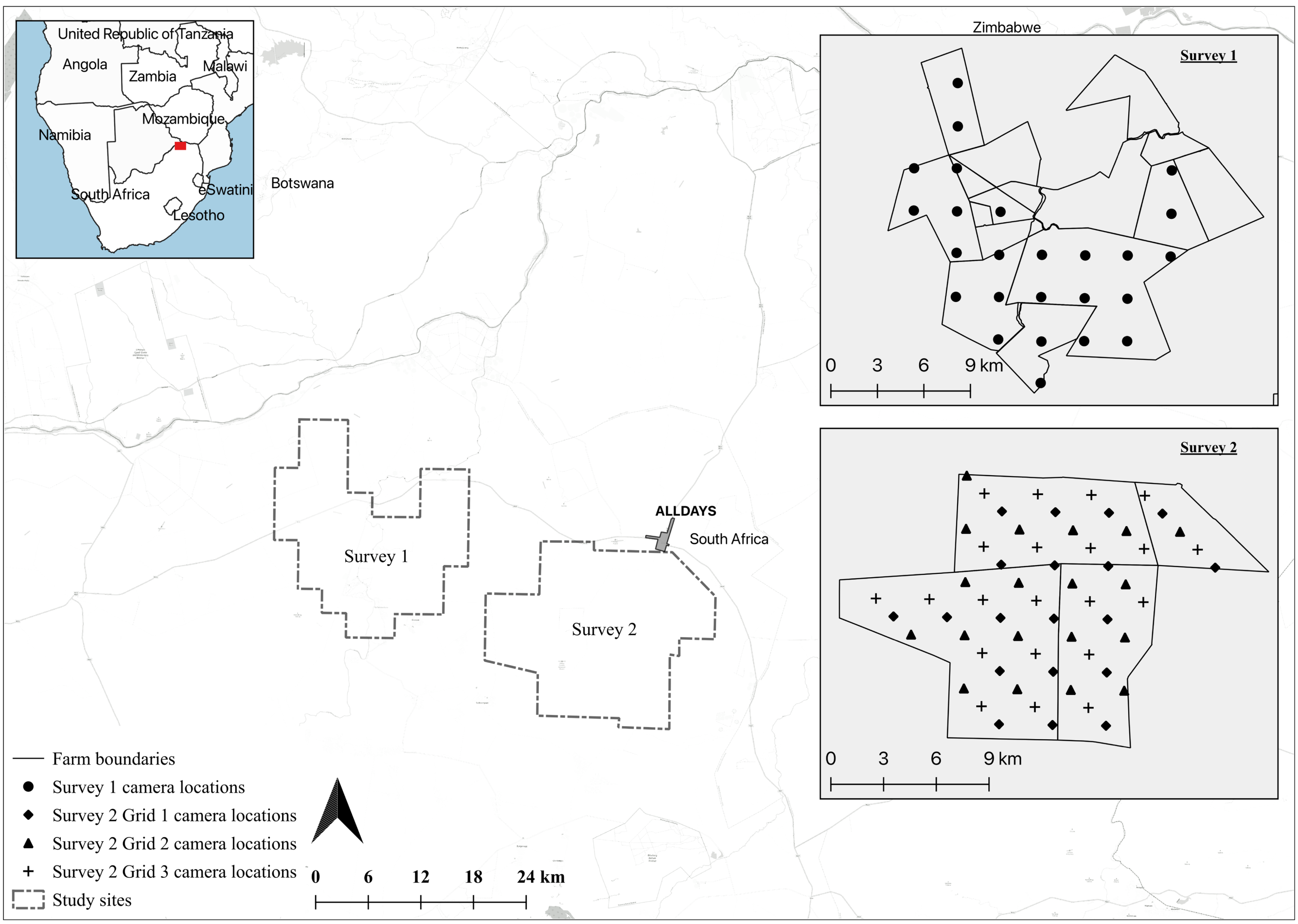

FIGURE 1 Location of the study area and the two camera surveys on farmland in the Alldays area of Limpopo Province, South Africa.

and March 2020 (Figure 1). Camera traps (Browning Strike Force HD Pro Model BTC-5HDP) were placed 3 km apart, on the intersections of a grid randomly placed over the study areas, allowing sample sites to be representative of the wider area within the constraints of the number of cameras available (Kays et al., 2020, 2021). Where it was not possible to place cameras in the exact location, for example because the point was in a water hole, they were all set up on suitable trees no further than 80 m away from the predefined grid position. Camera traps were placed at a height of 0.7 m, oriented north (±30°) and aligned to be exactly parallel to the ground. A customized spirit level was used during the setup to ensure each camera was set up identically in relation to the terrain, with a marker placed at 3 and 10 m from the camera to capture a distance reference photo for each location.

Each camera was set to 'rapid fire' burst mode, taking six photographs in quick succession (~0.3 s apart), with time between bursts set to the lowest possible (1 s) and quality set to 'Medium' (8MP). These settings were used to ensure the most continuous monitoring possible at each location without using video settings, which would have required that cameras were serviced too frequently. Cameras were serviced approximately every 2 weeks to change SD cards and batteries, if required, and to ensure the camera was still in its initial position. Where the camera had been moved or damaged, it was repositioned or replaced. One camera from each survey was stolen and neither was replaced.

