

Sampling design and analytical advances allow for simultaneous density estimation of seven sympatric carnivore species from camera trap data

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ABSTRACT

Population density is a fundamental parameter needed to assess wildlife populations but is difficult to obtain given species are often wide-ranging and elusive. Photographic capture-recapture techniques do not require direct observations and thus, have become a common approach for estimating wildlife densities. To date, however, these studies have typically focused on single species. Our research explores study design- and analytical-based approaches for expanding photographic capture-recapture studies to assess multiple species simultaneously. We developed a hybrid-sampling scheme that varied inter-camera distances and used simulations to test the efficacy of this design versus a systematically spaced grid in estimating densities of species with varied space use. Through simulations we found the hybrid design facilitated density estimates for a wider range of species with little or no cost in accuracy for most species. We implemented a hybrid camera design across a 1154-km² area in northern Botswana to estimate densities of lions, spotted hyenas, leopards, wild dogs, servals, civets, and aardwolves. We estimated densities of these small- to wide-ranging carnivores, where all or some portion of the population was individually identifiable, using spatially explicit capture-recapture and mark-resight models. Mean estimates ranged from 1.2 (95% CI = 0.72–1.99) lions to 10.1 (95% CI = 8.69–11.63) spotted hyenas/100 km² and provided empirical information needed for the conservation of these species in Botswana. Our research demonstrates how photographic capture-recapture studies can be expanded to estimate the densities of multiple species versus just a single species within a community, thus increasing the conservation value of this globally implemented approach.

1. Introduction

Among the most fundamental quantities needed to assess wildlife populations are abundance and/or density (Otis et al., 1978; Seber, 1982). Without such key, baseline parameters it is difficult to detect when common species are becoming uncommon, when invasive or exotic species are proliferating, or when climate- and land-use changes are acting as large-scale ecological stressors (Pereira et al., 2013; Schmeller, 2015; Steenweg et al., 2017). Consequently, estimating wildlife density is key to species conservation (Seber, 1982; Karanth and Nichols, 1998; Sollmann et al., 2012).

Information on the population dynamics of carnivorous mammals is of particular interest given their vulnerability to extinction and their

impacts on ecosystems as a whole (Woodroffe and Ginsberg, 1998; Ripple et al., 2014; Bauer et al., 2015). Among the 31 largest carnivores, 19 are listed as threatened by the International Union for the Conservation of Nature and many (e.g., African wild dogs- *Lycaon pictus* and African lions- *Panthera leo*) are disappearing from a large portion of their historical range (Ripple et al., 2014; Bauer et al., 2015). Tracking the status of these carnivore populations is challenging, however, given they are generally far-ranging, elusive and thus, difficult to count directly (Silver et al., 2004; Karanth et al., 2006). As a result of these challenges, photographic capture-recapture techniques have emerged as an increasingly common approach for estimating abundances and densities of carnivore populations as they do not require animals to be handled or observed directly. Remote sensing cameras detect passing

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animals using motion- and heat-sensing infrared technology, which allows them to collect data 24 h per day without a human being present (O'Brien et al., 2010; Rich et al., 2017). Abundance and density can then be estimated using capture-recapture techniques if the resulting photographic detections are identifiable to the individual-level (i.e., via natural or artificial markings; Otis et al., 1978; Karanth and Nichols, 1998; Williams et al., 2002).

To date, studies employing photographic capture-recapture techniques have almost exclusively focused on single, uniquely identifiable species (Karanth and Nichols, 1998; Silver et al., 2004; Maffei and Noss, 2008; Satter et al., 2019). This focus may be attributed to both the design constraints of camera trap surveys and the availability of analytical approaches. When employing traditional non-spatial capture-recapture approaches, sampling designs had to be tailored to the movements of a single focal species (Karanth and Nichols, 1998; Maffei and Noss, 2008). Recently developed spatially explicit capture-recapture (SECR) models, alternatively, directly incorporate locations where individuals were photographed, allowing them to be much more robust to varying trap array sizes and spacing relative to animal movement (Borchers and Efford, 2008; Royle et al., 2009; Sollmann et al., 2012; Sun et al., 2014). To estimate density with relatively low bias and high accuracy, SECR models still require multiple individuals to be photographed and at least a subset of these individuals to be photographed at multiple camera stations (Sollmann et al., 2012; Sun et al., 2014). Thus, a sampling design where cameras are evenly spaced based on the movements of a wide-ranging species would likely be limited in its ability to adequately sample and estimate densities of medium- to small-ranging species (i.e., individuals from such species are likely to be photographed at only a single camera). A sampling design where cameras are deployed across a range of distances, alternatively, may be more likely to collect the individual and spatial information required for simultaneously estimating the densities of multiple sympatric species.

Another factor that has contributed to photographic capture-recapture studies focusing on single, uniquely identifiable species, is the availability of analytical approaches. The first SECR model required populations to be identifiable to the individual-level (Borchers and Efford, 2008; Royle et al., 2009; see Rowcliffe et al., 2008 and Howe et al., 2017 for alternatives to capture-recapture methods). Only in recent years was the scope of spatial models expanded to include spatial mark-resight (SMR) models, which estimate the density of partially marked populations (e.g., from artificial or natural marks such as scars) by incorporating spatial data from marked, unmarked, and marked but not identifiable individuals (Sollmann et al., 2013; Rich et al., 2014; Royle et al., 2014). Applications of SMR models have been limited, likely because they had to be analyzed in a Bayesian framework (Sollmann et al., 2013; Royle et al., 2014). Efford and Hunter (2017) recently developed a likelihood-based SMR model, however, that estimates density by maximizing a pseudolikelihood that incorporates likelihood components from both marked and unmarked animals. This approach sacrifices some accuracy in parameter estimates, but reduces the computational overhead and in turn, increases the accessibility of SMR models to a broader audience (Efford, 2017; Efford and Hunter, 2017).

