Received: 1 March 2021 | Accepted: 23 December 2021

DOI: 10.1002/2688-8319.12129

Ecological Solutions and Evidence | BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Camera trapping and spatially explicit capture–recapture for the monitoring and conservation management of lions: Insights from a globally important population in Tanzania

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Paolo Strampelli and Charlotte E. Searle should be considered joint first authors.

Funding information
Natural Environment Research Council (NERC); National Geographic Society; Cleveland Metroparks Zoo; Chicago Zoological Society; Pittsburgh Zoo

Handling Editor: Marc Cadotte

Abstract

1. Accurate and precise estimates of population status are required to inform and evaluate conservation management and policy interventions. Although the lion (*Panthera leo*) is a charismatic species receiving increased conservation attention, robust status estimates are lacking for most populations. While for many large carnivores population density is often estimated through spatially explicit capture–recapture (SECR) applied to camera trap data, the lack of pelage patterns in lions has limited the application of this technique to the species.
2. Here, we present one of the first applications of this methodology to lion, in Tanzania's Ruaha-Rungwa landscape, a stronghold for the species for which no empirical estimates of status are available. We deployed four camera trap grids across habitat and land management types, and we identified individual lions through whisker spots, scars and marks, and multiple additional features.
3. Double-blind identification revealed low inter-observer variation in photo identification (92% agreement), due to the use of xenon-flash cameras and consistent framing and angles of photographs.
4. Lion occurred at highest densities in a prey-rich area of Ruaha National Park (6.12 ± SE 0.94 per 100 km^2), and at relatively high densities (4.06 ± SE 1.03 per 100 km^2) in a community-managed area of similar riparian-grassland habitat. Miombo woodland in both photographic and trophy hunting areas sustained intermediate lion densities (1.75 ± SE 0.62 and 2.25 ± SE 0.52 per 100 km^2, respectively). These are the first spatially explicit density estimates for lion in Tanzania, including the first for a trophy hunting and a community-managed area, and also provide some of the first insights into lion status in understudied miombo habitats.
5. We discuss in detail the methodology employed, the potential for scaling-up over larger areas, and its limitations. We suggest that the method can be an important

tool for lion monitoring and explore the implications of our findings for lion management.

KEYWORDS
camera trap, lion, *Panthera leo*, population monitoring, Ruaha-Rungwa, SECR, Tanzania, trophy hunting

1 | INTRODUCTION

The effective management of wildlife populations requires accurate and precise estimates of status, in order to assess threats, evaluate the impact of interventions, and identify areas of conservation importance (Campbell et al., 2002; Hayward et al., 2015). The African lion (*Panthera leo*) is classified as Vulnerable by the IUCN (Bauer et al., 2016), and the species is estimated to now occupy only 8% of its historical sub-Saharan range (Riggio et al., 2013; Wolf & Ripple, 2017). As a result of these patterns of loss, as well as the species' strong ecological, economic, and cultural value, lions have received increased conservation attention in recent years (Bauer et al., 2022; Macdonald et al., 2016). Nevertheless, most lion populations still lack reliable status estimates, particularly outside southern Africa (Bauer et al., 2016; Braczkowski, Gopalaswamy, Elliot, et al., 2020; Dröge et al., 2020).

In recent years, advances in spatially explicit capture–recapture (SECR) modelling have facilitated the estimation of large carnivore population status, by allowing density to be estimated directly as a state parameter (Borchers & Efford, 2008; Royle et al., 2009; Royle & Young, 2008). SECR models have since been employed to estimate lion population density primarily through unstructured search-encounter surveys, which rely on the direct observation of individuals (Braczkowski, Gopalaswamy, Nsubuga, et al., 2020; Elliot et al., 2020; Elliot & Gopalaswamy, 2017). However, collecting such data can be challenging where populations exist at low densities, or where individuals are elusive due to human persecution (Henschel et al., 2020).

For readily individually identifiable large carnivore species, this issue has been circumvented by applying SECR models to camera trap data. This has become the standard monitoring protocol for a range of species, including leopard (*Panthera pardus*; Strampelli et al., 2018), tiger (*Panthera tigris*; Karki et al., 2015), and jaguar (*Panthera onca*; Boron et al., 2016). However, the lack of easily identifiable pelage patterns on lions has resulted in this methodology being applied to the species only a handful of times, and only at single sites within a landscape (Kane et al., 2015; Rich et al., 2019), preventing comparisons across habitat and land management types. Possibly as a result of this, as well as of a lack of detailed methodological guidelines, the method has until now received little attention as a lion population assessment and monitoring tool (IUCN SSC Cat Specialist Group, 2018).

Here, we estimate lion population density through SECR modelling of data from modern, white-flash (xenon) camera traps at a number of sites, using a double-blind observer identification process to also assess ease of individual identification, which is a key requirement of SECR modelling (Efford, 2004). Our study area is the Ruaha-Rungwa landscape, a vast, mixed-use conservation complex in south-central Tanzania. Although considered one of only four lion strongholds in East Africa (Riggio et al., 2013), no published lion population status estimates are available for this area, which includes the region's second largest National Park and some of Tanzania's largest trophy hunting areas.

We modelled lion density at four sites in Ruaha-Rungwa: two within different habitat types in a photographic tourism area, one in a trophy hunting area, and one in a community-managed buffer area. We provide a detailed overview of the methodology employed, including with regard to data collection and individual identification. We discuss the potential applications and limitations of the method, and explore the implications of our findings for lion conservation management. Our study provides the first spatially explicit density estimates for a lion population in Tanzania, as well as some of the first insights into lion status in important yet understudied miombo woodland habitats.