2.3 | Data processing

To determine the distance of an animal from the camera, a distance overlay grid was created that could be superimposed over each image. To produce the distance overlay grid, a camera trap was set up at a height of 0.7 m, in a flat, open area, using a customized spirit level to ensure that it was exactly parallel to the ground. Arcs were drawn in the ground at 1 m intervals from the camera, with additional markers placed along these lines. A picture was taken on the camera trap to capture the distance arcs and all markers, providing a reference of distances from the camera. This image was uploaded to CorelDRAW (version 16) and digitally edited, constructing digital measurement lines over those drawn and marked in the ground in the camera trap photo (Figure 2; see Supporting Information Appendix S1 for further details). The digital grid was then saved as a Graphic Interchange Format file (.GIF) that could be overlaid on any image. The same spirit level and setup was then applied to cameras in the field allowing the distance overlay grid to be accurately calibrated to photos from each site. The distance overlay grid was then applied in bulk using XnConvert (version 1.80). Images were tagged with species, angle and distance from the camera trap using DigiKam (version 6.2.0) (Caullier, 2019) and the metadata downloaded using Exif Tool (version 11.87; Harvey, 2016). Distances to the mid-point of animals were tagged in half-metre intervals up to 10 m and then 1 m measures up to 25 m, as larger distances are harder to distinguish more precisely. To ensure the correct angle of view (AOV) was used for analysis, angles were tagged in categories (0–0.2, 0.2–0.4, 0.4–0.6, 0.6–0.8, 0.8–1.0) with 0 being the centre of the image and 1 being the vertical edges, before being converted to absolute angles in R (version 3.6.0) (R Core Team, 2013), based on the field of view.

2.4 | Survey effort

The sampling period at each camera location was the time a camera was available to capture data. Where a camera had been damaged or moved to face the ground (e.g. by an animal), effort was excluded until the camera was repositioned. Survey effort at each location (e_k) was:

$$e_k = \frac{\theta T_k}{2\pi t}.$$

A camera trap has a limited AOV (θ), and the fraction of a circle the AOV covers can be specified as $\frac{\theta}{2\pi}$. An effective angle of detection was calculated for each species per survey from the absolute angles and the relative value was used for the horizontal AOV for each species.

Within a sampling period (T_k), there are a predefined number of opportunities to obtain an image of an animal at a point (k). These opportunities are called snapshot moments and are defined as being t units of time apart. Ideally, snapshot moments would be predetermined and independent of camera triggering times (using time-lapse settings; see Howe et al., 2017), but cameras may not always perform to the selected criteria (Corlatti et al., 2020). Accordingly, we tested our camera performance (as recommended by Corlatti et al., 2020) by setting up two cameras opposite each other before walking randomly in front of both cameras continuously for approximately 5 min, at varying distances, with the camera recovery time set at its lowest value (1 s). We then used three different methods (see Figure 3) to determine snapshot intervals for analysis:

1. 'Handbook interval': Camera settings were assumed to work as described by the user manual, with $t = 1$ s used as the snapshot interval. Images from each camera placement were filtered so that those used were separated by a minimum interval of 1 s. Where there were multiple images with the same timestamp, the second image was used; choosing the first image might maximize sample size (the first image of the trigger is the most likely to contain the animal that triggered the camera), while choosing the third might minimize any positive bias in observed distances (by allowing the animal to have moved a significant distance and angle from first detection point) (E. Howe, personal comms., 2019). The second image was a compromise between these considerations.
2. 'Recovery-driven interval': The camera test data were used to calculate a 'mean burst time'—defined as the time taken to complete a six-photo burst plus the true camera recovery time (i.e. the time between the end of one burst and the start of the next in our

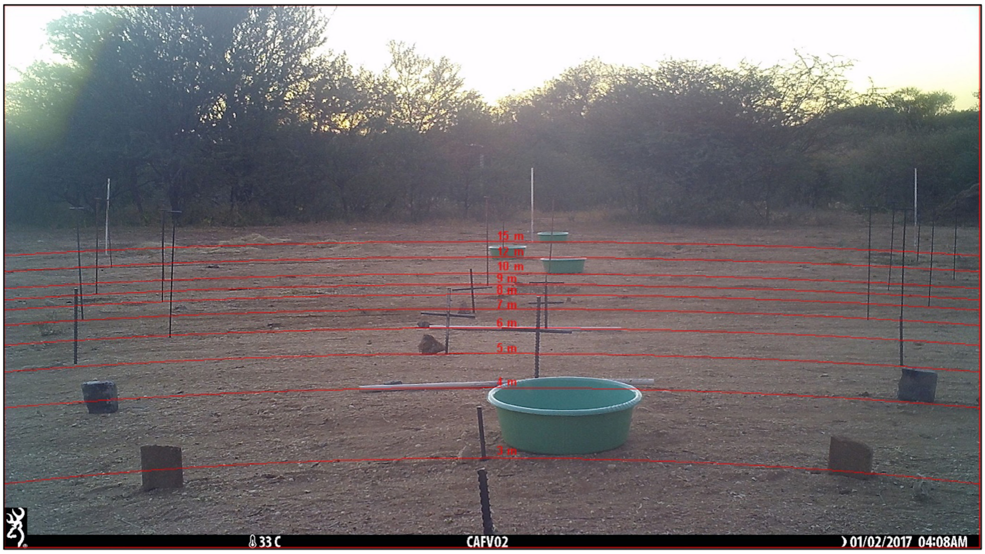

FIGURE 2 Distance measurements taken in the initial setup with the digitally created grid overlaid.