Our research explores two approaches designed to maximize our ability to estimate the densities of multiple species using a single camera trap survey. The first is design-based – a hybrid sampling grid that incorporates systematic and random components for establishing camera trap locations. The second is analytically-based – employing both SECR and SMR models to estimate densities of fully and partially-marked wildlife populations. We used simulations to test how our hybrid camera trapping grid compared to a more traditional, systematic grid in its ability to generate accurate density estimates for species that vary in their space use. We then implemented our proposed multi-species photographic capture-recapture approach in the Okavango Delta of Botswana, with the goal of estimating densities of carnivore

species ranging in size from aardwolves (~11 kg; *Proteles cristata*) to lions (~200 kg; Table 2). The Okavango Delta is a World Heritage Site, home to one of the highest diversities of carnivores in Africa and the most diverse assemblage of large (> 15 kg) carnivores in the world (Gittleman et al., 2001; Dalerum et al., 2008). Empirical data on this diverse wildlife community is generally lacking, yet urgently needed given recent reports of declining wildlife populations and increasing pressures from illegal hunting (Rogan et al., 2017). Maintaining Botswana's wildlife populations is important ecologically, but also economically; the wildlife-based tourism industry is one of the largest contributors to the country's gross domestic product (World Travel and Tourism Council, 2017). Our research aims to provide critically needed information on the densities of carnivore species in Botswana, as well as a general framework for expanding the scope of photographic capture-recapture studies from estimating the density of one focal species to estimating the densities of multiple, diverse species.

2. Material and methods

2.1. Study area

Our study was carried out in Ngamiland District of Northern Botswana (19°31'S 23°37'E), where the Okavango Delta is located. Dominant habitat types included floodplains, savanna grasslands, and mopane (*Colophospermum mopane*) shrub and woodlands. Our study site encompassed the eastern section of Moremi Game Reserve, wildlife management areas NG33/34, and a portion of the livestock grazing areas in Shorobe (Fig. 1). The game reserve and wildlife management areas were used primarily for photographic tourism while the livestock area was used primarily for cattle grazing. An extensive 1.3-m high cable veterinary fence separates the wildlife management areas from adjacent livestock grazing areas. Carnivores and other wildlife species, however, commonly passed through the fence (Keene-Young, 1999).

2.2. Simulations

We tested the efficacy of two camera trap spacing designs for simultaneously estimating the densities of sympatric species that varied in their space-use (Fig. 2). Both designs used the same number of traps ($n = 98$) and created coverage across the same unit area. The first design was an evenly spaced 10×10 grid that had one trap per grid cell. Traps were placed at the centroid of each grid cell and the first and 100th traps were removed (i.e., to keep the number of traps consistent between designs). The second design (hereafter “hybrid design”) used a 7×7 grid across the same unit area but had two traps per grid cell. Half of the traps were placed at the centroid of each 7×7 grid cell, and half of the traps were placed at a randomly selected location within each grid cell. This trap configuration resulted in an even coverage across the study area, but distances between traps fell across a greater range of values than with the completely systematic design. We considered data for 5 simulated species that varied in their density and space-use (Fig. 2, Table 1). We chose parameters so that total number of captures remained relatively constant across scenarios, thus enabling us to isolate the effect of species' relative amounts of movement on results. Space-use was represented by the parameters $g0$ (i.e., the probability of detecting an individual at a camera placed at the center of its home range) and σ (i.e., the spatial scale over which detection declines as you move away from the home range center, which is expected to increase as the animal's home range size increases; Borchers and Efford, 2008). We simulated 50 data sets for each combination of trap configuration and species-type (i.e., 500 simulated data sets total). We generated simulated data sets using the built-in simulation function in the SECR package, assuming a bivariate-normal utilization distribution around activity centers. We analyzed each data set using both a standard SECR model and a SMR model. For the hybrid design, which included a random component for trap placement, we generated a new trap

