Scent Lure Effect on Camera-Trap Based Leopard Density Estimates

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Abstract

Density estimates for large carnivores derived from camera surveys often have wide confidence intervals due to low detection rates. Such estimates are of limited value to authorities, which require precise population estimates to inform conservation strategies. Using lures can potentially increase detection, improving the precision of estimates. However, by altering the spatio-temporal patterning of individuals across the camera array, lures may violate closure, a fundamental assumption of capture-recapture. Here, we test the effect of scent lures on the precision and veracity of density estimates derived from camera-trap surveys of a protected African leopard population. We undertook two surveys (a ‘control’ and ‘treatment’ survey) on Phinda Game Reserve, South Africa. Survey design remained consistent except a scent lure was applied at camera-trap stations during the treatment survey. Lures did not affect the maximum movement distances (p = 0.96) or temporal activity of female (p = 0.12) or male leopards (p = 0.79), and the assumption of geographic closure was met for both surveys (p > 0.05). The numbers of photographic captures were also similar for control and treatment surveys (p = 0.90). Accordingly, density estimates were comparable between surveys (although estimates derived using non-spatial methods (7.28–9.28 leopards/100km²) were considerably higher than estimates from spatially-explicit methods (3.40–3.65 leopards/100km²)). The precision of estimates from the control and treatment surveys, were also comparable and this applied to both non-spatial and spatial methods of estimation. Our findings suggest that at least in the context of leopard research in productive habitats, the use of lures is not warranted.

Introduction

Camera-traps are widely used as a research tool to study cryptic species [1]. In particular, closed capture-recapture (CR) models are often used on camera-trapping data to estimate the
population abundance and density of large carnivores [2]. This method has recently been strengthened by incorporating data on spatial information of captured individuals into the CR framework, removing the edge effect typically associated with traditional non-spatial estimators [3], [4]. Importantly, the effective survey area is no longer defined by the inclusion of an ad hoc buffer extending beyond the camera-trap grid [5], but by a homogenous distribution of potential home-range centres, from which density is estimated [3], [6]. Previous non-spatial estimators did not allow for demographic processes like immigration or emigration in their statistical framework in order to interpret N in a meaningful way, and also assumed geographic and demographic closure [1]. Contrastingly new spatial methods relax geographic closure and allow for temporary movement of individuals around the state space [7].

Despite these recent advances, biologists continue to seek ways to improve camera-trap surveys; most notably, their precision given the low detection rates often associated with them [8]. Precise population estimates are required to inform appropriate conservation actions and to monitor the outcomes of management decisions [9]. Increasing the number of recaptures can reduce error but this may also violate the fundamental principles of CR; as sampling periods must be short enough to prevent any demographic processes to occur [10], [11]. Similarly, increasing sampling effort by increasing the number of camera-traps deployed is not always logistically feasible [12]. Increasing the precision of camera-trap studies can be improved by augmenting camera-trap data with ancillary biological information e.g. from faecal DNA [13], [14], but even this may be practically challenging and an inability to age scats or classify those of juveniles may overinflate density estimates. This was shown by Jenecka et al [15] working on snow leopards in the Gobi desert of Mongolia.

An alternative option increasingly used in camera-trap studies is to entice animals to camera-traps by placing an attractant nearby [16]. This may be a scent lure such as a perfume/cologne [17], [18] or a food attractant that is inaccessible to the animal [8]. Baiting is another strategy and entails the use of a food reward such as a carcass or meat [19], [20], [21]. However, the use of attractants can be laborious and expensive, and they are only likely warranted if they increase capture rates significantly [16]. Attractants may also influence the movement of individuals on and off the camera-trap array, potentially violating the assumption of geographic closure [8], but this is relaxed in SCR and individuals may move temporarily around the camera-trap grid [7]. They may also have variable effects on animals depending on their age, sex or resident status. Despite this, attractants have been used in camera-trap studies on species ranging from rodents to large carnivores [19], [20]. The use of lures could also be useful if the total number of animal detections at a sampling site may be used and no sub-division of captures into individual temporal occasions occurs [22].

Attaining a better understanding of the effects of attractants in camera-trap surveys is necessary to determine whether they are an appropriate means of improving the precision of population density estimates.

In this paper we examine how the use of a scent lure affects the behaviour of African leopards Panthera pardus during a camera-trap survey, and the precision of the resultant density estimates. We use leopards as a model species as, like many large carnivores, they are of conservation concern as they are sensitive to anthropogenic mortality and have suffered significant range loss in recent decades [23]. Leopards are also important revenue generators for trophy hunting [24] and photo-tourism [25] industries. Therefore, accurate and precise estimates of leopard population density are required to inform conservation and management practices [26], but leopard numbers are difficult to monitor. In this paper we assess (i) whether the use of lures violates the assumptions of geographic closure by examining the spatio-temporal patterning (as defined by the distances animals move between camera-traps, and the timing of photographic captures) of leopard captures in a control (i.e. non-lure) and treatment survey.
(scent lure), (ii) whether the use of lures significantly increases the number of leopard captures and recaptures, and finally (iii) how precision and density estimates varied between a traditional non-spatial CR density estimation method and two recent spatially-explicit CR approaches.

