One or two cameras per station? Monitoring jaguars and other mammals in the Amazon

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6 authors, including:

Carlos Fonseca
University of Aveiro

Eloy Revilla
Estación Biológica de Doñana

Nuno Negrões Soares
University of Aveiro

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ORIGINAL ARTICLE

Nuno Negrões · Rahel Sollmann · Carlos Fonseca
Anah T. A. Jácomo · Eloy Revilla · Leandro Silveira

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Abstract Camera trapping has become a popular technique to monitor carnivore populations due to its usefulness in estimating abundance. Nevertheless, there are a number of problems associated with study design which are motivating researchers to search for a compromise that ensures improvement of precision while being cost-effective. We have used data from a capture–recapture study in a forested area in central Brazil to evaluate the effectiveness of using one versus two cameras per trapping station for determining jaguar (*Panthera onca*) density and capture rates of several other mammals. The capture rate for the jaguar and other species recorded with only one camera was lower than that with two cameras. The number of jaguars identified using photos from one camera ranged between six and seven animals, but reached ten individuals when two-camera sets were used where pictures of both flanks could be positively individualized. These differences, combined with different estimates of effective sampled area size, resulted in jaguar densities estimates ranging from 2.18 to 5.40 and 3.99 individuals/100 km^2 when one and two cameras were used per station, respectively (using the half-MMDM and Heterogeneity model). Based on our results, we recommend the use of two cameras per station for jaguar density monitoring to ensure reasonable levels of reliability and accuracy of estimates despite a small sample size.

Keywords Camera-trapping · Closed mark–recapture models · Population density · *Panthera onca* · Relative abundance

N. Negrões (✉) · C. Fonseca
Center for Environmental and Marine Studies (CESAM) and Biology Department, Aveiro University,
Campus Universitário de Santiago, 3810-193 Aveiro, Portugal
E-mail: nunonegroes@gmail.com
Tel.: +351-277394467
Fax: +351-277394580

N. Negrões · E. Revilla
Department of Conservation Biology, Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas (CSIC), Calle Americo Vespucio s/n, 41092 Seville, Spain

N. Negrões · R. Sollmann · A. T. A. Jácomo · L. Silveira
Jaguar Conservation Fund, Caixa-Postal 193, GO-341 km 84, Zona Rural, Mineiros, GO 75.830-000, Brazil

R. Sollmann
Leibniz Institute for Zoo and Wildlife Research, Alfred-Kowalke-Str. 17, 10315 Berlin, Germany

Introduction

The use of camera trapping to study different aspects of animal ecology has become popular in recent years as an efficient tool to obtain data on rare and cryptic species (Kelly 2008; Rowcliffe and Carbone 2008). Camera trapping is currently a recurrent tool in both conservation biology and ecology, being commonly applied in species surveys, abundance estimations, nest depredation studies, and/or estimates of vital rates (Karanth 1995; Hernandez et al. 1997; Silveira et al. 2003; Trolle 2003; Trolle and Kéry 2005; Johnson et al. 2006; Karanth et al. 2006; Linkie et al. 2006; Dillon and Kelly 2007; Rowcliffe and Carbone 2008; Tobler et al. 2008; Negrões et al. 2011).

One of the most common uses of camera trapping is to determine the relative or absolute density of elusive species (Trolle and Kéry 2005), with the former usually based on photographic capture rates, i.e., number of photos per unit effort (O'Brien et al. 2003), and the latter based on a combination of camera trapping data and closed population capture–recapture modeling (e.g., Karanth and Nichols 1998). To apply such models to camera trapping data, several premises need to be fulfilled: (1) animals must bear individually identifiable marks (spots, stripes, scars, or artificial tags); (2) all animals inhabiting the study area must have a probability >0 of being detected; (3) sampling time should be short relative to the species population dynamics (for large felids about 2 months are suggested) to approximate a closed population; (4) sampling design should maximize capture probability (Karanth and Nichols

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1998, 2002; Stanley and Burnham 1999; Silver et al. 2004; Rowcliffe and Carbone 2008; Negrões et al. 2010; Sarmento et al. 2010).

For optimal individual identification in most species, pictures of both sides of an individual are needed and, therefore, the standard sampling protocol requires setting two camera-traps facing each other at each sampling station (Silver 2004). This considerably increases costs associated with sampling. However, as project resources are generally limited, researchers need to find a compromise that ensures the collection accurate data within economic constraints. A combined strategy that manages both the number of trapping stations and the trapping grid arrangement has been applied to address this issue (e.g., Karanth and Nichols 2002; O'Brien et al. 2003; Dillon and Kelly 2008), but such an approach may not always be feasible depending on the logistics at the study site. To date, no study has investigated the effect of using one versus two camera-traps at each sampling station on abundance and density estimates. Overall, sampling protocols are still open to debate, particularly in terms of trap distance and estimation of the sampled area (Soisalo and Cavalcanti 2006; Dillon and Kelly 2007; Maffei and Noss 2008; Balme et al. 2009), with only a few studies having looked at the consequences of different designs (Harmsen 2006; Dillon and Kelly 2007; Maffei and Noss 2008; Balme et al. 2009).

The jaguar *Panthera onca* (Linnaeus, 1758) is the largest cat in the Americas, with a wide distribution that stretches from the Southwestern USA/Mexico to Northern Argentina. The elusive nature of this species makes it difficult to detect and monitor populations (Rabinowitz and Nottigham 1986). In the last decade, the use of remote triggered photographic cameras has made a strong contribution to the increase in information on jaguar density and biology (Silver 2004; Silver et al. 2004). However, population status remains largely unknown throughout the majority of its range, and the declining status impairs research focused on population dynamics, which forms the basis for conservation guidance (Karanth et al. 2003; Sanderson et al. 2002).

Knowledge of a species' density per se does not provide enough information to evaluate population stability or design conservation policies (Harmsen 2006). Thus, our aim is to establish a long-term monitoring protocol to reliably estimate jaguar density and abundance of other species using camera trapping. To do so, we need to know how the use of one or two camera-traps per sampling station affects: (1) abundance and density estimates for the jaguar and (2) the photographic rates for most common large- and medium-sized species in the study area.