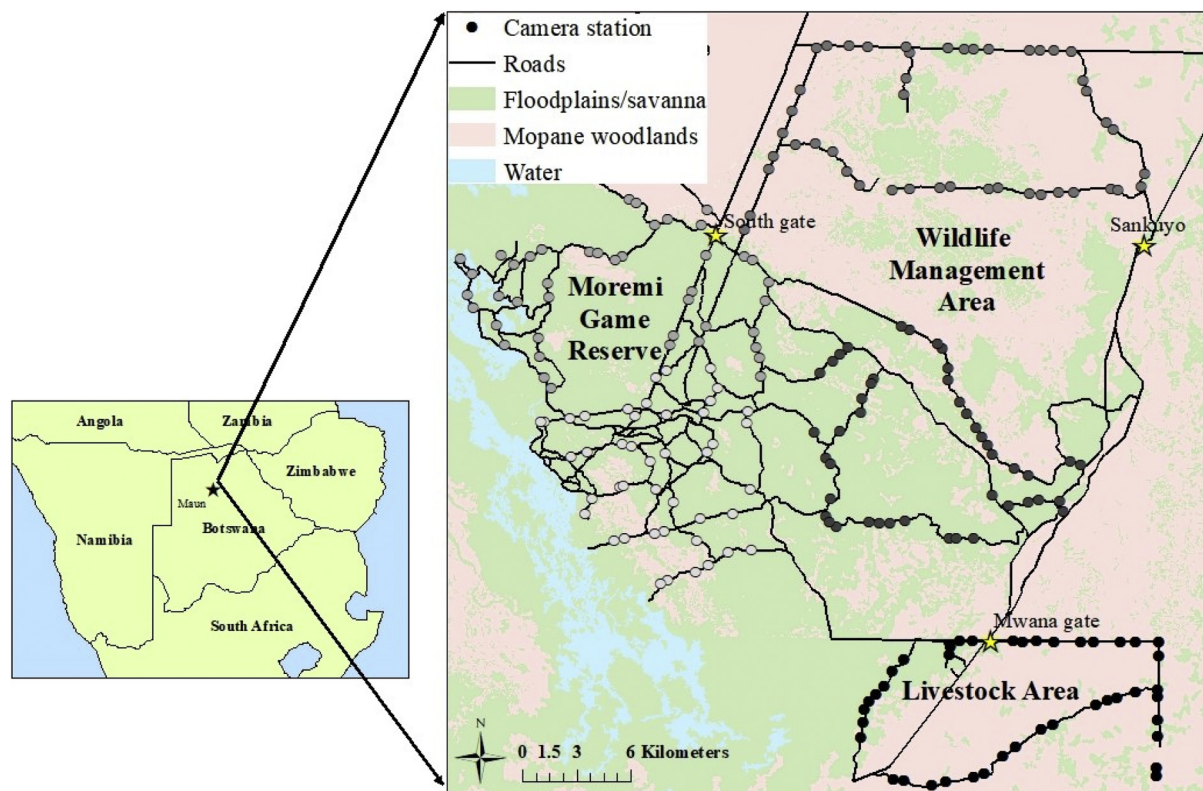


Fig. 1. Locations of camera stations, which are color coded by sampling blocks, during our survey in northern Botswana, 2015. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

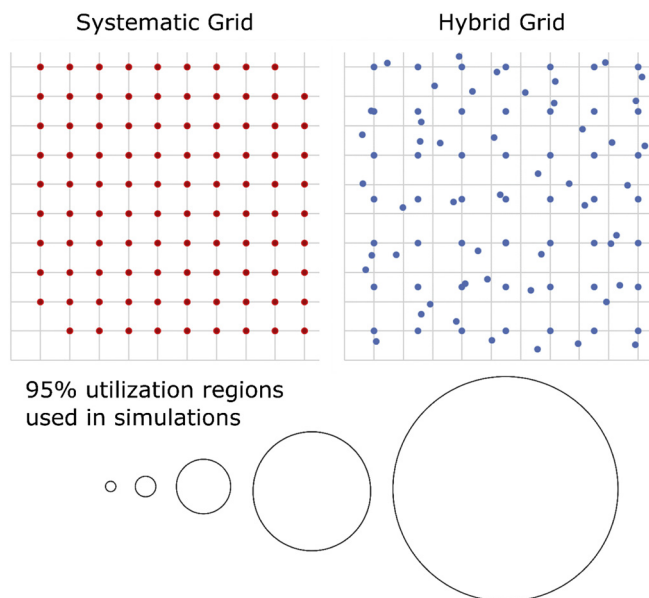


Fig. 2. Our simulation study used two alternative designs for the spacing of camera traps including a systematic 10×10 grid (below left) with traps placed at the centroid of each grid cell and a hybrid grid (below right) where half of the traps were placed at the centroids of a 7×7 grid and the remaining half were placed at a randomly selected location within each grid cell. We tested each design using simulated species that varied in their patterns of space-use. The circles at the bottom of the figure depict 95% utilization regions for the five simulated species (i.e., the areas in which 95% of use is expected to occur based on simulated σ values). While the species with larger utilization regions will overlap multiple camera locations when employing either grid, the smaller utilization regions will only overlap multiple cameras locations when employing the hybrid grid.

configuration for each simulated data set. For analyses using the SMR model, we simulated ~40% of individuals in each scenario to be unmarked. We determined the proportion of data sets for which estimates of density could be generated (i.e., at least one animal was caught at > 1 trap location) and estimated mean error rates (a measure of bias) and mean absolute error rates (a measure of accuracy) for density estimates. We used the secr package (vs. 3.1.3; Efford, 2017) through program R version 3.2.2 (R Development Core Team, 2017) to simulate and analyze all data sets.

2.3. Camera trap survey and photo classification

We deployed camera traps at 221 locations across our 1154-km² study area between February and July 2015 (Fig. 1). We used a combination of Panthera v4 incandescent-flash camera traps (0.18 s trigger speed) and Bushnell TrophyCam infrared camera traps (0.3 s trigger speed). To keep detection rates comparable among stations, we ensured every camera station included ≥ 1 Panthera camera. To guide the placement of cameras, we used 5-km² grid cells to ensure individuals from small ranging species (e.g., aardwolf) could be photographed at > 1 camera station. Within these grid cells, we placed cameras on sand roads to increase our probability of photographing carnivores as they often use lightly travelled roads as movement corridors (Forman and Alexander, 1998). We deployed two camera stations within each grid cell, one on the road closest to the predetermined center point of each grid cell and the second on the road closest to a predetermined random point within each grid cell. By moving camera locations to the closest road, our design did not completely mimic the simulated hybrid design. Specifically, we did not deploy cameras in the subset of cells where roads were sparse or missing and camera placement was concentrated in linear corridors. We were able to mimic, however, the distinguishing attribute of the design, which was having a range of intra-camera distances as compared to a consistent intra-camera distance. In our field design, camera stations were separated by a mean of 735 m with the

Table 1

We simulated 50 data sets for two camera trap configurations (systematic and hybrid grids; Fig. 2) and 5 sets of density (D), baseline encounter rate (g0), and movement (σ) parameter values. Results from spatially explicit capture-recapture (SECR) models and spatial mark-resight (SMR) models for each camera trap configuration and each set of parameter values include estimates of mean absolute error (Mean Abs. error; i.e., accuracy), mean error (i.e., bias), the percent of individuals that were photographed at a only a single camera trap (% no spatial recaptures), the number of individuals captured (# indiv. capt.), the number of captures per trap (# capt./trap), and the mean number of traps at which an individual was photographed (# traps/indiv.). For the SMR models, we simulated ~40% of individuals in each scenario to be unmarked.