**Methods**

**Ethics statement**

We obtained permission to perform leopard research on Phinda Game Reserve from the provincial conservation authority, Ezemvelo KwaZulu-Natal Wildlife (permit number HO/4004/07), and by & Beyond, the management authority on Phinda Game Reserve. Ethical clearance for this research was provided by the University of KwaZulu-Natal Ethics Committee (approval 051/12/Animal).

**Study area**

The study was conducted on Phinda Private Game Reserve (27° 51’ 30” S, 32° 19’ 00” E, hereafter Phinda) located in South Africa’s KwaZulu-Natal province, approximately 80 km south of the Mozambique border (Fig 1). Phinda (220 km²) is located adjacent to two large protected
reserves, the Mkhuze Game Reserve and the St Lucia Wetland Park. The landscape is dominated by savanna interspersed with broad-leaved woodland, grassland and relict patches of Licuati Sand Forest, a threatened and fragmented tropical dry forest with high levels of plant and animal endemism. Further details on the study area and its faunal assemblage may be found in [27]. Importantly, Phinda also borders a number of private game reserves, cattle ranches and local communities. However, leopard hunting on the ranches surrounding Phinda has largely stopped allowing for a population recovery of leopards [9]. We therefore feel experimenting with lures during camera-trap surveys is warranted as leopards who have home-ranges beyond Phinda’s border are unlikely to encounter intentionally placed scent trails.

Camera-trapping
We implemented two camera-trap surveys—a ‘control survey’ where no scent lures were deployed, which ran from 14 August–22 September 2012, and a ‘treatment survey’ where scent lures were deployed, which ran from 06 October–14 November 2012. Both surveys lasted 40 days and the camera-trap array remained consistent (Fig 1). We used Panthera IV digital camera-traps, set out in a paired format across 30 stations, totalling 60 camera-traps (1200 camera-trap nights). At least one camera-trap site was present per mean female leopard home-range (30 km$^2$) [28] to ensure no animal had a zero probability of capture (mean camera spacing = 1.68 km) [5]. Camera-traps were mounted to wooden posts, 40 cm from the ground and were monitored every four days to replace memory cards and batteries, and to administer lures.

Leopards regularly use roads during territorial patrols and are often attracted to decomposing carcasses upon which they scavenge [29], [30]. Our lure therefore comprised a scent trail of decomposed entrails from the three main leopard prey species in Phinda, nyala Tragelaphus angasii, impala Aepyceros melampus, and warthog Phacochoerus africanus [27] that was deposited on the roads along which our camera-traps were placed. The majority of entrails were from nyala that had died during game translocation operations, which Phinda facilitated between June-November 2012. The other species were used if found opportunistically. The scent trail was laid on roads for a distance of 500 metres on either side of camera-traps and refreshed every four days. This protocol is similar to that employed by trophy hunters wishing to attract a leopard to a bait near a shooting hide [31]. However, as we provided no reward for leopards, we considered our scent trail a lure rather than bait. We created separate capture histories for leopards photographed in the control and treatment surveys, in order to compare closure estimates, distances moved by individuals, the times of their captures and density estimates. The identity of leopards was determined by the unique spot patterns on their pelage [32], and their sex was estimated using distinctive morphological features [33]. We used a Fischer’s exact test [34] to examine differences in capture rates among sex classes in the control and treatment surveys.

Population closure
Leopards are long-lived (up to 19 years in the wild) [26]; hence, our survey period of 40 days seems sufficiently short to assume demographic closure [9]. We assessed geographic closure using the closure test of Otis et al [35] which assumes heterogeneity in recapture probability. We also used the closure test of Stanley and Burnham [36] which assumes a variation in time of recapture probability. Both tests were run in the statistical programme CloseTest version 3 (available online from: http://www.fort.usgs.gov/products/software/clostest/).
Spatio-temporal patterning

We followed [8] in assessing the influence of lures on the spatio-temporal behaviour of leopards during the control and treatment surveys. We compared the maximum distance moved by individuals detected at more than one camera-trap during both surveys using a Wilcoxon Signed Ranks test [34]. We also examined the distribution of times when male and female leopards were captured on camera-traps during the two surveys. We sub-divided the photographic events into five distinct periods (00:00–06:00; 06:00–12:00; 12:00–16:00; 16:00–20:00; 20:00–00:00) for both males and females and compared their frequencies for both the passive and treatment surveys using a Fishers exact test.

Density estimation

For comparison and consistency with previous non-spatial camera-trap surveys of leopards [5], [8], [21] we first used the software CAPTURE [35] to estimate leopard abundance. Following [5], we sub-divided our 40 sampling days into twenty 48-hour sampling occasions, and created a binary matrix of leopard detections, incorporating individual leopards only once during an occasion. CAPTURE provides the user with seven possible models for the computation of leopard abundance [35]. Each of these varies in its assumption regarding capture probability, which may be influenced by trap-specific response, time and individual heterogeneity [9].

CAPTURE computes a number of goodness-of-fit and between model statistics, and also has a discriminant function selection algorithm for objective model selection [35]. For each survey, we estimated the size of our effectively sampled area by adding a buffer equal to half the mean maximum distance moved by individuals photographed on more than one occasion (HMMDM) to our camera-trap grid [5] and removing zones of non-suitable leopard habitat (see supporting information). We divided the abundance estimate from CAPTURE by the effectively sampled area to estimate leopard density in the control and treatment surveys. We calculated variance for these density estimates using the delta method [10].