Materials and methods

Study area

The study was carried out at Santa Fé Ranch (SFR 09°34′S, 50°21′W), a 65,000-ha beef cattle ranch in southeastern Pará State (southern border of the Amazon in central Brazil), within the Araguaia River basin. Fieldwork was done in a 35,000-ha continuous patch of semi-deciduous tropical forest bordering the Araguaia River, which constitutes the farm's forest reserve (obligatory by Brazilian legislation). The rest of the farm is occupied by cattle pasture and human infrastructures (houses and offices). The climate presents a strong seasonality, with a characteristic rainy season from October to March (1,700 mm/year on average) and a dry season between April and September.

Camera trapping

The study was conducted from September to November 2007. Sampling consisted of 21 trap stations placed along roads and trails, concentrated within the patch of tropical forest located inside the farm's reserve (Fig. 1). Each trap station location was established following signs of jaguar or prey use in order to increase detection probability (Harmsen et al. 2010). The distance between stations varied from 1.5 to 3.4 km (mean 2.9 km). The minimum home range size of a jaguar is considered to be 10 km^2 (Rabinowitz and Nottigham 1986); therefore, theoretically, this design ensures that all jaguars in the sampled area were to some extent exposed to camera-traps and thus had a probability of capture >0 (Karanth and Nichols 2002; Silver 2004; Silver et al. 2004). Each station consisted of two passive infrared camera-traps (model LeafRiver C1-BU; Vibrashine, Taylorsville, MS) strapped to trees approximately 50–70 cm above the ground (Silver 2004). The cameras were placed on each side of the roads/trails, facing each other with a lateral offset of about half a meter to avoid flash interference between them (Karanth 1995), and were programmed to take photographs 24 h/day with a 5-min interval between consecutive photos. The state of the film and battery was checked on a regular basis (15–20 days) throughout the 80-day survey period. For each sampling station, cameras were assigned to Set 1 or Set 2, with Set 1 representing the first choice location that would have been used if only one camera trap had been available, taking direct sunlight exposition and distance to the path into account.

Photographic rates

For each photograph we recorded the species, number of individuals, date, and hour. For each species we considered consecutive photos as independent records—if taken more than 1 h apart or if different individuals could be identified (O'Brien et al. 2003). We calculated photographic rates [relative abundance indices (RAI)] using the formula of O'Brien et al. (2003):

$$\mathrm{RAI}_i = (g_i \Sigma_j n_{ij} / \Sigma_j \mathrm{tn}_j) \times 100 \qquad (1)$$

where g_i is an average group size for ith species, n_{ij} is the number of independent "detections" for the ith species

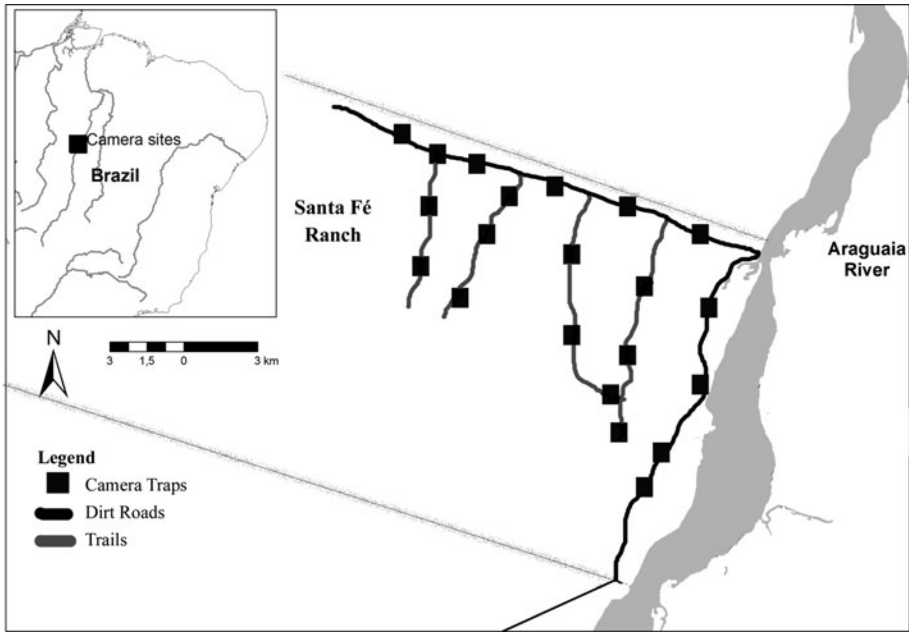

Fig. 1 Study area location on the Araguaia River basin in Brazil and location of the 21 camera trap stations deployed during this study

at the *j*th trap location, and tn_j is the total number of trap-nights at the *j*th trap location (O'Brien et al. 2003; Kawanishi and Sunquist 2004). For further analysis, we only used species of which we obtained ≥5 independent events. We evaluated the differences of using one or two cameras in the estimation of relative abundance of jaguars and other mammals by comparing overall capture rates (RAI) using linear regression. Hypothetically, if RAI results obtained from one camera (both Set 1 or Set 2) and two cameras were similar, they would present a correlation with an intercept estimate of 0 and a slope of 1, while departures from this null prediction will indicate a bias in photographic rates. We performed a Wilcoxon signed-rank test to determine the significance in differences between species RAI obtained using Set 1, Set 2, and both cameras. We also performed Spearman's rank-correlation analysis to evaluate the influence of a species' weight on its capture rate (RAI) (average species weight compiled from IUCN et al. 2008).

Jaguar identification and density estimation

Jaguar numbers were estimated through identifying individuals by their spot patterns in two different ways: (1) for data collected with single camera sets (Set 1 or 2), we identified animals by their left and right flanks separately; (2) for data collected with the double camera set, we pooled data from both cameras and used both flanks simultaneously for individual identification. We divided the sampling period into eight 10-day sampling sessions, and using the individualized photographs we built a total of five capture–recapture histories: (1) two for Sets 1 and 2, each corresponding to right and left flank pictures and (2) one for the double camera set. To estimate jaguar abundance from these capture histories, we followed procedures described by Otis et al. (1978), White et al. (1982), and Karanth and Nichols (1998) using the CAPTURE program (Rexstad and Burnham 1991). This program tests seven models, with each assuming different sources of variation in capture probability *p*, and determines the best fitting model using a series of goodness-of-fit tests followed by a discriminant function analysis (Jackson et al. 2006; Sharma et al. 2010). The simplest model (M_0), also known as the null model, assumes no variation in *p*. The other models are more complex and include the heterogeneity model (M_h), which assumes individual variation in *p*, the time variation model (M_t), the behavior model (M_b), which assumes distinct probabilities for first capture and recaptures, and three combinations of these models (time and behavior; behavior and heterogeneity; time, behavior, and heterogeneity). The M_h model is considered to be the most biologically plausible for large felids because it assumes individual heterogeneity in capture probability (Karanth and Nichols 1998). The program also includes a test for population closure (Rexstad and Burnham 1991).