	Simulated parameter values			Systematic grid					Hybrid grid						
	D	g0	σ	Mean Abs. error	Mean error	% no spatial recapt.	# indiv. capt.	# capt./trap	# traps/indiv.	Mean Abs. error	Mean error	% no spatial recapt.	# indiv. capt.	# capt./trap	# traps/indiv.
SECR model results	8	0.50	0.1	— ^a	— ^a	100	144.3	3.5	1.00	1.23	0.99	0	137.2	3.6	1.05
	4	0.18	0.2	0.66	−0.03	14	186.5	1.9	1.01	0.67	0.11	0	161.5	2.2	1.15
	2	0.08	0.5	0.32	−0.03	0	193.6	2.4	1.73	0.37	0.02	0	195.1	2.4	1.77
	1	0.03	1	0.28	0.01	0	129.7	2.8	2.50	0.29	0.04	0	133.5	2.8	2.45
	0.5	0.01	2	0.21	0.00	0	93.8	2.9	2.73	0.23	−0.01	0	93.0	2.8	2.71
SMR model results	8	0.5	0.1	— ^a	— ^a	100	102.7	3.5	1.00	1.25	0.60	0	85.3	3.6	1.05
	4	0.18	0.2	0.60	−0.14	38	121.8	1.9	1.01	0.74	0.22	0	97.7	2.2	1.15
	2	0.08	0.5	0.38	−0.02	0	127.4	2.4	1.73	0.43	−0.02	0	111.8	2.4	1.74
	1	0.03	1	0.31	−0.01	0	74.9	2.8	2.47	0.28	−0.01	0	71.2	2.8	2.44
	0.5	0.01	2	0.27	0.01	0	55.3	2.9	2.72	0.26	0.00	0	53.3	2.9	2.72

^a We were not able to calculate absolute error because there were no spatial recaptures.

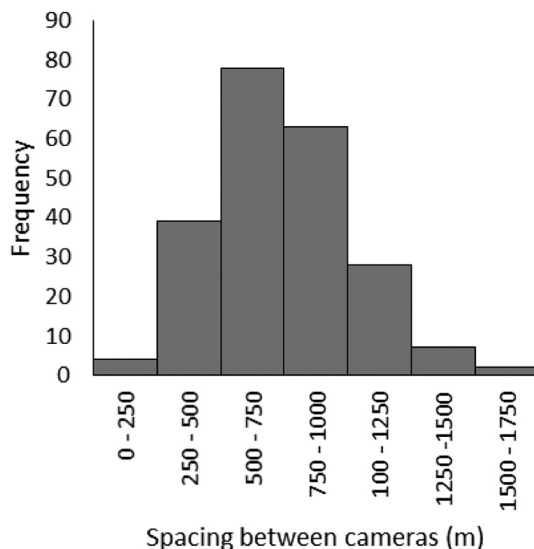


Fig. 3. The nearest neighbor distance separating 221 camera stations during a survey in Ngamiland District, Botswana, 2015. We spaced cameras at a range of distances to adequately reflect movements of small and wide-ranging carnivore species.

distance to the nearest neighbouring camera station ranging from < 500 m for 20% of the cameras to over 1 km for 17% of the cameras (range = 212 m to 1661 m; Fig. 3).

We used a rotational system for camera deployment that allowed us to extend our spatial coverage. We divided our study area into five sub-areas and sequentially sampled each area for 30 nights. Each camera station included two opposing cameras mounted on trees or, if no trees were available, on metal fence posts that we hammered into the ground. We secured cameras at knee height and positioned cameras to photograph both flanks of passing carnivores. We programmed cameras to take three photos when triggered in the day with a delay of 30 s between photo events. At night-time, the infra-red cameras took three photos when triggered but the flash cameras could only take one photo every 15 s due to the flash having to re-charge. We checked cameras every 5–10 days to download photos, replace batteries, and ensure cameras were operational.

Our analysis included 7 species of meso- and large carnivores

(Table 2); each species had a minimum of 25 photographic detections and all or a subset of each population was identifiable to the individual-level. We identified photographic detections of spotted hyenas (*Crocuta crocuta*), leopards (*Panthera pardus*), African wild dogs (*Lycaon pictus*), African civets (*Civettictis civetta*), servals (*Leptailurus serval*), and aardwolves to the individual-level using pelage patterns. For each identification, we noted whether it was based on photographic detections of both-sides, the left-side, or the right-side of the animal. If we could not identify a photo to the individual level (e.g., image was blurry or only captured part of the body), we classified the photo as unresolved. We identified detections of lions to the individual level using natural and artificial markings such as ear nicks, manes, whisker spot patterns, scars, and radio-collars (a subset of the population was collared). We again noted if the identification was based on both- or single-sided detections and if we could not identify a lion to the individual level, we labelled the photo as unresolved. Our inability to identify photographs to the individual-level was likely random with respect to individual. Unidentifiable images resulted mainly from an animal being either too far away from a camera or at an angle that did not allow a view of the flank. These events occurred at numerous stations across the grid and in no particular pattern. Lastly, the behavior and space use of many felids differs between sexes (Sollmann et al., 2011). Thus, for leopards and lions, we also distinguished males from females using secondary sexual traits.

For each species, we then determined if there were more individual identifications from left- or right-sided only detections. We retained individual identifications from the side with the greater number, and reclassified the remaining identifications as unresolved. Our approach ensured we did not double count individuals, but we note that we may have introduced some heterogeneity and thus negative bias into our estimates of density (Augustine et al., 2018).