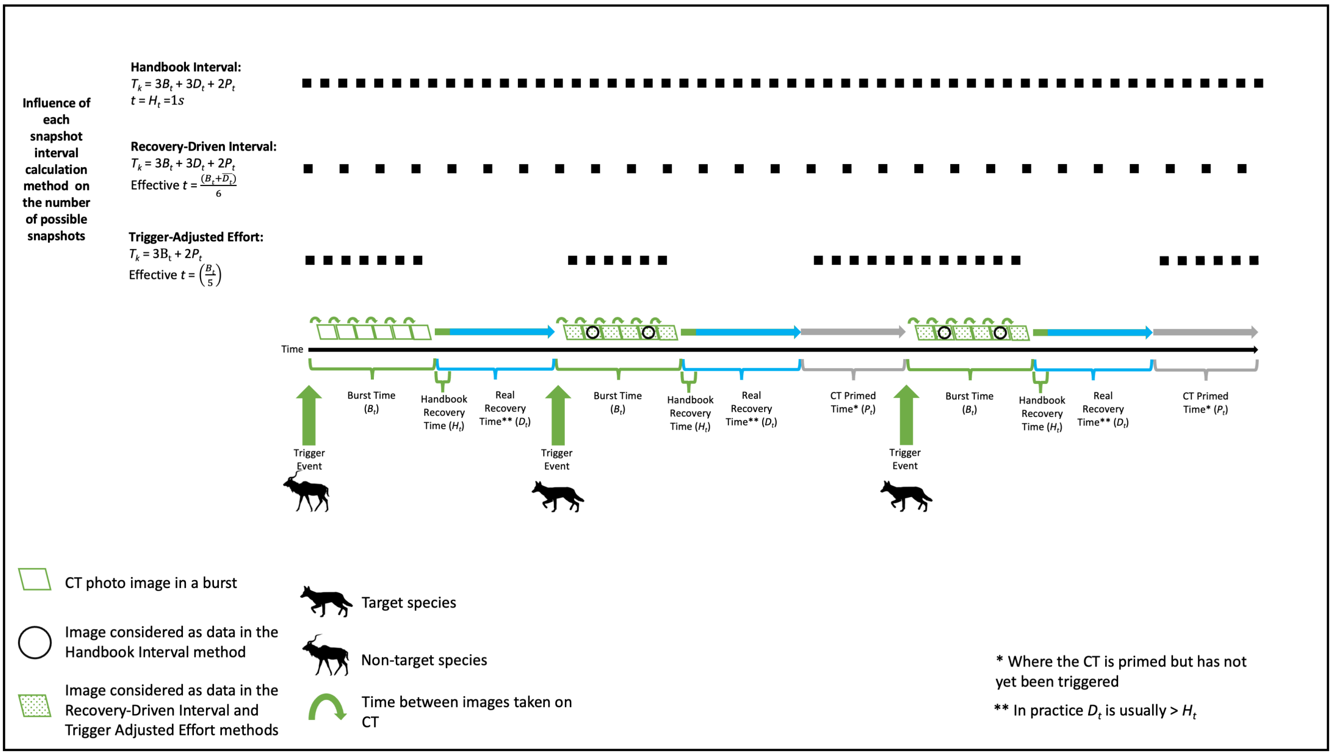

FIGURE 3 The impact of camera trap (CT) performance and snapshot interval calculation method on the number of possible snapshots. CTDS deploys a CT at a point k over a time period T_k, set to capture images throughout the duration of the camera's deployment. Howe et al. (2017) predetermine a finite set of snapshot moments during T_k at which the CT can be triggered and a set of images can be captured; these are assumed to be t units of time apart. Temporal effort at point k is, thus, T_k/t or, where an 'effective t' (Corlatti et al., 2020) is used, T_k/(effective t). Formulae given are for the case where burst duration and subsequent downtime are fixed properties of the camera; if these vary, their values should be replaced by means.

test). We then calculated the snapshot interval as the number of photos in a burst (six) divided by the 'mean burst time'. In this case, the snapshot interval is significantly influenced by how long the camera takes to recover between possible trigger events, as this is absorbed within the snapshot interval calculation.

3. 'Trigger-adjusted effort': Snapshot intervals were defined as the average time between each photo within only the burst itself (five recoveries for a 6-photo burst) in the test data. The true recovery time between triggers, where the camera was inactive, was removed from survey effort for each trigger event. The survey

effort removed is dependent on how many actual trigger events occur.

The availability of a species for capture is considered fundamental to accurate density estimates from CTDS (Howe et al., 2017). We used Rowcliffe et al.'s (2014) ACTIVITY package in R, which assumes that all animals in a population are active and available for capture when the camera trapping rate achieves its maximum in a daily cycle. Overall activity level is then a measure of the extent to which this daily maximum is sustained throughout the 24 h period. To this end, the 'fitact' function was used to fit a kernel density distribution to the temporal distribution of photographic captures. To ensure independence of detection times, an observation of the same species 30 min since the last capture was considered a new event (Williams et al., 2021), with only the first image from each sequence included in these calculations.

2.5 | Data analysis

Density estimation was completed in R using the DISTANCE package (Miller et al., 2019). Data were binned and truncated (discarded distance observations from analysis outside of lower and upper bounds) to help more precise model fitting and stratum-specific modelling was employed in survey 2, where each camera grid is treated as an individual strata and fitted with its own detection function. We followed Buckland et al. (2001) and Howe et al. (2017) closely, fitting a standard set of distance sampling candidate models that we compared using QAIC (Howe et al., 2019). Variance was estimated using bootstrapping. Further details on our data analysis are available in Supporting Information Appendix S1.

Only naturally monotonically decreasing models were selected for final analysis (Buckland et al., 2001). Images in which animals showed a reaction to the cameras were excluded to avoid bias in encounter rates. These images were identified where the animal showed a clear change in initial direction of movement, with many occurrences resulting from the animal directly interacting with the camera. For distance sampling, a minimum of 60 observations are typically recommended for a reliable density estimate (Buckland et al., 2001); however, we relaxed this rule of thumb, where necessary, to enable comparisons between results based on different snapshot intervals. In such cases sample size never dropped below 25 observations.

