MethodsX 7 (2020) 101042

Contents lists available at ScienceDirect

MethodsX

journal homepage: www.elsevier.com/locate/mex



Method Article

A baited-camera trapping method for estimating the size and sex structure of African leopard (*Panthera pardus*) populations



Christoffel J. Joubert^a, Allan Tarugara^{b,c,*}, Bruce W. Clegg^b, Edson Gandiwa^c, Victor K. Muposhi^c

^a Selati Game Reserve, Post Office Box 296, Gravelotte, South Africa

^b Malilangwe Wildlife Reserve, Private Bag 7085, Chiredzi, Zimbabwe

^c Chinhoyi University of Technology, Private Bag 7724, Chinhoyi, Zimbabwe

ABSTRACT

Amongst Africa's large predators, leopards (Panthera pardus) are arguably the most elusive carnivore. Information on the species is lacking in most areas where they are found. This is because leopards are largely solitary, cryptically coloured and nocturnal making the collection of accurate population data difficult. As a result, population estimates from methods such as spoor and scat counts are less reliable. This is a concern because accurate census data are essential for informed policy and management of threatened species such as leopards. Camera trapping has emerged as a powerful tool for inventorying and monitoring carnivores in their natural habitats. Pictures from camera traps allow unambiguous individual identification making these data useful for generating accurate population estimates from capture-recapture analysis. Conventionally, camera trapping uses two cameras to record passing subjects at unbaited stations but the design usually suffers from low capture rates. Here we report on the Baited-Camera Trapping (BCT) method which uses bait and single cameras at sampling stations to survey free ranging leopards. Using bait to improve the quality of data collected in population studies is not a new strategy but arranging baits and cameras according to the BCT method is a novel approach to achieving this goal. We show that the method can significantly enhance capture rates, improve individual identification and reduce cost when sampling leopards. Furthermore, the method allows easy sex determination and collection of morphometric data from camera trap photographs. The BCT method has been tested in semi-arid savannas and we give recommendations for application in other environments and species.

- The BCT method uses baits and single cameras to record leopards at sampling stations.
- The provision of a leading pole enables easier individual identification and sex determination.

https://doi.org/10.1016/j.mex.2020.101042

2215-0161/© 2020 Elsevier B.V. This is an open access article under the CC BY-NC-ND license. (http://creativecommons.org/licenses/by-nc-nd/4.0/)

^{*} Corresponding author at: Malilangwe Wildlife Reserve, Private Bag 7085, Chiredzi, Zimbabwe.

E-mail addresses: gm@selatigamereserve.co.za (C.J. Joubert), allantarugara@gmail.com (A. Tarugara), bruce@malilangwe.com (B.W. Clegg), edson.gandiwa@gmail.com (E. Gandiwa), vkmuposhi@gmail.com (V.K. Muposhi).

• The method can be used to investigate multiple population monitoring questions which enhances its cost-benefit ratio.

© 2020 Elsevier B.V. This is an open access article under the CC BY-NC-ND license. (http://creativecommons.org/licenses/by-nc-nd/4.0/)

ARTICLE INFO

Method name: Baited-camera trapping method for surveying leopard poulations

Keywords: Capture-recapture analysis, Cost-effectiveness, Detection probability, Large carnivore, Non-invasive, Savanna ecosystems

Article history: Received 11 June 2020; Accepted 19 August 2020; Available online 22 August 2020

Specifications table

Subject Area:	Agricultural and Biological Sciences
More specific subject area:	Carnivore population ecology
Method name:	Baited-camera trapping method for surveying leopard populations
Name and reference of original method:	n/a
Resource availability:	Applicable hardware and software discussed in the relevant sections

Method details

Background

Camera trapping of rare or elusive carnivores conventionally uses two cameras facing each other to photograph unsuspecting individuals as they pass unbaited sampling stations. Two cameras are needed as images of either flank are required for identification since the direction in which subjects pass is unknown. The cameras collect presence and identification data which can be used to derive population estimates using capture-recapture analysis, but the design often suffers from low capture rates. This is a concern, as low sample sizes preclude in-depth population analyses [1,2]. Here we describe the baited-camera trapping (BCT) method which uses single cameras and baits at trapping stations and can significantly improve capture rates and individual identification when surveying leopards (*Panthera pardus*) in savanna ecosystems. We use a study by Tarugara et al. [3] at Malilangwe Wildlife Reserve (MWR), southeast Zimbabwe (20°58' and 21°15'S and 31°47' and 32°01'E) as an example. There is a growing body of evidence indicating that the BCT method has advantages over traditional methods and this paper brings together information published under peer review in demonstrating the validity and scientific credence of the method.