Next, for each species, we determined the proportion of detections that were identifiable to the individual-level. If at least 70% of a species' photographic detections were individually identifiable, then we opted to use SECR models and if not, then we used SMR models. African civets (63%) and lions (62%) were the only species where < 70% of their detections were individually identifiable (Table 2). To implement SMR models for these species, we had to classify unresolved detections as (1) marked but unidentifiable or (2) unmarked. Making this distinction proved to be extremely difficult, so we adopted an approach aimed at minimizing positive bias (i.e., the chance of misidentifying a marked individual as an unmarked individual). For lions, we classified all

Table 2

The total number of detections of seven carnivore species (Det.) during a camera trap survey in Ngamiland District, Botswana, 2015, the number of individuals identified based on both-side or single-side detections (Both, Left, Right), classification of the detections based on whether they were individually identifiable (i.e., detections of individuals from 'both' category + single-side category with larger number; Indiv. ID) or unresolved (i.e., detections of individuals from single-side category with smaller number + photos that were not individually identifiable), median number (range) of detections per individual (Det./indiv.), and median number (range) of camera traps where an individual was photographed (Traps/indiv.).

Species	Scientific name	Det.	Individuals			Detection classifications		Det./indiv.	Traps/indiv.
			Both	Right	Left	Indiv. ID	Unresolved		
Spotted hyena	<i>Crocuta crocuta</i>	947	167	27	16	764	183	3 (1–25)	2 (1–14)
Leopard (F)	<i>Panthera pardus</i>	120	28	3	1	93	27	2 (1–10)	2 (1–6)
Leopard (M)	<i>Panthera pardus</i>	232	28	2	0	218	14	5 (1–33)	4 (1–23)
Wild dogs	<i>Lycan pictus</i>	302	50	0	0	280	22	5 (1–15)	5 (1–12)
Serval	<i>Leptailurus serval</i>	46	12	10	5	38	8	1 (1–6)	1 (1–4)
African civet	<i>Civettictis civetta</i>	325	41	45	50	205	120	1 (1–18)	1 (1–6)
Aardwolf	<i>Proteles cristatus</i>	36	10	5	6	27	9	1 (1–5)	1 (1–3)
Lion	<i>Panthera leo</i>	156	26	0	0	96	60	4 (1–8)	2 (1–7)

unresolved detections as marked but unidentifiable. For civets, we noted that in two of our sampling blocks the majority of civet detections were classified as unresolved. Instead of including the nominal amount of information from marked animals, we opted to re-classify all civet detections within these sampling blocks as unmarked. Civets tend to range over small areas (Ayalew et al., 2013) so it was unlikely that civets detected within these sampling blocks were previously identified individuals. In the remaining sampling blocks, we classified all unresolved detections as marked but unidentifiable. We note that some of our 'marked but unidentifiable' detections of lions and civets could have been of new individuals. Thus, our estimates of civet and lion densities are likely biased low. Given likelihood-based SMR models are a relatively new class of models, we compared estimates of civet and lion density based on SMR models to those based on SECR models to determine if (1) the estimates were similar and (2) SMR models had improved accuracy.

2.4. Spatial models

We collapsed daily camera trapping data into 20, 1-week sampling occasions and created species-specific capture histories. We also created camera trap input files, which included camera locations, sampling histories (1 = camera station active; 0 = camera station not active) and estimates of vegetation density for each camera. Vegetation density was a coarse measure of forb, shrub, and tree cover in the area surrounding the camera station (see Rich et al., 2016 for details). Lastly, we created input files with camera- and sampling-occasion specific counts of the number of sightings classified as marked but not identifiable or unmarked.

We used the secr package (vs. 3.1.3; Efford, 2017) through program R version 3.2.2 (R Development Core Team, 2017) to implement both the SECR and the SMR models. For both models, we assumed each individual had an activity center and that activity centers were distributed across the state space S (Borchers and Efford, 2008). To define S , we trialed different buffer sizes in secr and selected the buffer size that was large enough to include the activity centers of all individuals exposed to trapping (i.e., buffer was at least $3 \times$ the size of σ and density estimate stayed comparable if the buffer size was increased). We used buffers surrounding our camera station grid ranging in size from 5 km for the small-ranging species to 25 km for the wide-ranging species (Table 3). Further, we overlaid S with a habitat mask that we developed using vegetation data from Bennitt et al. (2014). By assuming that activity centers followed an inhomogeneous Poisson spatial distribution, we were able to estimate density within each of the two major habitat strata, mopane woodlands (49% of area) and floodplains/savanna grasslands (51% of area), and to calculate an overall density estimate as the area-weighted mean.

For individually identifiable animals (i.e., marked animals), which

constituted the entire population for the SECR models and a portion of the population for the SMR models, we assumed the number of photographic detections of individual i at camera station j during sampling occasion k , y_{ijk} , was a Poisson random variable with a mean encounter rate λ_{ijk} (Borchers and Efford, 2008; Royle et al., 2009). We assumed λ_{ijk} would decline with distance between the camera trap and an individual's activity center and modeled this decline using a half-normal detection function, where the shape was dependent on g_0 , the baseline encounter rate, and σ , the spatial scale parameter. We included vegetation density as a covariate for g_0 as it is negatively related to the detection probability of mammals in northern Botswana (Rich et al., 2016). For each of the individually identifiable animals (i.e., the SECR models), we then used the secr package to estimate habitat-specific and overall densities by fitting Poisson processes through likelihood maximization. Additional steps were necessary for the SMR models to account for sightings classified as marked but unidentifiable or unmarked (Efford and Hunter, 2017). Using the secr package, we were able to implement these steps and then estimate density by maximizing a pseudolikelihood (i.e., a weighted combination of likelihood components for marked and unmarked animals) adjusted for spatial overdispersion (see Efford and Hunter, 2017 for details).

