BIOLOGICAL CONSERVATION 129 (2006) 487–496

available at www.sciencedirect.com

SCIENCE DIRECT®

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

Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture–recapture sampling in combination with GPS radio-telemetry

Marianne K. Soisalo[a,*], *Sandra M.C. Cavalcanti*[b,c]

[a]*Wildlife Research Group, Department of Anatomy, University of Cambridge, Downing Street, Cambridge, CB2 3DY, UK*
[b]*Department of Forest, Range, and Wildlife Sciences, Utah State University, Logan, UT 84322-5230, USA*
[c]*Instituto Pró-Carnivoros, Caixa Postal 10, Atibaia, SP, 12940-970, Brazil*

ARTICLE INFO

Article history:
Received 23 June 2005
Received in revised form
16 November 2005
Accepted 21 November 2005
Available online 9 January 2006

Keywords:
Jaguar
Panthera onca
Camera-traps
Capture–recapture
Population density estimation
Effective sampled area

ABSTRACT

The jaguar (*Panthera onca*) is the largest feline in the Americas and third largest world-wide, smaller in size only to the tiger (*P. tigris*) and lion (*P. leo*). Yet, in comparison, relatively few studies on jaguar population densities have been conducted and baseline data for management purposes are needed. Camera trapping and capture–recapture sampling methods were used to estimate the size of a jaguar population in the Pantanal's open wet grassland habitat, an important area for the long-term survival of the species. This study is the first jaguar population estimate conducted in co-operation with a GPS-telemetry study providing an important opportunity for comparing different methods of density estimation. An accessible area within a 460 km^2 privately-owned ranch was sampled with equal effort during the dry seasons of 2003 and 2004. Thirty-one and twenty-five individual jaguars were identified in 2003 and 2004, respectively. Estimates of jaguar abundance were generated by program CAPTURE. Density estimates were produced according to different methods used to calculate the effectively sampled areas which ranged from 274 to 568 km^2. For 2003, the currently-used mean maximum distance moved (MMDM) method produced a density of 10.3 jaguars/100 km^2, while GPS-telemetry-based calculations produced a mean density of 6.6 jaguars/100 km^2. For 2004, the MMDM method produced an estimate of 11.7 jaguars/100 km^2 while GPS-telemetry calculations produced a density of 6.7 jaguars/100 km^2. Our results suggest that the widely-used MMDM method used to calculate effectively sampled areas is significantly under-reflecting maximum distances moved by jaguars and their range-use and, thereby, considerably inflating cat density estimates. This overestimation could place a population in a difficult situation by lengthening the time taken to initiate protection measures because of underestimating the risk to that population.

1. Introduction

The jaguar is the largest cat in the Neotropics and third largest world-wide. It is an important species within its ecosystem, occupying the position of top predator and is considered an umbrella species within a wide range of habitats (Seymour, 1989). Culturally significant throughout the Americas, jaguars have long been revered as an important

---

[*] *Corresponding author*: Tel.: +44 1223 333753/2073 723543; fax: +44 1223 333786.
E-mail addresses: mks23@cam.ac.uk, mariannesoisalo@hotmail.com (M.K. Soisalo), cavalcanti1@yahoo.com (S.M.C. Cavalcanti).

0006-3207/$ - see front matter © 2005 Elsevier Ltd. All rights reserved.
doi:10.1016/j.biocon.2005.11.023

symbol of power and beauty (Saunders, 1998; Luna and Amaringo, 1999), so that when considering conservation strategies, the strong image of the jaguar, coupled with its ecological importance, make it an ideal flagship species to enlist both local and global support for conservation.

Continual loss of habitat has reduced the jaguar's historical range of occupation by more than 50% since 1900 (Sanderson et al., 1999a,b) and many jaguar populations currently coexist with humans and their activities. Large areas continue to be converted for agriculture, cattle ranching and human settlement, bringing jaguars and humans into direct conflict (Conforti and Azevedo, 2003; Polisar et al., 2003). Livestock predation is the primary cause of people's intolerance of these large cats (Sanderson et al., 1999a,b).

Information regarding the jaguar is still lacking, especially in the field of population ecology, which forms the basis for any conservation management strategy. Many hunting and natural history anecdotes exist (Siemel, 1953; de Almeida, 1990; Hoogesteijn and Mondolfi, 1992), but reliable data on jaguar population densities are critically needed. Relatively few such studies have been carried out to date (Schaller and Crawshaw, 1980; Rabinowitz, 1986; Rabinowitz and Nottingham, 1986; Crawshaw and Quigley, 1991; Ceballos et al., 2002; Nuñez et al., 2002; Wallace et al., 2003; Maffei et al., 2004; Silver et al., 2004) due to the difficulties of monitoring a species of cryptic nature inhabiting extensive areas in difficult terrain.

