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Estimating jaguar densities with camera traps: Problems with current designs and recommendations for future studies

Mathias W. Tobler [a,*], George V.N. Powell [b]

[a] San Diego Zoo Global, Institute for Conservation Research, 15600 San Pasqual Valley Road, Escondido, CA 92027-7000, USA
[b] World Wildlife Fund Conservation Science Program, 1250 24th Street, NW, Washington, DC 20037, USA

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ABSTRACT

Camera traps have become the main method for estimating jaguar (*Panthera onca*) densities. Over 74 studies have been carried out throughout the species range following standard design recommendations. We reviewed the study designs used by these studies and the results obtained. Using simulated data we evaluated the performance of different statistical methods for estimating density from camera trap data including the closed-population capture–recapture models M_o and M_h with a buffer of ½ and the full mean maximum distance moved (MMDM) and spatially explicit capture–recapture (SECR) models under different study designs and scenarios. We found that for the studies reviewed density estimates were negatively correlated with camera polygon size and MMDM estimates were positively correlated. The simulations showed that for camera polygons that were smaller than approximately one home range density estimates for all methods had a positive bias. For large polygons the M_h MMDM and SECR model produced the most accurate results and elongated polygons can improve estimates with the SECR model. When encounter rates and home range sizes varied by sex, estimates had a negative bias for models that did not include sex as a covariate. Based on the simulations we concluded that the majority of jaguar camera trap studies did not meet the requirements necessary to produce unbiased density estimates and likely overestimated true densities. We make clear recommendations for future study designs with respect to camera layout, number of cameras, study length, and camera placement. Our findings directly apply to camera trap studies of other large carnivores.

1. Introduction

It has been over 16 years since camera traps (infrared activated cameras) and capture–recapture models were first used to estimate the density of a large cat (Karanth, 1995). Many studies have adopted the methodology and design developed by Karanth and Nichols (1998) for their species and few changes or improvements have been made to this method. Besides the tiger (*Panthera tigris*), the jaguar (*Panthera onca*) is the species that has been most studied with camera traps. Maffei et al. (2011) documented 83 different surveys that have been carried out from Arizona to Argentina with the goal of documenting the presence and estimating density of the jaguar. Many of these surveys have based their design on a manual with recommendations on field design and data analysis for jaguar surveys (Silver, 2004).

Jaguar density is usually estimated from camera trap data using closed population capture–recapture models and most studies use the software package CAPTURE (Otis et al., 1978; Rexstad and Burnham, 1991; White et al., 1982) to estimate abundance. In most cases the jackknife implementation of the M_h model which accounts for heterogeneity in the capture probabilities among individuals is chosen over model M_0 which assumes capture probabilities to be equal for all individuals (Burnham and Overton, 1979). Other implementations of the M_h model such as estimating functions (Chao et al., 2001) or the maximum likelihood mixture models (Dorazio and Royle, 2003; Pledger, 2000), which allow for individual covariates, have rarely been used in camera trap studies.

There are two main assumptions made by these closed population capture–recapture models that influence the design of camera trap studies (1) population closure, and (2) no individual can have zero capture probability. To ensure population closure, most studies use a short survey length (between 30 and 90 days) during which it is assumed the population will experience no birth, deaths, immigration or emigration. Given that capture probabilities are generally low for jaguars, survey length is a trade-off between keeping the survey short enough to assume closure and colleting enough data for a robust abundance estimation (Harmsen et al., 2011). In order to satisfy the second assumption, that no individual has zero probability of being photographed, the design has to ensure that at least one camera station is placed within the home range of every individual in the study area. In other

* Corresponding author. Tel.: +1 760747 8702.
E-mail address: matobler@gmx.net (M.W. Tobler).

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words, there should be no hole between cameras that could fit an entire home range of an individual. Many studies cite a minimum home range of 10 km^2 for a female jaguar as estimated by Rabinowitz and Nottingham (1986) based on footprint surveys in Belize and consequently space cameras at about 2–3 km intervals (e.g. Kelly, 2003; Silveira et al., 2010; Silver et al., 2004). However, given that the number of cameras available for a study is usually limited, this minimum distance between cameras also determines the maximum area surveyed, something that has typically received little attention.

In order to convert abundance into density one needs to estimate the effective trapping area (ETA). This is generally done by estimating the mean maximum distance moved (MMDM), which is supposed to be a proxy for home range diameter and is calculated by taking the average of the maximum distance between capture locations for all individuals captured at a minimum of two camera stations and then calculating the ETA by applying a buffer of width ½ MMDM around the camera polygon (Karanth and Nichols, 1998; Wilson and Anderson, 1985). Three potential problems arise when using this technique for jaguars which typically have large home ranges and low capture probabilities: (1) the possible maximum distance is limited by the maximum distance between cameras which is insufficient to represent home range size of jaguars, (2) with few recaptures the cameras do not capture the actual maximum distance moved of an individual within the grid, and (3) the maximum distance moved is underestimated for individuals whose home range only partly overlaps the camera grid. These sampling errors can lead to an underestimation of the true MMDM and subsequently the ETA which in turn results in an overestimation of density. This has been realized when researchers compared the MMDM obtained from camera traps to the MMDM from telemetry data, and lead to the suggestion that the full MMDM might be a more representative buffer than ½ MMDM (Dillon and Kelly, 2008; Sharma et al., 2010; Soisalo and Cavalcanti, 2006).