To provide a reference for the plausibility of our results, we conducted a literature review identifying papers covering our target carnivores. Several databases (Web of Science, Google Scholar and Wiley) were searched using species name (e.g., African civet) and scientific name (e.g. *C. civetta*) as initial search criteria. Search criteria were further refined by searching titles, keywords and topics for the terms: 'population size', 'density', 'abundance' and 'management'. Results not directly related to wild population studies or not relevant were discarded. Additional records were obtained from the Red List of Mammals of South Africa, Swaziland and Lesotho (Child et al., 2016). Search results of relevant theses and dissertations were included as these can provide valuable information, especially of understudied species, even if they might not experience the same level of scrutiny as peer-reviewed publications (du Plessis et al., 2015).

3 | RESULTS

A total of 411,956 images of animals were captured across the two surveys—2250 trap days in Survey 1, 1770 in Survey 2—including 39 different mammal species (Supporting Information Table S1). Caracal were captured 102 times, African civet 743 times, brown hyena 1197 times and black-backed jackal 4148 times.

3.1 | Snapshot intervals

Our three methods to establish a snapshot interval produced different snapshot interval values. Handbook interval used $t = 1$ s, but reduced sample size to about 40% of the original data (Table 1), where the others retained all images. Where camera capture delay was set to 1 s, the true camera recovery time, where the camera was inactive, averaged 10.35 s (SE ±0.52). The mean burst time for one six-photo burst was 2.44 s (SE ±0.07). Accordingly, the mean interval between photos (including recovery time) was 2.11 s (SE ±0.08) and so we used $t = 2$ s for the recovery-driven interval. Within a burst, the five trigger intervals gave a mean of 0.49 s (SE ±0.07), and so for trigger-adjusted effort we used $t = 0.5$ s.

3.2 | Capture availability

Both brown hyena and African civet were exclusively nocturnal (see Supporting Information Appendix S2). Caracal activity was predominantly nocturnal, with two crepuscular highs, while jackal demonstrated a greater variability although nocturnal activity was dominant. This proportion of time active was assumed to represent the probability of availability for capture of each species (Table 1) and was included in survey effort.

3.3 | Density estimation

Density estimates varied between the two surveys, as well as between the different snapshot interval methods used (Table 2). Model fitting QAIC scores resulted in the Hazard rate with no adjustments being applied in almost all cases, with the uniform model with one cosine adjustment being used only for African civet in Survey 2 (Table 1; see Supporting Information Appendix S2 for probability of detection histograms). For all species, estimates using the recovery-driven interval produced density estimates that were approximately four-five times larger than those from the other two methods.

TABLE 1 Species-specific information from camera traps, with model fitting information (Survey 1 in grey and Survey 2 in white). Analysis method is the snapshot interval used (a = handbook interval (1 s), b = recovery-driven interval (2 s), c = trigger-adjusted effort (0.5 s)); detection locations is the number of CT locations where detections >0; total radial distances is the total number of radial distances measured; % of total captures (%) is the percentage of observations used in analysis; availability (%) is the proportion of a 24-hour day that a species was available for detection; truncation (m) is the left and right-truncation of radial distances in metres; model is the model fitted to estimate species abundance in the study area; adj.: is the adjustment terms applied to the model (Cos = Cosine, - = no adjustments); order is orders of adjustment; effective detection radius (m) is the distance from the camera where number of observations beyond this distance equals the number of observations missed within; mean encounter rate is the mean number of observations per t − s time interval (a = 1, b = 2, c = 0.5); detection probability variance (%) is percentage of variance attributable to detection probability; encounter rate variance (%) is percentage of variance attributable to encounter rate.

Species	Analysis method	Detection locations	Total radial distances	% of total captures (%)	Availability (%)	Truncation (m) left–right	Model	Adj.	Order	Effective detection radius (m)	Mean encounter rate	Detection probability variance (%)	Encounter rate variance (%)
African civet	(a)	17	266	39.2	0.39	0–21	Hazard-rate	-	-	11.98	4.83×10^{-5}	0.51	99.49
Black-backed jackal	(a)	18	1299	40.9	0.47	1–21	Hazard-rate	-	-	13.18	1.99×10^{-4}	0.25	99.75
Brown hyena	(a)	11	328	40.2	0.43	2.5–17	Hazard-rate	-	-	11.24	3.55×10^{-5}	2.82	97.18
Caracal	(a)	6	30	38.5	0.51	3–16	Hazard-rate	-	-	13.06	2.82×10^{-6}	5.79	94.21
African civet	(b)	17	678	100	0.39	0–21	Hazard-rate	-	-	11.88	2.47×10^{-4}	0.22	99.78
Black-backed jackal	(b)	18	3176	100	0.47	1–21	Hazard-rate	-	-	13.21	1.01×10^{-3}	0.10	99.9
Brown hyena	(b)	11	816	100	0.43	2.5–17	Hazard-rate	-	-	11.07	1.80×10^{-4}	1.19	98.81
Caracal	(b)	6	78	100	0.51	3–23	Hazard-rate	-	-	13.03	1.76×10^{-5}	1.81	98.19
African civet	(c)	17	678	100	0.39	0–21	Hazard-rate	-	-	11.88	6.20×10^{-5}	0.22	99.78
Black-backed jackal	(c)	18	3176	100	0.47	1–21	Hazard-rate	-	-	13.21	2.53×10^{-4}	0.10	99.9
Brown hyena	(c)	11	816	100	0.43	2.5–17	Hazard-rate	-	-	11.07	4.48×10^{-5}	1.19	98.81
Caracal	(c)	6	78	100	0.51	3–23	Hazard-rate	-	-	13.03	4.40×10^{-6}	1.81	98.19
African civet	(a)	6	25	38.5	0.21	1–18	Uniform	Cos	1	10.19	4.16×10^{-6}	8.14	91.86
Black-backed jackal	(a)	34	419	43.1	0.46	1.5–18	Hazard-rate	-	-	14.39	7.95×10^{-5}	4.90	95.10
Brown hyena	(a)	18	162	42.5	0.39	0–20	Hazard-rate	-	-	10.34	2.72×10^{-5}	41.78	58.22
African civet	(b)	6	65	100	0.21	1–18	Uniform	Cos	1	10.14	2.18×10^{-5}	2.94	97.06