The camera-trap capture–recapture method used in this survey has proved to be an effective tool for estimating tiger densities in Asia and has been recommended for use with other individually identifiable animals (Karanth and Nichols, 1998, 2000, 2002; Carbone et al., 2001). Like tigers, jaguars can be identified unambiguously by their distinctive coat markings. Although extensively used to estimate tiger populations (Karanth, 1995; Karanth and Nichols, 1998, 2000; Franklin et al., 1999; Smith et al., 1999; Karanth et al., 2001; O'Brien et al., 2003; Kawanishi and Sunquist, 2004), the use of camera-traps in combination with capture–recapture sampling methods to estimate jaguar populations has only recently been initiated in Latin America (Wallace et al., 2003; Maffei et al., 2004; Silver et al., 2004; Soisalo, 2004).

This is both the first study to estimate a jaguar population in Brazil based on camera-traps and capture–recapture, and to use camera-trap data in conjunction with radio-telemetry data (Cavalcanti, unpublished data) on the same population. Specific objectives of this study were: (1) to estimate the abundance of jaguars at the study site, using a capture–recapture sampling approach with the use of camera-traps, (2) to estimate the effectively sampled area and use this information to calculate the jaguar density expressed as the number of jaguars/100 km^2, (3) to compare the estimates of effectively sampled areas based on camera-traps, with estimates of effectively sampled areas based on an independent estimate of home-range size and animal movement obtained from radio-telemetry data, and use this comparison to provide information for a future calibration of the mean maximum distance moved (MMDM) method for large cats, and (4) to provide baseline data from which to begin a long-term population monitoring programme.

2. Methods

2.1. Study area

This study was carried out in the Pantanal wetlands of Mato Grosso do Sul, south-western Brazil. The area is the largest natural floodplain in the world, covering over 140,000 km^2 (Alho et al., 1988), and is characterised by low terrain with an annual flooding regime. Due to substantial jaguar populations, a stable prey base and adequate habitat, the Pantanal has recently been considered an important area for the long-term conservation of jaguars (Sanderson et al., 1999a,b). Ranching activities within the Pantanal watershed have a 250-year history. With about 4 million cattle, it is the main economic activity in the region where most of the land is privately-owned (Fortney, 2000).

The survey was conducted within Fazenda Sete (19°57′S, 56°25′W), a 460 km^2 privately-owned beef cattle ranch. Altitude ranges between 89 and 120 m above sea level. The climate is seasonal, with a rainy season between October and March and an average monthly precipitation of 161.5 mm. The dry season occurs between April and September with a monthly precipitation of 49.3 mm (Crawshaw and Quigley, 1984). Temperatures range from 21.5 °C in June and July to 43.5 °C in October. Relative humidity varies from 60–75% in the dry season to 80–95% in the wet season (Crawshaw and Quigley, 1984).

The vegetation consists of marginally-flooded semi-deciduous forest and other major habitat types in the area are marsh, grassland, open forest or *cerrado*, forest patches and riverine forest (Crawshaw and Quigley, 1991). A detailed description of Pantanal vegetation has been published elsewhere (Prance and Schaller, 1982).

White-lipped peccaries (*Tayassu pecari*), marsh deer (*Blastocerus dichotomus*), caiman (*Caiman crocodilus yacare*), armadillos (*Euphractus sexcinctus*), and giant anteaters (*Myrmecophaga tridactyla*) are found in the area and are considered important prey species for jaguars (Schaller, 1983; Polisar et al., 2003; Cavalcanti, unpublished data). Puma (*Puma concolor*), ocelot (*Felis pardalis*), giant river otter (*Pteronura brasiliensis*), and crab-eating foxes (*Cerdocyon thous*) are sympatric carnivores that also inhabit the area (Schaller, 1983).

2.2. Field methods

The sampling design and statistical framework used in this study were based on tiger studies in India (Karanth, 1995; Karanth and Nichols, 1998, 2000; Karanth et al., 2001) and recent jaguar studies in Latin America (Wallace et al., 2003; Maffei et al., 2004; Silver et al., 2004). A closed model capture–recapture sampling approach (Otis et al., 1978; White et al., 1982) was used to survey an area within the ranch using camera-traps to obtain photographs of jaguars. This camera-trapping survey was carried out simultaneously with a radio-telemetry study (Cavalcanti, unpublished data).

2.2.1. Camera-trap systems

Fifteen Trailmaster® TM1550 active infra-red systems (Goodson Associates Inc., KS, USA) and one Camtrakker® passive infra-red system (Cam Trak South Inc., GA, USA) were used.