Over recent years new spatially explicit capture–recapture models (SECR) have been developed that use the spatial location of captures to estimate activity centers, distance parameters (σ), encounter rates at the activity center (λ_0), and abundance for all individuals in a pre-defined area, avoiding the choice of a buffer to estimate the ETA (Efford, 2004; Efford et al., 2009; Royle and Gardner, 2011; Royle and Young, 2008). These models further have the advantage that they can incorporate both individual-level covariates such as sex or age class as well as station level covariates such as road vs trail, camera type or habitat (Sollmann et al., 2011), whereas classical capture–recapture models for closed populations based on a maximum likelihood estimator only allowed for individual covariates and the jackknife estimator does not allow for any covariates. SECR models make some additional assumptions to the closed population capture–recapture models (1) home ranges are stable over the time of the survey, (2) activity centers are distributed randomly (as a Poisson process), (3) home ranges are approximately circular, and (4) encounter rate (the expected number of encounters/photographs per sampling interval) declines with increasing distance from the activity center following a predefined detection function. These models can be analyzed both within a maximum-likelihood (Borchers and Efford, 2008; Efford et al., 2009) as well as a Bayesian framework (Royle and Gardner, 2011; Royle and Young, 2008). Simulations showed that the SECR models work well and produce unbiased results for adequate sample sizes (N = 200, σ smaller than grid size) but bias increased with low capture probabilities and when the home range size was getting closer to the size of the study area (Marques et al., 2011; Royle and Young, 2008). Sollmann et al. (2011) were the first to apply these models to a jaguar camera trap study and they found that including sex as well as camera location (on/off road) as covariates improved estimates over the classical method using MMDM and models without covariates.

A recent review based on a literature review and the authors own experience has brought up several potential problems with camera trap density studies including misidentification of individuals, low capture probabilities, small sample sizes, camera failure, and small study area size (Foster and Harmsen, 2012). However, to date there exist no clear recommendations on what minimum survey effort is needed for jaguar surveys in order to produce accurate density estimates. Especially the question of the minimum survey area needed in relation to home range size has never been well addressed. Maffei and Noss (2008) compared camera trap data to telemetry data from ocelots and concluded that the survey area should be three to four times the average home range size, but there is little theoretical justification for that. Given the widespread use of camera trap data for estimating jaguar densities, it is important to evaluate the potential bias of current camera trap studies caused by inadequate study designs and to make clear recommendations for future studies. We implemented an extensive series of simulations to quantitatively measure the bias in jaguar density calculations as a function of camera polygon size and shape, camera numbers, sampling period and jaguar density. We simulated spatially explicit capture–recapture data using realistic parameters for jaguars and camera trap survey designs. Based on our simulations we make specific recommendations for future studies, taking into account both statistical as well as logistic considerations.

2. Materials and methods

2.1. Review of field studies

We compiled a database of published and unpublished jaguar density surveys recording the number of cameras used, the number of survey days, the camera spacing, the area of the survey polygon, the number of individuals captured, the number of recaptures, the estimated MMDM, the estimated abundance, the estimated trapping area, and the estimated density. We also reviewed available publications on jaguar home range size.

We used a linear regression to look at the relationship between the estimated MMDM and the survey polygon area using a log-transformation for polygon area. We used a second linear regression to look at the relationship between estimated density and the survey polygon using a log-transformation for both variables. For the second regression we excluded one outlier with a density of 18.3 ind. km^{-2}. All analysis were carried out in R 2.14 (R Development Core Team, 2011).

2.2. Simulations

We simulated datasets to evaluate which factors influenced both the accuracy and precision of the classic MMDM based estimators as well as different SECR models. We chose parameters that we consider realistic for jaguar populations and camera trap studies based on our literature review (Table 1). To simulate the data we used the function sim.capthist() from the secr package (Efford, 2011b) in R 2.14 (R Development Core Team, 2011). This function simulates spatially explicit capture recapture data based on randomly distributed activity centers, circular home ranges, and an encounter rate that declines with distance from the activity center following a half-normal function ($g(d) = \lambda_0 * exp(-d^2/(2\sigma^2)$; with λ_0 = base encounter rate at the activity center, σ = distance parameter related to the home range radius and d = distance between the activity center and the camera). This is the same model that is used by the SECR model to estimate density. We truncated the distance function at $2.45 * \sigma$ which corresponds approximately to a 95% home range estimate. Not truncating the data would in some cases