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

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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.

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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

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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

Table 1
Parameters used to simulate spatial capture–recapture data for evaluating camera trap study designs for estimating jaguar densities.

Parameter	Values
Population	
Density (ind. 100 km^{-2})	1, 2, 4
λ_0	0.005, 0.01
σ (m)	2857, 4592[a]
Study design	
Cameras (N)	36, 49, 64
Polygon size (km^2)	33, 55, 90, 148, 245, 403, 665, 1097, 1808, 2981, 4915,8103,13360
Occasions (days)	30, 60, 90

[a] Corresponds to a circular home range of 150 and 400 km^2 or a home range diameter of 14 and 22.5 km respectively.

increase the MMDM estimates due to rare captures at very large distances from the activity center in larger grids. All simulated camera grids for our baseline simulation had a square shape and activity centers were distributed over an area that incorporated the camera grid plus a $6 * \sigma$ wide buffer on each side of the grid. We only considered scenarios with a minimum of five captured individuals given that a lower number of captured individuals often resulted in failed estimates. We estimated densities with the M_0 and M_h jackknife estimators and a buffer of ½ MMDM and the full MMDM as well as with a basic SECR model implemented in secr (Efford, 2011b; Efford et al., 2009). For the basic model with no covariates the maximum likelihood and the Bayesian implementation of the SECR model give almost identical results and we therefore decided to use the maximum likelihood implementation based on the significantly lower computational time required for each simulation run. We ran 110 repetitions for each of the 1404 parameter combinations (Table 1), resulting in 154,440 simulation runs. Simulations were run in parallel using the snowfall package (Knaus, 2010).

After analyzing the results from our baseline simulations we conducted further simulations to investigate the effect of camera grid shape, and sex-specific encounter rates and sex-specific home range sizes on estimates as well as to evaluate the possibility of correcting estimates setting the MMDM or σ value to the know value used for the simulations. For these simulations we used a reduced set of parameters at intermediate levels. We used 60 survey days, densities of 2 and 4 ind. 100 km^{-2}, and all the polygon sizes used for the original simulations. For the simulations where we set MMDM and σ to the simulated value we used a 7×7 grid, σ values of 2857 m and 4592 m and a λ_0 of 0.01. Due to truncation the estimated σ is lower than the simulated σ so that we used a correction factor of 0.92 when fixing σ. For the grid shape simulations we used a λ_0 of 0.01, a σ of 4592 and the following grid configurations: 7×7, 5×10, 4×12, 3×16, and 2×24. For the sex covariate simulation we used the following parameter for males: $\sigma = 4592$, $\lambda_0 = 0.01$ and females: $\sigma = 2857$, $\lambda_0 = 0.005$, and a sex ratio of 1:1.5 (male:female). These parameters correspond approximately to parameters we obtained from a large dataset from Peru (Tobler et al., in press-a). We ran 110 repetitions for each parameter combination.

2.3. Analysis of simulated data

For all analyses we filtered out unrealistically high estimates ($\hat{D} > 100$ ind. km^{-2}) and estimates with very large coefficients of variation (CV(σ)>2, CV($\hat{D}$) > 10) caused by non-convergence of the likelihood function.

In order to compare density estimates to the true density across scenarios we calculated the relative bias ($RB = (\hat{D} - D)/D * 100$), where D = density). Given the non-linear relationships, strong interactions, and unequal variance observed across our simulated parameter combinations, we chose to explore the relationships between parameters and the observed bias graphically instead of trying to fit a linear or additive model. We looked at two main metrics, accuracy and precision. Accuracy is defined as the mean bias for all simulations with a certain parameter combination and is highest when it equals zero. Precision is defined as the distribution of the estimates around the means and is higher when all estimates are close to the mean and there is little variation between estimates.

In a first step we looked at the accuracy of different estimators in relation to camera polygon size and home range size. For each simulated home range size we then chose the minimum camera polygon size required to obtain unbiased results, and evaluated the influence of different study design parameters on the accuracy and precision of the estimates by using box plots. We did the same for simulations with covariates and simulations with density corrections using the true MMDM or σ value.

3. Results

3.1. Review of field studies

We analyzed data from 74 different camera trap surveys that were intended for estimating jaguar densities covering the entire range of the species from Mexico to northern Argentina (Appendix A). Designs varied greatly among surveys. The number of camera stations used ranged from 11 to 134 (N = 65, mean = 30, median = 24) with 38% of the surveys using less than 20 stations, 46% using 20–40 stations, and only 15% using more than 40 stations. Survey days ranged from 20 to 90 (N = 65, mean = 55) with 61% of all surveys lasting between 50 and 70 days. Cameras were spaced 0.8–6 km apart (N = 56, mean = 2.4) with 32% of all surveys spacing cameras at 1–2 km and 53% of all surveys spacing cameras at 2–3 km. Survey polygon sizes ranged from 20 to 1320 km^2 (N = 72, mean = 123, median = 80) with 54% of all surveys having a survey polygon between 50 and 100 km^2. The number of captured individuals ranged from 1 to 31 (N = 56, mean = 8, median = 6) with 32% of all studies having photographed less than 5 individuals and only 11% having photographed more than 10 individuals (Fig. 1). When looking at the relationship between the number of individuals photographed (N_{obs}) versus the estimated abundance (N_{est}) we found almost 80% of all surveys captured 70% or more of the mean estimated number of individuals (N = 52, mean = 81%).

We found a strong positive relationship between the size of the camera polygon and the estimated MMDM ($R^2 = 0.49$, $p < 0.001$, $F = 50.04$, $df = 52$) and a negative relationship between the camera polygon and the estimated density ($R^2 = 0.33$, $p < 0.001$, $F = 28.58$, $df = 59$) (Fig. 1). If results were unbiased we would not expect any relationship between these variables. We would like to note at this point that several studies did report densities other than those obtained with ½ MMDM and some pointed out the shortcoming of using ½ MMDM, however, for comparison purposes we only considered densities estimated with that method for this analysis. When necessary for the purposes of this comparison, we calculated ½ MMDM for those studies that did not provide the parameter.

There are 13 studies from five different countries that used radio or GPS telemetry to estimate jaguar home ranges (Appendix B). Home range sizes varied widely with female home ranges generally being smaller than male home ranges. Female home ranges ranged from 8.8 to 492 km^2 (mean: 103 km^2), while male home ranges were between 5.4 and 1291 km^2 (mean: 196 km^2). Within

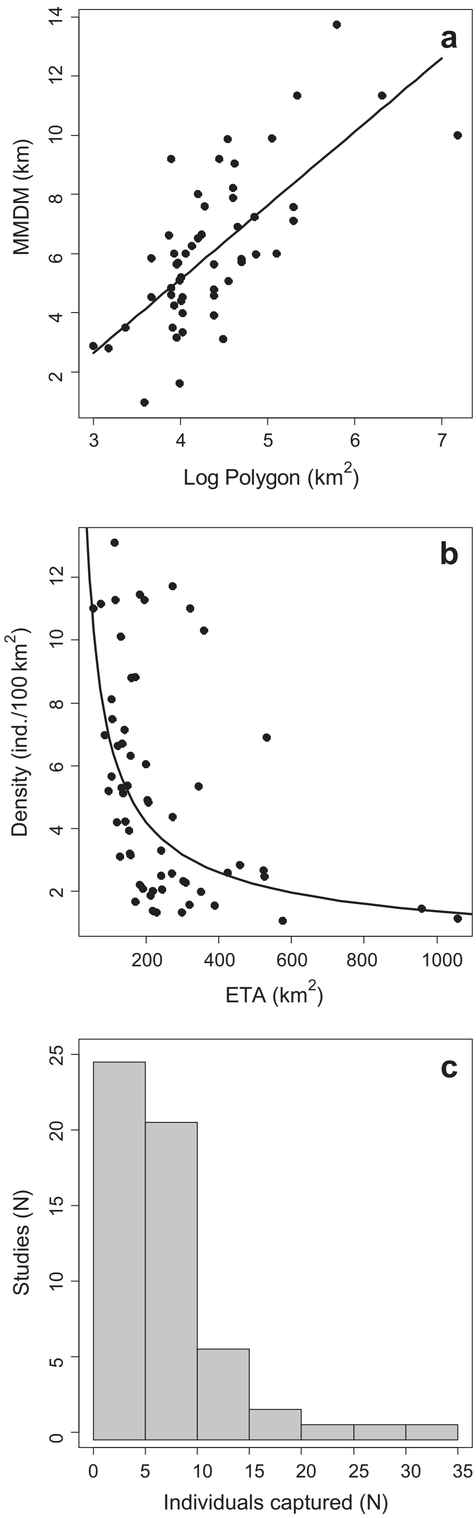

Fig. 1. (a) Relationship between the size of the camera polygon and the estimated mean maximum distance moved (MMDM) for 64 jaguar density studies ($R^2 = 0.49$, $p < 0.001$). (b) Relationship between the size of the camera polygon and the density estimated using the M_h model and a buffer of ½ MMDM for 56 jaguar camera trap studies (regression on a log–log scale: $R^2 = 0.33$, $p < 0.001$). (c) Histogram of the number of jaguar photographed by 56 jaguar density studies.

site and within sex variation of home range size was high with the largest recorded home range on average being three times larger than the smallest home range for individuals of the same sex (range: 1.1–26).