Density and positioning of baited-camera traps

An essential requirement of a camera trapping survey is that the entire study area be covered with trapping stations. No large gaps should be left in which the study species can exist for the full sampling period without the chance of being photographed [4]. Also, to avoid sampling bias, we suggest that stations be randomly placed. To achieve the above, a grid and random sampling are used for camera site placement. Dimensions for each grid square are calculated as;

$$g1, g2 = \sqrt{\frac{A}{n_t}} \tag{1}$$

where **g1**, **g2** = grid square length, width (km); **A** = study area size (km²) and **n**_t = the total number of sampling stations needed to survey the study area. The minimum and maximum coordinates of the study area are used to define the spatial extents of the grid (Fig. 1a) which is then clipped to the boundary of the study area using a Geographic Information System (GIS) (Fig. 1b). For surveying leopards using BCT in semi-arid savannas, the optimum sampling density has been determined as 0.24 cameras km⁻² [3] therefore **n**_t in these environments is derived as **A** x 0.24. Using MWR



Fig. 1. Placement of sampling points using a map of Malilangwe Wildlife Reserve as an example. Overlaying a grid onto the study area (a), clipping the grid to study area boundary (b), random placement of sampling points in grid squares (c) and placement of points along the road network (d).

 $(A = 490 \text{ km}^2)$ as an example, n_t therefore rounds to 120 sampling stations, with g1, g2 rounding down to 2 km. In each grid square, a sampling station is placed at random (Fig. 1c). However, since leopards frequently use roads in their movements, detection probability is increased if sampling stations are placed next to a road or an intersection [5]. Therefore, the position of each randomly placed sample point is moved to the nearest road intersection (Fig. 1d). In grid squares without road intersections, the baited-camera trap is placed next to the closest road. In cases where there are no roads, placement is as close as possible to the nearest road in one of the adjoining grid cells. Since trap sites are usually visited using a vehicle, placing them near roads facilitates easy access and also protects the environment from the detrimental effects of off-road driving.

To determine whether sampling effort has been sufficient to get an accurate population estimate, several recaptures are needed. For semi-arid savannas, we recommend splitting the overall sampling effort (n_t) into four (4) repetitions (sampling occasions) [3]. The number of trap sites required for each sampling occasion is derived as;

$$\frac{\mathbf{n}_t}{4}$$
 (2)

To obtain four (4) sets of evenly distributed sampling points, the total number of sampling points (\mathbf{n}_t) is subsampled four (4) times without replacement using a GIS (Fig. 2).

Baited-camera trap setup

Camera sites are located in the field using a map and a Global Positioning System (GPS) device. At the site, two trees spaced 2–4 m apart are selected within 50 m radius of the GPS point; one for the bait and the other for the camera. For the bait-tree, it is advisable that a tree with a broad and leafy canopy be chosen to provide cover from vultures (*Gyps spp.*) and birds of prey. Bait can be



Fig. 2. An example of subsampling points for baited-camera trapping from Malilangwe Wildlife Reserve (Tarugara et al. 2019a).

5



Fig. 3. Researchers arranging material at baited camera stations (a) and an example of the setup in operation (b).

in the form of either skinned meat portions or carcasses of medium sized ungulates such as impala (Aepyceros melampus). Experience has shown that skinning prolongs the working life of the bait by delaying decomposition. Where portions are used, they should be sufficiently large (>20 kg) to last the period of sampling. Baits should be tied to the bait-tree with wire and a forked leading pole (3-4 m long, 0.2–0.3 m diameter) placed against the tree at an angle of approximately 45° to provide easy access for leopards (Fig. 3). Tying the bait with wire prevents leopards or lions (Panthera leo) from removing it and feeding out of sight of the camera. To prevent feeding by spotted (Crocuta crocuta) and brown hyena (Hyaena brunnea), baits should be hung such that the lowest parts are at least 2 m above the ground. Leafy branches are used to cover exposed parts of baits, further camouflaging them. A camera trap is secured to the camera-tree to the right-hand side of each bait, with its line of sight at 90° to the leading pole. Camera units can be housed in metal boxes to protect them from damage from animals and weather. Offal and stomach contents are dragged along the road for the last 300 m of the route to the camera site in anticipation that leopards will pick up the scent and follow the trail. It is assumed that detection distances of drags and baits are small thereby limiting attraction to resident individuals only. When a leopard or other animal climbs up the pole to feed, the camera is triggered and a photograph is taken. Due to its position to the right of the leading pole, the camera consistently takes photographs of an animal's right profile. We recommend that trigger delay be set to 1 min between photographs and picture quality set at >5 megapixels to allow unambiguous identification.