Each trap station was set with two cameras opposite each other, positioned to photograph both asymmetrical flanks of the animal for positive identification. The beam was set at a height of about 45 cm and the two cameras were placed on either side, 7–8 m apart facing the centre of the beam. The systems were programmed to run for 24 h and to fire as soon as the beam was broken with a delay of 3 min between pictures. Stations were checked daily, or at least every two days, due to heavy cattle traffic. No bait or lure was used at any station to attract jaguars.

2.2.2. *Radio telemetry*

Eight jaguars were captured with the help of trained hound dogs and an experienced local hunter (de Almeida, 1990) at sites of frequent use. Treed cats were immobilised with Telazol (tiletamine-zolazepan, Fort Dodge do Brasil), or a combination of Telazol and ketamine hydrochloride. Individuals were fitted with a Global Positioning System (GPS) telemetry collar (Televilt, Sweden) and released. These GPS collars provided coverage over large areas and operated 24-h a day throughout the year, collecting 12 locations/day for each cat and storing them "on-board". We downloaded data from the collars at 21-day intervals with the help of a Cessna aircraft. This large amount of locations on an individual provided information on animal movement continuously and the use of GPS collars allowed for the simultaneous location of several individuals. All jaguar locations ($n = 5.600$) were plotted on a base map of the study area (Landsat TM Satellite Image).

2.3. *Sampling design considerations*

One of the most important aspects of camera trapping is to capture as many different individuals and to obtain as many photo recaptures of each individual as possible (Karanth and Nichols, 2000, 2002). Thus, it is critical to optimise trap placement to maximise the chances of capturing a jaguar. As this study is the first to estimate a jaguar population using the camera-trapping method in combination with GPS radio-telemetry data collected at the same study site, the study design was adapted accordingly to include the radio-telemetry movement data during the calculations and general planning of the survey.

Like tigers, jaguars use regular travel routes. Information on previous use was derived from both direct sign (tracks, scats, scrapes, kill sites and sightings) and the telemetry dataset from GPS collars collected at the site (Cavalcanti, unpublished data). Since all jaguar locations were plotted on a map of the study area, optimal sites for trap placement were selected based on these jaguar locations. Areas with clusters of locations, which indicated quite heavy use of a particular site, usually by more than one individual, were selected for the placement of camera-traps (Fig. 1). In this manner, trap placement was greatly optimised to photograph as many individuals as possible over the largest accessible area.

The size of the area to be sampled was driven by the number of camera-traps available ($n = 16$), and accessibility within the area. As the study site was located in the Pantanal wetlands, many areas remained too wet and inaccessible, even

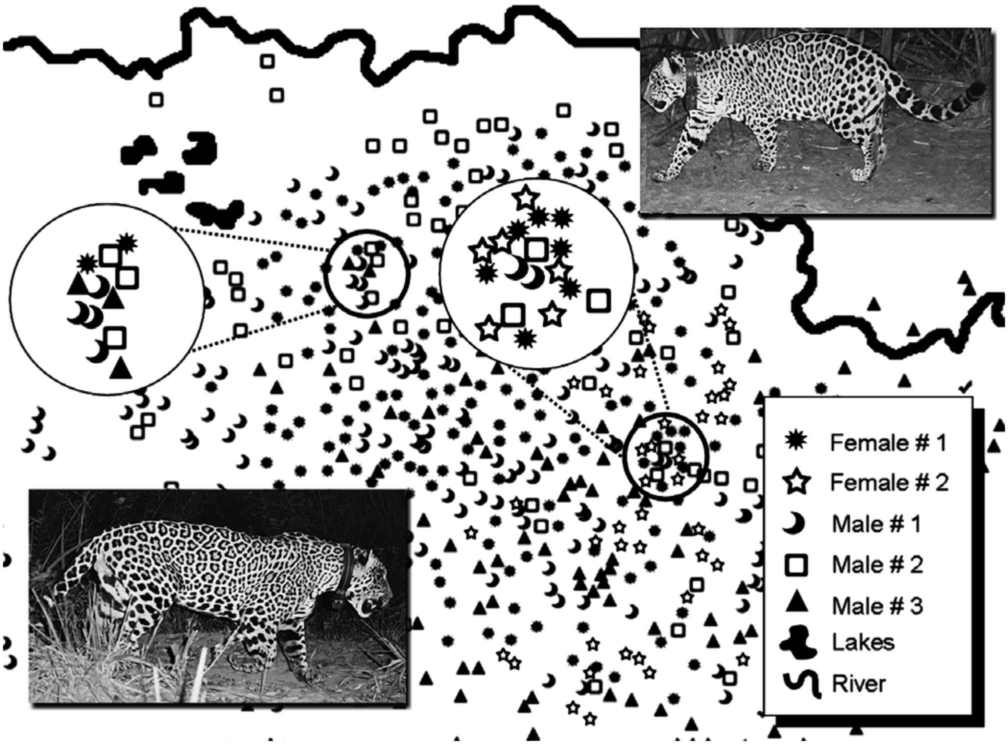

Fig. 1 – Choice of camera-trap locations based on GPS-locations of collared cats. Areas within circles indicated use of that area by more than one individual cat and were therefore thought to be good sites for camera-trap placement.