3.2. Simulations

For our first set of simulations we observed a large positive bias for all methods when the camera polygon was small compared to the size of the home range (Fig. 2). The M_h jackknife estimator combined with a buffer of ½ MMDM resulted in a large positive bias even when the camera polygon was much larger than the simulated home range size. In contrast, using a buffer of a full MMDM resulted in a small negative bias when the camera polygon was the size of one home range or larger. The M_0 estimator consistently resulted in lower density estimates than the M_h estimator, leading to a negative bias in combination with the full MMDM. The SECR model resulted in a very similar bias to the M_h MMDM method, with density estimates starting to be unbiased once the camera polygon size was between half and the full home range depending on the other parameters.

The precision of the estimates was very low for small camera polygons and rapidly increased as the polygon size approached the size of one home range. After that, precision did not increase much further with increasing polygon size but decreased slightly for very large camera polygons due to the large spacing of cameras (Fig. 3). We found that the maximum camera spacing that still gave accurate results was about half a home range diameter.

Both jaguar density and the study design influenced the precision and accuracy of the estimates (Fig. 4). For low jaguar densities ($D = 1$ ind. $100\,\text{km}^{-2}$), and a small home range size ($\text{HR} = 150\,\text{km}^2$) estimates were positively biased even when the camera polygon was the size of one home range and there was a high survey effort. For these scenarios the number of individuals recorded was very low. If the expected mean number of individuals photographed was smaller than our imposed minimum of 5, our limit favored simulation runs that had a higher local density around camera polygon which led to a positive bias. The minimum camera polygon required for this low density was 665 km^2 or about four times the home range size. The simulations show that for low densities, increasing both the number of survey days and the number of cameras leads to an increase in precision but even for the scenarios with higher densities a minimum survey effort of 60 days seems to be required to obtain reliable estimates.

Using asymmetrical camera grid layouts reduced the bias even for small grids for the SECR models (Fig. 5). Examining the results we found density estimates started being unbiased when the longer side of the camera grid equaled one home range diameter. However, for large grids density estimates from elongated grids had a lower precision than estimates from a square grid.

If males and females have different home range sizes and encounter rates, using models that do not account for this can introduce additional bias. In the case of jaguars, females usually have smaller home ranges and lower encounter rates (Sollmann et al., 2011; Tobler et al., in press-a) which leads to a negative bias for both the M_h MMDM and SECR models (Fig. 6). Models with sex covariates for both σ and λ_0 had a low bias but also a relatively low precision. This can be explained by the fact that categorical covariates divide the data into distinct groups reducing effective sample size. The data are especially sparse for females which are encountered much less frequently. We can further observe the importance of camera polygon size and camera spacing when home range sizes vary by sex. Results for the SECR model with sex covariates were unbiased when the polygon was equal to or larger than the size of one male's home range, but they started being biased when the camera spacing was larger than the female home range radius (Fig. 6).

Fixing σ at the simulated value for the SECR model effectively corrected the bias introduced by small camera polygon sizes

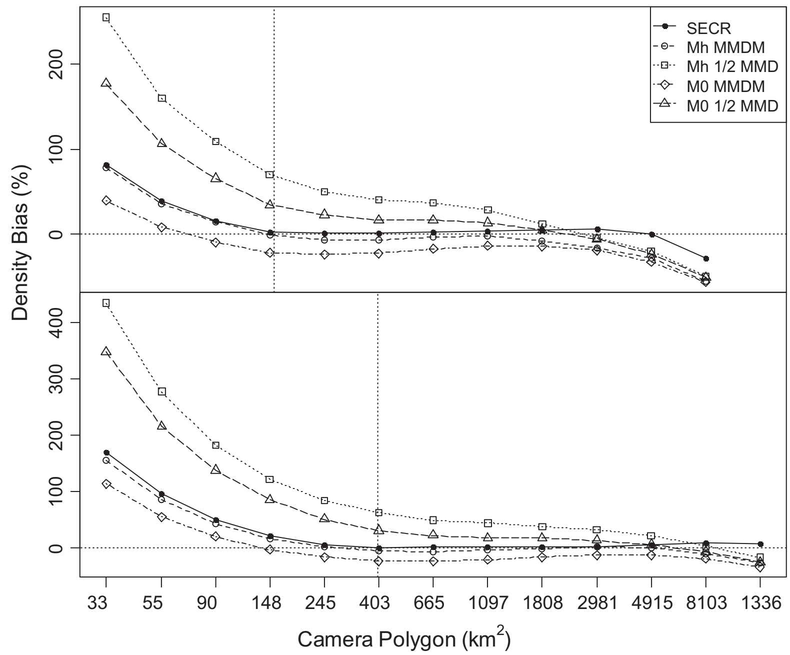

Fig. 2. Mean bias of different density estimators in relation to the camera polygon for simulated jaguar capture–recapture data using two different home range sizes (top: 150 km^2 and bottom: 400 km^2) indicated by the vertical lines. The data shown combines simulation runs with the following parameters: $\lambda_0 = 0.01$, number of cameras (49, 64), number of occasions (60, 90), simulated density (2, 4 ind. 100 km^{-2}).

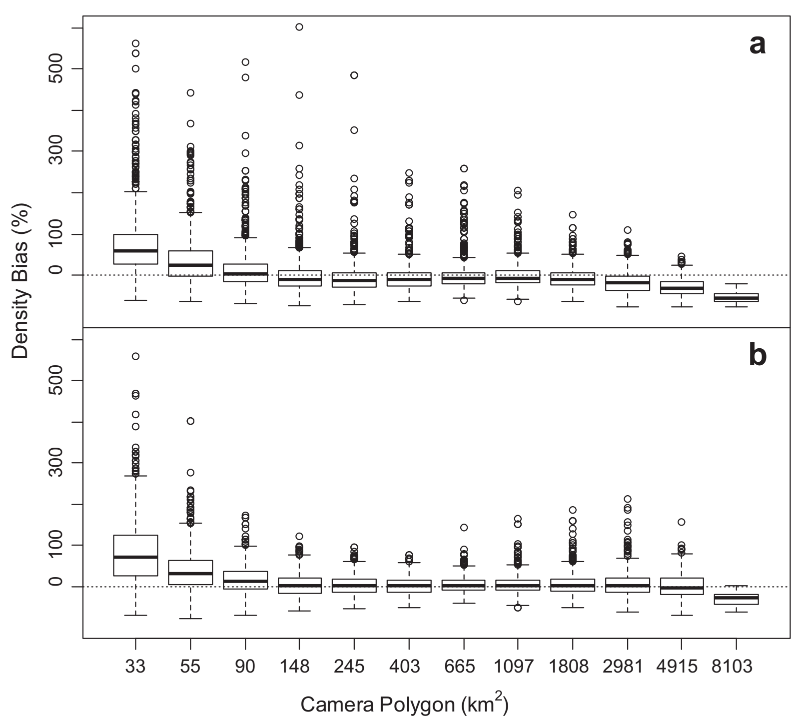

Fig. 3. Distribution of the bias of densities estimated using the M_h MMDM (a) and SECR (b) method in relation to the camera polygon size for simulated jaguar capture–recapture data. The data shown combine simulation runs with the following parameters: $\lambda_0 = 0.01$, number of cameras (49, 64), number of occasions (60, 90), simulated density (2, 4 ind. 100 km^{-2}), home range = 400 km^2 ($\sigma = 4592$). The bottom and top of the box show the 25th and 75th percentiles, respectively, the horizontal line indicates the median and the whiskers show the range of the data except for outlier indicated by circles.

(Fig. 7). The results also show that a large portion of the variation of estimates for small polygons is caused by the σ estimate, while for larger polygons it can largely be attributed to the estimate of λ_0 or random variation in the local density of the simulated animals. The same is true for the M_h MMDM method.