3. Results

3.1. Simulations

Our results were largely similar for SECR and SMR data sets, with the primary difference being greater accuracy for SECR and spatial recaptures occurring less frequently for SMR (Fig. 4; Table 1; Appendix A). For species with small home-ranges (i.e., σ is small), the hybrid design generated data that allowed for density to be estimated in many cases where the systematic design would not (Table 1). In 100% of the simulated data sets for our smallest σ value, and in 14 and 38% of the data sets for our next smallest σ value (analyzed using SECR and SMR models, respectively), animals were never photographed at > 1 camera trap when employing the systematic grid configuration. This stands in contrast to the hybrid grid, where for all σ values at least some individuals were photographed at > 1 camera, which allowed us to estimate density for all values of σ .

Estimates were unbiased for all but the smallest σ (i.e., mean error was close to 0; Fig. 4; Table 1). In the case of the smallest σ , where estimates could only be achieved for the hybrid design, density was overestimated (i.e., positively biased) by 12 and 8% on average when employing SECR and SMR models, respectively (Appendix A). Accuracy in density estimates, as measured by mean absolute error, was similar between the designs for the largest σ value when employing both SECR and SMR models (Table 1). For intermediate values of σ ($\sigma = 0.5$), alternatively, the systematic grid was 15% more accurate than the hybrid

Table 3

Summary statistics (estimated mean parameter values and 95% confidence intervals) from spatially explicit capture-recapture and spatial mark-resight models based on photographic captures of carnivores in Ngamiland District, Botswana, 2015, including buffer widths and the resulting state space areas, and estimates of baseline encounter rate g_0 and scale parameter σ .

Common name	Buffer width (km)	State space (km ²)	g_0	σ (km)
Spotted hyena	25	6337	0.07 (0.06–0.08)	4.2 (4.01–4.46)
Leopard (F)	15	3738	0.1 (0.07–0.15)	2.4 (2.06–2.70)
Leopard (M)	20	4969	0.2 (0.15–0.22)	3.2 (2.93–3.51)
Wild dogs	25	6337	0.07 (0.054–0.079)	4.8 (4.40–5.23)
Serval	5	1666	0.06 (0.027–0.147)	1.2 (0.85–1.55)
African civet	6	1867	0.3 (0.28–0.42)	1.3 (1.20–1.44)
Aardwolf	5	1666	0.06 (0.026–0.130)	2.2 (1.64–3.03)
Lion	25	6337	0.09 (0.044–0.110)	3.6 (3.26–4.56)

grid. In the case of SMR, accuracy was also lower for the hybrid grid when $\sigma = 0.2$. However, this comparison is not direct since 38% of the systematic data sets did not allow for density to be estimated at all (i.e., no spatial recaptures; Table 1). In most cases, the hybrid design was successful in allowing us to estimate density for a wider range of species with negligible decreases in accuracy.

3.2. Field density estimation

We recorded 2167 photographic detections of our 7 focal carnivore species over 6607 trap nights. Spotted hyenas were photographed most often with 947 detections while aardwolves were photographed least with 36 detections (Table 2). We identified high numbers of individual spotted hyenas, African civets, and leopards, and low numbers of aardwolves, servals, and lions (Table 2).

Our hybrid camera trapping configuration resulted in at least some individuals from all species being photographed at multiple camera

stations. Among the species, individual male leopards and individual wild dogs were detected the greatest number of times at the greatest number of cameras (Table 2). Conversely, individuals from the smaller ranging species (i.e., aardwolves, servals, and civets) were detected the fewest number of times at the fewest cameras (Table 2). Male leopards and African civets had the highest estimated baseline encounter rates, g_0 , whereas wild dogs and spotted hyenas had the largest estimated movement parameters, σ (Table 3). Estimates of g_0 and σ were higher for male leopards than for females, supporting that the space use of felids can differ between sexes (Table 3; Sollmann et al., 2011). For lions, however, σ was similar for adult male lions ($\sigma = 3.8$) and young male lions and females ($\sigma = 4.2$), so we opted to model all lion detections together. Our resulting density estimates ranged from 1.2 lions per 100 km² to 10.1 spotted hyenas per 100 km² (Fig. 5). For the majority of species, estimated densities were greater in non-mopane habitats (i.e., open areas) than in mopane woodlands but these relationships were weak (i.e., 95% confidence intervals overlapped; Fig. 5). We were