(Continues)

TABLE 1 (Continued)

Species	Analysis method	Detection locations	Total radial distances	% of total captures (%)	Availability (%)	Truncation (m) left–right	Model	Adj.	Order	Effective detection radius (m)	Mean encounter rate	Detection probability variance (%)	Encounter rate variance (%)
Black-backed jackal	(b)	34	972	100	0.46	1.5–18	Hazard-rate	-	-	13.13	3.99×10^{-4}	2.34	97.66
Brown hyena	(b)	18	381	100	0.39	0–20	Hazard-rate	-	-	9.70	1.40×10^{-4}	22.86	77.14
African civet	(c)	6	65	100	0.21	1–18	Uniform	Cos	1	10.14	5.45×10^{-6}	2.94	97.06
Black-backed jackal	(c)	34	972	100	0.46	1.5–18	Hazard-rate	-	-	13.13	9.98×10^{-5}	2.34	97.66
Brown hyena	(c)	18	381	100	0.39	0–20	Hazard-rate	-	-	9.70	3.49×10^{-5}	22.86	77.14

TABLE 2 Densities of African civet, black-backed jackal, brown hyena and caracal in the Alldays area using the three snapshot moment methods (*D* is estimated density (individuals/100 km^2); SE is standard error; LCI is the lower 95% confidence interval; HCI is the higher 95% confidence interval; %CV is the percent coefficient of variation).

		(a) Handbook interval					(b) Recovery-driven interval					(c) Trigger-adjusted effort				
			Bootstrap					Bootstrap					Bootstrap			
Survey	Species	*D*	SE	LCI	UCI	%CV	*D*	SE	LCI	UCI	%CV	*D*	SE	LCI	UCI	%CV
1	African civet	10.8	5.0	3.0	22.0	54.0	55.9	28.0	18.0	116.0	53.0	14.0	8.0	5.0	31.0	56.0
	Black-backed jackal	36.5	15.0	13.0	72.0	40.0	184.6	75.0	65.0	352.0	41.0	46.2	19.0	18.0	91.0	41.0
	Brown hyena	9.0	6.0	3.0	23.0	54.0	46.5	28.0	13.0	121.0	55.0	11.6	5.0	3.0	23.0	48.0
	Caracal	0.5	1081.0	0.0	2678.0	184254.0	3.3	3873.0	1.0	95.0	108490.0	0.8	1.0	0.0	2.0	70.0
2	African civet	2.3	3.0	0.0	10.0	149.0	6.8	18911.0	0.0	28756.0	395867.0	1.7	20.0	0.0	7.0	144.0
	Black-backed jackal	24.8	21.0	6.0	68.0	85.0	119.1	80.0	31.0	322.0	68.0	29.8	20.0	8.0	79.0	65.0
	Brown hyena	27.2	28.0	1.0	104.0	123.0	146.5	92674.0	6.0	37846.0	62956.0	36.6	43.0	1.0	162.0	144.0

Brown hyena attraction to the cameras was evident in Survey 2 through a lower effective detection radius and the greater contribution of detection probability variance to total variance (Table 2). Variance around our other estimates in both surveys was almost exclusively due to encounter rate, a result of highly varied observation numbers across camera locations (Table 1). Stratum-specific model fitting for jackal and brown hyena from Survey 2, further demonstrated the negative role of encounter rate in the precision of CTDS density estimates. Despite similar numbers of camera locations and radial observations for both species across the three grids, as well as the same activity and effective angle of detection estimates (Table 2), there was extremely wide variability in density and precision estimates (Table S2).

The literature search yielded 69 articles (six on African civet; 31 on black-backed jackal; 30 on brown hyena; two on caracal) with abundance estimates. The articles providing population density estimates from southern Africa are detailed in Figure 4 (and Supporting Information Table S3) with estimated densities (/100 km^2) ranges of 3.6–18.26 for civet, 1.8–1305 for black-backed jackal, 0.74–24.01 for brown hyena and 23–47 for caracal.

4 | DISCUSSION

We conducted two CTDS surveys using rapid-fire photo burst modes to estimate mesocarnivore densities in a commercial farmland area of South Africa. Both surveys provided density estimates for African civet, black-backed jackal and brown hyena, with an estimate for caracal from Survey 1. Estimates were highly variable when we used different values for the snapshot interval, a key parameter in determining survey effort, demonstrating the importance of specifying this parameter in future studies using burst modes with still images. The higher coefficients of variation suggests imprecision across the estimates, with encounter rate variance from spatial heterogeneity in capture rates at each camera location the dominant cause of this; however, brown hyena estimates from one survey also showed some detection function variance, most likely because attraction to the camera traps made model fitting less reliable. Using a migrating grid did not reduce encounter rate variance at the scale of our study. Owing to its influence on the interpretation of our ecological findings, we begin by discussing the methodological considerations before considering the validity, precision and management implications of our mesocarnivore estimates.