4. Discussion

Over the last decade a large amount of work and funding has been invested in camera trap studies with the goal of estimating jaguar densities across the range of the species. Recommendations

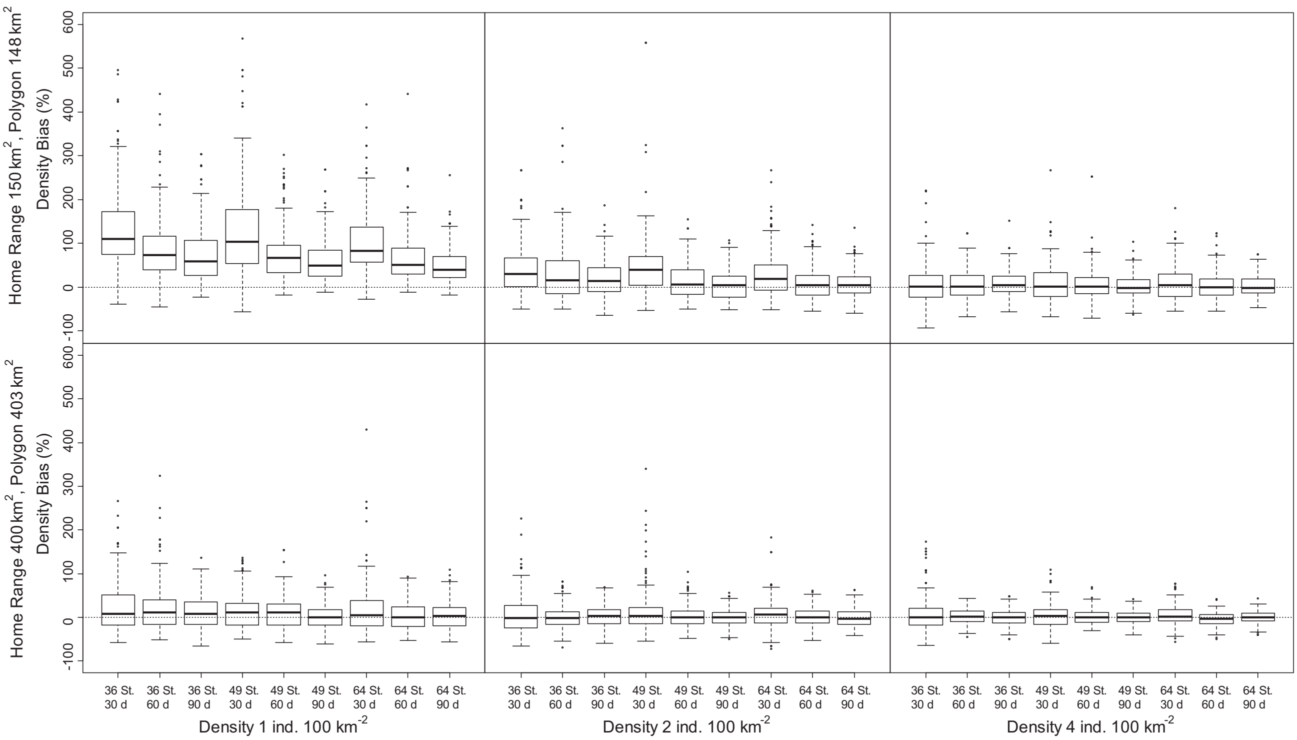

Fig. 4. Bias of densities estimated by a spatially explicit capture–recapture model (SECR) in relation to different densities and camera trap survey parameters for simulated jaguar capture–recapture. The graph shows the distribution of the bias from 110 simulation runs for each parameter combination. The bottom and top of the box show the 25th and 75th percentiles, respectively, the horizontal line indicates the median and the whiskers show the range of the data except for outlier indicated by circles. St.: camera station.

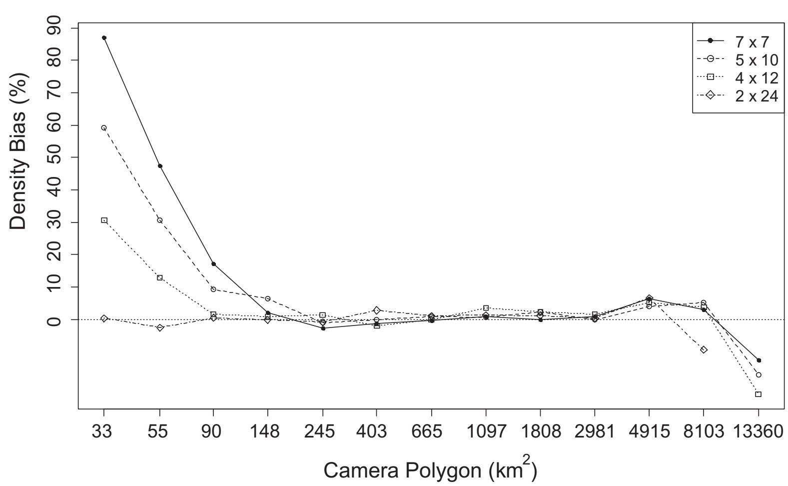

Fig. 5. Mean bias of densities estimated by a spatially explicit capture–recapture model (SECR) in relation to different camera grid shapes for simulated jaguar capture–recapture data. The data shown combines simulation runs with the following parameters: $\lambda_0 = 0.01$, home range = 400 km^2 ($\sigma = 4592$), number of occasions = 60, simulated density (2, 4).

were made on how to best setup such surveys and on how to analyze the resulting data (Silver, 2004), and these standardized methods have been used by many projects. Unfortunately, these recommendations did not consider the minimum camera trap polygon size and sampling effort necessary to study a species that occurs at low densities, has a low capture probability and can have a home range the size of several hundred square kilometers. Our results indicate that about 90% of all studies carried out so far do not fulfill minimum requirements and produce highly biased results that overestimate jaguar densities. Consistent with our simulations we found that density estimates increase with decreasing camera polygon size which is caused by an underestimation of the MMDM. Only nine studies had a camera polygon covering an area larger than 200 km^2, and even some of those studies might still be too small given that maximum home ranges in many places are larger than 200 km^2 and can be over 1000 km^2 (Conde, 2008; McBride, 2007). Over one third of all surveys used a very low number of camera stations (<20) and/or estimated densities based on less than five photographed individuals. Our results also showed that using ½ MMDM as a buffer almost doubles estimated densities and in combination with a small study areas can lead to an overestimation of density by 200–400% or 3–5 times the actual

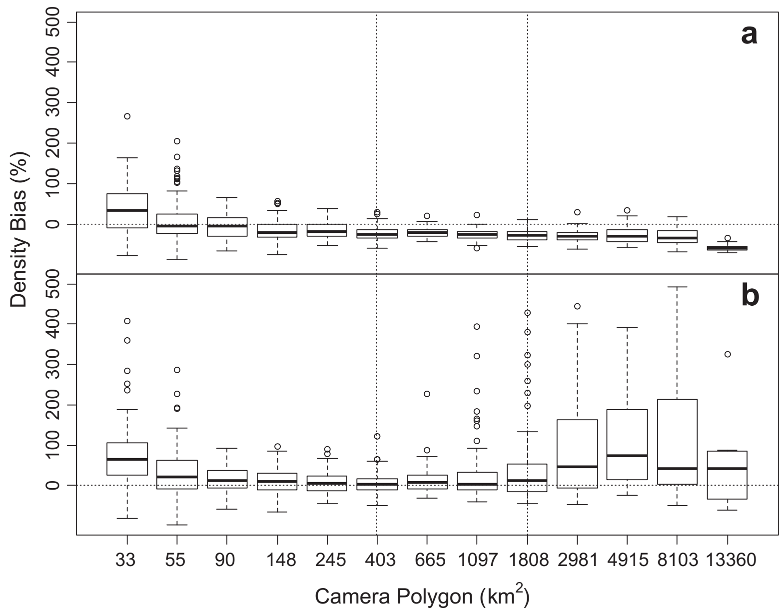

Fig. 6. Comparison of the performance of spatially explicit capture–recapture models (SECR) without (a) and with (b) sex covariates for σ and λ_0 for data simulated with different values for σ and λ_0 for male and female jaguars. The first vertical line indicates the size of the male home range; the second line indicates the point where camera spacing was equal to the female home range radius. The following simulation parameters were used: number of cameras = 49, number of occasions = 60, density 4 ind. 100 km^{-2}, Male: λ_0 = 0.01, home range = 400 km^2 (σ = 4592), Female: λ_0 = 0.005, home range = 150 km^2 (σ = 2857). The bottom and top of the box show the 25th and 75th percentiles, respectively, the horizontal line indicates the median and the whiskers show the range of the data except for outlier indicated by circles.