To translate jaguar abundance into an estimate of density, the effective sampled area needs to be identified. When home range information for the species in the study area is not available, the standard method uses a buffer around the traps whose width corresponds to half the mean maximum distance moved by all individuals captured at least twice (half-MMDM) (Karanth and Nichols 2002; Wallace et al. 2003; Maffei et al. 2004; Silver et al. 2004). Nevertheless, there is some debate on bias associated with this method for estimating sampled area. Based on a combined analysis of data from camera-traps and radio-tracking, some authors consider that half-MMDM could lead to density overestimation; these authors favor the use of full-MMDM (Soisalo and

Table 1 Photographic rate[a] of the main species captured for one (Set 1 and Set 2) and two cameras (Total) during 1,681 trap-nights at Santa Fé Ranch, central Brazil in 2007

Mammals	Set 1	Set 2	Total	Percentage detection by only 1 camera[b]
Tapir, *Tapirus terrestris*	2.74 (0.90)	2.55 (0.92)	3.45 (1,06)	51.9
Gray brocket deer, *Mazama gouazoupira*	0.83 (0.26)	0.77 (0.20)	1.02 (0,27)	56.3
Red brocket deer, *Mazama americana*	3.00 (0.60)	3.13 (0.63)	4.02 (0,72)	55.6
Collared peccary, *Pecari tajacu*	1.72 (0.52)	1.02 (0.29)	2.23 (0,65)	57.1
Crab-eating fox, *Cerdocyon thous*	5.23 (1.75)	3.32 (1.05)	6.89 (2,01)	55.6
Margay, *Leopardus wiedii*	0.13 (0.10)	0.26 (0.14)	0.32 (0,18)	80.0
Ocelot, *Leopardus pardalis*	1.09 (0.36)	1.21 (0.39)	1.40 (0,45)	31.8
Puma, *Puma concolor*	2.17 (0.56)	3.38 (1.20)	4.08 (1,26)	46.7
Jaguar, *Panthera onca*	2.87 (0.75)	3.32 (0.92)	4.08 (1,05)	47.2
Tayra, *Eira barbara*	0.32 (0.15)	0.13 (0.11)	0.38 (0,19)	66.7
South American coati, *Nasua nasua*	0.70 (0.26)	0.57 (0.16)	0.89 (0,23)	71.4
Azara's agouti, *Dasyprocta azarae*	0.77 (0.34)	0.45 (0.16)	0.96 (0,40)	60.0
Capybara, *Hydrochaeris hydrochaeris*	0.38 (0.16)	0.45 (0.20)	0.45 (0,20)	14.3
Giant armadillo, *Priodontes maximus*	0.19 (0.09)	0.19 (0.10)	0.32 (0,12)	80.0
Nine-banded armadillo, *Dasypus novemcinctus*	0.26 (0.14)	0.38 (0.17)	0.51 (0,21)	87.5

Data are presented at the mean photographic rate (RAI), with the standard error (SE) given in parenthesis
[a]Relative abundance indices (RAI) were calculated from the photographic rate
[b]The percentage of species detection that triggered only one of the two cameras of the trap station

Cavalcanti 2006; Dillon and Kelly 2008), while others suggest the opposite (Balme et al. 2009). Consequently, and for comparison reasons, both full-MMDM and half-MMDM (using data from all recapture individuals within each capture history) have been computed to calculate the effective sampled area (Karanth and Nichols 2002; Silver 2004; Soisalo and Cavalcanti 2006; Salom-Pérez et al. 2007; Balme et al. 2009).

We used logistic regression to evaluate the probability that any new jaguar photo was from a known (response variable = 0) or unknown individual (response variable = 1) as a function of the sampling event (defined by the eight 10-day consecutive sampling sessions). We assessed model fit using likelihood ratio test statistics (Hosmer and Lemeshow 2000). Non-parametric statistics were performed employing R v.8.2 free statistical software, while linear and logistic regressions were executed using SigmaPlot 11.0 (Systat Software, San Jose, CA).

Results

Photographic rates

During a sampling effort of 1,680 camera-nights we obtained a total of 3,619 photographs; of these, species of interest, including mammals ($N = 505$), birds ($N = 215$), and reptiles ($N = 1$) could be positively identified on 724 photographs. There were three photos of domestic animals that were not considered in the analysis. The crab-eating fox (*Cerdocyon thous*) was the most frequently photographed species, followed by the jaguar and the puma (*Puma concolor*) (both with RAI = 4.08) (Table 1). Among the other species, the red brocket deer (*Mazama americana*) and the tapir (*Tapirus terrestris*) presented the highest photographic capture indexes (Table 1). Rates obtained with only one camera (either Set 1 or 2) did not differ between sets ($z = 0.42$, $p = 0.6373$; Fig. 2), showing that our a priori identification of Set 1 as the most favorable side of the station was unjustified. However, we consistently obtained higher rates using two cameras per station (Table 1, Fig. 2), with overall rates of 1.45 ± 0.05 [standard error (SE)] and 2.05 ± 0.13 for sets with 1 and 2 cameras, respectively. The differences were significant (Set 1 vs. Total $z = -3.30$, $p = 0.0007$; Set 2 vs. Total $z = -3.28$, $p = 0.0011$). On average, there was an increase of 29% in photographic rate when two cameras were used, and for the majority of the species, more 50% of the detections resulted from the triggering of only one camera of the set (Table 1). No correlation was found between RAI and mean species weight ($r_s = 0.476$, $p = 0.073$, $N = 15$).

Jaguar identification and abundance

We obtained a total of 64 individual jaguar photos (considering photos of the same jaguar taken simultaneously by both cameras of the set as one photo), but in 47.2% of the cases only one of the two cameras per set registered the passing individual. A jaguar's full body extension was captured in only 45.7% of the photos, while 22.8% revealed the animal's body except for the head. Only the posterior three-quarters of the body was visible in 16.3% of the photos, and only the tail was photographed in 13% of the photos. The remaining photos (2.2%) showed frontal or posterior views of the animal.

The number of jaguars identified using only one camera per station varied from six to seven animals (Set 1 or Set 2); this reached ten individuals when two opposingly placed cameras were used (Table 2).