We also estimated leopard population density from both surveys using two spatially-explicit CR approaches (also using the 20 sampling occasion framework for comparability). Spatially-explicit CR estimates animal density from a set of individual animal detections made at capture locations nested within a broader network of potential leopard home-range centres [3], [6]. Through the incorporation of spatial information in the detection process the method is considered more robust to the “edge effects” common to non-spatial estimators and eliminates the need of a user-defined sampling area from which density is calculated [3]. We used the maximum likelihood based estimator secr version 2.9.3 [37] and the Bayesian estimator SPACECAP version 1.1 [6] in R version 2.15.2 [38]. Both methods make use of three input files: 1) detection history (information on animal identity, trap location and sampling occasion), 2) trap deployment (location of camera-traps, sampling occasions and camera function details) and 3) potential home-range centres file (a mesh of potential leopard home-range centres located in areas of suitable leopard habitat; these are demarcated by a 1 for suitable, and a 0 for non-suitable). We followed Gopalaswamy et al [6], and Athreya et al [39] in eliminating potential home-range centres from areas of non-leopard habitat. We used the raster [40] and rgdal [41] packages in R to create a rectangle around our outermost camera-traps. We then applied a 15-km buffer around a homogenous distribution of potential home-range centres spaced at 578 m intervals [6] and removed non-suitable leopard habitat (>3 settlements per 0.34 km² grid and the St Lucia water body. A detailed habitat mask creation procedure is provided (S1 Protocol). Large felids are known to exhibit trap-specific and sex-specific traits in their ranging behaviours [9] and males are generally recorded at higher capture rates when compared to females [42], [43]. We therefore followed [19] and fitted models, in secr, which
incorporated potential trap-specific responses of individuals and sex-specific detection probability (full model definitions created in secr may be found in Table 1). We maximised models in secr using conditional likelihood as this results in a likelihood, which ignores nuisance parameters within the model. We assessed candidate models in secr using AICc criteria [34] and evidence ratios (ER) [44]. In order to present leopard density, capture probability at home-range centre (g0) and sigma, we compared our top-ranked model with the next best-ranked model. We used the following formula:

\[ ER = \frac{w_j}{w_i} \]

where \( w_j \) is the AICc weight of our best-ranked model and \( w_i \) is the AICc weight of the next best model (ie. Model being compared; Table 2). SPACECAP presently allows two models, 1) a base model which considers equal capture probabilities among individuals and 2) a model which incorporates a “trap-specific” response with detection probability increasing after initial capture in a trap [6]. Both models were fitted using a half-normal detection function and Bernoulli’s encounter model. The number of Markov-Chain Monte Carlo (MCMC) iterations and burn in varied per survey in order to achieve convergence (Table 3). SPACECAP uses data-augmentation, which adds to a dataset of known leopards with an enlarged set of all zero-encounter histories [6]. We set this augmentation value to 20 times the number of photographed individuals. We assessed model adequacy in SPACECAP through examination of the Bayesian P-value which is deduced from individual encounter frequencies. A Bayesian P-value

Table 1. Models used in secr analysis to estimate leopard density on Phinda.

| Variable | Description | Variable function |
|----------|-------------|-------------------|
| g0–1     | Constant    | g0 and sigma kept constant |
| g0–b     | Learned response | Step change in parameter after initial detection of animal |
| g0–h2    | 2-class mixture | Finite mixture model with two latent classes |
| g0–bk    | Animal x site response | Site-specific step change |
| g0–Bk    | Animal x site response | Site-specific transient response |
| g0–Sex*  | Sex of animal | Male and female specific detection |

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Table 2. Model definitions and selection criteria for density models fitted for the control and lure surveys in secr.

| Survey   | Model definition | Parameters | Log likelihood | AIC | AICc | Delta AIC | AIC weight | Evidence ratio |
|----------|------------------|------------|----------------|-----|------|-----------|-------------|----------------|
| Control  | g0–bk            | 4          | -213.34        | 434.67 | 438.67 | 0         | 0.97        | 1              |
|          | g0–1             | 3          | -219.14        | 444.29 | 446.47 | 7.78      | 0.02        | 48.5           |
|          | g0–b             | 4          | -218.21        | 444.42 | 448.42 | 9.75      | 0.01        | 97             |
|          | g0–h2            | 4          | -218.59        | 445.18 | 449.18 | 10.5      | 0           | -              |
|          | g0–Bk            | 4          | -218.66        | 445.32 | 449.32 | 10.65     | 0           | -              |
|          | g0–sex           | 4          | -218.59        | 445.18 | 449.18 | 10.5      | 0           | -              |
|          | g0–sex, sigma–sex| 5          | -199.69        | 409.38 | 416.88 | 0         | 0.31        | 1              |
|          | g0–bk            | 4          | -202.27        | 412.54 | 416.98 | 0.1       | 0.3         | 1.03           |
|          | g0–1             | 3          | -205.21        | 416.42 | 418.82 | 1.94      | 0.12        | 2.58           |
| Lure     | g0–sex           | 4          | -203.31        | 414.62 | 419.07 | 2.18      | 0.11        | 2.82           |
|          | g0–h2            | 4          | -203.31        | 414.82 | 419.07 | 2.18      | 0.11        | 2.82           |
|          | g0–Bk            | 4          | -204.56        | 417.13 | 421.57 | 4.69      | 0.03        | 10.33          |
|          | g0–b             | 4          | -205.2         | 418.4  | 422.85 | 5.96      | 0.02        | 15.5           |