Data collection

For surveying leopards in semi-arid savannas using the BCT method, a sampling period of nine (9) days is recommended to derive an accurate population estimate [3]. Data are therefore collected over four (4) sampling occasions with each occasion comprising a 9-day period over which baited camera traps collect picture data. Camera trapping begins with sampling occasion 1 and progresses to occasions 2, 3 and 4. To ensure uniformity of data it is advisable that all BCT stations be set up in one day. Where logistics do not permit this, we recommend that set-up is done in the shortest possible time over consecutive days. In environments where elephants (*Loxodonta africana*), lions and hyena are present these species often visit BCT stations and sometimes disturb the set-up. For this reason, camera stations should be monitored approximately every 3 days. Lions usually rob baits while hyenas knock over the leading pole. Baits removed by lions before leopards encounter them should be replaced and the leading poles repositioned where necessary. Photographs stored on the memory cards should be downloaded regularly onto a laptop computer as a contingency. On the 10th day, baits are taken down, batteries checked for power and the cameras are moved to the sites for the next sampling occasion.



Fig. 4. Determination of optimal sampling effort. Dotted lines represent increased effort to establish population estimate stabilization. Error bars indicate 95% confidence estimates of population estimates. (Data from Tarugara et al. 2019a).

Data analyses

Population size and sex structure

Photographs are scrutinised and individual leopards are identified from their unique rosette patterns. The presence or absence of a visible scrotal sac is used to distinguish adult males from females. The scrotum is less distinct in males <2 years old and therefore sex in the sub-adult class cannot be distinguished [6]. Sub-adults (>1 year) are counted, while cubs are not recorded because they do not have distinct rosettes. An identikit of individuals is created and capture histories for each sampling occasion are constructed. The histories are then fed into capture-recapture software, e.g., SECR [7], CAPTURE [8] or SPACECAP [9] and population estimates with 95% confidence intervals are generated for each occasion. When estimates and confidence intervals of two consecutive occasions stabilize, sufficient sampling effort has been attained and sampling can be stopped (Fig. 4). It has been found that for surveying leopards in semi-arid savannas using the BCT method, a sampling effort of 4 occasions and 9 days is required to provide accurate population estimates [3]. For populations where the optimum has not yet been established and population estimates have not stabilized by the 4th sampling occasion, additional occasions can be added (Fig. 4).

Advantages of the BCT method

Improved individual identification

Using bait to improve the quality of data collected in population studies is not a new strategy but arranging baits and cameras according to the BCT method is a novel approach to achieving this goal. The BCT method can improve individual identification for studies of distinctly marked carnivore species. The setup ensures that subjects standing on the leading pole consistently have their right side available for scrutiny and for species with unique coat patterns, e.g., leopards, jaguars (*Panthera onca*), ocelots (*Leopardalis pardus*) and clouded leopards (*Neofelis nebulosa*), individuals can be unambiguously distinguished. This applies even where photographs contain partial shots of the animal or where postures vary. In addition, feeding subjects are often stationary and spent longer in front of the camera thereby providing many photographs for reference [10]. In two separate studies conducted in Zimbabwe comparing the BCT method to conventional unbaited cameras when surveying



Fig. 5. Estimating body dimensions of leopards from camera trap photographs. Image showing a male leopard with an outline of a body length measurement.

leopards, Grant [11] and du Preez et al. [12] recorded an increase in capture frequencies at baited stations by up to x7.3 and x6.2 respectively. On the other hand, unbaited camera traps usually record a single image as the subject walks past and fast moving animals usually produce photographs with blank or partial shots [13]. In some cases, the subject may pass too close or too far from the camera resulting in indistinct images [12]. Even where the animal may be well positioned weather conditions such as rain, fog or sunlight can render images unusable resulting in weaker data sets [10].