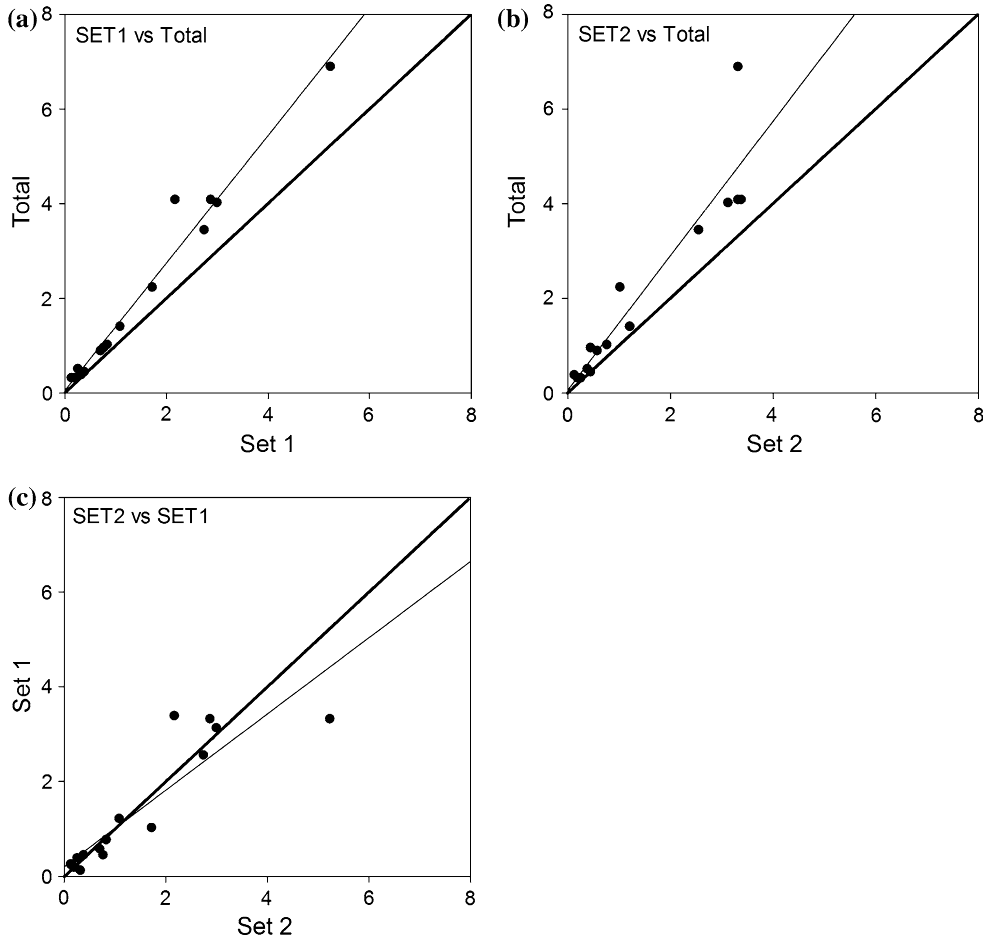

Fig. 2 Cross-species comparison of overall photographic rates (records/100 trap-nights) using one camera (*SET 1*, *SET 2*) and both cameras (*Total*) per station. *Thin line* Regression of the photographic rates of the different sets, *thick line* expected regression if both estimate similar rates (i.e., $a = 1$)

For all single-camera set analyses, CAPTURE selected the null model (M_0) as the most suitable, followed by the heterogeneity model (M_h) (Table 2). There were considerable differences in the estimates of jaguar abundance between these models, particularly in Set 1, where values obtained for M_h ($N = 15$–22) were up to threefold higher than estimates by M_0 ($N = 6$–7). Estimates of capture probability (*p*-hat) varied from 0.080 to 0.438 (Table 2) and, consequently, generally lay above the threshold of 0.1 required for reliable estimates of population size (White et al. 1982). *p*-hat was also consistently higher for the M_0 model when compared to M_h. For the two cameras per station, CAPTURE selected the M_{bh} model as the most suitable, followed by the M_h model, but both presented the same abundance estimates ($N = 12$) (Table 2). Capture–recapture analysis fail to produce captures probabilities for M_{bh} models due to the absence of new capture on sampling occasion 2. CAPTURE did not indicate any violation of the closure assumption for any of capture–recapture histories.

The estimates of the buffer strip width did not differ significantly when using 1 (average MMDM 12 ± 4.06 km) or two cameras (MMDM 11.4 ± 4.01 km) (Kruskal–Wallis $K = 4.585$, $p = 0.3326$ for all sets; Kruskal–Wallis $K = 4.144$, $p = 0.2463$ for comparison between single-camera sets) (Table 3). Nevertheless, when applied to the estimates of effective sampled area, there were considerable differences in sampled area, varying from 529 to 1,065 km^2 for one camera per set (mean 777.3 km^2) and a mean of 753 km^2 for the two cameras per set.

The differences in the estimates of jaguar abundance and sampled area resulted in different density estimates for the different camera sets (Table 3). The null model generated a lower density estimate for single-camera sets, with values ranging from 1.72 to 3.26 jaguars/100 km^2 for half-MMDM (0.66–1.32 jaguars/100 km^2 for full MMDM) compared to 3.35 jaguars/100 km^2 (vs. 1.33 jaguars/100 km^2 for full-MMDM) for the two cameras per set. In contrast, the heterogeneity model in most cases generated a higher density estimate for one camera per station, with values ranging from 2.18 to 5.40 jaguars/100 km^2 for half-MMDM (vs. 0.86–2.13 jaguars/100 km^2 for full-MMDM) compared to 3.99 jaguars/100 km^2 (vs. 1.59 jaguars/100 km^2 for

Table 2 CAPTURE[a] results for the population closure test, model selection, capture probabilities, and estimated abundance of jaguar for one and two cameras per station in the Santa Fé Ranch forest reserve (central Brazil), 2007