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close to either 0 or 1 is indicative of an inadequate model [6]. SPACECAP also provides a set of Geweke diagnostic statistics, which indicate whether MCMC chains have converged around a solution; if values range between -1.6 and 1.6 then convergence has been achieved [6]. We supplemented Geweke diagnostics supplied by SPACECAP by performing the Gelman-Rubin diagnostic and assessed potential shrink reduction factors for each parameter [45]. To do this we ran two more chains for each survey (including models incorporating the trap response variable), using different start values on the same data set (Table 4). Shrink Reduction Factors for each parameter should be <1.1 [45]. Finally we examined if estimates of density decreased using larger buffer spacings than the 15 km allocated in our models in secr using the mask check function in secr, as too narrow a buffer is likely to produce inflated density estimates [46].

Results

Photographic captures and population closure

Fifteen leopards (eight males, seven females) were captured on 40 occasions during the control survey, and fourteen leopards (10 males, four females) on 39 occasions in the treatment survey. Only one female with cubs was detected once during both surveys and those cubs were not considered in the analyses. Of the 15 leopards captured in the control survey, nine of these were present during the lure survey (six males, three females). We detected no significant difference in sex-specific captures between surveys (Fischer’s exact test, p = 0.90). The closure test of Otis et al [35] suggested no violation of permanent population closure for either the control (Z = 1.16, p = 0.88) or treatment (Z = 1.35, p = 0.91) surveys. Similarly, the test of Stanley and Burnham [36], which incorporates time variation in recapture probability, suggested population closure was achieved for both the control ($X^2 = 16.94$, d.f = 14, p = 0.26) and treatment ($X^2 = 12.20$, d.f = 15, p = 0.66) surveys.

Spatio-temporal patterning

The maximum distance moved by leopards captured on more than one occasion was similar for the control (mean = 4.95 km, range = 0–11.8 km) and treatment (mean = 5.34 km,

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Table 3. Geweke diagnostic statistics and Bayes p-values generated from the four models run for the control and treatment surveys in SPACECAP.

| Model Description                  | Iterations | Burn in |
|------------------------------------|------------|---------|
| Control survey trap absent         | 100 000    | 50 000  |
| Control survey trap present        | 80 000     | 40 000  |
| Treatment survey trap absent       | 80 000     | 30 000  |
| Treatment survey trap present      | 80 000     | 40 000  |

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Table 4. Shrink reduction factors generated using the Rubin-Gelman diagnostic in R.

| Model Description                  | sigma Point est | sigma Upper C.I | lam0 Point est | lam0 Upper C.I | beta Point est | beta Upper C.I | psi Point est | psi Upper C.I | psi Point est | psi Upper C.I | N |
|------------------------------------|-----------------|-----------------|---------------|---------------|---------------|---------------|--------------|---------------|--------------|---------------|---|
| Control survey trap absent         | 1.02            | 1.02            | 1.01          | 1.01          | -             | -             | 1            | 1             | 1            | 1             |   |
| Control survey trap present        | 1.09            | 1.07            | 1.02          | 1.02          | 1.07          | 1.06          | 1.02         | 1.01          | 1.02         | 1.01          |   |
| Treatment survey trap absent       | 1.01            | 1.01            | 1             | 1             | -             | -             | 1.01         | 1.01          | 1.01         | 1.01          |   |
| Treatment survey trap present      | 1               | 1               | 1.07          | 1.05          | 1.16          | 1.12          | 1.01         | 1             | 1.01         | 1             |   |

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range = 0–10.4 km) surveys. Similarly, we found no difference in the maximum distance moved by specific individuals captured in both surveys (W = 31, p = 0.96). We found no difference in time-specific captures between the passive and treatment survey for males (Fisher’s Exact test, p = 0.79) and females (Fisher’s Exact test, p = 0.12).

**Photographic captures and density estimates**

The heterogeneity model M(h) fit our data best for both the control and treatment surveys in CAPTURE. Using the jackknife estimator, CAPTURE estimated population abundance (SE) at 17±4.3 leopards for the control survey, yielding a density (SE) of 7.28±2 leopards/100 km² when a buffer based on HMMDM (2.48 km) was applied to our survey area. Population abundance (SE) estimated by CAPTURE for the treatment survey was 23±6.6 leopards, resulting in a density (SE) of 9.28±2.9 leopards/100 km² with a HMMDM buffer of 2.67 km.