2 | MATERIALS AND METHODS

2.1 | Study area

The Ruaha-Rungwa ecosystem is a ~45,000-km^2 unfenced multiple-use conservation complex in south-central Tanzania, and is considered a Key Landscape for Conservation (European Commission, 2016). The largest Protected Area (PA) in the complex is Ruaha National Park (NP), which at 20,226 km^2 is the second largest NP in East Africa. Only photographic tourism is permitted within the NP. To the north are Rungwa (9175 km^2), Kizigo (5140 km^2) and Muhesi Game Reserves (GRs; 2720 km^2). GRs hold similar legal protection status as NPs, but rely on consumptive use of wildlife through trophy hunting as their primary revenue generation mechanism. To the east of Ruaha NP are MBOMIPA (947 km^2) and Waga Wildlife Management Areas (WMAs; 344 km^2), community-managed PAs which form a buffer between Ruaha NP and unprotected village lands. Although both photographic tourism and trophy hunting are permitted in the WMAs, neither were taking place at the time of study. A multiple-use Game Controlled Area (GCA) and Open Area (OA) complete the complex (Figure 1).

Ruaha-Rungwa is located at the intersection of three ecoregions: southern *Acacia–Commiphora* bushland and grasslands, and both Central Zambezian and Eastern miombo woodlands (Olson et al., 2001). The climate of the region is semi-arid to arid, with an average annual

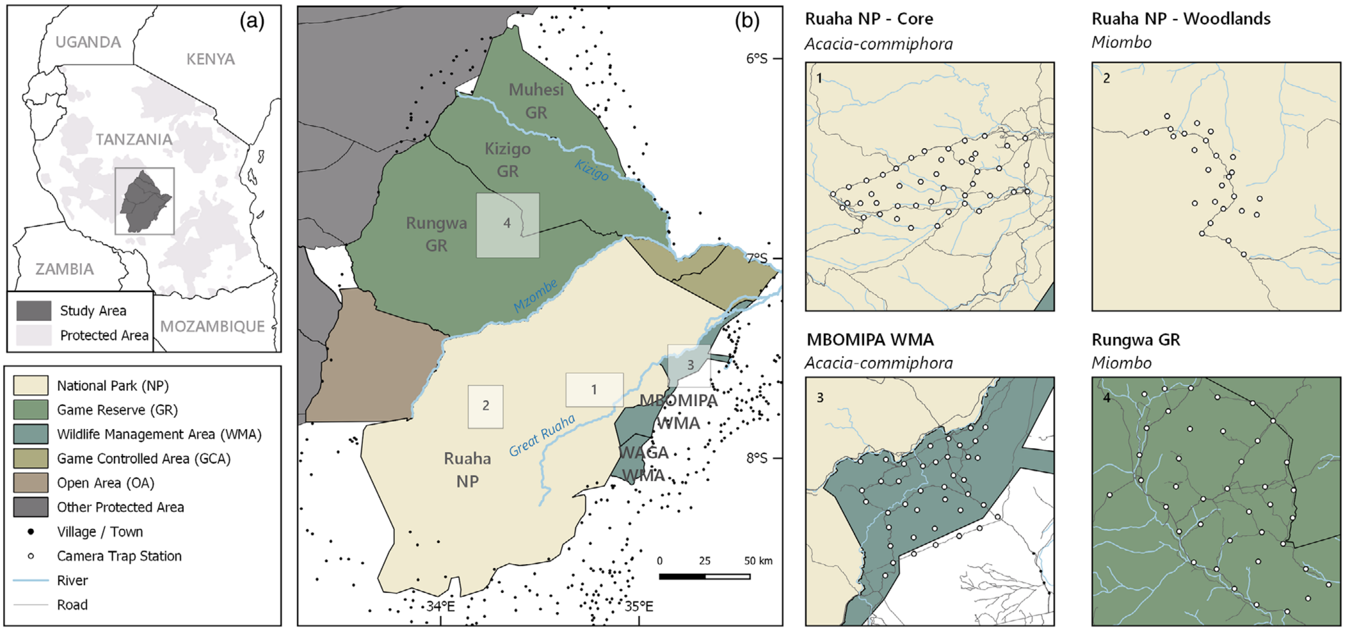

FIGURE 1 The Ruaha-Rungwa conservation landscape (b), located within the context of Tanzania's protected area network (a). Protected areas not typically considered part of the Ruaha-Rungwa conservation complex are shaded in grey. Map includes the largest rivers in the complex. Only villages in close proximity of the PA complex are shown. Insets 1–4: Camera traps survey grids carried out in 2018 and 2019, and the main vegetation type of the area

precipitation of 600 mm (Fick & Hijmans, 2017). The complex has been identified as a priority for large carnivore research and conservation in Tanzania (TAWIRI, 2009).

2.2 | Camera trap survey design

We carried out systematic camera trap surveys at four sites in Ruaha-Rungwa, between June and November 2018 and July and October 2019 (Table 1). Forty-four stations (88 cameras) were deployed for 83 nights over 223 km^2 in the core tourist area of Ruaha NP, a well-protected and prey-rich (TAWIRI, 2019) *Acacia–Commiphora* habitat near the Great Ruaha River, which is a key source of dry season surface water for wildlife (Figure 1). Twenty-six stations (52 cameras) were deployed for 90 nights over 152 km^2 in an area of miombo woodland habitat in the north-west of Ruaha NP. Forty stations (80 cameras) were deployed for 70 nights over 270 km^2 in MBOMIPA WMA, in primarily *Acacia–Commiphora* habitat, also near the Great Ruaha River and relatively prey rich. Due to its proximity to unprotected village lands, however, the area experiences greater levels of human disturbance than the core tourist area of Ruaha NP (TAWIRI, 2019). Finally, forty stations (80 cameras) were deployed for 91 nights over 555 km^2 in central Rungwa GR, within the actively hunted Rungwa Ikiri block, in an area of miombo woodland and seasonal floodplains. The area also experiences greater levels of anthropogenic impact than the core tourist area of Ruaha NP (TAWIRI, 2019).