Camera	Side	N_{jag}	Test for closure		Model selection rankings[b]				Population estimates[b]					
									Null model (M_0)		Heterogeneity model (M_h)		Heterogeneity and behavior model (M_{bh})	
			z	p	M_0	M_h	M_b	M_{bh}	p-hat	N ± SE (95% CI)	p-hat	N ± SE (95% CI)	p-hat	N ± SE (95% CI)
Set 1: 1 camera per station	Right	7	1.311	0.905	1.00	0.90	0.36	0.64	0.238	7 ± 1.176 (7–14)	0.080	22 ± 8.481 (13–48)	Not computed	Not computed
	Left	6	−0.422	0.337	1.00	0.89	0.30	0.58	0.313	6 ± 0.624 (6–6)	0.125	15 ± 5.086 (10–31)	Not computed	Not computed
Set 2: 1 camera per station	Right	7	0.829	0.796	1.00	0.80	0.16	0.57	0.339	7 ± 0.559 (7–7)	0.264	9 ± 1.897 (8–16)	Not computed	Not computed
	Left	7	0.418	0.662	1.00	0.90	0.22	0.57	0.339	7 ± 0.559 (7–7)	0.339	7 ± 2.412 (7–20)	Not computed	Not computed
Total: two cameras per station	-	10	−1.030	0.151	0.74	0.98	0.86	1.00	0.438	10 ± 0.329 (10–10)	0.365	12 ± 3.200 (11–29)	Not computed	12 ± 3.170 (11–29)

N_{jag}, Number of jaguars identified; CI, confidence interval; p-hat, capture probability; N, estimated abundance

[a]CAPTURE program (Rexstad and Burnham 1991): tests seven models, with each assuming different sources of variation in capture probability p, and determines the best fitting model using a series of goodness-of-fit tests followed by a discriminant function analysis

[b]M_0, null model, which assumes no variation in capture probability between individuals over time; M_h, the heterogeneity model, which assumes individual variation in capture probability; M_b, the behaviour model, which assumes distinct probabilities for first capture and recaptures; M_{bh}, the behavior and heterogeneity model

Table 3 Jaguar density for the different CAPTURE models for abundance estimation on the Santa Fé ranch, 2007, based on one and two cameras per station

Camera	Side	MMDM (km) ± SE	Sampled area (km^2)		Estimated density (per 100 km^2) ± SE					
					Null model (M_0)		Heterogeneity model (M_h)		Heterogeneity and behavior model (M_{bh})	
			MMDM	Half-MMDM	MMDM	Half-MMDM	MMDM	Half-MMDM	MMDM	Half-MMDM
Set 1: 1 camera per station	Right	14.39 ± 2.05	1,065	408	0.66 ± 0.28	1.72 ± 0.61	2.01 ± 1.13	5.40 ± 2.67		
	Left	10.88 ± 1.82	704	283	0.85 ± 0.42	2.12 ± 0.842	2.13 ± 1.26	5.30 ± 2.71		
Set 2: 1 camera per station	Right	8.76 ± 2.29	529	215	1.32 ± 1.05	3.26 ± 2.03	1.70 ± 1.39	4.19 ± 3.73		
	Left	12.00 ± 1.95	811	322	0.86 ± 0.42	2.18 ± 0.86	0.86 ± 0.51	2.18 ± 1.13		
Total: 2 cameras per station	-	11.40 ± 1.63	753	301	1.33 ± 0.70	3.35 ± 1.36	1.59 ± 0.94	3.99 ± 1.95	1.59 ± 0.93	3.99 ± 1.94

MMDM mean maximum distance moved

full-MMDM) computed for two cameras per set. This last estimate for two cameras per station matched the density computed for the M_{bh} model.

As expected, the probability that a jaguar photo was from a new unknown individual previously undetected decreased with the sampling event, from a maximum of around 0.6 down to a non-negligible 0.1 during the last sampling event (likelihood-ratio test 5.94, $p = 0.015$ rejects the null model of no effect, Wald $\chi^2 = 5.1$; $p = 0.024$ for the parameter estimate; Fig. 2).

Discussion

Although camera-trap studies designed for specific target species are unlikely to supply a complete inventory of medium- to large-sized mammals, this study design can be used for monitoring purposes and for providing information on which to base conservation actions (Ahumada et al. 2011; Gray and Phan 2011). Species detection by camera-trapping can be influenced by several factors in addition to abundance, namely, species size/body mass, characteristics of the camera model, environmental conditions, and species behavior (e.g., speed) among others (Rowcliffe et al. 2011). Some of these factors were not evaluated within the scope of this study, which limits the conclusions that can be drawn to only a comparison of the efficiency one versus two cameras per camera location. Photographic rates of jaguars and other species were significantly lower when one camera was used per station than when two cameras were used per station. These results are intuitive, since by placing two cameras per station we increased the probability of photographing an animal passing the station. When both cameras of a given station were compared, there were no considerable differences in the outcome from each individual camera, since both presented the same technical characteristics, similar spatial position relative to the road/trail, and equivalent environmental conditions. The number of false events (pictures without animals) was twofold higher than the number of pictures with animals and could mostly be attributed to sun/heat exposition or human passage. However, a considerable number of false events (about 10% of total photos) could be attributed to slow trigger response. These were characterized by being night photos without any sign of what could have caused the picture to be taken other than a passing animal that at the moment of trigger had already left the camera's range. The fact that only half the jaguar photos were shot simultaneously by both cameras of the set and that 10% of these photos caught only the tail again highlights the influence of trigger speed and possible camera detection failure on the results. With a faster and more reliable camera model, it is well possible that results from one versus two cameras per station would not have been as different as we experienced in this study. A number of variables need to be controlled in order to compare species RAI between places and time, particularly those associated with camera detection ability. Further information on species behavior (e.g., speed) and estimation of the detection zone for each camera model under specific conditions are required to improve further comparisons (Rowcliffe et al. 2011).