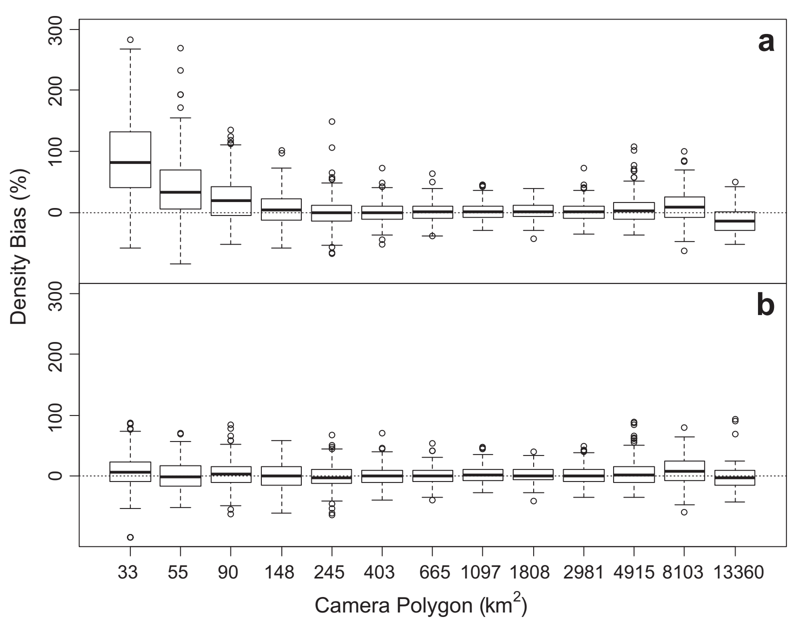

Fig. 7. Correction of bias by small camera polygons by fixing σ to the true value for a spatially explicit capture–recapture models (SECR). (a) σ Estimated by from data, (b) σ set to the true simulated value. The following simulation parameters were used: λ_0 = 0.01, number of cameras = 49, number of occasions = 60, simulated density (2, 4 ind. 100 km^{-2}), home range = 400 km^2 (σ = 4592). The bottom and top of the box show the 25th and 75th percentiles, respectively, the horizontal line indicates the median and the whiskers show the range of the data except for outlier indicated by circles.

density. This could explain very high densities of 8–12 jaguar 100 km^{-2} reported by some studies (e.g. Harmsen, 2006; Miller, 2005; Moreira et al., 2008a, 2008b; Silver et al., 2004).

4.1. Evaluation of methods and study designs

There were large differences in density estimates for the different methods used. The best results were obtained with the SECR model and with the M_h jackknife estimator and a full MMDM buffer. The M_o estimator on the other hand consistently underestimated the true abundance. This confirms that the M_h is a better choice in the presence of spatial heterogeneity and, assuming that real data show an even higher degree of heterogeneity due to additional heterogeneity in individual capture probabilities, justifies the default choice of this estimator for camera trap studies. However, the precision of this estimator for small capture probabilities (<0.1) has been shown to be quite poor even for a relatively large number of individuals (N = 50) which very few camera traps studies reach (Harmsen et al., 2011), and we saw a similar effect in our simulations. It has been suggested that collapsing data from multiple days into one survey period (e.g. using 5 days as one sampling day) would increase capture probability and improve estimates (Foster and Harmsen, 2012; Maffei et al., 2011), however, given that the jackknife estimator only uses the final capture frequencies (number of animals captured once, twice etc.), the number of survey occasions has no influence on the estimate and collapsing data might actually result in poorer or more biased estimates as it can reduce the number of individuals captured multiple times. The only ways to improve estimates if capture probabilities are low are to either add more cameras or extend the survey period.

For all our simulations a buffer ½ MMDM produced large positive biases under all conditions whereas the full MMDM produced unbiased results for adequate camera polygon sizes (equal or larger than one home range). We found that for unbiased density estimates the value of the estimated MMDM was slightly lower than the simulated home-range radius, and not, as often assumed, equal to the home range diameter. That the full MMDM is a better choice for the buffer width was previously suggested by Soisalo and Cavalcanti (2006) and Sharma et al. (2010) based on their comparison with telemetry data from the same site, by Parmenter et al. (2003) based on field studies with small rodents, and by Ivan (2011) based on simulations studies.

For square polygons all methods evaluated showed a large positive bias and low precision for small camera polygon sizes. Estimates started being unbiased once the size of the camera polygon was approximately equal to the size of a simulated home range and both accuracy and precision remained fairly stable until the distance between cameras exceeded the home range radius, at which point density estimates started showing a negative bias. Sollmann et al. (2012) found that SECR models can produce unbiased density estimates even when the camera polygon size is about half the size of a home range. For some scenarios with a high simulated density we could confirm that result, however under other scenarios, this polygon size still produced positively biased results.

Using the simulated values for MMDM or σ in the models removed the polygon size bias even for small polygons and produced accurate results for the SECR model and resulted in a slightly negative bias for the Mh MMDM model. Not only did the accuracy increase, the precision of the estimate was also much higher for small grids. This shows that the main source of imprecision for both the Mh MMDM and the SECR models is the estimation of the home range parameter. This also means that data from telemetry studies or larger camera polygons could potentially be used to correct for the bias in small polygons (Tobler et al., in press-a).

Using rectangular grids increased accuracy for small polygon sizes under the SECR model. In fact, the absolute polygon size seems to be less important than the length of the longer side of the grid. Once the length of the camera grid equaled one home range diameter, density estimates were relatively unbiased, although precision was lower than for large square grids of the same size. Rectangular grids also increased the number of individuals exposed to the cameras, effectively increasing sample size. While highly rectangular camera polygons do improve density estimates for small grids, they might be problematic when home ranges are asymmetrical and could be oriented perpendicular to the grid. Ivan (2011) simulated asymmetrical home ranges for snow shoe hares and found that the M_h MMDM method performed better than the SECR model under those conditions.

Something we have not considered in our simulations is the effect of varying home range sizes on density estimates. Telemetry studies show a large variation of home range sizes for individuals of the same sex while all models assume a constant home range size. We suspect that this heterogeneity would lead to a negative bias of the SECR models. While it would be possible to build models that include heterogeneity for σ either as a fixed or continuous mixture (Borchers and Efford, 2008), this would further increase the necessary sample size.

When encounter rates and home range size differed for males and females, both the M_h MMDM and the SECR model underestimated density. This has been shown for field data (Tobler et al., in press-a) and was confirmed by our simulation. Including sex as a covariate in the SECR model corrected for this bias but lowered the precision of the estimate.

4.2. Recommendations for jaguar density studies

4.2.1. Polygon size

Based on our findings, the camera polygon for a density study should be at least the size of one home range. Since male home ranges tend to be much larger than female ranges, the polygon size should be determined by the male home range. While in some places such as the Pantanal of Brazil this means that a polygon of 200–300 km^2 is sufficient (Cavalcanti and Gese, 2009), in other places a camera polygon of 1000 km^2 would be necessary (Conde, 2008; McBride, 2007). As we have shown, in areas with low jaguar densities (<2 jaguar 100 km^{-2}) the camera polygon might need to cover several home ranges in order to produce reliable estimates, rising the required minimum size even more. In areas with high densities (3–4 jaguar 100 km^{-2}) on the other hand camera polygon sizes somewhere between half and one home range might be sufficient. Extending the survey area not only reduces the bias and increases the sample size, it has the additional advantage of including more habitat heterogeneity, making the survey more representative for the general area and making extrapolation more valid. When the area that can be covered by a camera polygon is limited, using a more rectangular grid should improve density estimates by SECR models. In that case, the design should attempt to have the long side of the polygon be at least the length of one home range diameter.