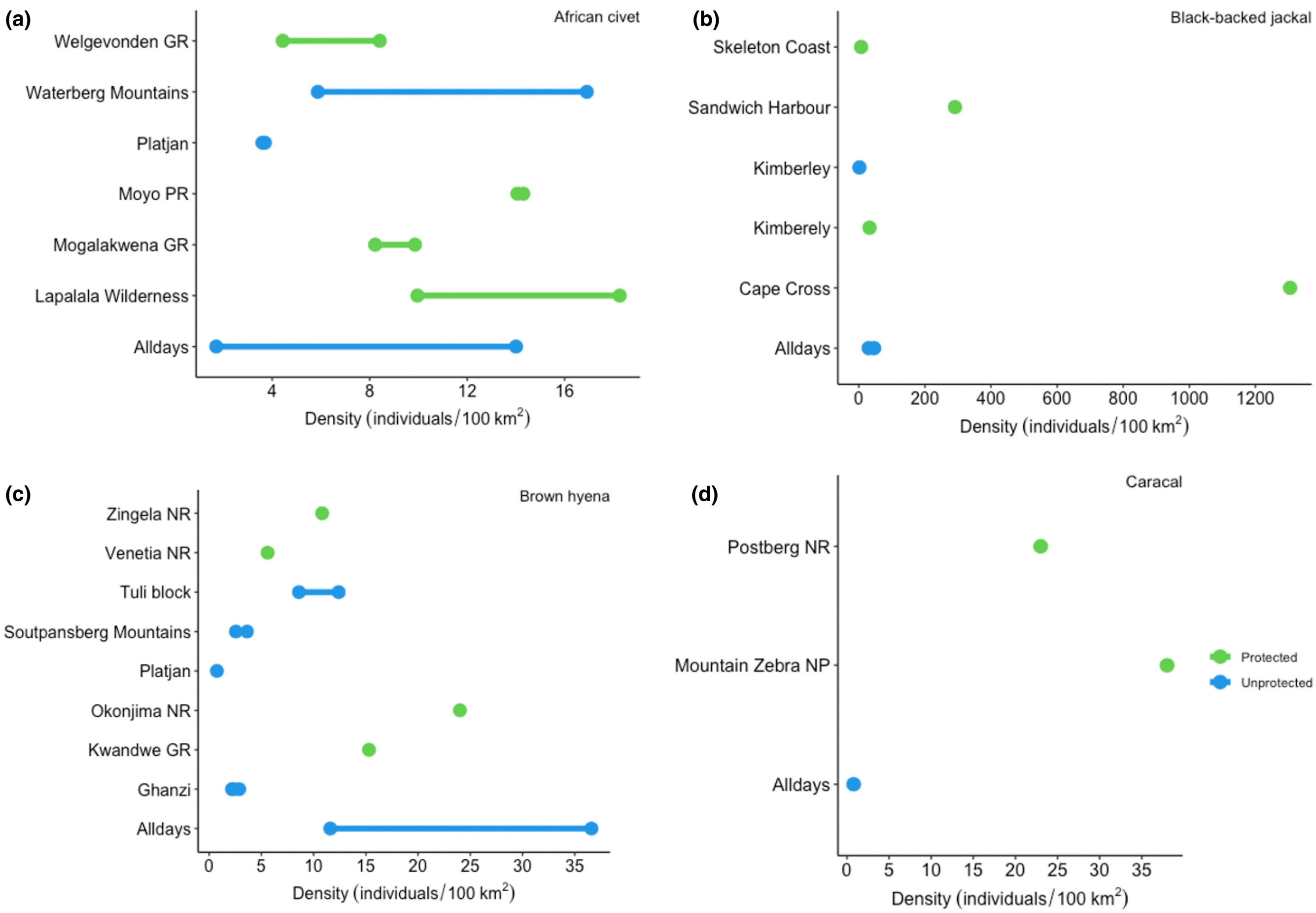

FIGURE 4 Density estimates (individuals/100 km^2) from studies of (a) African civet, (b) black-backed jackal, (c) brown hyena, and (d) caracal in protected and unprotected areas across southern Africa, including this study (Alldays). See Table S3 in SI Appendix S2 for details of sources. GR, Game Reserve; NR, Nature Reserve; NP, National Park.

4.1 | Methodological considerations

We explored the sensitivity of our density estimates to methods for determining the value of the 'snapshot interval', a key component in defining survey effort (Howe et al., 2017). We used three methods for calculating the snapshot interval and our results suggest that measuring camera trap recovery time under local conditions is critical to estimating this parameter. Our handbook interval method, based on the camera performance stated in the user manual, assumed that cameras were active for longer than they could have been, in practice. We found that, on average, cameras had a 10.35 s downtime between photo bursts, especially when the camera was being continuously triggered, suggesting that the handbook interval method overestimates survey effort.

Our recovery-driven interval method using $t=2$ s, and our trigger-adjusted effort method using $t=0.5$ s led to considerably different density estimates. As the recovery time of our cameras was much longer than stated in the camera handbook, survey effort estimated by our calculated recovery-driven interval was very low, leading to considerably larger density estimates, well outside the range of those observed in southern Africa (Figure 4). The formula to estimate survey effort accounts for activity and snapshot interval such that doubling t effectively halves survey effort. In the case of the handbook interval estimates, the effect of reduced survey effort is further exacerbated as capture numbers dropped between a half and two thirds as images were filtered. These differences mathematically account for the approximately four- and five-fold higher density estimates (Table 2), as well as the differing mean encounter rates between analyses, even where other factors such as truncation, total radial distances and effective detection radius were identical or very similar (Table 1). For this reason, we used the trigger-adjusted effort method to estimate densities. Our trigger-adjusted effort method created an 'effective-t' of only the burst itself, discretising the number of times an animal was detected over the time that the camera was actually being triggered, using a method similar to Corlatti et al. (2020). This ensured that survey effort was not falsely estimated by assuming that the camera was always active and maximizes the data for such elusive animals through a smaller snapshot interval, as advised by Howe et al. (2017). Had the recovery time matched that stated in the handbook, then the recovery-driven interval method would not display a substantive difference, and theoretically, it would be possible to use the stated recovery time as an effective snapshot interval. Similarly, if numbers of triggers are low, then recovery times will make little difference to the time during which the cameras were available to be triggered. However, because the number of triggers is affected by all trigger events, it is important to quantify the impact since even a study of a rarely encountered species will be subject to substantially reduced effort in an area in which non-target species or false triggers increase the frequency of triggers. The CTDS technique was originally proposed for video and the influence of assumed recovery periods on survey effort could be equally important when using the video method.