The two main components that affect the final density estimate, namely, abundance and sampled area, must be evaluated in order to establish an efficient camera-trapping protocol for jaguar population monitoring. Estimates of abundance are affected by the capacity to distinguish individuals and, using capture–recapture analysis, the effectiveness in computing quantitative unbiased estimates that reflect the true population size (Karanth and Nichols 1998). Model selection by CAPTURE is known to lack power when sample sizes and capture probabilities are low (Otis et al. 1978; Pollock et al. 1990). Although the null model (M_0) is considered to be unrealistic for carnivore species because it does not account for any variation in capture probability—a situation that is almost never true in a field study—and because it can underestimate true density (Karanth and Nichols 1998), it has been ranked as the best model for all analyses except for the two-camera set. Alternatively, the Jackknife population estimator accounting for individual heterogeneity in p (M_h) is considered to be a more robust model, but it does not provide an adequate estimation if only few animals are recaptured (Otis et al. 1978; Boulanger et al. 2004), which was the case in our study for all single-camera set analyses. A clear advantage of using two simultaneous cameras in our study was the higher detection probability and, more importantly, an increased capacity to identify individuals by obtaining photographs of both flanks that allowed a more solid capture–recapture history to be built. The use of one camera per station represented an overall reduction of 30–40% in the number of individual jaguars identified ($N = 10$ for 2 cameras and $N = 6$ or 7 for 1 camera set). Also, by incorporating more photos into the capture–recapture history, researchers can use data more efficiently, resulting in a higher number of detected individuals for use in further analyses. Thereby, sources of unreliability (low captures rates and extreme levels of heterogeneity) can be reduced (Menkens and Anderson 1988; Harmsen 2006). In our study, one camera per station supplied a lower number of capture events and increased the number of individuals captured only once (i.e., decreased recaptures) when compared with the two-camera station. The fact that a 10% probability of a jaguar not being detected during sampling remained even with two cameras per set underlines the importance of using models that account for imperfect detection, rather that using mere count statistics (Fig. 3). This is even more important if we consider that this probability can be underestimated, since the logistic regression is conditioned on the number of animals detected and not on all animals present in the population.

The test for population closure included in CAPTURE is not considered to be statistically robust

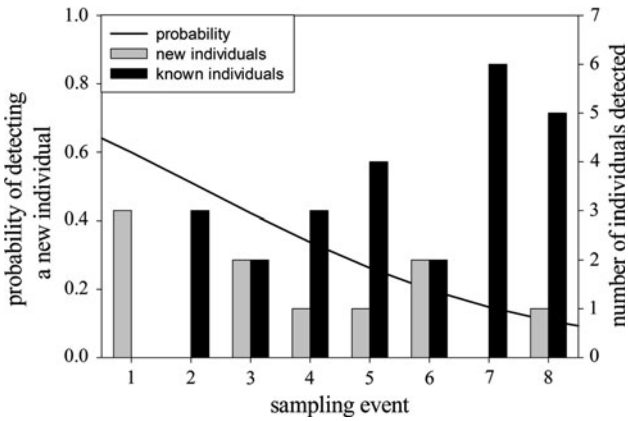

Fig. 3 Probability of capturing new unknown individuals as a function of the sampling event (*left y*-axis) and the number of new (*grey bar*) and known (*black bar*) individual jaguars detected in each sampling event (*right y*-axis)

(Rexstad and Burnham 1991), and although an alternative test does exist (CloseTest program provided by Stanley and Burnham 1999), it is generally agreed that closure should best be approximated and judged on a biological basis (Otis et al. 1978). We believe that 2 months is a proper survey length for the jaguar to meet this assumption, even more so since we only consider adult individuals in our analysis. However, we do acknowledge the lack of data on territorial and spatial behavior that could support this assumption.

The standard approach of estimating a sampled area is an ad hoc method that is open to debate due to a lack of theoretical background—more specifically, its relation to territory and home range size (Royle et al. 2009). According to Maffei and Noss (2008), the area covered by traps should include an area that is more than fourfold larger than the size of the average home range of the species in question. The lack of data on jaguar home range in our study area impairs any evaluation of the effectiveness of our sampling design and our reliability in terms of sampled area estimates. The variation that can be observed in our sampled area estimates is directly associated with differences in maximum distance moved (MDM), which in turn depends on the distance between the cameras and recaptured animals. Since camera position is the same, differences in the results of single- versus two-camera sets are a consequence of limitations in individualizing jaguar pictures in the single-camera sets and, consequently, in observing recaptures. This decrease in the probability of recapturing individuals increases the bias in the estimates. The relatively recent development of new spatially explicit capture–recapture analysis allows effective sampled area to be estimated using observed spatial encounter history data and can potentially be explored to overcome the conceptual limitation of the traditional closed population estimators (Borchers and Efford 2008; Gardner et al. 2009; Obbard et al. 2009; Royle et al. 2009).

In addition to differences in estimates of sampled area, jaguar density estimates based on data from one or two cameras per station were influenced by different estimates of abundance, which were further influenced by the model (M_0, M_h, M_{bh}) used (Tables 2, 3; Fig. 3). While the null model (M_0) estimates can be considered to be conservative, densities obtained for one camera per station using the Jackknife estimator (M_h) were revealed to be unrealistically high and probably to overestimate abundance (Harmsen 2006). These differences in density estimates are relevant for monitoring programs, since they affect the capacity to correctly characterize a population's status and detect annual trends, especially when populations are present at low densities (Balme et al. 2009).

Although any comparison of the results from this study with other jaguar densities estimates should take into account differences in methodology, a pattern can be discussed using the premises that have been observed in the majority of published data (that is, using data pooled from two camera sets and estimates from the M_h model and half-MMDM). With an estimate of four jaguars/100 km^2, the jaguar density in our study area is somewhat intermediate between that of tropical forest areas [e.g., 7.48–8.80 jaguars/100 km^2 in Belize (Silver et al. 2004); 6.98 jaguars/100 km^2 in Costa Rica (Salom-Pérez et al. 2007); 3.41–5.11 jaguars/100 km^2 in Bolivia (Maffei et al. 2004)] and dryer regions [2.67 jaguars/100 km^2 for Brazilian Caatinga (Silveira et al. 2009); 2.00 jaguars/100 km^2 for Brazilian savannahs (Silveira 2004). Although our study location was a forest environment, jaguar densities in the Atlantic forest of Brazil and Argentina are lower than that determined in our study (0.2–2.22 jaguars/100 km^2; Cullen et al. 2005; Paviolo et al. 2008), possibly because the biome is much more degraded and fragmented (Sollmann et al. 2008). In some regions of the open seasonally flooded plains of the Pantanal, jaguar densities are comparable to or even higher than those in tropical forests (10.3–11.7 jaguars/100 km^2; Soisalo and Cavalcanti 2006), probably due to the abundant mammal fauna (Astete et al. 2008). The availability of prey is considered to be an important limiting factor for the species and could explain density variation, but in order to confirm this hypothesis further research combining information on jaguar and prey species abundance is needed (Maffei et al. 2004; Salom-Pérez et al. 2007).