4.2.2. Camera spacing

The maximum distance between cameras depends on the female home range which is generally much smaller than the male home range. While some studies reported female home ranges of less than 10 km^2, these may be sampling artifacts due to small sample sizes (Crawshaw et al., 2004; Rabinowitz and Nottingham, 1986). But seasonal home ranges as small as 34 km^2 have been documented with GPS collars (Cavalcanti and Gese, 2009); these would require a maximum distance between cameras of 3 km. However, in many cases it can be assumed that female home ranges are larger (Conde, 2008; Cullen, 2006; McBride, 2007) allowing for a camera spacing of 4 km or even 5 km (corresponding to a circular home range of 50 and 80 km^2), which would reduce the number of cameras required to cover the necessary area. Still, we believe that a minimum of 40–50 stations are required to carry out a reliable survey and a larger number of stations would be desirable. According to our simulations, surveys with fewer stations will likely result in biased or imprecise results unless capture probabilities are very high. If the number of cameras available is smaller than the total number needed, a blocked design can be used where cameras are moved during the survey (Di Bitetti et al., 2006; Foster and Harmsen, 2012; O'Brien et al., 2003; Soisalo and Cavalcanti, 2006).

4.2.3. Sampling duration

For all our simulations a 30 day sampling period resulted in reduced precision and larger confidence intervals. We therefore recommend a minimum survey period of 60 days if densities and encounter rates are high or a block design is used, or else 90 days or even 120 days. While violating the population closure assumption is a concern for long survey periods, currently there are insufficient data from jaguar studies to indicate for how long population closure can be assumed. But in most situations the data gained by extending the survey period should outweigh the risk of violating closure.

4.2.4. Camera placement

A higher capture probability will increase the precision of the estimate and reduce the necessary survey time. Cameras should therefore be placed to maximize capture probabilities. This means placing them on well-established trails and logging roads that are frequently used by jaguars (Harmsen et al., 2010; Sollmann et al., 2011; Tobler et al., in press-a). Other habitat features that can concentrate jaguar movements are canyons, ridges or river edges. While placing cameras in optimal locations could favor certain individuals over others (Foster and Harmsen, 2012), in our experience cameras that are randomly placed in the landscape have a very low capture probability for jaguars and will result in poor data. If some cameras are placed on roads or trails and others not, it is important to include the camera placement as a covariate to account for the difference in capture probabilities, which can easily be done in a SCER model (Sollmann et al., 2011).

4.2.5. Data analysis

While SECR models still require a minimum camera polygon size they have several advantages over MMDM based methods. They allow for the inclusion of both site and individual covariates and in most cases produce unbiased results with adequate data. Male and female jaguars usually have different home range sizes and encounter rates and not accounting for this can lead to biased density estimate. We therefore recommend that all jaguar density studies include sex covariates both for the λ_0 and the σ parameter. While the maximum likelihood implementation of the SECR model does require the sex of every individual to be known, the Bayesian implementation allows for missing data (Sollmann et al., 2011; Tobler et al., in press-a). With the inclusion of covariates, however, the data are divided up into smaller groups and larger sample sizes are needed. SECR models with sex covariates have been run with 10 individuals (Sollmann et al., 2011), but a sample size of 30 or more individuals will result in more precise estimates with smaller confidence intervals (see Appendix C).

Increasing the camera polygon size usually increases the sample size, but another possible way of increasing sample size is to combine data from multiple surveys. If it can be assumed that home range sizes or even encounter rates do not vary much from one survey to another (e.g. if the surveys were carried out in the same area over multiple years or in the same general habitat), sharing those parameters across surveys can improve density estimates for each survey, or parameters estimated from a larger survey could be used to correct for polygon size bias of a smaller survey (Tobler et al., in press-a,-b; Wilting et al., 2012). Furthermore, carrying out multiple surveys allows the validation of results and the detection of erroneous estimates.

A last advantage of the SECR models is that it is straight forward to include the exact number of days each camera was active. This provides an easy way of dealing with camera failure or blocked designs where not all cameras were active at the same time. Not accounting for camera failure can lead to biased density estimates due to an underestimation of capture probabilities (Foster, 2008).

We highly recommend researchers to carry out simulation studies with reasonable parameters in order to test their study design before putting camera traps out in the field. These simulations can relatively easily be implemented using the secr package in R (Efford, 2011b) or the software DENSITY (Efford, 2011a). Both allow users to use a real camera trap layout and to define realistic parameters as the basis for simulations. By varying parameters such as density, home range size or encounter rates researchers can evaluate the range of conditions for which their study design will likely give unbiased results.

5. Conclusions

Unfortunately, after over a decade of jaguar camera traps studies, our knowledge of the true densities of jaguars in different habitats remains poor. A large number of camera trap surveys have documented the presence of the species, but mostly produced density estimates that are biased and therefore cannot be reliably compared across studies. Given that actual densities for most regions are likely significantly lower than current estimates, there are real implications for jaguar conservation. Populations that were thought to be sufficiently large for long-term survival might actually be too small and in need of urgent actions. For example, if we assumed that densities presented by Maffei et al. (2004) were overestimated by a factor of two, the extrapolated total populations in the Kaa-Iya National Park would be 500 individuals instead of 1000 individuals, if the overestimation was by a factor of three the population could be as small as 300 individuals, well below the number generally assumed to be required for long-term viability (Eizirik et al., 2002). Since it will take time to produce reliable density estimates, it might be worth calculating densities for surveys with a reasonable amount of data using the full MMDM or a SECR model and to use that number as a maximum population estimate to evaluate possible changes in conservation priorities. Alternatively, if telemetry data or other estimates of home range sizes are available, one could correct for the polygon size bias by using those data to estimate the spatial parameters necessary for modeling density.

It is time to rethink the way we study jaguars and to focus resources. It is clear that large-scale studies with camera polygons of 500–1000 km^2 and 60–100 or more camera stations are needed. These studies will not only provide use with better density estimates, they will also allow us to confirm some of the simulation results by sub-sampling the data. Ideally at least one such study would be carried out in each of the major ecoregions the jaguar occupies (e.g. tropical moist forest, wet savannas [e.g. Pantanal, Llanos], Chaco, Cerrado, Caatinga) and would be combined with GPS telemetry studies. We understand that the logistic and financial requirements of such studies are large, but using this as an excuse to continue with designs that are known to be flawed will be unproductive and even seriously counterproductive given that inadequate designs primarily produce overly optimistic results. If the requirements for density estimates cannot be met by a project it would be better to use a design that focuses on the presence and distribution of the species, habitat preferences, or on the use of corridors (Zeller et al., 2011). Many important questions can be answered without the need for an absolute density estimate.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2012.12.009.

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Appendix A.

Design parameters and density estimates for camera trap surveys used to estimate jaguar (*Panthera onca*) densities. Densities are based on the Mh model and a buffer of ½ MMDM, which was the method most commonly used. In addition several studies also reported density estimates based on other methods.

[a] Density estimates based on the Mh MMDM method
[b] Density estimates based on a spatially explicate capture-recapture (SECR) model
[c] Approximate density estimate not based on capture-recapture method

Country	*Survey*	*Stations (N)*	*Days*	*Spacing (km)*	*Polygon (km^2)*	*Captures (N)*	*Estimate (N)*	*MMDM (km)*	*Area 1/2 MMDM (km^2)*	*Density ½ MMDM (Ind. 100 km^{-2})*	*Reported density (Ind. 100 km^{-2})*	*Reference*
Argentina	Iguazu 2004	39	45	2	209	4	5±1.41	11.33±2.7	576	1.07±0.33	0.49±0.16[a]	(Paviolo et al. 2008)
Argentina	Iguazu 2006	47	45	2.6	555	11	14±2.45	11.33±2.7	958	1.46±0.34	0.93±0.2[a]	(Paviolo et al. 2008)
Argentina	Urugua-i	34	45	1.25	81	1	-	11.33±2.7	368	0.3[c]	0.12[a]	(Paviolo et al. 2008)
Argentina	Yaboti	42	45	2.43	549	2	-	11.33±2.7	1001	0.2[c]	0.11[a]	(Paviolo et al. 2008)
Belize	Cockcomb basin	20	59	2.5	80	11	14±3.57	3.9±2.36	159	8.8±2.25		(Silver et al. 2004)
Belize	Cockcomb basin				80		-	-	322	11		unknown, in (Maffei et al. 2011)
Belize	Cockcomb basin 2002	20	59	2.5	80	11	14±3.57	3.9±2.36	159	8.8±3.69		(Harmsen 2006)
Belize	Cockcomb basin 2003	19	65	2.5	80	9	10±1.53	5.62±1.04	207	4.82±0.96		(Harmsen 2006)
Belize	Cockcomb basin 2004	19	72	2.5	80	20	35±9.17	4.78±0.88	191	18.29±5.21		(Harmsen 2006)
Belize	Cockcomb basin 2005	19	77	2.5	80	20	21±9.72	4.58±1.08	183	11.45±5.54		(Harmsen 2006)
Belize	Cockcomb basin 2005	17	62		130		-	-		-		(Foster 2008)
Belize	Cockcomb basin 2006	13	62		79		-	-		-		(Foster 2008)
Belize	Cockcomb basin 2007	21	40		165		-	-		-		(Foster 2008)
Belize	Cockcomb basin 2008	44	62		290		-	-		-		(Foster 2008)
Belize	Chiquibul	15	27	2.5	89	7	8±2.51	3.1±1.62	107	7.48±2.74		(Silver et al. 2004)
Belize	Fireburn	16	63	3	55	5	7	5.2	132	5.3±1.76		(Miller 2006)
Belize	Gallon Jug Estate 2004	28	62	2.5	105		15	6.9	195	11.28±2.66		(Miller 2005)
Belize	Gallon Jug Estate 2005	24	62	2.5	95	12	22	5.06	170	8.82±2.27		(Miller 2005)
Belize	Mountain Pine Ridge		80		105		-	-	302	2.32		M. Kelly unpubl. data, in (Maffei et al. 2011)