From the seven models we created for the control survey in secr, there was very strong support for the trap-specific model, with the next best model being 48.5 times less likely. The trap-specific model estimated a density (SE) of 3.40±1.20 leopards/100 km² (capture probability at home-range centre (g0 with SE) = 0.01±0.005; sigma (σ) = 4454.23±916.40 m). From the seven models created for our treatment survey, there was equal support for a model incorporating sex (as a function of both g0 and sigma) and the trap-specific model (ER 1 vs 1.03). The base model was also a candidate being 2.58 times less likely compared to the sex model. The sex model estimated a density (SE) of 3.47±1.22 leopards/100 km²; (capture probability at home-range centre for females (g0 with SE) = 0.03±0.01; sigma (σ) = 2541.03±674.90 m and (g0 with SE) = 0.03±0.01; sigma (σ) = 4366.64±969.99 m for males). The trap-specific model estimated a density (SE) of 3.26±1.27 leopards/100 km² (capture probability at home-range centre (g0 with SE) = 0.02±0.007; sigma (σ) = 3843.36±935.87 m). Similarly, the base model from the treatment survey estimated a density (SE) of 3.30±1.15 leopards/100 km² (g0 = 0.03 ±0.009; σ = 3414.81±712.49 m). The SPACECAP estimator yielded a density (SD) of 3.55±1.04 leopards/100 km² (g0 = 0.03±0.01; σ = 3970±709 m) for the control survey in the absence of the trap response variable, and 3.65±1.22 leopards/100 km² (g0 with SD = 0.01±0.001; σ = 4700±1010 m) using the trap response variable. The SPACECAP density (SD) estimate for the treatment survey was 3.43±1.12 leopards/100 km² (g0 with SD = 0.03±0.01; σ = 3630±751 m) in the absence of the trap response variable, and 3.49±1.26 leopards/100 km² (g0 with SD = 0.02±0.01; σ = 4170±1000 m) with the trap response variable. The 15 km buffer appeared to be adequate as density estimates remained unchanged with buffer increases at 22.38 and 28.84 km using the mask.check function in secr. Bayes p values and Geweke diagnostic statistics suggested model adequacy and convergence for all four models run in SPACECAP (Table 5). This was further confirmed by shrink reduction factors for key parameters which were all <1.1 (Table 4).

**Table 5. Geweke diagnostic statistics and Bayes p-values generated from the four models run for the control and treatment surveys in SPACECAP.**

| Model                        | sigma | lam0 | beta * | psi    | N     | Bayes p-value |
|------------------------------|-------|------|--------|--------|-------|---------------|
| Control survey trap absent   | 0.16  | -1.15| -       | -0.11  | -0.11 | 0.53          |
| Control survey trap present  | -0.80 | 0.42 | -0.25  | 1.01   | 1.09  | 0.53          |
| Treatment survey trap absent | 0.66  | -0.36| -       | -1.37  | -1.17 | 0.59          |
| Treatment survey trap present| 0.26  | 0.31 | 0.81   | 0.37   | -1.07 | 0.57          |

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Discussion

An important foundation for estimating population abundance and subsequent estimates of density using capture-recapture sampling is geographic closure [9]. Lures and other attractants may compromise geographic closure by prompting temporary immigration or emigration of animals into or out of a survey area. Although our results from the two closure tests suggest that there was no breach of geographic closure during the lure survey, this does not rule out a movement of individuals either inside or outside the camera-trap grid. We had no GPS collared leopards at the time of both surveys to confirm this. We however cannot discount the possibility that our closure tests suffered from a Type II statistical error. Gerber et al [8] suggested that the Pradel model [47] was more suitable for evaluating population closure (as it is highly flexible in modelling recapture variation and less susceptible to statistical errors when there is a trap-specific effect), but our sample sizes were inadequate to run this analysis. Importantly however, assumptions of geographic closure in SCR are more relaxed and are robust to temporary movements of individuals on the borders of the camera-trap grid [7].

The use of lures also did not appear to have a significant effect on the distances moved by leopards or the timing of leopard captures. Gerber et al [8] also found that the presence of a lure did not influence the distances moved by Malagasy civet *Fossa fossana* or the temporal distribution of their captures.

Importantly our model selection process revealed substantial evidence for the “site-specific learned response” model bk, with individuals becoming “trap happy” in the control survey. This result may seem surprising as the camera trap sites were not baited nor lured in the control survey. We would have rather expected trap shyness. The “site-specific learned response” also did not become more strongly positive when scent lures were used in the treatment. Instead there was an equal support for a model incorporating sex, the site specific behavioural model and the base model. The fact that we observed a behavioural effect when there was no lure, there is a possibility that there was some other unmodelled effect (possibly site-site detector differences). Additionally although the use of lures did not appear to affect the behaviour of leopards (behaviour being defined as the distances they moved between camera-traps and when they were caught on camera-traps), they also did not improve capture or recapture rates, and hence the precision of our density estimates. This may be due to the limited range over which our lures were effective. Felids do not possess a particularly acute sense of smell [48]; hence, leopards were only likely to detect scent trails in close proximity. It is also possible that leopards may be more predisposed to scavenging, and thus to respond to lures, in more arid areas where prey abundance is lower. Phinda is a productive system and earlier research demonstrated that the leopard population was not constrained by prey availability [49].