Measuring body dimensions from photographs

A useful application of the BCT method is that it facilitates measurement of body dimensions from camera trap photographs. A study by Tarugara et al. [14] used steel nails driven 20 cm apart into the underside of the leading pole as a scaling standard and in this way, leopards photographed from each sampling station could be measured (Fig. 5). The study showed that body length of leopards in a level back-straight forelimb-parallel tail posture can be measured accurately from camera trap photographs (mean variance from actual body length = 2.0 cm, 95% CI = 1.5-2.7 cm). Photographs that fit these criteria can be filtered from the dataset for remote measurement. These data are important for monitoring growth rates and investigating variations in body sizes. Morphometric information may have management relevance especially where leopards are hunted and size-minimum harvesting regulations are observed.

Age and sex determination

Age classification of carnivores in camera-trapping is subjective and, in most cases, depends on the distance of the subject from the camera. Sub-adults passing close to the camera can appear deceivingly bigger while adults passing further away may appear smaller [12]. Because in the BCT method the distance between the bait and the camera-tree is fixed, images from the same station are on an identical scale thereby allowing age to be judged with more confidence. In mane-less species such as leopard and jaguar, the presence of male genitalia in a photograph can be used to tell sexes apart; a distended scrotum distinguishes males from females (see Fig. 5). In the BCT method, the leading pole ensures that subjects are always aligned broadside to the camera's line of sight thereby revealing the presence or absence of male genitalia. Without a clear view of genitals, young males may be difficult to distinguish from adult females [12]. Furthermore, the method often collects many



Fig. 6. Modeling space use from baited-camera trapping data in Malilangwe Wildlife Reserve. A surface showing the distribution of leopards across the study area. Scale ranges from 0 to 5 leopards. (Created using data from Tarugara et al. 2019a).

photographs of an individual subject per station thus presenting many examples for comparison. In this regard, the BCT method allows a more accurate demographic population assessment compared to unbaited camera trapping.

Determination of space use

Presence data from BCT surveys can be used for modeling space use in leopards. This information provides an important benchmark for understanding ranging behavior of less studied populations where more advanced methods, e.g., telemetry are not available. Due to the presence of food, some camera stations may be visited by multiple individuals over the duration of sampling and these records can be used to construct maps showing the density and spatial distribution of leopards in the study area (Fig. 6). In addition, inventory, population and distribution data for other key species that visit BCT stations (e.g., lions and hyenas) can also be collected as ancillary information.

Large amount of data collected

A common application of camera trapping is surveying animals that are ordinarily difficult to study, e.g., shy, elusive or species occurring at low densities [15]. For such species capture rates are inherently low and conventional unbaited camera trapping sometimes record insufficient data [11]. Where data are insufficient, analysis is limited to less robust methods which may provide unreliable results and incorrect inferences [10,13]. The BCT method has been shown to significantly increase the probability of leopards encountering cameras and consequently being photographed [11,12], thereby increasing the size of the dataset. Large sample sizes are preferable as they allow detailed analyses to be performed on study populations. In a study that tested BCT and the traditional unbaited method to survey leopards in Mangwe District, Zimbabwe, Grant [11] identified 13 leopards using the BCT stations and only one individual from unbaited cameras. In a similar study conducted at Bubye Valley

Conservancy, Zimbabwe, du Preez et al. [12] recorded up to x1.5 higher detections of leopards from the BCT method when compared to unbaited camera trapping. Similarly, Tarugara et al. [3] recorded a high detection probability ($p \ge 0.93$) when surveying a leopard population at MWR, Zimbabwe using the BCT method.

Lower hardware costs

Since project resources are generally limited, researchers usually seek to balance camera quality and affordability. Cameras models with fast trigger speeds, wide detection zones and minimal motion blur are ideal for recording elusive or fast moving animals such as leopards. Despite advances in technology having lowered prices of camera-traps, decent models fitting capture-recapture studies are generally expensive, with single units ranging from US\$ 250 to 450 and up to US\$ 1 000 for more advanced types [16,17]. The BCT method uses a single camera per sampling station thereby halving the number of cameras required for the same sampling effort in conventional camera trapping [3,11,12]. In addition, because stationary subjects are photographed, costly functionalities such as fast trigger speed, wide detection zones and minimal motion blur are not required. As a result, fewer, cheaper cameras are able to provide adequately identifiable photographs at a significantly lower cost.