Belize	Mountain Pine Ridge		64		140		-	-	345	5.35		M. Kelly unpubl. data, in (Maffei et al. 2011)
Bolivia	Cerro Cortado I Kaa-Iya	38	60	1.7	49	7	7±3.01	4.82±2.24	137	5.11±2.1		(Silver et al. 2004)
Bolivia	Cerro Cortado II Kaa-Iya	28	60	2.5	52	7	8	5.62	149	5.37±1.79		(Maffei et al. 2004)
Bolivia	El Encanto	20	60	2	36	4	6	0.97	106	5.66±2.33		(Arispe et al. 2007)
Bolivia	Estacion Isoso I, Kaa-Iya 2005	22	56	3.5	48	4	5±1.59	6.6	158	3.16±1.17		(Maffei et al. 2006)
Bolivia	Estacion Isoso II, Kaa-Iya 2006	20	64	3.5	51	4	6±3.18	5.99	153	3.93±0.27		(Romero-Muñoz et al. 2007)
Bolivia	Guanaco, Kaa-Iya I	16	60	3	49	5	5±0.35	9.2	243	2.05±0.21		(Cuéllar et al. 2004a)
Bolivia	Guanaco, Kaa-Iya II	18	60	3	62	4	4±0.35	6.26	191	2.09±0.45		(Cuéllar et al. 2004b)
Bolivia	Palmar I, Kaa-Iya 2006	23	61	2	72	3	3±0.035	7.6	230	1.32		(Romero-Muñoz et al. 2006)
Bolivia	Palmar II, Kaa-Iya				434		-	-	1058	1.13±0.13		(Montaño et al. 2007)
Bolivia	Ravelo I, Kaa-Iya	36	60	2.5	100	5	7	7.88	309	2.27±0.89		(Maffei et al. 2004)
Bolivia	Ravelo II, Kaa-Iya			2.5	100	5	7	8.2	319	1.57		(Cuéllar et al. 2003)
Bolivia	Rios Tuichi and Hondo, Madidi	66	28	2.5	200	9	13±8.16	7.1±2.8	458	2.84±1.78		(Silver et al. 2004)
Bolivia	Rios Tuichi and Hondo, Madidi	45	30		54		-	1.6	127	-		(Wallace et al. 2003)
Bolivia	Rios Tuichi and Hondo, Madidi	32	29		77		-	-	170	1.68±0.78		(Wallace et al. 2003)
Bolivia	San Miguelito	28	60	1.5	24	5	6±1.54	2.8	54	11		(Rumiz et al. 2003)
Bolivia	San Miguelito	25	60	1.5	54	6	6±1.57	5.1	142	4.23±1.43		(Arispe et al. 2005)
Bolivia	Tucavaca I, Kaa-Iya	32	60	1.7	130	7	7±2.63	5.98±1.78	272	2.57±0.77		(Silver et al. 2004)
Bolivia	Tucavaca II, Kaa-Iya	16	60	2.5	49	4	4	4.6	128	3.1±97		(Maffei et al. 2004)
Brazil	Emas National Park		62	1.5			-	-	500	2		(Silveira 2004)
Brazil	Emas National Park	119	85	3.5	1320	10	-	10	1,750	0.51±0.19	0.29±0.10[b]	(Sollmann et al. 2011)
Brazil	Fazenda Santa Fe				80		-	-	425	2.59±1.03		L. Silveira and N.M. Negrões, in (Maffei et al. 2011)
Brazil	Fazenda Sete 2003	42	20		165	31	37±5.52	6	360	10.3±1.53	5.7±0.84[a]	(Soisalo and Cavalcanti 2006)
Brazil	Fazenda Sete 2004	16	60		110	25	32±5.53	5.8	274	11.7±1.94	5.8±0.97[a]	(Soisalo and Cavalcanti 2006)
Brazil	Moro do Diablo	73	20	6	330	10	13±2.46	13.74	526	2.47±0.46		(Cullen 2006)
Brazil	Serra da Capivara	20	84	2.9	157	12	14±3.643	9.9±3.86	524	2.67±1.06	1.28±0.62[a]	(Silveira et al. 2010)
Colombia	Amacayacu				32		-	-	120	4.2		(Payan 2009)
Colombia	Calderon river valley				70		-	-	242	2.5		(Payan 2009)
Costa Rica	Corcovado	11	30	2.75	29	4	6±1.96	3.48±0.47	86	6.98±2.36		(Salom-Perez et al. 2007)
Costa Rica	Golfo Dulce / Golfito	134	35	1	102	4	5±0.71	9.04	218	2±1.49		(Bustamante 2008)

Costa Rica	San Cristobal	15	43	2.3	50	4	9±11.9	3.48	134	6.7		(Rojas 2006)
Costa Rica	Talamanca	24	30	1.75	85	4	4±0.3	9.2	298	1.34±0.48		(Gutiérez and Porras 2008)
Costa Rica	Talamanca ZPLT (Coton)	10	60	1.5	19	4	5±2.12	5.77	92	5.42±2.3	2.25[a]	(Gonzáles-Maya 2007)
Ecuador	Yasuni-Waorani				94		-	-	218	1.38±0.6		S. Espinoza unpubl. data, in (Maffei et al. 2011)
Ecuador	Yasuni ITT	32	64	2.5	58	4	4±2.62	6	182	2.2		(Araguillin et al. 2010)
French Guiana	Counami Forest	19	90	2.5	60	6	8	-	242	3.3		(Association Kwata 2009)
French Guiana	Montagne de Fer	19	90	2.5	70	9	10	6.63	204	4.9		(Association Kwata 2009)
Guatemala	Carmelita-AFISAP	20	45	2.5	51	10	13±2.6	4.24	115	11.28±3.51		(Moreira et al. 2008a)
Guatemala	La Gloria-Lechugal	33	46	2.5	128	6	6±2.59	7.22	390	1.54±0.85		(Moreira et al. 2007)
Guatemala	Mirador, Oeste	33	47	2	94	7	7±0.82	9.87	351	1.99±1.57	0.9±0.48[a]	(Moreira et al. 2005)
Guatemala	Dos Lagunas Rio Azul	25	47	2.5	39	6	-	5.84	76	11.14±7.45	7.02±6.44[a]	(Moreira et al. 2008b)
Guatemala	Tikal	15	34		39	7	8±3.015	4.52±4.14	121	6.63±2.46	3.39[a]	(García et al. 2006)
Guatemala	Melchor de Mecos	23	45	2	67	9	12±2.63	6.5	199	6.04±1.68	2.91±0.72[a]	(Moreira et al. 2010)
Guatemala	Laguna del Tigre	24	49	2.5	55	9	10±1.23	4.4	158	6.32±1.66	3.73±0.49[a]	(Moreira et al. 2009)
Honduras	La Mosquitia	20	60	0.8	20	5	5	2.87	96	5.2[c]		(Portillo Reyes and Hernández 2011)
Mexico	Sonora	26	60	3.5	100	5	-	-	140	1±1.3[c]		(Rosas-Rosas 2006)
Mexico	San Luis Potosi 2007	13	81	1.5	61	3	3±1.22	-	70	-		(Avila Nájera 2009)
Mexico	San Luis Potosi 2008	27	31	1.5	53	3	5±1.93	5.672	156	3.2±1.9	1.55±1.93[a]	(Avila Nájera 2009)
Panama	Darian	23	35	2.2	67	3	4±5.1	8	213	1.87	0.71[a]	(Moreno 2006)
Panama	Darian	22	50	3.2	110	4	12±5.8	5.7	274	4.38	2.69[a]	(Moreno 2006)
Peru	Los Amigos 2005	24	62	2	56	9	13±3.69	3.987	130	10.1±2.04		(Tobler et al. submitted)
Peru	Los Amigos 2006	40	62	2	56	10	10±2.56	4.521±0.907	141	7.13±2.05	4.5±1.4[b]	(Tobler et al. submitted)
Peru	Los Amigos 2007	40	62	2	56	12	15±2.57	3.343±0.561	114	13.1±2.56	4.0±1.3[b]	(Tobler et al. submitted)
Peru	Bahuaja Sonene, Tambopata	43	62	2	52	6	9±3.56	3.155±0.951	105	8.1±3.6		(Tobler et al. submitted)
Peru	Espinoza	38	122	3	250	26	36±6.26	7.569±1.154	532	6.9±1.3	4.9±1.0[b]	(Tobler et al. submitted)

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Appendix B.