In conclusion, the use of one camera per station can be a useful approach in estimating relative abundance—if the consequent decrease in detection probability is acknowledged. The use of two camera-traps at selected stations to calibrate the error of single-camera sets may be an approach to guarantee the comparability of data from single- versus two-camera sets. In all other cases, such as when we intend to apply mark–recapture models to obtain actual accurate density estimates, the use of two cameras per station should be preferred. The increase in data available for analysis and the resulting improved model choice and reliability of parameter estimates are especially important when dealing with a rare and cryptic species that will almost inevitably yield a low sample size, even with the best sampling design possible. When designing a study, researchers should locate stations on roads and well-established open trails (Harmsen et al. 2010). When available, site-specific information on jaguar home range size should be considered for deciding on the spacing of cameras, and a uniform sampling design should be established that allows possible exploration of a new spatially explicit capture–recapture analysis as an alternative to the traditional one (Royle et al. 2009).

Camera-trapping, although limited by various methodological constraints, has proved to be a useful tool for accessing the density of several large carnivore species; as such, it has provided valuable data that have been used to evaluate the success of conservation efforts and human impact on natural populations. However, small datasets, which are likely to arise from sampling rare and cryptic species, can cause erroneous model selection for the estimation of abundance, as well as lead to biased estimates of spatial parameters (here the MDM). Both aspects largely influence the final density estimate. Further, insufficient data can lead to estimates that lack the reliability needed for management decisions or biological inference. Here, we show that for the jaguar, which is a species of conservation concern, the use of two camera traps per sampling station has clear advantages over the use of single-camera stations and that the former should be used whenever possible to achieve reasonable levels of reliability in parameter estimates. Additional studies should be performed to further optimize this method, particularly in the setting of spatially explicit capture–recapture approaches that could overcome standard methodological constraints.

The Brazilian Amazon basin is suffering from increased human pressure due to deforestation, which is especially evident at the southern border of the Amazon, where it merges with the Cerrado savannahs—an area called the arc of deforestation. Here, the agricultural frontier is moving into the Amazon forest, leaving the landscape extremely fragmented. Although the establishment of protected areas (PA) has increased in recent years (Schulman et al. 2007), these may not be enough to secure jaguar population dynamics at a larger scale. The importance of private forest reserves for landscape-scale jaguar conservation is highlighted by our results, given that they can sustain considerable densities of this species, and others. Especially in the context of fragmentation, these reserves can also play an important role in landscape connectivity when considering a meta-population structure for the jaguar. Understanding this species' population status and landscape use, not only inside PA, is essential in order to establish national and regional management plans.

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References

Ahumada JA, Silva CEF, Gajapersad K, Hallam C, Hurtado J, Martin E, McWilliam A, Mugerwa B, O'Brien TG, Rovero F, Sheil D, Spironello WR, Winarni N, Andelman SJ (2011) Community structure and diversity of tropical forest mammals: data from a global camera trap network. Philos Trans R Soc B 366:2703–2711

Astete S, Sollmann R, Silveira L (2008) Comparative jaguar ecology in Brazil. Cat News 4:9–14

Balme GA, Hunter LTB, Slotow R (2009) Evaluating methods for counting cryptic carnivores. J Wildl Manag 73:433–441

Borchers DL, Efford MG (2008) Spatially explicit maximum likelihood methods for capture–recapture studies. Biometrics 64:377–385

Boulanger J, Stenhouse G, Munro R (2004) Sources of heterogeneity bias when DNA mark-recapture sampling methods are applied to grizzly bear (*Ursus arctos*) populations. J Mammal 85:618–624

Cullen L Jr, Abreu KC, Sana D, Nava AFD (2005) Jaguars as landscape detectives for the upper Paraná River corridor, Brazil. Natureza e Conservação 3:147–161

Dillon A, Kelly MJ (2007) Ocelot *Leopardus pardalis* in Belize: the impact of trap spacing and distance moved on density estimates. Oryx 41:469–477

Dillon A, Kelly MJ (2008) Ocelot home range, overlap and density: comparing radio telemetry with camera trapping. J Zool 275:391–398

Gardner B, Royle JA, Wegan MT (2009) Hierarchical models for estimating density from DNA mark–recapture studies. Ecology 90:1106–1115

Gray TNE, Phan C (2011) Habit preferences and activity patterns of the larger mammal community in Phnom Prich Wildlife Sanctuary, Cambodia. Raffles Bull Zool 59:311–318

Harmsen BJ (2006) The use of camera traps for estimating abundance and studying the ecology of jaguars (*Panthera onca*). PhD dissertation, University of Southampton, Southhampton

Harmsen BJ, Foster RJ, Silver S, Ostro L, Doncaster CP (2010) Differential use of trails by forest mammals and the implications for camera-trap studies: a case study from Belize. Biotropica 42:126–133

Hernandez F, Rollins D, Cantu R (1997) An evaluation of Trailmaster camera systems for identifying ground-nest predators. Wildl Soc Bull 25:848–853

Hosmer DW, Lemeshow S (2000) Applied logistic regression. Wiley, New York

IUCN, Conservation International, Arizona State University, Texas A & M University, University of Rome, University of Virginia, Zoological Society London (2008) An analysis of mammals on the 2008 IUCN Red List. http://www.iucnredlist.org/mammals. Downloaded on 9 October 2008

Jackson RM, Roe JD, Wangchuk R, Hunter DO (2006) Estimating snow leopard population abundances using photography and capture–recapture techniques. Wildl Soc Bull 34:772–781

Johnson A, Vongkhamheng C, Hedemark M, Saithongdam T (2006) Effects of human–carnivore conflict on tiger (*Panthera tigris*) and prey population in Lao PDR. Anim Conserv 9:421–430

Karanth KU (1995) Estimating tiger *Panthera tigris* populations from camera-trap data using capture–recapture models. Biol Conserv 71:333–338

Karanth KU, Nichols JD (1998) Estimating tiger (*Panthera tigris*) populations form camera-trap data using capture–recaptures. Ecology 79:2852–2862

Karanth KU, Nichols JD (2002) Monitoring tigers and their prey. A manual for researchers, managers and conservationists in tropical Asia. Center for Wildlife Studies, Bangalore

Karanth KU, Nichols JD, Seidensticker J, Dinerstein E, Smith JLD, McDougal C, Johnsingh AJT, Chundawat RS, Thapar V (2003) Science deficiency in conservation in practice: the monitoring of tiger populations in India. Anim Conserv 6:141–146

Karanth KU, Nichols JD, Kumar NS, Hines JE (2006) Assessing tiger population dynamics using photographic capture–recapture sampling. Ecology 87:2925–2937