Shorter sampling periods

A requirement of capture-recapture studies is being able to sample the study area in as few repeats as possible [18]. However, due to the inherently low detection rates of unbaited camera trap surveys, sampling periods sometimes need to be extended in order to collect sufficient data. In contrast, the BCT method improves detection rates and subjects are ideally positioned in front of cameras allowing the collection of many usable photographs over a short period of time [12]. Furthermore, the use of single cameras in the BCT method allows available cameras to cover twice the area that can be covered by unbaited cameras thereby allowing the study area to be sampled in fewer repetitions. Short survey periods are preferable as running costs and the risk of violating geographic and reproductive closure are reduced.

Sampling design and camera location

To obtain an accurate representation of density and distributions of the target species, habitats in the study area must be evenly sampled [15]. This can be achieved by subdividing the area using a grid and placing camera stations at random [19]. However, habitat characteristics often skew movement patterns and rates of camera encounter by target species [20] with passages through vegetation, roads and game trails being frequently used by carnivores in their movements [21,22]. As such, unbaited surveys often target the placement of camera traps on game trails to maximize detection rates. While targeted camera placement improves detection probability, it however introduces bias by creating an uneven sampling effort as habitats without trails are often underrepresented [19]. In the BCT method, bait and drags attract subjects to the camera station thereby facilitating sampling in most habitats.

Limitations

Exclusion of bait-shy individuals

A potential limitation of the BCT methodology is the preferential recording of individuals that would readily take baits. This introduces bias as bait-shy individuals in the population may not be recorded. Where hunting is practiced, baits are often used to attract leopards and this can lead to baits being associated with risk. However, in a study conducted at Bubye Valley Conservancy, Zimbabwe comparing baited and unbaited camera trap surveys, du Preez et al. [12] found no evidence for bait shyness in leopards. In their study, more leopards were recorded at baited than unbaited stations despite the study site being a hunting area suggesting that leopards were not bait-shy. This may however be a concern where the method is used to investigate species other than leopards.

Influence on ranging behavior

Using baits to attract animals to camera stations can potentially influence the ranging behavior of target species. It is possible that during the duration of sampling subjects may be conditioned to the presence of baits and spend more time in areas with baited sites or they may increase their patrol effort in order to discover additional reward. However, in their study, du Preez et al. [12] found that the presence of baited sites in their study area did not influence space use in 10 GPS collared leopards. Similarly, a study by Gerber et al. [23] in Ranomafana National Park, Madagascar, also found that baits had no effect on ranging or temporal activity in Malagasy civets (*Fossa fossana*).

Pull effect of baits

Baits can potentially introduce bias by attracting non-resident animals onto the sampling grid which, if recorded, can misrepresent population sizes and distributions [23,24]. The BCT method fundamentally assumes that the maximum bait and drag detection distance is small thereby limiting attraction to resident individuals. In addition, territorial forces are known to prevent conspecifics from moving into an area where they do not ordinarily occur, thereby limiting bias. An analysis of GPS collar data from eight collared leopards (four males and four females) at MWR (unpublished data) showed that male and female conspecifics had clear cut boundaries and seldom wandered into each other's territories.

Interference from competitors

A potential source of bias is introduced when lions and vultures consume baits before leopards have an adequate chance of finding them. Lions can ably climb trees and vultures flying above can discover baits. To remedy this, trees with a leafy canopy should be chosen and leafy branches used to cover exposed parts of the baits. During the sampling window, baits that are consumed before leopards can feed on them are continually replenished [3]. In addition, baited sites may simulate natural kills in the field and as such can become points of conflict. The presence of dominant competitors may introduce bias by preventing some individuals from being recorded due to agonistic behaviour. However, the ability of leopards to skillfully climb trees helps them to avoid kleptoparasitism and predation risk from lions and spotted hyenas.

High turnover of consumables

Baited camera-traps ordinarily have high battery usage since each camera site yields many photographs. Batteries can represent a significant cost in study designs that use many camera units. Where rechargeables are used, batteries from active camera sites may have to be recharged at least once a week (*A. Tarugara 2017, personal observation on Moultrie I60 camera traps*), representing time and monitoring costs. However, this cost is offset by the value of the numerous accumulated photographs in individual identification and statistical analyses. Furthermore, technological advancement has given recent camera models the capability of long battery life (for example up to 12 months in Cuddeback X-Change Series camera traps).