Summary of published home range estimates for the jaguar (*Panthera onca*). MCP: minimum convex polygon, KHR: kernel home range, HM: harmonic mean.

		Female Home Range (km^2)				Male Home Range (km^2)							
Country	Habitat	N	min	max	mean	N	min	max	mean	Estimator	Telemetry	Comments	Reference
Belize	Moist forest	1			11	4	28	40	33	MCP	VHF	females based on tracks	(Rabinowitz and Nottingham 1986)
Brazil	Atlantic forest	5	18	192	92	2	89	471	280	KHR 95%	VHF		(Cullen 2006)
Brazil	Atlantic forest	2	135	289	212	1			299	KHR 95%	VHF		(Cullen 2006)
Brazil	Moist forest	2	8	70	39	7	5	138	57	MCP	VHF	very few locations	(Crawshaw et al. 2004)
Brazil	Pantanal	4	30	83	57	6	72	231	152	MCP 98%	GPS	Wet season	(Cavalcanti and Gese 2009)
Brazil	Pantanal	4	40	97	69	6	73	268	170	MCP 98%	GPS	Dry season	(Cavalcanti and Gese 2009)
Brazil	Pantanal	4	34	89	62	6	83	197	140	KHR 90%	GPS	Wet season	(Cavalcanti and Gese 2009)
Brazil	Pantanal	4	40	87	63	6	73	258	165	KHR 90%	GPS	Dry season	(Cavalcanti and Gese 2009)
Brazil	Pantanal	4	97	168	139	1			152	MCP	VHF		(Crawshaw and Quigley 1991)
Brazil	Pantanal	1			193	3	253	472	337	HM 95%	VHF	Harmonic mean HR	(Silveira 2004)
Brazil	Pantanal				38				67	KHR 95%	VHF		(de Azevedo and Murray 2007)
Brazil	Pantanal	1			34						VHF		(Schaller and Crawshaw 1980)
Mexico	Deciduous dry forest	2			60					MCP?	VHF		(Núñez et al. 2000)
Mexico	Moist forest	2	31	59	45	2	33	40	36		VHF		(Ceballos et al. 2002)
Mexico	Moist forest		122	293			280	970		MCP	GPS		(Conde 2008)
Paraguay	Chaco	2	388	492	440	3	390	1291	692	KHR	GPS	Probably KHR 95%	(McBride 2007)
Paraguay	Pantanal	2	69	72	70					KHR	GPS	Probably KHR 95%	(McBride 2007)
Venezuela	Llanos	1			83	2	93	108	100	KHR 95%	VHF	Dry season	(Scognamillo et al. 2003)
Venezuela	Llanos	2	47	66	56	0				KHR 95%	VHF	Wet season	(Scognamillo et al. 2003)

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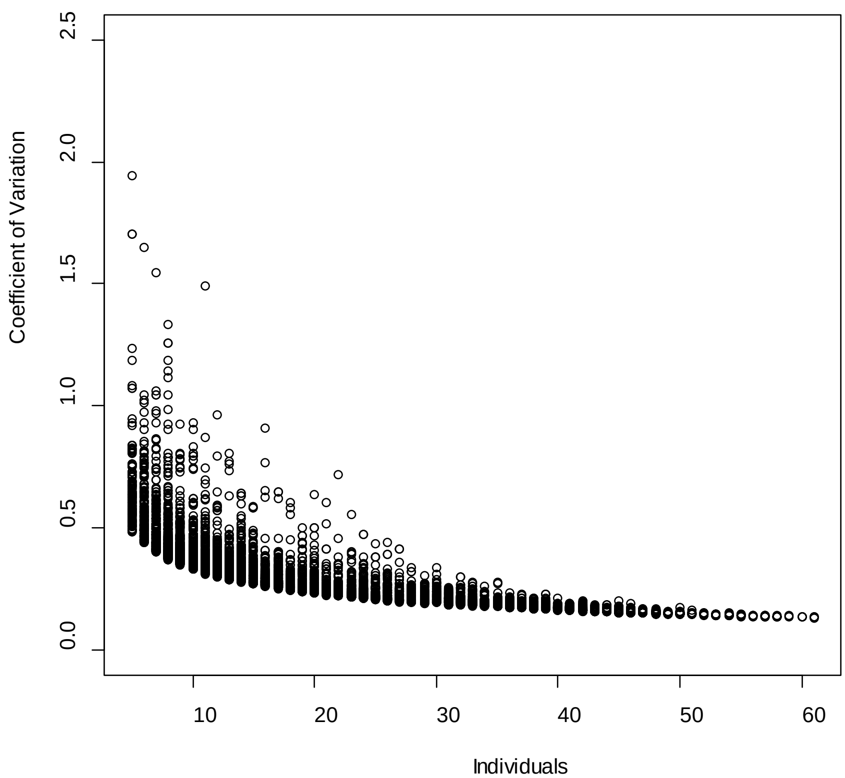
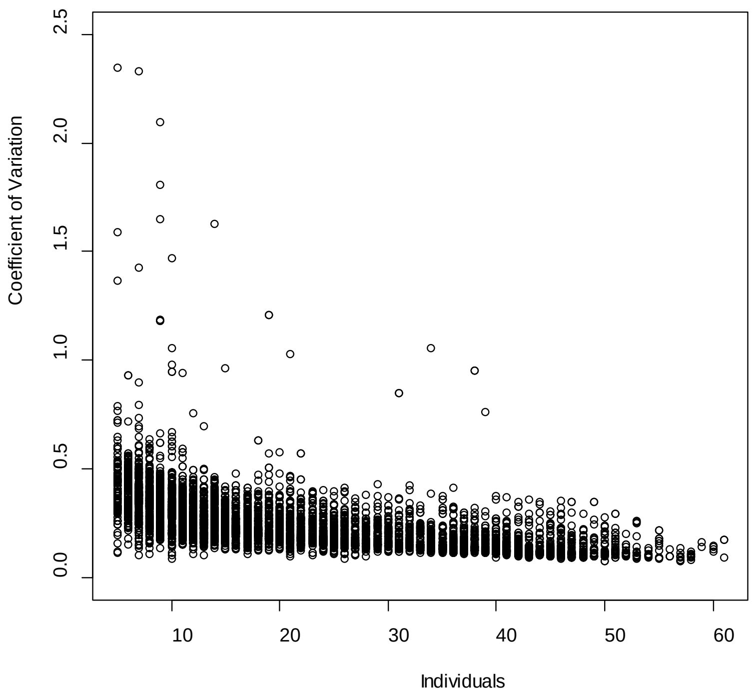
Appendix C.

Additional graphs for different parameter combinations.