Studies on leopards elsewhere and carnivores more broadly suggest that capture rates may be increased by using baits (i.e. where the target species is rewarded) rather than lures. Grant [21] placed stillborn cattle foetuses near camera-traps in Mangwe, Zimbabwe, and showed a twenty-fold increase in the number of leopard captures when compared to a failed non-baited survey. Similarly, a study in the Bubye valley conservancy [19] found that the presence of baits near camera-traps increased leopard captures four-fold. Although at the outset these results appear promising, the precision estimates of Du Preez et al. [19] only increased marginally with the presence of baits (2–4%) and at an additional cost of 314 man-hours per survey [50]. Leopards can remain sedentary, feeding on a single carcass for up to a week if it is large enough [29]. Such a change in an individual’s daily routine may be significant in the context of a 40-day camera-trap survey, especially if non-spatial methods are used. Specifically in reducing the number of detections of an individual leopard on different camera-traps,
which could underestimate the movement parameter sigma. However SCR models enable the
user to adjust the encounter probability, sigma and density when a trap-specific response is
added to the model. Even when using non-spatial HMMDDM [19] suggested no significant
changes in the ranging behaviours of leopards in their study, although they did not explicitly
test for closure violations. The detection distance of baits may also be larger than lures,
artificially drawing individuals into the sampling area and potentially biasing population
estimates.

The density estimates from the two spatially-explicit capture-recapture approaches (maxi-
mum likelihood and Bayesian) were comparable, but were significantly lower than estimates
derived using traditional, non-spatial methods. This concurs with previous research which
shows that non-spatial CR analyses typically overestimate population density by underestimat-
ing the distances moved by animals [51], [52], [53]. Furthermore, spatially-explicit CR models
are generally more robust to changes in the camera-trap array, the sizes of sampled areas and
the movement patterns of individuals [54]. This was reflected in our study by a 22% increase in
density estimates between the control and treatment surveys using the non-spatial estimator,
compared to a nominal change using spatial estimators. It was highly unlikely that leopard
density varied much over our study given its duration and the short interval between surveys.
This was reflected by the similar density estimates obtained from our candidate models in secr
and SPACECAP over the combined survey period.

The application of scent trails was laborious and difficult to justify for our study given the
lack of improvement in the precision of density estimates. However, capture probabilities at
home-range centre among our surveys were similar to other recent studies employing spa-
tially-explicit CR methods to estimate leopard density (eg. in the Limpopo province of South
Africa [46], p = 0.03; and a post conflict landscape of Cambodia [55], p = <0.01–0.04), and
were sufficiently high to produce reliable population estimates even in the absence of attrac-
tants. This may not be the case in lower density populations, or for species, which are less
routine in their movement patterns and thus more difficult to camera trap. In such cases the
use of an attractant may be warranted. For felids, this may require the deployment of baits
rather than lures; however, we strongly recommend that this only be done after the effects of
baiting on population and spatial parameters have been assessed, preferably using a similar
approach as this study (i.e. with a control and treatment period). Lures may be adequate for
species with superior olfactory senses such as hyaenids [16] or viverrids [8], where they are
likely preferable to baits. The use of lures could potentially also be warranted if a certain
variety is found to be particularly successful. Thorn et al [16] and Braczkowski et al [18] fol-
lowed this approach in the Limpopo and Cape respectively, and attempted to examine lure
preference.

An alternative way to increase the capture rates of animals during surveys (and conse-
quently measures of precision) is by lengthening the duration of surveys. This is indeed recom-
mended by Tobler et al [2], who suggest that higher captures be preferred over short survey
periods. Borchers et al [56] also developed a continuous time SCR model and showed that
using count (rather than binary) data improved parameter estimates. Both of these approaches
could help to increase the precision of density estimates.

Our results suggest that although using lures do not lead to the violation of CR model
assumptions in a savanna environment, they also do not improve the precision of density esti-
mates, so may be of limited use for leopard researchers. Insights such as these are important in
assisting biologists and conservation managers in determining which approaches should be
applied or avoided for the most cost- and time-efficient method to enumerate leopards and
potentially other large carnivores.
Supporting Information

S1 Dataset. SPACECAP control survey captures.
(CSV)

S2 Dataset. SPACECAP lure survey captures.
(CSV)

S3 Dataset. SPACECAP trap layout.
(CSV)

S4 Dataset. SPACECAP habitat suitability mask.
(CSV)

S5 Dataset. secr control survey captures.
(TXT)

S6 Dataset. secr lure survey captures.
(TXT)

S7 Dataset. secr survey trap layout.
(TXT)

S1 Protocol. Suitable leopard habitat mask creation procedure implemented in the R statistical environment.
(DOCX)

S1 Results. SPACECAP control survey trap absent output.
(TXT)

S2 Results. SPACECAP control survey trap present output.
(TXT)

S3 Results. SPACECAP lure survey trap absent output.
(TXT)

S4 Results. SPACECAP lure survey trap present output.
(TXT)

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Author Contributions

Conceived and designed the experiments: AB GB PJ AD. Performed the experiments: AB TD. Analyzed the data: AB JF. Contributed reagents/materials/analysis tools: GB LH. Wrote the paper: AB GB AD JF PJ DM LH.

References

1. O'Connell AF, Nichols JD, Karanth KU. (2010) Camera traps in animal ecology: methods and analyses. Springer Science & Business Media.
2. Tobler MW, Carrillo-Percastegui SE, Zúñiga Hartley A, Powell GV. (2013) High jaguar densities and large population sizes in the core habitat of the southwestern Amazon. Biological Conservation 159: 375–381.