Kawanishi K, Sunquist ME (2004) Conservation status of tigers in a primary rainforest of Peninsular Malaysia. Biol Conserv 120:329–344

Kelly MJ (2008) Design, evaluate, refine: camera trap studies for elusive species. Anim Conserv 11:182–184

Linkie M, Chapron G, Martyr DJ, Holden J, Leader-Williams N (2006) Assessing the viability of tiger sub-populations in a fragmented landscape. J Appl Ecol 43:576–586

Maffei L, Noss AJ (2008) How small is too small? Camera trap survey areas and density estimates for ocelots in the Bolivian Chaco. Biotropica 40:71–75

Maffei L, Cuellar E, Noss AJ (2004) One thousand jaguars (*Panthera onca*) in Bolivian Chaco? Camera trapping in the Kaa-Iya National Park. J Zool 262:295–304

Menkens GE, Anderson SH (1988) Estimation of small-mammal population size. Ecology 69:1952–1959

Negrões N, Sarmento P, Cruz J, Eira C, Revilla E, Fonseca C, Sollmann R, Tôrres NM, Furtado MM, Jácomo ATA, Silveira L (2010) The use of camera trapping to estimate puma (*Puma concolor*) density and influencing factors in a forest habitat of Central Brazil. J Wildl Manag 74(6):1195–1203

Negrões N, Revilla E, Fonseca C, Soares AMVM, Jácomo ATA, Silveira L (2011) Private forest reserves can aid in preserving the community of medium and large-sized vertebrates in the Amazon arc of deforestation. Biodivers Conserv 20:505–518

O′Brien T, Kinnard MF, Wibisono HT (2003) Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. Anim Conserv 6:131–139

Obbard ME, Howe EJ, Kyle CJ (2009) Empirical comparison of density estimators for large carnivores. J Appl Ecol 47:76–84

Otis DL, Burnham KP, White GC, Anderson DR (1978) Statistical inference from capture data on close population. Wildl Monogr 62:1–135

Paviolo A, De Angelo CD, Di Blanco YE, Di Bitetti MS (2008) Jaguar *Panthera onca* population decline in the Upper Paraná Atlantic Forest of Argentina and Brazil. Oryx 42:554–561

Pollock KH, Nichols JD, Brownie C, Hines JE (1990) Statistical inference for capture–recapture experiments. Wildl Monogr 107:1–97

Rabinowitz AR Jr, Nottigham BG (1986) Ecology and behaviour of the jaguar (*Panthera onca*) in Belize, Central America. J Zool 210:149–159

Rexstad E, Burnham KP (1991) User's guide for interpretative program CAPTURE. Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins

Rowcliffe JM, Carbone C (2008) Surveys using camera traps: are we looking to a brighter future? Anim Conserv 11:185–186

Rowcliffe JM, Carbone C, Jansen PA, Kays R, Kranstauber B (2011) Quantifying the sensitivity of camera traps: an adapted distance sampling approach. Methods Ecol Evol 2:464–476

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

Salom-Pérez R, Carrillo E, Sáens JC, Mora M (2007) Critical condition of the jaguar in Corcovado National Park, Costa Rica. Oryx 41:51–56

Sanderson EW, Redford RH, Chetkiewicz CB, Medellin R, Rabinowitz A, Robinson J, Taber A (2002) Planning to save a species: the jaguar as a model. Conserv Biol 16:58–72

Sarmento P, Cruz J, Eira C, Fonseca C (2010) Habitat selection and abundance of common genets *Genetta genetta* using camera capture–mark–recapture data. Eur J Wildl Res 56:59–66

Schulman L, Ruokolainen K, Junikka L, Saaksjarvi IE, Salo M, Juvonen S-K, Salo J, Higgins M (2007) Amazonian biodiversity and protected areas: do they meet? Biodivers Conserv 16:3011–3051

Sharma RK, Jhala Y, Quershi Q, Vattakaven J, Gopal R, Noyak K (2010) Evaluating capture–recapture population and density estimation of tigers in a population with known parameters. Anim Conserv 13:94–101

Silveira L (2004) Ecologia comparada e conservação da onça-pintada (*Panthera onca*) e onça-parda (*Puma concolor*), no Cerrado e Pantanal. PhD dissertation University of Brazilia, Brazilia

Silveira L, Jácomo ATA, Diniz-Filho JAF (2003) Camera trap, line transect census and track surveys: a comparative evaluation. Biol Conserv 114:351–355

Silveira L, Jacomo ATA, Astete S, Sollmann R, Tôrres NM, Furtado MM, Marinho-Filho J (2009) Jaguar density in the Caatinga of Northeastern Brazil. Oryx 44:104–109

Silver S (2004) Assessing jaguar abundance using remotely triggered cameras. Wildlife Conservation Society, New York

Silver S, Ostro LE, Marsh LK, Maffei L, Noss AJ, Kelly MJ, Wallace RB, Gómez H, Ayala G (2004) The use of camera traps for estimating jaguar *Panthera onca* abundance and density using capture/recapture analysis. Oryx 38:148–154

Soisalo MK, Cavalcanti SMC (2006) Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture–recapture sampling in combination with GPS radio-telemetry. Biol Conserv 129:487–496

Sollmann R, Tôrres NM, Silveira L (2008) Jaguar conservation in Brazil: the role of protected areas. Cat News 4:15–20

Stanley TR, Burnham KP (1999) A closure test for time-specific capture–recapture data. Environ Ecol Stat 6:197–209

Tobler MW, Carrillo-Percastegui SE, Leite Pitman R, Mares R, Powell G (2008) An evaluation of camera traps for inventorying large- and medium size terrestrial forest mammals. Anim Conserv 11:169–178

Trolle M (2003) Mammal survey in the southeastern Pantanal, Brazil. Biodivers Conserv 12:823–836

Trolle M, Kéry M (2005) Camera-trap study of ocelot and other secretive mammals in the northern Pantanal. Mammalia 69:409–416

Wallace RB, Gomez H, Ayala G, Espinoza F (2003) Camera trapping for jaguar (*Panthera onca*) in the Tuichi Valley, Bolivia. Mastozool Neotrop 10:5–11

White GC, Anderson DR, Burnham, KP, Otis DL (1982) Capture–recapture and removal methods for sampling closed populations. Los Alamos National Laboratory Publication LA-8787-NERP. Los Alamos National Laboratory, Los Alamos