Survey grids consisted of paired camera trap stations (Cuddeback Professional Color Model 1347, Non Typical Inc., Wisconsin, USA), spaced between 1.5 and 4.5 km from each other (see Table 1 for mean camera spacing for each grid). This was based on estimated female lion dry season home range size in the study area (~170 km^2; RCP, unpublished data), to ensure that all individuals in the survey area had a non-zero capture probability (Noss et al., 2013). Although ideally the sampled area would have exceeded mean male dry season home range (~290 km^2; RCP, unpublished data), logistical constraints meant that in our case this was achieved with certainty for only one grid (Rungwa GR). Survey duration for each grid was restricted to 3 months; this is generally considered appropriate to minimize demographic closure violations in studies of large felids (Alexander et al., 2015; Karanth, 1995).

Camera stations were set along roads, game trails, and near water points, to maximize captures of large carnivores (Tobler et al., 2013). Cameras were mounted on trees at a height of 30–40 cm on opposite sides of the road or trail, facing inwards, to attempt to photograph both flanks of animals. We selected trees located 3–5 m from the centre of the road or trail, as recommended for other large carnivores (Noss et al., 2013). Cameras were set perpendicular to the road or trail, to ensure consistent framing and angles in order to facilitate individual identification and minimize known issues related to this process (Johansson et al., 2020). Cameras were placed within metal protective cases and camouflaged, to prevent damage by animals or people. Cameras were set to take pictures during both day and night, and to take one photograph per trigger (white-flash cameras are only able to take one photograph per trigger at night). Trigger interval was set on 'Fast as Possible' (<5 s during the day, and ~20 s at night), and image resolution was set to 'high quality' (20 MP). Flash strength was set at 'close' or 'medium', depending on the distance to the centre of the road or trail.

TABLE 1 Survey design details and summary results for the four camera trap grids in Ruaha-Rungwa

	Ruaha NP (Core)	Ruaha NP (Woodland)	MBOMIPA WMA	Rungwa GR
Primary habitat type	*Acacia–Commiphora*	Miombo	*Acacia–Commiphora*	Miombo
Survey period	June–September 2018	August–November 2018	September–November 2018	July–October 2019
Survey duration (nights)	83	90	70	91
Stations	45	26	40	40
Trap nights	3380	2172	2689	3206
Mean trap nights per camera	80	84	67	80
Average station spacing	1.96 km	1.88 km	2.08 km	3.46 km
Survey area[a]	223 km^2	152 km^2	270 km^2	555 km^2
Flank with most captures	Right	Left	Right	Left
Independent lion captures[b]	390	67	53	80
Proportion of identifiable captures[b,c]	90%	79%	95%	83%
Individuals recorded[b,c]	48	14	18	21
Female	30	9	9	11
Male	18	5	9	10
Recapture rate[b,c,d]	74%	71%	67%	61%

[a] Area of the minimum convex polygon around all stations (does not include buffer).
[b] Based on the flank with most captures for each grid. Includes both identifiable and non-identifiable captures.
[c] For sites with two investigators (MBOMIPA WMA and Rungwa GR), figures from the consensus capture histories are presented.
[d] Percentage of identified individuals recaptured at more than one station during the survey period.

2.3 | Individual identification

For each survey grid, we used captures of the flank with the greater number of photographs, to avoid biasing capture probabilities for individuals whose flanks could not be matched. The primary means of identifying lions were whisker spots (Braczkowski, Gopalaswamy, Nsubuga et al., 2020) and scars and marks; in addition, pelage patterns (for younger individuals), mane size and shape (for males), ear notches, and nose shape were all also used to facilitate and expedite identification. A positive identification was deemed to be achieved only if whisker spots matched; the only exception was if a characteristic scar or mark was present, in which case identification was achieved even if whisker spots were not clearly visible, but the characteristic scar or mark matched exactly (Figure 2). Due to scars and marks potentially fading over time, the absence of a scar or a mark was not deemed sufficient to exclude individuals during identification, except if photographs with that same scar or mark were available from both before and after the time of the photograph lacking the scar or mark of interest. Photographs were only considered to depict a new individual if it was clear that they did not depict any of the identified individuals; if this could not be determined conclusively (Figure 3), the photograph was discarded. See Appendix S1 for additional details and worked examples of the identification process.

Only individuals estimated to be >1 year of age (i.e. adults or subadults; Miller et al., 2016) were considered. Although all efforts were made to exclude lions younger than this, and to accurately sex individuals, we acknowledge the difficulties associated with ageing and sexing young lions with certainty through camera traps. Lions were never identified based solely on social patterns (e.g. identification based on certain individuals often noted to be captured together).

We used a double-blind observer identification process to determine how differences in photo identification between researchers might influence density estimation, as previously done for other species (e.g. puma, *Puma concolor*; Kelly et al., 2008; Rich et al., 2014). For two of the four sites (MBOMIPA WMA and Rungwa GR), we had two investigators independently identify photographs of lion, with each unaware of how the other had identified and categorized captures. This approach was implemented at two sites only due to logistical and financial constraints; nevertheless, sites within both *Acacia–Commiphora* and miombo woodland habitats were subject to the double-blind process.