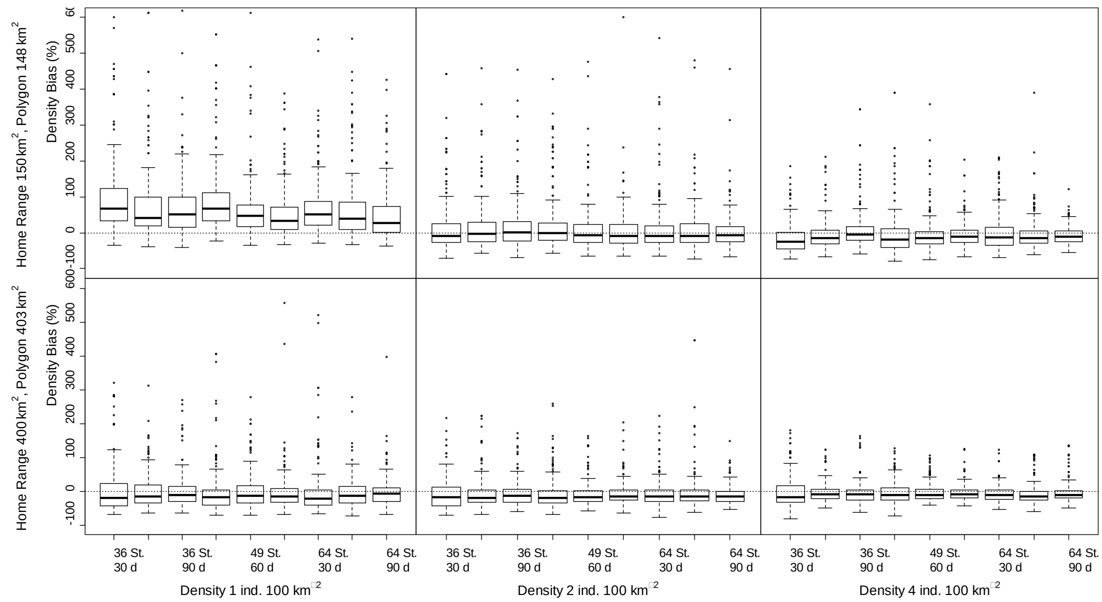
Coefficient of variation of the density (standard error / mean) in relationship to the number of captured individuals for simulated capture-recapture analyzed with a spatially explicit capture-recapture (SECR) model. The data shown combine simulation runs with the following parameters: grid size=403 km^2, λ_0 (0.05,0.1), number of cameras (36,49,64), number of occasions (30, 60, 90), simulated density (1, 2, 4 ind. 100 km^{-2}), home range=400 km^2 (σ=4592).



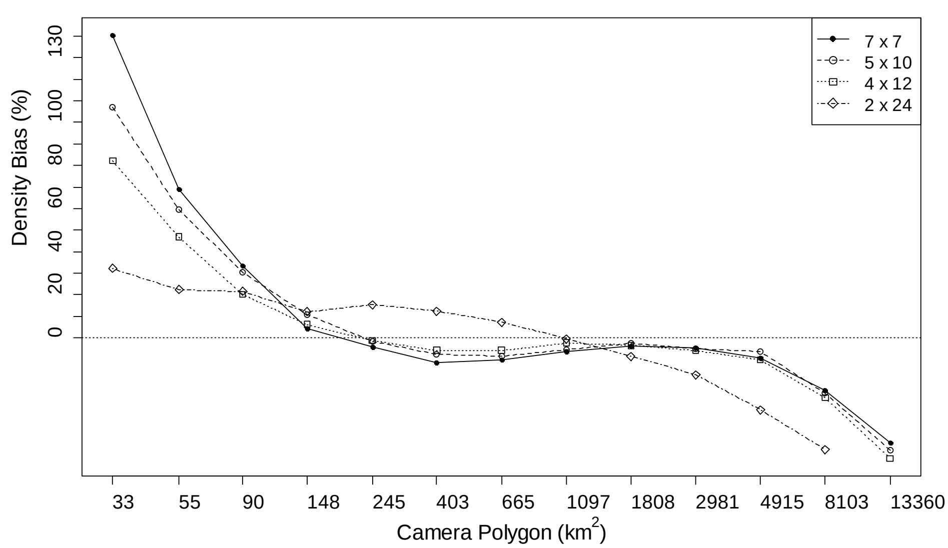
Coefficient of variation of the density (standard error / mean) in relationship to the number of captured individuals for simulated capture-recapture analyzed with the M_h full MMDM method. The data shown combine simulation runs with the following parameters: grid size=403 km^2, λ_0 (0.05,0.1), number of cameras (36,49,64), number of occasions (30, 60, 90), simulated density (1, 2, 4 ind. 100 km^{-2}), home range=400 km^2 (σ=4592).



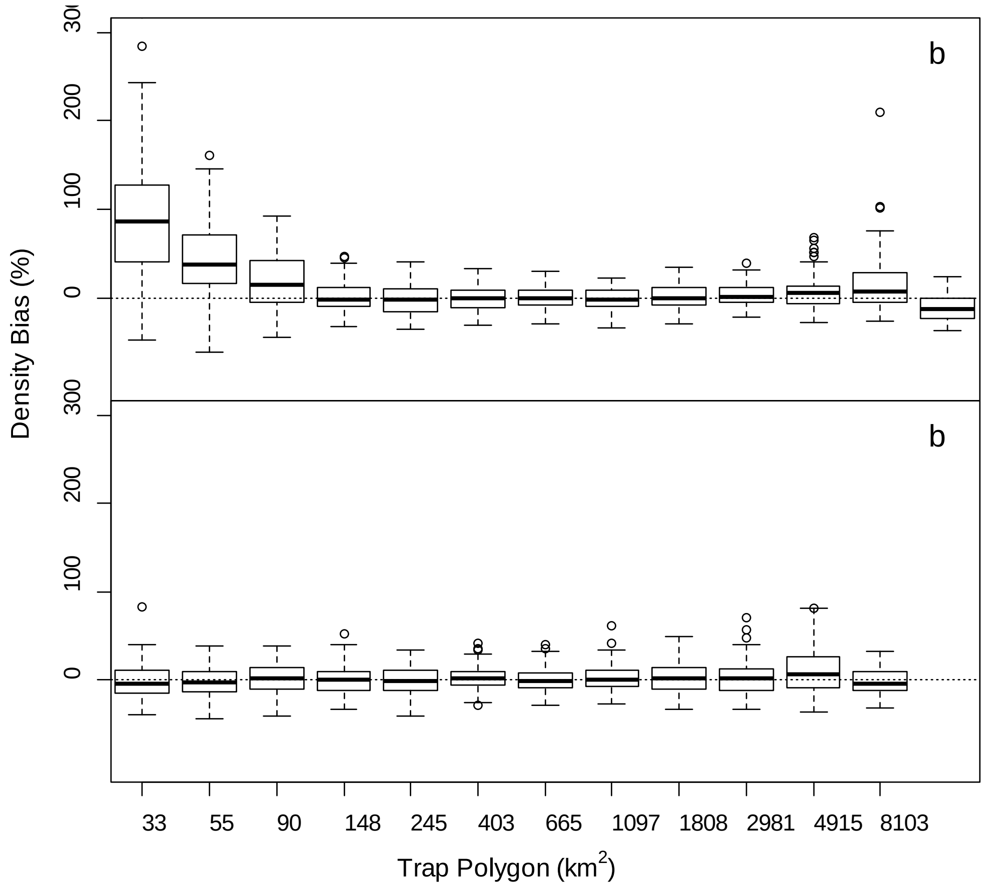
Bias of densities estimated by the M_h full MMDM method in relation to different densities and camera trap survey parameters for simulated jaguar capture-recapture (analog to Figure 4 in the main article). The graph shows the distribution of the bias from 110 simulation runs for each parameter combination. The bottom and top of the box show the 25th and 75th percentiles, respectively, the horizontal line indicates the median and the whiskers show the range of the data except for outlier indicated by circles. St.: camera station.



Mean bias of densities estimated by the M_h full MMDM method in relation to different camera grid shapes for simulated jaguar capture-recapture data (analog to Figure 5 in the main article). The data shown combines simulation runs with the following parameters: λ_0=0.01, home range=400 km^2 (σ=4592), number of occasions=60, simulated density (2, 4).



Bias of densities estimated by a spatially explicit capture-recapture model (SECR) for two different grid shapes (a) 7 x 7 cameras, (b) 3 x 16 cameras. The data shown combines simulation runs with the following parameters: λ_0=0.01, home range=400 km^2 (σ=4592), number of occasions 60, simulated density (2, 4). The bottom and top of the box show the 25th and 75th percentiles, respectively, the horizontal line indicates the median and the whiskers show the range of the data except for outlier indicated by circles.



Correction of bias by small camera polygons by fixing MMDM to the true value for the M_h full MMDM method (analog to Figure 7 in the main article). (a) MMDM estimated by from data and full MMDM used for density etimstes, (b) MMDM set to the true simulated value and ½ MMDM used for density estimates. The following simulation parameters were used: λ_0=0.01, number of cameras=49, number of occasions=60, simulated density (2, 4 ind. 100 km^{-2}), home range=400 km^2 (σ=4592). The bottom and top of the box show the 25th and 75th percentiles, respectively, the horizontal line indicates the median and the whiskers show the range of the data except for outlier indicated by circles.