Seasonality and study area size

The BCT method is best suited for use during the dry seasons and its applicability may be limited in wet conditions. Leopards are ambush predators and rely on the cover of vegetation for concealment when approaching or stalking prey. Because vegetation cover is low during the dry season, hunting efficiency is reduced thereby increasing the likelihood of leopards taking baits and thus the success of the BCT method. On the contrary, kill rates of leopards improve during the wet season due to abundant vegetation cover and the presence of juveniles of most prey species, which make easier prey targets. As a result, leopards are less likely to visit baits during this time. In addition, high humidity and moisture levels experienced during the wet season affect bait condition and longevity by quickening the rate of putrefaction and this has cost implications. On the other hand, the BCT method is logistically demanding, labor and time intensive rendering its applicability challenging where the study area size is large. Cost of bait procurement and monitoring increases with study area size potentially limiting the method's suitability to small and medium size properties.

Generalizability

We do not have in-depth knowledge on the ecology and habits of species beyond the African leopard but the methodology described above could be applicable to other boldly marked, individually identifiable carnivores such as jaguar, clouded leopards and ocelots provided the species will readily take baits and climb up the leading pole. Applicability of the method to other species has to take careful consideration of the leading pole as it is central to the BCT design. The leading pole ensures that subjects are aligned at right angles to the camera's field of view thereby enabling the full body profile of the animal to be photographed. By ensuring that a chosen flank of the animal's body is consistently photographed, the pole facilitates individual identification and use of only one camera per sampling station. Furthermore, the pole facilitates the fixing of a measurement standard allowing the investigation of morphological development and also ensures that subjects are aligned broadside in photographs which aids in sex determination.

The BCT method may be limited when used to study tigers (*Panthera tigris*), lions and snow leopards (*Panthera uncia*). Although tigers may readily take baits, it is likely that they do not balance well on a leading pole because they are heavy. In a previous study, Tarugara et al. [3] reported that lions that visited camera sites could not balance on the leading pole and therefore tigers being larger, may have the same challenge. Regarding snow leopards, BCT may not be suitable due to the lack of adequate trees in the environment in which they exist. The BCT method may have scope for viverrids and with careful consideration may be modified for studying carnivore species that cannot climb up the leading pole. For example, a brush wall or similar obstruction could be used to coax the target species into a particular position such that a side profile is consistently photographed. Where this method is applied outside the tropics, sampling effort will be guided by the method of determining optimal sampling effort discussed above.

Conclusion

Maximizing capture rates is especially important in capture-recapture studies of species whose detectability is inherently low. The BCT method can improve the quality and quantity of data collected from leopard surveys and it has potential to provide novel information. With regard to carnivores, the BCT method can provide useful information for policy and management decisions. We recommend baited-camera trapping as a reliable method that enhances the cost-benefit ratio of carnivore population surveys especially in savanna ecosystems.

Acknowledgements

Field applications of this method were funded by Sango Wildlife Conservancy and The Malilangwe Trust, Zimbabwe. The funders had no role in the study design, data collection and analysis, preparation of the manuscript and/or decision to publish. We acknowledge Colin Wenham, Philmon Chivambu and Nathan Chinhondo for assistance with fieldwork. The authors declare no conflict of interest.

References

- [1] A.F. O'Connell, J.D. Nichols, K.U. Karanth, 1 ed., Springer, New York, 2011, p. 271.
- [2] K.M. Harkins, D. Keinath, M. Ben-David, It's a trap: optimizing detection of rare small mammals, PLoS One 14 (3) (2019) e0213201.
- [3] A. Tarugara, B.W. Clegg, E. Gandiwa, V.K. Muposhi, Cost-benefit analysis of increasing sampling effort in a baited-camera trap survey of an African leopard (*Panthera pardus*) population, Glob. Ecol. Conserv. 18 (2019) e00627.
- [4] L. Maffei, A.J. Noss, S.C. Silver, M.J. Kelly, Abundance/density case study: Jaguars in the Americas, in: A.F. O'Connell, J.D. Nichols, K.U. Karanth (Eds.), Camera Traps in Animal Ecology: Methods and Analyses, 1 ed., Springer, New York, 2011, pp. 119–144.