2.4 | Density estimation

Population density was modelled within a maximum-likelihood SECR framework, using the package *secr 4.2.0* (Efford, 2020) in R v. 3.6.3 (R Core Team, 2019). SECR models estimate density explicitly while accounting for imperfect detection (Borchers & Efford, 2008), and simulations have shown that the method provides accurate results for social animals (as are lions) even when their ranging patterns may violate assumptions of independence between activity centres and individuals' movements (López-Bao et al., 2018). A SECR approach was chosen over spatial mark-resight (SMR), which has been employed for lions elsewhere (Kane et al., 2015; Rich et al., 2019), because (a) current SMR models do not permit the modelling of sex as a covariate, and lions

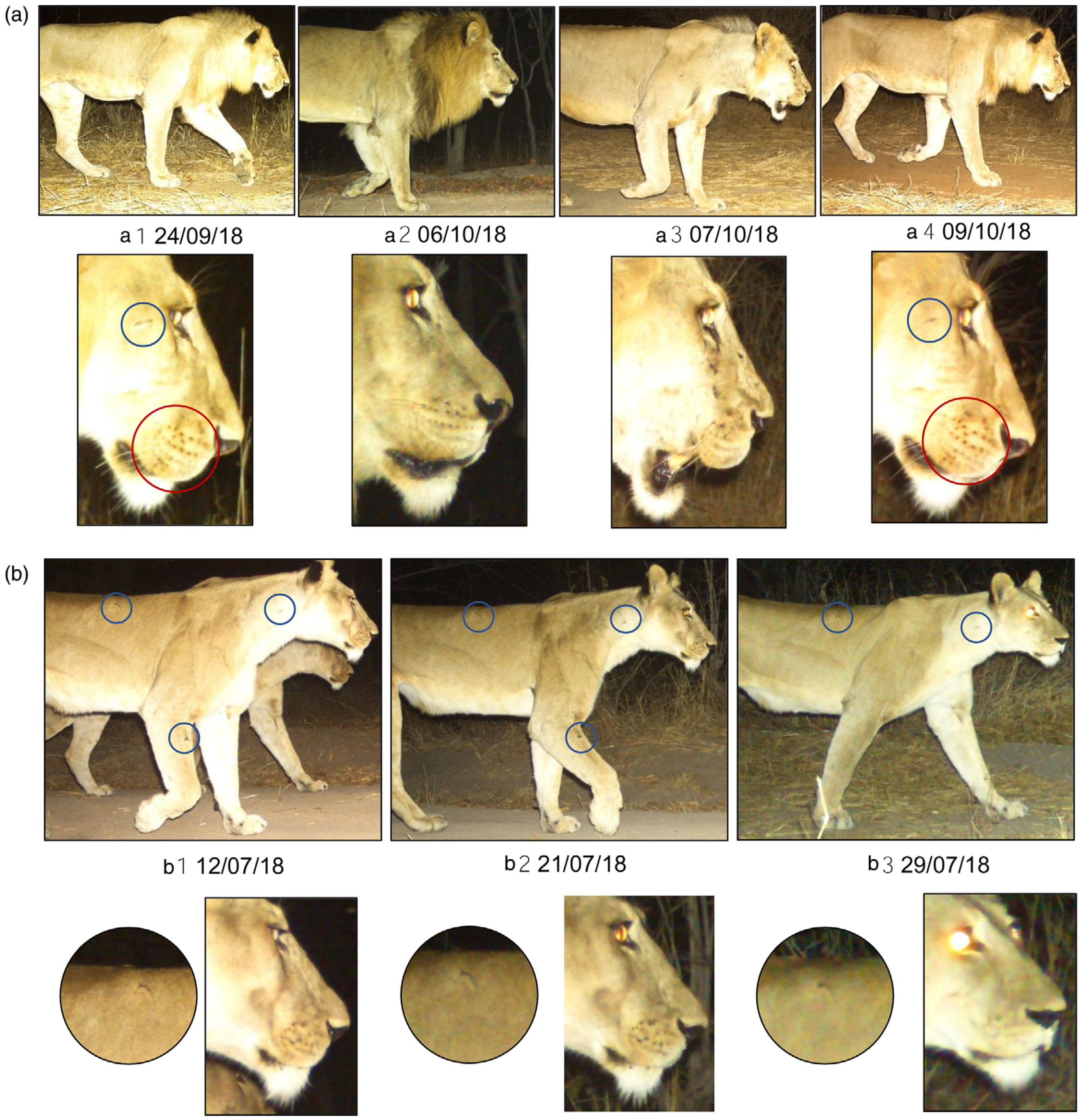

FIGURE 2 Two examples of individual identification. (a) 1: Two photographs of the same (a1, a4) and of two different (a2, a3) male lions, including dates of capture. Note that whisker spots match in a1 and a4, and not in the others. Similarly, marks and scars, mane size and shape, nose shape, and knee hair tufts also all match in photographs a1 and a4, and not in the others. (b) 1: Three photographs of the same female lion, including dates of capture. Note the characteristic mark on the back present in all three pictures, as well as marks on the neck (also present in all three pictures—may require magnification) and on the leg (present in the first two pictures). These allowed us to identify photograph b3 as depicting the same individual, even though whisker spots were less clearly defined. While marks and scars fade over time, the fact that new ones appeared regularly led to these being a very useful feature to aid identification. See Appendix S1 for additional examples of how individual identifications were carried out, and of different types of scars and marks used in the process

exhibit sex-specific traits in their ranging behaviours (Loveridge et al., 2009), and (b) the use of white-flash cameras resulted in a relatively high proportion of captures being suitable for individual identification, permitting the application of SECR models.

Capture and trap effort histories were developed for each site following recommended procedures (Efford, 2020), with each night (24 h—12:00 PM to 12:00 PM) treated as a separate sampling occasion (Goldberg et al., 2015). For the two sites with two investigators carrying out identifications, three capture histories were created: two from the classification of each investigator, and one employing only the captures for which both had independently agreed on the identification (the final ‘consensus’ input data; Rich et al., 2014). To ensure that identifications were completely independent, no comparisons were carried out post-identification, so that the consensus capture history consisted only of captures for which agreement had been reached independently. All SECR input files can be accessed in Appendix S2.