A key assumption of distance sampling is that distance to subject estimates are accurate (Buckland et al., 2001). We applied a method to measure distances from a camera trap without requiring significant apparatus in the field. In addition to streamlining camera placement and reducing effort in the field, this method can also maximize usable data, even if changes to the camera position are made during the survey. Specifically, animals may move cameras, invalidating the initial measurement grid for that location; however, as long as the camera is not moved dramatically, the robustness of the initial setup means that a new grid can be applied to account for the change in perspective, potentially salvaging considerable quantities of data that would otherwise have to be discarded. We recommend that 2–3 distance measures at each camera location are sufficient to apply the measurement grid accurately for each location without requiring the use of a spirit level device, although more reference points might be required in more variable terrain.

4.2 | Validity and precision of mesocarnivore estimates

With the actual population density of our study area unknown, we compared our estimates to those from other sites. Our species estimates using the trigger-adjusted effort may be considered slightly high in the context of previous density estimates from unprotected land (Figure 4). However, although there are likely several drivers of mesocarnivore population abundance, the limited extent of top-down pressure on the Alldays mesocarnivore populations might account for some of these higher estimates (Minnie et al., 2016; Yarnell et al., 2016). The majority of large carnivore species have been hunted to extirpation around Alldays, with small populations of lion (Snyman et al., 2015), cheetah (Marnewick et al., 2017) and wild dog (Pretorius et al., 2019) restricted to just the north of Alldays around the Venetia Limpopo Nature Reserve and into Botswana. Our data also suggest limited numbers of spotted hyena in the Alldays area (Supporting Information Table S1). Furthermore, our first survey area included several crop farms and this might account for slightly higher civet and particularly jackal estimates. Both species are noted crop foragers (Findlay, 2016), with our cameras capturing jackals eating melons. High rodent populations associated with crop farming would also provide a further food resource (Williams et al., 2018). Nel et al. (2013) showed considerably higher jackal densities where food resources were more abundant. Civet estimates from agricultural land in the Waterberg Mountains (Isaacs et al., as cited by Swanepoel et al., 2016) were similar to ours. Although the temporal difference between our surveys is likely to have little impact on three of our species, civet densities could also have been lower in Survey 2 as they are known to have young between August and January, meaning more individuals were likely in dens and unavailable for capture (Stuart & Stuart, 2015) during the survey.

Even given the limited top-down pressure, our brown hyena estimates appear high, with attraction to the cameras likely responsible for upward bias and imprecise estimates. Despite removing all images that visibly demonstrated attraction to the camera traps, as suggested by Howe et al. (2017) and Bessone et al. (2020), the bias was not removed. Placing cameras for a period before the survey starts to habituate animals to their presence has also been advised (Howe et al., 2017) but, again, this did not appear successful here as hyena damage to cameras continued throughout the three-month deployments. The attraction of hyenas to camera traps is recognized (Apps & McNutt, 2018) and is an important factor to consider for future studies of this species and others known for similar behaviour (see Caravaggi et al., 2020). Aside from these concerns, however, brown hyena density estimates vary widely in southern Africa (Williams et al., 2021) and our 11.6 individuals/100 km^2 estimate appears more plausible in light of a recent study from the nearby Tuli block in Botswana (Vissia et al., 2021) that reported a density estimate of 8.6–12.4 individuals/100 km^2, despite a high spotted hyena population. Despite the difficulties of using spatially explicit capture-recapture for brown hyena, Faure et al. (2021) successfully estimated their density in nearby Platjan at 0.74/100 km^2 using this method; for now, spatially explicit capture-recapture may remain a more robust method for brown hyena as it does not require the distance measures required by CTDS that are inherently vulnerable to positive biases for this species.

We provided one of the only density estimates for caracal, and the first using camera traps. A density estimate of 0.8 individuals/100 km^2 represents a sparse caracal population. This remains true regardless of the snapshot method used, and all are very low compared to historic estimates from protected areas that used home range collar data (Figure 4). Caracal densities are often expected to be low where jackals are abundant (Pohl, 2015), despite fine-scale spatial and temporal separation (Avenant et al., 2016). The number of observations for caracal was very low across both surveys, with the second survey area capturing too few observations to yield a density estimate. To estimate densities of extremely rare species, future studies might combine datasets from the same environment and season to obtain a detection function for a species, that can then be applied to only the dataset for the specific survey period required (Buckland et al., 2001).

Estimates from both surveys were imprecise and, in most cases, almost all variance was accounted for by encounter rate variation among camera stations. The first survey showed evidence of heaping, with a large proportion of observations at the same or very similar distances from the camera. This was caused by just one or two cameras with very high encounter rates. The non-random movements of carnivores, which are known to make considerable use of roads and trails (Swanepoel et al., 2016), will exacerbate this problem. Our second survey used a migrating grid, not only to increase survey locations, but also to reduce the time each location was surveyed, limiting the accumulation of observations from any one site. The detection probabilities for each species for each grid of cameras showed no evidence of heaping, but it is not possible to be sure whether the migrating grid mitigated such observation accumulation or whether this was simply a feature of the surveyed area. Indeed, despite similar sample sizes, the jackal and hyena estimates differed in the stratum-specific analysis results, further highlighting that encounter rate variability is the biggest barrier to greater precision in CTDS, regardless of survey design. Re-sampling the same survey areas repeatedly with different and more camera locations may provide more confidence in the estimates (Cappelle et al., 2021; Kays et al., 2020), although combining data in this way does require consistent detectability throughout.