3. Efford MG, Dawson DK, Robbins CS. (2004) DENSITY: software for analysing capture-recapture data from passive detector arrays. Animal Biodiversity Conservation 27: 217–228.

4. Royle JA, Karanth KU, Gopalaswamy AM, Kumar NS. (2009) Bayesian inference in camera trapping studies for a class of spatial capture-recapture models. Ecology 90: 3233–3244. PMID: 19967878

5. Balme GA, Hunter LTB, Slotow R. (2009a) Evaluating methods for counting cryptic carnivores. Journal of Wildlife Management 73: 433–441.

6. Gopalaswamy AM, Royle JA, Hines JE, Singh P, Jathanna D, Kumar N, et al. (2012) Program SPACECAP: software for estimating animal density using spatially explicit capture–recapture models. Methods in Ecology and Evolution 3: 1067–1072.

7. Chandler RB, Royle JA, King DJ. (2011) Inference about density and temporary emigration in unmarked populations. Ecology 92: 1429–1435. PMID: 21870617

8. Gerber BD, Karpanty SM, Kelly MJ. (2012) Evaluating the potential biases in carnivore capture–recapture studies associated with the use of lure and varying density estimation techniques using photograph-sampling data of the Malagasy civet. Population Ecology 54: 43–54.

9. Balme GA, Slotow R, Hunter LTB. (2009b) Impact of conservation interventions on the dynamics and persistence of a persecuted leopard (Panthera pardus) population. Biological Conservation 142: 2681–2690

10. Karanth KU, Nichols JD. (1998) Estimation of tiger densities in India using photographic captures and recaptures. Ecology 79: 2852–2862.

11. Williams BK, Nichols JD, Conroy MJ. (2002) Analysis and management of animal populations. Academic Press, San Diego, California, USA.

12. Marmewick K, Funston PJ, Karanth KU. (2008) Evaluating camera trapping as a method for estimating cheetah abundance in ranching areas. South African Journal of Wildlife Research 38: 59–65.

13. Gopalaswamy AM, Royle JA, Delampady M, Nichols JD, Karanth KU, Macdonald DW. (2012) Density estimation in tiger populations: combining information for strong inference. Ecology 93: 1741–1751. PMID: 22919919

14. Sollmann R, Törres NM, Furtado MM, de Almeida Jácomo AT, Palomares F, Roques S, et al. (2013) Combining camera-trapping and noninvasive genetic data in a spatial capture–recapture framework improves density estimates for the jaguar. Biological Conservation 167: 242–247.

15. Janečka JE, Munkhtsog B, Jackson RM, Narambaatar G, Mallon DP, Murphy WJ. (2011) Comparison of noninvasive genetic and camera-trapping techniques for surveying snow leopards. Journal of Mammalogy 92: 771–783.

16. Thorn M, Scott DM, Green M, Bateman PW, Cameron EZ. (2009) Estimating brown hyaena occupancy using baited camera traps. South African Journal of Wildlife Research 39: 1–10.

17. Thomas P, Balme G, Hunter L, McCabe-Parodi J. (2005) Using scent attractants to non-invasively collect hair samples from cheetahs, leopards and lions. Animal Keepers Forum 7/8: 342–384.

18. Braczkowski A, Watson L. (2013) Observations of leopard and caracal responses to novel scents in South Africa. CAT News 58: 13–15.

19. du Preez BD, Loveridge AJ, Macdonald DW. (2014) To bait or not to bait: a comparison of camera-trap methods for estimating leopard Panthera pardus density. Biological Conservation, 176, 153–161.

20. Ariefiandy A, Purwandana D, Seno A, Ciofi C, Jessop TS. (2013) Can camera traps monitor komodo dragons a large ectothermic predator? PLOS ONE. doi: 10.1371/journal.pone.0058800

21. Grant TL. (2012) Leopard population density, home range size and movement patterns in a mixed land-use area of the Mangwe District of Zimbabwe. PhD dissertation. Rhodes University, Grahamstown.

22. Royle JA, Chandler RB, Sollmann R, Gardner B. (2013) Spatial Capture-Recapture. Academic Press, USA.

23. Ray JC, Hunter L, Zigouris J. (2005) Setting conservation and research priorities for larger African carnivores. Wildlife Conservation Society, New York.

24. Lindsey PA, Alexander R, Frank LG, Mathieson A, Romanach SS. (2006) Potential of trophy hunting to create incentives for wildlife conservation in Africa where alternative wildlife-based land uses may not be viable. Animal Conservation, 9(3), 283–291.