As camera traps do not physically capture animals, stations were classified as proximity detectors, acting independently of one another, and a half-normal detection function was fitted to model the distance between home range centre and camera stations (Boron et al., 2016;

FIGURE 3 Examples of photographs of lions which could not be identified at an individual level. (a) Individual too far, leading to features necessary for identification not being visible. (b) Although the framing of the picture is good, the station was placed too far from the trail, meaning a lack of clear whisker spots or characteristic scars or marks meant identification was not possible. Ideally stations should be placed between 3 and 5 m from the centre of the road or trail, to allow for pictures where features are better defined. (c) Individual not identifiable due to poor framing of the picture, and to the body lacking characteristic marks or scars. (d) The male in the background was not identifiable due to the presence of the female in the foreground obscuring its face and body. The social nature of lions, combined with the ~20 s of recharge time required by the xenon flash, meant that some captures had to be discarded for this reason. (e) Individual not identifiable due to flash overexposure. Overexposure is a risk if the flash is set too strong, if the camera is deployed too close to the road, or if lions walk on the bank of the road (as in this case). (f) Capture from a camera trap model with an infrared flash (model: Reconyx HC500 HyperFire), for comparison purposes. As can be seen, even when the framing of the capture is fairly optimal, the lack of definition and contrast associated with an infrared flash results in individuals being unlikely to be identifiable unless they exhibit a very clear mark or scar. See Appendix S1 for examples of suboptimal captures that were nonetheless identifiable due to the individual possessing a characteristic scar or mark

Efford, 2020). This describes the probability of capture (P) of an individual i at a trap j as a function of distance d from the activity centre of the individual to the trap, as follows: $Pij = g0 \exp(-dij^2/(2\sigma^2))$, where $g0$ is the capture probability at the home range centre, and σ is a spatial parameter related to home range size. A Bernoulli or binomial encounter model was fitted to the data, as this is most relevant to camera trap studies (Efford, 2020).

Sex was modelled as a covariate by fitting a hybrid mixture model (Efford, 2020). In addition, as large carnivores often use roads to travel (Mckenzie et al., 2012), whether a station was located on- or off-road might impact the capture parameter ($g0$). At all sites, the impact of sex on both the capture ($g0$) and movement (σ) parameters, and of road placement on $g0$, was therefore tested by fitting eight alternative models (Table 2; Boron et al., 2016). Models were ranked using the Akaike

TABLE 2 Candidate models of population density fitted to lion camera trap data, testing the influence of sex and camera location (on- or off-road) on model parameters

Model name	*g0~*	*σ~*
secr.0	1	1
secr.sex.g	Sex	1
secr.sex.s	1	sex
secr.sex	Sex	sex
secr.road	road	1
secr.road.sex.g	road + sex	1
secr.road.sex.s	road	sex
secr.road.sex	road + sex	sex

Note: *g0*, capture probability at home-range centre; *σ*, spatial movement parameter; 1, parameter modelled as constant; sex, parameter modelled as a function of sex; road, parameter modelled as a function of camera placement on-/off-roads.

information criterion, adjusted for small sample size (AICc; Burnham & Anderson, 2004), and the top-ranked model was employed to derive density estimates. For each analysis, following Efford (2004) we first set the buffer area for the SECR mask (state-space) as four times the estimated root pooled spatial variance (RPSV), which is the overall distance between camera locations an animal was detected at during the study. Once the top model was identified, we re-ran analyses increasing the buffer size by 1 km in each run (Appendix S4), until the density estimates stabilized (Kalle et al., 2011).

3 | RESULTS

Across the four survey sites, a total sampling effort of 11,447 camera trap nights across 150 camera stations yielded 1491 images of lion. Including only images of the flank with the greatest number of captures for each survey grid resulted in 590 unique capture events of lion (Table 1).

3.1 | Individual identification and inter-observer variability

Across the four grids, the majority of individuals (83% in MBOMIPA WMA; 73% in Ruaha NP core; 66% in Ruaha NP miombo; and 63% in Rungwa GR) exhibited at least one highly characteristic scar or mark that facilitated individual identification across multiple captures. With regard to whisker spots, 67% of captures in MBOMIPA WMA, 58% of captures in Ruaha NP core, 53% of captures in Ruaha NP miombo, and 52% of captures in Rungwa GR depicted whisker spots well enough to assist with individual identification. The combination of the relatively high number of photographs depicting whisker spots, a scar or mark, or both, as well as additional features (mane size and development, knee hair tufts for males, and nose shape), resulted in a large proportion of photographs being suitable for individual identification (Table 1). Although proportions of identifiable photographs varied between surveys, these were always relatively high in the context of SECR modelling (Tourani et al., 2020). See Table 3 for information on inter-observer variability and agreement.

TABLE 3 Summary of inter-observer variability and agreement in the survey grids with double-blind individual identification

	MBOMIPA WMA	Rungwa GR
Flank used	Right	Left
Photographs of males	37	46
Agreement	36 (97%)	40 (87%)
(Same individual)	35	36
(Unidentifiable)	1	4
Photographs of females	23	47
Agreement	23 (100%)	42 (89%)
(Same individual)	23	30
(Unidentifiable)	0	12
Overall agreement (both sexes)	98%	92%

3.2 | Lion population density

Buffer width stabilized at between 15 and 18 km for the different grids. The top ranked model was secr.road.sex.g for the Ruaha NP core grid, secr.0 for the Ruaha NP miombo grid, secr.sex.s for the MBOMIPA WMA grid, and secr.road.sex.s for the Rungwa GR grid (see Appendix S4 for full model outputs). Population density was highest in the Ruaha NP core grid, at 6.12 ± 0.94 lions per 100 km^2. The next highest density, at 4.05 ± 1.02 (Investigator 1) / 4.06 ± 1.03 (Investigator 2 and consensus) lions per 100 km^2, was estimated in the MBOMIPA WMA grid. This was followed by 2.74 ± 0.66 (Investigator 1), 2.30 ± 0.54 (Investigator 2), and 2.50 ± 0.64 (consensus) per 100 km^2 in Rungwa GR, and 1.75 ± 0.62 per 100 km^2 in the miombo woodland of Ruaha NP (Figure 4; see Appendix S3 for additional model parameter estimates).