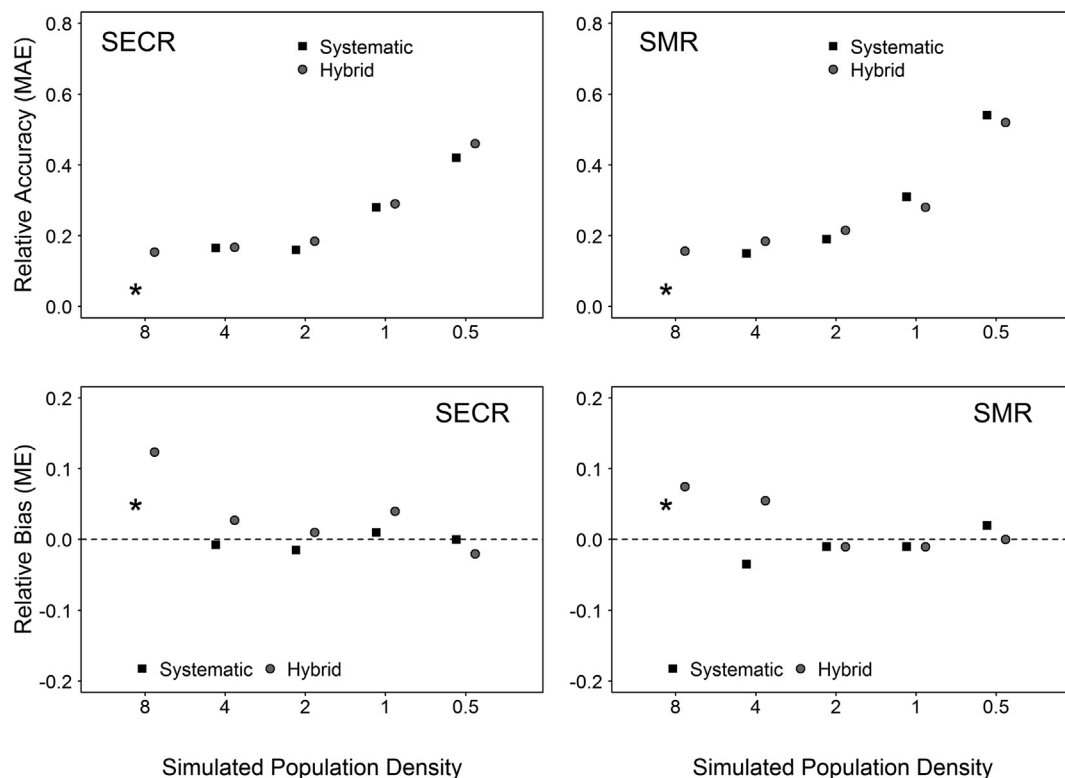


Fig. 4. We simulated 50 data sets using two camera trap configurations (systematic and hybrid grids; Fig. 2) and 5 sets of density, baseline encounter rate, and movement parameter values, and then analyzed the data using both spatially explicit capture-recapture (SECR) and spatial mark-resight (SMR) models. Here, we present the resulting estimates of relative accuracy (mean absolute error - MAE) and relative bias (mean error - ME) for each camera trap configuration, each simulated population density, and each modeling approach. A star indicates there were no spatial recaptures and consequently, that we were not able to estimate relative accuracy and bias.

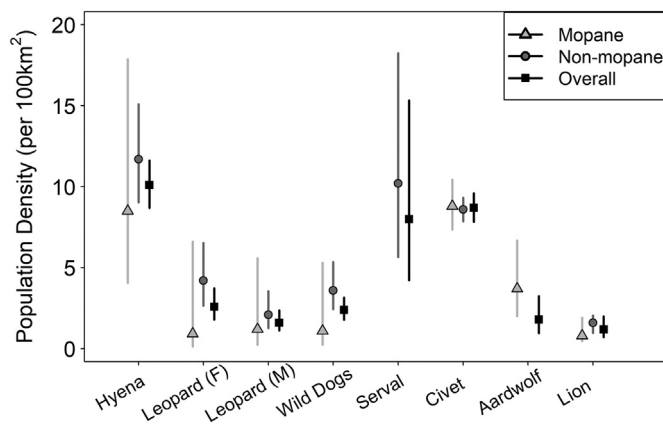


Fig. 5. Mean density estimates (D) and 95% confidence intervals from likelihood-based models for spotted hyena, female leopard, male leopard, African wild dog, serval, African civet, aardwolf, and lion in Ngamiland District of Botswana, 2015. We include density estimates for these species in mopane (*Colophospermum mopane*) habitat, non-mopane habitat, and the study area overall.

unable to estimate the densities of servals in mopane areas and aardwolves in non-mopane areas given the low detection rates of these species in the respective habitat type. Lastly, estimates of lion (SMR: 1.2, 95% CI = 0.72–1.99; SECR: 1.5, 95% CI = 0.97–2.33) and civet (SMR: 8.7, 95% CI = 7.84–9.59; SECR: 10.7, 95% CI = 8.46–13.58) densities (animals/100 km²) were comparable when using SECR and SMR models, but estimates were lower and had smaller confidence intervals when employing SMR techniques, particularly for civets.

4. Discussion

Our research demonstrates that a single camera trap survey, in combination with capture-recapture techniques, can be used to estimate the densities of multiple small- to wide-ranging species. Camera traps have become a mainstream tool in conservation ecology because they allow collection of information on a diversity of wildlife populations, 24 h per day, and in all weather conditions (O'Brien et al., 2010; Steenweg et al., 2017; Rich et al., 2017). Attention is typically focused on a single species, however, meaning a wealth of community information is underutilized (Karanth and Nichols, 1998; Silver et al., 2004; Karanth et al., 2006). By employing a carefully designed camera trapping grid, where cameras were spaced by a range of distances, and applying the full range of spatial capture-recapture models, we were able to estimate the densities of lions, spotted hyenas, leopards, African wild dogs, African civets, servals, and aardwolves simultaneously. Our multi-species approach facilitated a more comprehensive and efficient use of available field equipment and data collected, and likely resulted in considerable savings in money, time, and personnel costs when compared to single species approaches. Maximizing the amount of information gained from field studies is increasingly necessary given the limited funding available to many conservation agencies and organizations across the world (Zipkin et al., 2009).

The ability of spatial capture-recapture models to produce reliable estimates of animal movement and density depends on the number of individuals photographed and the number of spatial recaptures (Borchers and Efford, 2008; Sollmann et al., 2012; Sun et al., 2014). Thus, if the goal is to use a single camera trapping grid to estimate the densities of multiple species, grid design is paramount. We used simulated data for species that varied in density and space use to test the efficacy of two camera trap spacing designs. We show that a hybrid design that uses elements of systematic and random camera placement can be used to estimate density for a wider range of species. The hybrid design results in even coverage across a large study area as with a

systematic grid, but also results in some traps being located more closely together. Consequently, species with small home ranges have the opportunity to be photographed at more than a single camera station. The hybrid design resulted in little loss in accuracy for animals with large home ranges, and a minor loss in accuracy for species with medium-sized home ranges. We cannot say with certainty why in a subset of the cases the standard trapping grid was more accurate than the hybrid grid. These results suggest, however, that there is a tradeoff between being able to estimate the density of numerous species, in which case the hybrid design performs better, and accuracy, in which case a systematic design may perform better, particularly if trap spacing is tailored to the movements of an individual species. Further work to better understand how the dispersion of recaptures affects accuracy of estimates may provide additional insights into how to optimally space traps when movement patterns differ among species. An alternative to our hybrid design, which would likely achieve similar results, would be to locally cluster traps (Sun et al., 2014). Both our hybrid design and local clustering of traps will maximize community coverage, facilitating density estimation for an array of species that vary widely in space-use.