25. Di Minin E, Fraser I, Slotow R, MacMillan DC. (2012) Understanding heterogeneous preference of tourists for big game species: implications for conservation and management. Animal Conservation 16: 249–258.
26. Balme GA, Lindsey PA, Swanepoel LH, Hunter LT. (2013) Failure of research to address the rangewide conservation needs of large carnivores: leopards in South Africa as a case study. Conservation Letters 7: 3–11
27. Balme G, Hunter L, Slotow R. (2007) Feeding habitat selection by hunting leopards Panthera pardus in a woodland savanna: prey catchability versus abundance. Animal Behaviour, 74(3), 589–598.
28. Fattebert J. (2013) Spatial ecology of a leopard population recovering from over-harvest. PhD thesis. University of Kwazulu-Natal, Kwazulu-Natal.
29. Bailey TN. (1993) The African leopard: ecology and behavior of a solitary felid. New York, Columbia University Press, USA.
30. Bothma JDP, Walker C. (1999) Larger carnivores of the African savannas. Berlin, Springer. Germany.
31. Braczkowski AR, Balme GA, Dickman A, Macdonald DW, Fattebert J, Dickerson T, et al. (2015) Who Bites the Bullet First? The Susceptibility of Leopards Panthera pardus to Trophy Hunting. PLOS ONE 10(4): e0123100. doi: 10.1371/journal.pone.0123100 PMCID: 25860139
32. Miththapala S, Seidensticker J, Phillips LG, Fernando SBU, Smallwood JA. (1989) Identification of individual leopards (Panthera pardus kotiya) using spot pattern variation. Journal of Zoology 218: 527–536.
33. Balme GA, Hunter L, Braczkowski AR. (2012) Applicability of age-based hunting regulations for African leopards. PLOS ONE. doi: 10.1371/journal.pone.0035209
34. Zar JH. (1999) Biostatistical analysis. Prentice Hall, New Jersey.
35. Otis DL, Burnham KP, White GC, Anderson DR. (1978) Statistical inference from capture data on closed animal populations. Wildlife Monographs 62: 1–135.
36. Stanley TR, Burnham KP. (1999) A closure test for time-specific capture-recapture data. Environmental and Ecological Statistics 6: 197–209.
37. Efford M. (2015) Package secr version 2.9.3.R language for statistical computing.
38. R Development Core Team. (2008) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna: Austria.
39. Athreya V, Odden M, Linnell JD, Krishnaswamy J, Karanth U. (2013) Big cats in our backyards: persistence of large carnivores in a human dominated landscape in India. PLOS ONE. doi: 10.1371/journal.pone.0057872
40. Hijmans RJ. (2013) Raster package in R. Version 2.2–2.31.
41. Keitt T. (2013) Rgdal package in R. Version 0.8–16.
42. Maputia NW, Chimimba CT, Ferreira SM. (2013) Calibrating a camera trap–based biased mark–recapture sampling design to survey the leopard population in the N’wanetsi concession, Kruger National Park, South Africa. Afr J Ecol 51: 422–430.
43. Martins Q, Harris S. (2013) Movement, activity and hunting behaviour of leopards in the Cederberg mountains, South Africa. Afr J Ecol 51: 571–579.
44. Mazerolle MJ. (2006) Improving data analysis in herpetology: using Akaike's Information Criterion (AIC) to assess the strength of biological hypotheses. Amphibia Reptilia, 27(2), 169–180.
45. Gelman A, Rubin DB. (1992) Inference from iterative simulation using multiple sequences. Statistical science, 457–472.
46. Grey JNC, Kent VT, Hill RA. (2013) Evidence of a High Density Population of Harvested Leopards in a Montane Environment. PloS One. doi: 10.1371/journal.pone.0082832
47. Pradel R (1996) Utilization of capture-mark-recapture for the study of recruitment and population growth rate. Biometrics 52: 703–709.
48. Sunquist M, Sunquist F. (2002) Wild cats of the world. Chicago, University of Chicago Press, USA.
49. Balme GA, Slotow R, Hunter LTB. (2010) Edge effects and the impact of non-protected areas in carnivore conservation: leopards in the Phinda–Mkhuzu Complex, South Africa. Animal Conservation 13: 315–323.
50. Balme G, Hunter L, Robinson H. (2014) Baited camera-trap surveys—Marginally more precise but at what cost? A response to du Preez et al. (2014). Biological Conservation 179: 144–145.
51. Obbard ME, Howe EJ, Kyle CJ. (2010) Empirical comparison of density estimators for large carnivores. Journal of Applied Ecology 47: 76–84.
52. Noss AJ, Gardner B, Maffei L, Cuéllar E, Montaño R, Romero-Muñoz A, et al. (2012) Comparison of density estimation methods for mammal populations with camera traps in the Kaa-nya del Gran Chaco landscape. Animal Conservation 15: 527–535.
53. Pesenti E, Zimmermann F. (2013) Density estimations of the Eurasian lynx (Lynx lynx) in the Swiss Alps. Journal of Mammalogy 94: 73–81.

54. Sollmann R, Furtado MM, Gardner B, Hofer H, Jácomo AT, Tórres N, et al. (2011) Improving density estimates for elusive carnivores: accounting for sex-specific detection and movements using spatial capture–recapture models for jaguars in central Brazil. Biological Conservation, 144(3): 1017–1024.

55. Gray TNE, Prum S. (2012) Leopard density in post-conflict landscape, Cambodia: Evidence from spatially explicit capture–recapture. Journal of Wildlife Management 76: 163–169.

56. Borchers D, Distiller G, Foster R, Harmsen B, Milazzo L. (2014) Continuous-time spatially explicit capture–recapture models, with an application to a jaguar camera-trap survey. Methods in Ecology and Evolution, 5: 656–665.