- [5] P. Funston, L. Frank, T. Stephens, Z. Davidson, A. Loveridge, D. Macdonald, et al., Substrate and species constraints on the use of track incidences to estimate African large carnivore abundance, J. Zool. 281 (1) (2010) 56–65.
- [6] G.A. Balme, L. Hunter, A.R. Braczkowski, Applicability of age-based hunting regulations for African leopards, PloS One 7 (4) (2012) e35209.
- [7] M.G. Efford, R.M. Fewster, Estimating population size by spatially explicit capture-recapture, Oikos 122 (6) (2013) 918–928.
 [8] E. Rexstad, K.P. Burnham, E. Rexstad, K. Burnham (Eds.), Colorado Cooperative Fish and Wildlife Research Unit, Colorado,
- 1991 Available from: https://www.mbr-pwrc.usgs.gov/software/doc/capture/capture.htm (Accessed date: 22 June 2019).
 [9] A. Gopalaswamy, J. Royle, J. Hines, P. Singh, D. Jathanna, N. Kumar, et al., SPACECAP: A Program to Estimate Animal Abundance and Density using Bayesian Spatially-Explicit Capture-Recapture Models, Wildlife Conservation Society—India
- Program, Centre for Wildlife Studies, Bangalore, India, 2012 Version 1. 0. 5.
 [10] D. Rocha, E. Ramalho, W. Magnusson, Baiting for carnivores might negatively affect capture rates of prey species in camera-trap studies, J. Zool. 300 (3) (2016) 205–212.
- [11] T.-L. Grant, Leopard population density, home range size and movement patterns in a mixed landuse area of the Mangwe District of Zimbabwe, Rhodes University, 2012.
- [12] B.D. du Preez, A.J. Loveridge, D.W. Macdonald, To bait or not to bait: a comparison of camera-trapping methods for estimating leopard *Panthera pardus* density, Biol. Conserv. 176 (2014) 153–161.
- [13] N. Negroes, R. Sollmann, C. Fonseca, A.T. Jacomo, E. Revilla, L. Silveira, One or two cameras per station? Monitoring jaguars and other mammals in the Amazon, Ecol. Res. 27 (3) (2012) 639–648.
- [14] A. Tarugara, B.W. Clegg, E. Gandiwa, V.K. Muposhi, C.M. Wenham, Measuring body dimensions of leopards (Panthera pardus) from camera trap photographs, PeerJ 7 (2019) e7630.
- [15] K.U. Karanth, J.D. Nichols, Monitoring tigers and their prey: a manual for researchers, managers, and conservationists in tropical Asia, Centre for Wildlife Studies Bangalore, India, 2002.
- [16] F. Rovero, F. Zimmermann, D. Berzi, P. Meek, "Which camera trap type and how many do I need?" A review of camera features and study designs for a range of wildlife research applications, Hystrix 24 (2) (2013) 148–156.
- [17] F. Trolliet, C. Vermeulen, M.-C. Huynen, A. Hambuckers, Use of camera traps for wildlife studies: a review, Biotechnol. Agron. Soc. Environ. 18 (3) (2014) 446–454.
- [18] K.U. Karanth, J.D. Nichols, Estimation of tiger densities in India using photographic captures and recaptures, Ecology 79 (8) (1998) 2852–2862.
- [19] E. Brassine, D. Parker, Trapping elusive cats: using intensive camera trapping to estimate the density of a rare African Felid, PloS One 10 (12) (2015) 1–15.
- [20] F. Belbachir, N. Pettorelli, T. Wacher, A. Belbachir-Bazi, S.M. Durant, Monitoring rarity: the critically endangered Saharan cheetah as a flagship species for a threatened ecosystem, PloS One 10 (1) (2015) e0115136.
- [21] S. Ferreira, P.J. Funston, Age assignment to individual African lions, S. Afr. J. Wildl. Res. 40 (1) (2010) 1–9.
- [22] J.M. Kelly, T. Tempa, Y. Wangdi, Camera trapping protocols for wildlife studies (With emphasis on tiger density estimation), in: L.S. Mills, T. Tempa, E. Cheng (Eds.), Wildlife Research Techniques in Rugged Mountainous Asian Landscapes, Ugyen Wangchuck Institute for Conservation and Environment, Bhumtang, 2013, pp. 93–124.
- [23] B.D. Gerber, S.M. Karpanty, M.J. Kelly, Evaluating the potential biases in carnivore capture-recapture studies associated with the use of lure and varying density estimation techniques using photographic-sampling data of the Malagasy civet, Popul. Ecol. 54 (1) (2012) 43–54.
- [24] P. Lukacs, Closed population capture-recapture models, in: E.G. Cooch, G.C. White (Eds.), Program Mark: A Gentle Introduction, 2014 14.1-.38Available from: http://www.phidot.org/software/mark/ (Accessed date: 28 June 2019).