4 | DISCUSSION

4.1 | Individual identification of lions from white-flash camera trap data

Individual identification was possible for the majority of lion captures (Table 1), and was consistent between observers (Table 3). Inter-observer differences in photo identification did not lead to significant differences in density estimates (Figure 4). Agreement was particularly high in the grid with higher road density (WMA dataset; 98%); this is likely a result of roads allowing cameras to be set at an exact perpendicular angle and at the ideal distance, thus providing consistent

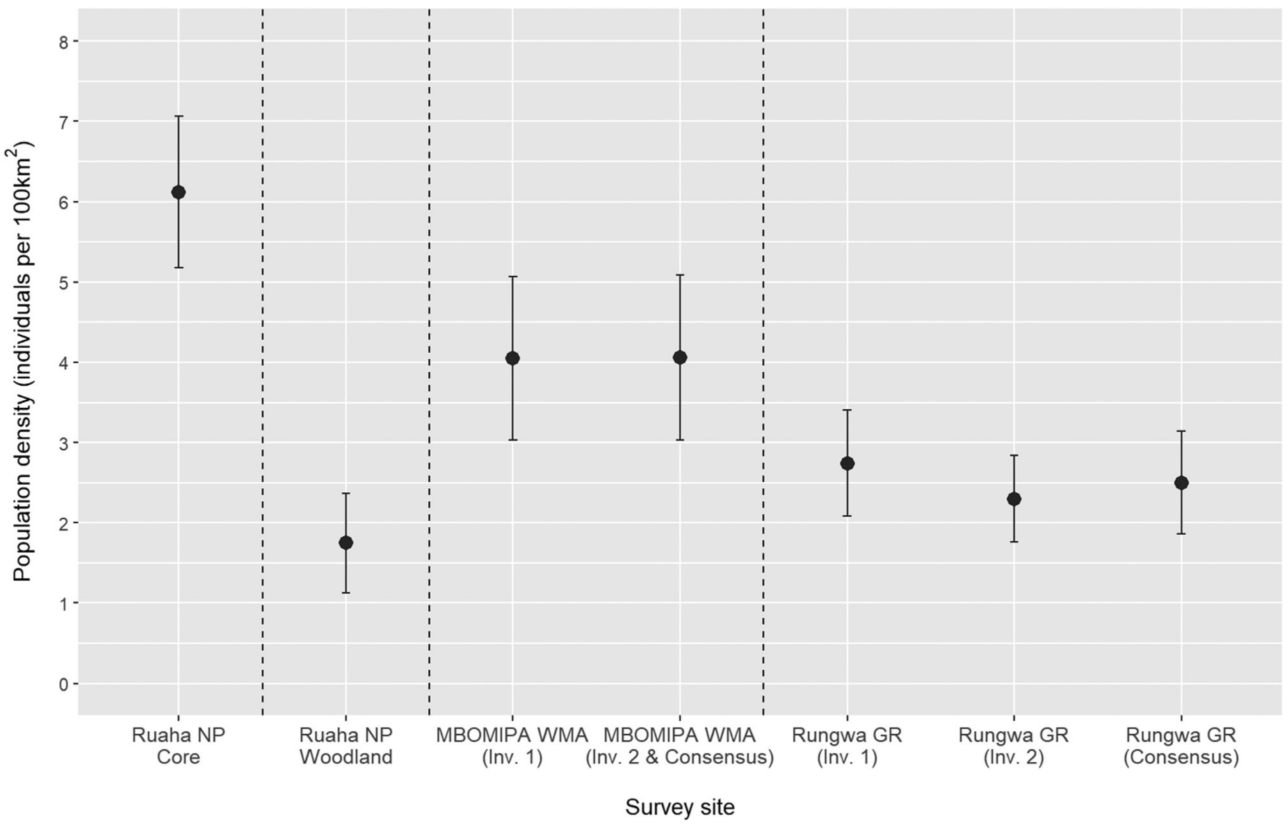

FIGURE 4 Lion population density estimates (and associated standard errors) for the four surveyed sites in Ruaha-Rungwa. For sites where a double-blind multiple investigator approach was employed (MBOMIPA WMA and Rungwa GR), density estimates from individual capture histories, as well as from an independently reached consensus capture history, are presented

framing of individuals, which aided identification. Nevertheless, even in the dataset with lower levels of agreement (88%; Rungwa GR), density estimates from the investigators (and their consensus) were similar.

Inter-observer agreement was higher than reported for similar investigations with pumas (Kelly et al., 2008; Rich et al., 2014), possibly due to identification being facilitated by variation in manes of male lions, and to the high proportion of individuals with marks or scars. Indeed, scars and marks proved very useful due to the large number of individuals exhibiting these, and these often remaining visible for the duration of the survey. As this was also noted by Kane et al. (2015) in their study in Senegal, it is likely to be a feature common to lion populations. While some scars and marks will fade over time, thus decreasing their usefulness for the identification of individuals over repeat (e.g. multi-year) surveys, multiple photographs with clearly visible whisker spots were obtained for all individuals identified. As a result, scars and marks can serve as a tool to greatly facilitate identification during the period of a single survey, with whisker spots instead being the primary tool employed to pair individuals between inter-annual surveys. Mane size and development also proved useful for males, with considerable variation observed between mature individuals (see Appendix S1 for examples). Nevertheless, as with scars and marks, the fact that this may change over time should be taken into account in multi-year studies. Knee hair tufts (for males) and nose shape were similarly also useful features for identification (Appendix S1). On the other hand, coat patterns—while at times visible even in adult individuals—were the least commonly used feature for identification, due to similarities being common between individuals.