Our estimated densities ranged from 1.2 lions to 10.1 spotted hyenas per 100 km². We could not find density estimates for aardwolves for comparison, but we were able to determine that our estimated densities for spotted hyenas, leopards, civets, and servals fell within the range of previously published estimates in southern Africa (Balme et al., 2010; Boast and Houser, 2012; Cozzi et al., 2013; Ramesh and Downs, 2013; Amiard, 2014). Our estimate of wild dog densities also seemed reasonable based on known pack and home range sizes in the region (Pomilia et al., 2015). Our estimated lion density (1.2 lions/100 km²; 95% CI = 0.72–1.99) was substantially lower than a previous estimate from our study region that was based on call stations (5.8 lions/100 km²; Cozzi et al., 2013). Converting call station responses to population estimates is dependent on the researcher's ability to estimate the proportion of animals that respond, and by accurately calculating the distance from which the species respond to the call station (Midlane et al., 2015). Consequently, differences in estimated densities are likely attributed to the differing sampling and estimation techniques and not to an actual decline in the study area's lion population. We note that our sampling design (i.e., deploying cameras on sand roads) may have affected results if certain species preferentially used or avoided roads, but we believe these effects were minimal given 1) these were low-use, 4-wheel drive roads distributed throughout the major habitat types and 2) estimates were comparable to those from similar habitats in southern Africa. We recommend further work assessing the impacts of camera placement, as it would help elucidate potential impacts.

While our multispecies approach was successful in estimating the densities of a range of species, it also had several limitations. Our primary limitation was the challenge of distinguishing between marked but unidentifiable and unmarked detections. To avoid labeling detections of previously identified individuals as unmarked (i.e., falsely augmenting the population), we classified the majority of unresolved sightings as marked but unidentifiable. If some of these sightings were of new individuals, however, then our approach likely introduced a source of negative bias. Further, for civets, we classified all detections within a subset of the study area as unmarked as very few photos were identifiable to the individual level. Spatial mark-resight models analyzed in a likelihood framework assume (1) marked individuals represent a random sample of the population and (2) failure to identify marked individuals occurs at random throughout the population and space (Royle et al., 2014). Our approach for classifying civet detections likely violated this assumption, but appears to have had a nominal influence on density estimates given the comparability of estimates from SMR and SECR models. It is also possible that we violated this assumption if animals with activity centers closer to camera stations had a higher probability of being photographed on both-sides and in turn, a higher capture probability. In this case, we may have introduced individual heterogeneity in capture probability and secondary source of

negative bias in abundance and density (Augustine et al., 2018). When relying on natural marks, we expect that many practitioners will also have difficulty distinguishing between these unresolved classifications and face similar limitations. Thus, we encourage the development of a likelihood-based SMR model where detections of unknown status could be grouped together potentially as an overall correction factor for detection.

Our multispecies capture-recapture framework demonstrates (1) the utility of a hybrid sampling design when the goal is to inform community-level conservation and (2) the practicality of likelihood-based, spatial models for estimating the densities of partially to fully marked populations (Borchers and Efford, 2008; Efford and Hunter, 2017). This framework is applicable to not only the growing number of camera trap studies worldwide (Steenweg et al., 2017; Rich et al., 2017), but also to survey methods (e.g., hair snares) that produce encounter history data with corresponding spatial information (Royle et al., 2009). We applied our multispecies approach to a camera trap survey in northern Botswana, specifically, to provide vitally needed information on the population status of 7 carnivore species, including the first published density estimates for aardwolves, civets, servals, wild dogs, and leopards in the country. Conserving carnivore populations in the Okavango Delta of Botswana is vital given it is a stronghold for many wildlife populations and home to one of the highest diversities of carnivores in Africa (Gittleman et al., 2001). Similar to continent-wide trends, however, wildlife is perceived to be declining within the country and the data needed to quantify this trend is generally lacking (Ripple et al., 2014; Bauer et al., 2015; Rogan et al., 2017). We encourage continued research focused on improving our knowledge and understanding of wildlife densities and abundances in Botswana, as well as elsewhere in the world. Only then, will we be able to empirically detect population declines and develop conservation plans aimed at effectively curtailing or reversing these declines (Collen et al., 2013; Pereira et al., 2013, Ripple et al., 2014; Bauer et al., 2015).

Data accessibility

We will publish our data in the Dryad Digital Repository upon manuscript acceptance.

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Appendix A

We simulated 50 data sets for all combinations of five population densities, two statistical estimators, and two camera trap configurations. Our simulations included 98 cameras arranged in either a systematic grid or a hybrid design, which combined systematic and random locations. Data generated in the simulations followed a spatially explicit capture-recapture (SECR) or spatial mark-resight (SMR) design and were analyzed using the respective estimator in the secr package in R. Finally, we simulated 5 different densities (0.5, 1, 2, 4, 8

animals per unit area), and assumed a strong negative correlation between density and home range size. In all cases, we were unable to estimate density for the systematic grid when density was high (and movement low) because spatial recaptures did not occur. We were also unable to generate estimates of density in 7 cases for the SECR data and 19 cases for the SMR data when the simulated density of 4 was used.

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