The imprecision of CTDS estimates is not only a feature of nocturnal and crepuscular species (Bessone et al., 2020; Cappelle et al., 2021). Improving precision is, thus, likely to dictate how widely the method is used in future. Nevertheless, a strength of CTDS is the size of dataset that can be achieved; small snapshot intervals allow for a large number of sampling occasions maximizing the potential for capturing cryptic and elusive species; other methods, such as the Random Encounter Model, might have smaller datasets because of independence assumptions, while spatially-explicit capture recapture might lose data from blurred or distant photos that prevent individual identification. In addition, grid-based survey design allows for occupancy modelling of any species captured insufficiently frequently for distance analysis.

Farmers in the Alldays area believe that mesocarnivores are locally abundant and that their population is increasing (Chloe Lucas and Jamie McKaughan, unpublished data). While the precision of CTDS estimates make longer-term trends difficult to monitor accurately, our estimates nonetheless provide the first density estimates for these species in the area. These suggest a high abundance of brown hyena, but do not support the idea that the other species are unusually abundant. Greater abundance information will improve understanding of how these human modified landscapes might be supporting mesocarnivore populations more widely, and will provide a foundation to review whether populations need to be managed.

5 | CONCLUSIONS

Our density estimates for four species showcase the potential of CTDS for monitoring elusive mesocarnivores in anthropogenic environments and provide valuable insights into the status of our focal species in commercial farming landscapes in South Africa. Where observations were more limited, the observed imprecision resulted from encounter rate variance between camera placements, rather than from small sample size per se, suggesting CTDS could be applied to estimate mesocarnivore densities, globally. Additional camera locations will increase the area surveyed and should improve precision, but the random placements of cameras means encounter rate variance will still impact precision for these species (Cappelle et al., 2019, 2021; Kays et al., 2020). Despite avoiding heaping, a migrating grid was not successful in improving precision for the species in our survey; we speculate that the migrating grid might be more successful on a larger scale (Cappelle et al., 2021). Studies using burst modes should pay specific attention to study-specific camera trap recovery time in defining their snapshot interval parameter, as this can drastically affect density estimates. Future research should maximize number of sampling locations to improve the reliability and precision of mesocarnivore estimates from CTDS. Finally, more studies that compare CTDS estimates to known population numbers, similar to Cappelle et al. (2019), would be useful to understand accuracy of CTDS estimates across other taxa.

AUTHOR CONTRIBUTIONS

Jamie E. T. McKaughan, Russell A. Hill and Philip A. Stephens conceived the ideas and designed methodology; Jamie E. T. McKaughan collected and analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

None of the authors have a conflict of interest.

DATA AVAILABILITY STATEMENT

The data and code used in this article will be openly available on OSF at https://doi.org/10.17605/OSF.IO/CKZVE (McKaughan et al., 2023).

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SUPPORTING INFORMATION

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

Figure S1. All camera traps were setup as identically as possible relative to the slope of the ground in front of them using the nylon wire. This ensured that the distance overlay grid could be reliably calibrated to photos from each site accurately. The camera traps were repositioned until the nylon wire ran directly through the middle of the copper piping, not touching any of the pipe.

Figure S2. Scaled histograms of the probability of detecting African civet, black-backed jackal, brown hyena and caracal (top), and probability density functions of observed distances to each species (bottom) from Survey 1, Analysis (a).

Figure S3. Scaled histograms of the probability of detecting African civet, black-backed jackal and brown hyena (top), and probability density functions of observed distances to each species (bottom) from Survey 2, Analysis (a).

Figure S4. Scaled histograms of the probability of detecting African civet, black-backed jackal, brown hyena and caracal (top), and probability density functions of observed distances to each species (bottom) from Survey 1, Analysis (b).

Figure S5. Scaled histograms of the probability of detecting African civet, black-backed jackal and brown hyena (top), and probability density functions of observed distances to each species (bottom) from Survey 2, Analysis (b).

Figure S6. Scaled histograms of the probability of detecting African civet, black-backed jackal, brown hyena and caracal (top), and probability density functions of observed distances to each species (bottom) from Survey 1, Analysis (c).

Figure S7. Scaled histograms of the probability of detecting African civet, black-backed jackal and brown hyena (top), and probability density functions of observed distances to each species (bottom) from Survey 2, Analysis (c).

Figure S8. Availability for capture of African civet, black-backed jackal, brown hyena and caracal, based on time of independent capture by camera traps from survey 1.

Figure S9. Availability for capture of African civet, black-backed jackal and brown hyena, based on time of first capture by camera traps from survey 2.

Table S1. Mammals observed across both study sites and whether there were enough observations, as indicated by Y (yes) or N (no), for a density estimation to be achieved based on the suggested minimum number of observations required for model fitting (Buckland et al., 2001) in distance sampling.

Table S2. Strata results for black-backed jackal and brown hyena from Survey 2, using the trigger-adjusted effort.

Table S3. Key literature results of population size information for African civet, black-backed jackal, brown hyena and caracal. N.B. (Isaacs et al., as cited in Swanepoel et al., 2016; Moolman, 1986, as cited in Dobamo, 2019). *Estimate made assuming impermeable fence line.

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