Our study also provides insights into some limitations related to individual identification. Firstly, camera traps should use white flash, as most night-time photographs from infrared variants are unlikely to be suitable to distinguish individual lions (Figure 3). In addition, both capture and identification are aided by stations being located on roads or large trails, as is the case for other large carnivores (e.g. jaguars; Tobler et al., 2013). Nevertheless, this proved to not be a strict requirement: although our miombo grid in Ruaha NP had only a single major road traversing it (Figure 1), capture and identification rates were still high (Table 1).

Finally, while identification rates were sufficiently high in our study to employ SECR models, we recommend the further development of SMR models (especially to allow for the inclusion of finite-mixture covariates such as sex), for cases where identification rates are lower. We also similarly recommend testing the suitability of other models of xenon-flash camera traps for the individual identification of lions, as this may not be equal across models.

4.2 | Potential applications and limitations of SECR and camera traps for the assessment and monitoring of lion populations

We show that camera trap surveys combined with SECR modelling can be an effective way to obtain relatively precise density estimates for lion populations, and explore how population status varies across habitat types and land management strategies. In our case, we applied this method over areas of between 150 and 550 km^2, in line with the sizes of areas commonly surveyed when estimating population densities of other large carnivores (e.g. leopard, Davis et al., 2021; tiger, Ngoprasert & Gale, 2019; jaguar, Boron et al., 2016). At the same time, scaling the method to considerably larger areas has been done for other large carnivores (e.g. tiger, Tempa et al., 2019; leopard, Mann et al., 2020), and should similarly be possible for lion. However, this is likely to becostly and/or challenging to implement over particularly vast areas, particularly given the ongoing shortage in conservation funding for African PAs (Lindsey et al., 2018). Surveying an area of 5000 km^2, with cameras placed at regular 5-km intervals (wider than in our study, but likely still suitable for lion), would require ∼200 stations (400 cameras, if paired). At ∼150 USD per camera (https://www.cuddeback.com/shop), this would amount to ∼ USD 60,000 of camera trap costs, in addition to significant accessory costs (for import fees, batteries, memory cards, and protective cases). It is furthermore unlikely that many large PAs will have a sufficiently developed road network to allow for the access of all areas by road, considerably increasing the logistical requirements of the fieldwork. Deploying and checking such a large number of cameras would also require considerable time, as would the identification of a considerably greater number of individuals.

Nevertheless, while acknowledging these challenges, we encourage further studies to explore the scalability of this method to larger areas. This would likely involve both a wider spacing than that employed here (e.g. 5–7 km), possibly the use of single-camera stations and/or models aimed at improving single-sided identification (e.g. Augustine et al., 2018), and/or rotating camera grids to cover larger areas (e.g. Rich et al., 2019). At the same time, however, we also echo Dröge et al. (2020) in suggesting that a number of precise estimates, representative of habitat types, land management strategies, and anthropogenic impact gradients, could serve as an effective framework to monitor lion populations over considerably vaster landscapes. While this would require a shift from attempting to estimate absolute population abundance, monitoring the status of lion populations through the regular estimation of density across a number of 300–500 km^2 representative grids may be more practical for management than scaling the methodology to obtain landscape-scale estimates of abundance. This is especially the case if such efforts are accompanied by complementary landscape-scale indicators of status (e.g. sign-based occupancy surveys; Everatt et al., 2019; Henschel et al., 2020).

Indeed, as shown for other large carnivores, density estimates over scales such as those presented in our study can be employed to help inform conservation management (e.g. Ramesh et al., 2017; Rosenblatt et al., 2016). In Ruaha-Rungwa, for example, MBOMIPA WMA plays a key buffer role for the wider population, and monitoring lion status here would give indications of the changing impact of edge effects (Woodroffe & Ginsberg, 1998) and act as an early warning system for the wider population. Additionally, in the years following our survey MBOMIPA received a series of protection and applied conservation interventions (STEP, 2020); regularly repeating our survey would provide an accurate and relatively efficient way to evaluate the impact of these on lions. Elsewhere, regular surveys in the core of hunting blocks (as in Rungwa GR) would provide insights on population trends that could be used to employ an adaptive approach to their management (e.g. by modifying offtake quotas accordingly). Thus, we suggest this approach be used instead of, or as a complement to, SECR modelling through direct observation (Elliot & Gopalaswamy, 2017) in areas where this is challenging (due to low densities, closed habitat, or lions being particularly elusive), or where assessments are also required for other large carnivore species (e.g. leopard, spotted hyaena; Searle et al., 2021). We recommend studies comparing the relative suitability of these methods (as well as promising alternatives, such as SECR modelling of DNA-based analysis of scats—Gopalaswamy et al., 2012) across a range of lion populations, as well as their integration into single frameworks. We also recommend further research into survey design advancements that can lead to improved precision of the density estimates produced.

4.3 | Possible violations of model assumptions and implications

The assumption of SECR models that all individuals are uniformly and independently distributed is inherently violated by social species such as lions. However, simulations have shown that SECR models can be reliably applied to species violating this assumption with minimal impact on density estimates (Efford et al., 2009; López-Bao et al., 2018). This has led SECR models to be considered appropriate for a range of social species, from primates (Arandjelovic & Vigilant, 2018) to wolves (Roffler et al., 2019). Nevertheless, recent research suggests that violations of these assumptions may have greater implications than previously thought (Bischof et al., 2020), and we recommend further investigations into the potential effects of social cohesion and aggregation on SECR parameters, as well as the continued development of approaches that incorporate this within the modelling process (e.g. Emmet et al., 2021).

Survey grids are recommended to be larger than the estimated average male home range (Noss et al., 2013; Tobler & Powell, 2013). This was likely achieved for one of grids, and possibly for two others; however, it is likely that the survey grid in the miombo woodland of Ruaha NP did not meet this recommendation. This may have resulted in artificially lowered movement parameters (σ), which in turn may lead to density estimates exhibiting a positive bias (Foster & Harmsen, 2012). Nevertheless, simulations suggest that even assuming particularly large lion home ranges (400 km^2) and low detection probabilities at home range centre ($g0 = 0.01$) the resulting density bias would be less than 10% (Tobler & Powell, 2013). Additionally, reduced grid size has been found to not be as much of an issue as only surveying high-density 'hotspots' (Suryawanshi et al., 2019), which we made efforts to avoid. We nonetheless recommend that future studies attempt to avoid violating this assumption.

Finally, capture–recapture models assume there is no misidentification of individuals (Efford, 2004), and the fact that identifications varied slightly between the two investigators suggests this assumption was violated to some extent. Nevertheless, results of the double-blind approach, as well as the density estimates being very similar, indicate that misidentification was low.

4.4 | Lion population densities in Ruaha-Rungwa

Lion population density was highest in the core tourist area of Ruaha NP, at 6.12 ± SE 0.94 adult and sub-adult lions per 100 km^2. The area holds some of the highest dry season prey densities in the landscape, and exhibits relatively low levels of anthropogenic impacts (TAWIRI, 2019). The high density observed is therefore in line with our knowledge of the species' ecology (Ferreira & Funston, 2010; Henschel et al., 2016).

Lion density in MBOMIPA WMA was estimated at 4.06 ± SE 1.03 individuals per 100 km^2 (consensus estimate). Although lower than in the core area of Ruaha NP, this is still high for the species (Bauer et al., 2016). The grid was located in similarly productive habitat, also exhibiting high dry-season prey densities. However, the area is more anthropogenically impacted, with greater levels of human disturbance (TAWIRI, 2019). The area also experiences high levels of human–lion conflict, with at least 17 lions killed in retaliation for livestock predation in MBOMIPA and adjacent unprotected areas between 2017 and 2020 (RCP, unpublished data).

Lion densities at the two miombo woodland sites, one in Ruaha NP and one in Rungwa GR, were relatively similar (Figure 4). While lower than densities near the Great Ruaha River, these estimates are similar to those obtained using SECR methods elsewhere (Braczkowski, Gopalaswamy, Nsubuga, et al., 2020; Rich et al., 2019). Thus, even though miombo woodlands are a low-productivity habitat, supporting relatively low ungulate biomass (only 20%–30% of other savannah habitats with comparable rainfall; Frost, 1996), our findings indicate that lions can nevertheless exist at intermediate densities in these habitats.

Finally, heterogeneous densities are common in large carnivore populations (Sarmento & Carrapato, 2019). By revealing significant heterogeneity in lion densities across the landscape, our results bring attention to the importance of sampling populations across habitat and land management types, and not only in the areas likely to host the highest densities, which can lead to flawed inferences (Suryawanshi et al., 2019). As a result, understanding density gradients, and identifying high-density areas that are likely to be acting as population sources for wider areas—in turn enabling the prioritisation of areas of key conservation importance—should be seen a priority for threatened lion populations.

ACKNOWLEDGEMENTS

Fieldwork for this research was carried out under permits 2018-368-NA-2018-107, 2019-96-ER-97-20 and 2019-424-NA2018-184, granted by the Tanzania Commission for Science and Technology (COSTECH) and the Tanzania Wildlife Research Institute (TAWIRI). We would like to thank the Government of Tanzania, TAWIRI, Tanzania National Parks Authority (TANAPA), Tanzania Wildlife Management Authority (TAWA), and Idodi-Pawaga MBOMIPA WMA for their support of this research. We also thank the field staff of the Southern Tanzania Elephant Program (STEP) and the Ruaha Carnivore Project (RCP) for their assistance with data collection, Mdonya Old River Camp, Essential Destinations, and Nomad Tanzania for their support in Ruaha, Tanzania Big Game Safaris for their assistance in Rungwa Ikiri, and all WMA Village Game Scouts, TANAPA Rangers and TAWA Game Scouts who contributed to fieldwork. We also thank Tatiana Chapman for serving as a second observer. Scholarship funding for PS and CS was provided by the University of Oxford NERC Environmental Research DTP. AD was funded by a Recanati-Kaplan Fellowship. Additional funding was provided for the fieldwork for this research by grants from National Geographic Society Early Career Grants, Cleveland Metroparks Zoo Africa Seed Grants, Chicago Zoological Society Chicago Board of Trade (CBOT) Endangered Species Fund, and Pittsburgh Zoo & PPG Aquarium Conservation & Sustainability Fund.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

PS and CS conceived the research idea and designed the methodology. CS, JS, LM and PS collected the data, with support from AD and PH. PS and CS analysed the data. PS wrote the manuscript, with inputs from CS, JS, PH, DI, DM and AD.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1002/2688-8319.12129.

DATA AVAILABILITY STATEMENT

All input files employed for the analyses in this study have been archived in Zenodo: https://doi.org/10.5281/zenodo.5846471 (pstrampelli, 2022).

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How to cite this article: Strampelli, P., Searle, C. E., Smit, J. B., Henschel, P., Mkuburo, L., Ikanda, D., Macdonald, D. W., & Dickman, A. J. (2022). Camera trapping and spatially explicit capture–recapture for the monitoring and conservation management of lions: Insights from a globally important population in Tanzania. *Ecological Solutions and Evidence*, *3*, e12129. https://doi.org/10.1002/2688-8319.12129