in the dry period, and a thorough preliminary reconnaissance defined the outer boundaries of the sampling area each year.

An additional consideration in determining the size of the sampling area was the average size of an adult female's home range (Karanth and Nichols, 2002). Since an adult female jaguar has the smallest range within a population (Crawshaw and Quigley, 1984, 1991; Rabinowitz and Nottingham, 1986; Cavalcanti, unpublished data), the placement of a minimum of 2–3 traps as recommended by Karanth and Nichols (2002) within such an area, ensures that animals of other sex and age classes are also likely to be exposed to more traps.

A mean of four female home ranges during the same period in which the sampling was conducted, the dry period (June–October), was calculated at 40 km^2 (ranging from 33.9 to 50 km^2). This a priori knowledge of a female home range size was then used to determine trap spacing. It is crucial for the design that the area be evenly covered with traps to minimise the chance that an individual cat could be living in the area and have a zero chance of being captured by at least one camera-trap during the sampling period. No gaps larger than 40 km^2 were left within the area and the areas surveyed both years contained no holes of unsuitable jaguar habitat.

In the 2003 survey, three similarly-sized contiguous blocks (mean = 65 km^2) were sampled sequentially using 16 stations in each block for the same amount of time ($n = 20$ days). The capture history data of the first sampling day, in each of three blocks were combined to form one sampling occasion. The same procedure was used for the second, third, fourth, and remaining days within the 20-day sampling period. In 2004, accessibility in the area was reduced by water levels, and thus, the design was different. The 16 camera-traps covered the accessible area but remained stationary during the 60-day period. It is important that equal effort is invested into each sampling period as was done and that this period is short enough in order to meet the general assumption of a closed population in mark-recapture studies (Karanth and Nichols, 2002). As the life span of jaguars is similar to that of tigers (Hoogesteijn and Mondolfi, 1992; Sunquist and Sunquist, 2002), we assumed that the use of a short sampling period of 20 sampling occasions over a two-month period in this study would allow us to consider demographic closure.

2.4. *Analysis*

To minimise bias in the identification process, all jaguar photographs were examined by the authors independently. Each photograph of an individual represented a capture occasion. Capture histories were then compiled into a matrix for use in program CAPTURE (Otis et al., 1978; White et al., 1982; Rexstad and Burnham, 1991). For the 2003 survey in which the area was divided into blocks, we followed Karanth and Nichols (2002) so that the three blocks were combined to form one final matrix, with all animals captured during the survey making up the rows, and the combined 20 sampling occasions making up the columns. The sampling occasions of the three blocks were combined so that the first day in all blocks formed occasion number one, the second day in all blocks combined formed the second occasion and so on. Program CAPTURE computed an estimate of population size or abundance (N) and *var* (N) for jaguars within the effectively sampled area $A(W)$. The abundance estimate was then used to derive an estimate of jaguar density, defined as $D = N/A$, where N is animal abundance and A is the area sampled. The area used in this calculation is not simply the area defined by the outer trap polygon. Typically, a buffer or a boundary strip of width W is added to the area defined by the outer traps, so that the sampling area also includes areas covered by the outer traps beyond the outer polygon limits (Otis et al., 1978; White et al., 1982; Karanth and Nichols, 1998, 2002). An overestimate would occur if the outer trap polygon area alone was used.

Karanth and Nichols (1998, 2002) used and recommended the approach formulated and tested by Wilson and Anderson (1985) to estimate the buffer width of their tiger camera-trapping surveys. This method has also been used in other jaguar camera-trap capture–recapture surveys carried out (Wallace et al., 2003; Maffei et al., 2004; Silver et al., 2004). When home range information is not available, once the trapping is concluded, the "mean maximum distance moved" (MMDM) by all those cats that were trapped more than once is used to compute a boundary or buffer strip. Each cat's maximum linear distance moved from one trap to another during the sampling period is recorded and an average of all the cats' maximum distances is calculated to reflect an estimate of home-range diameter. This figure is then halved to produce an estimation of the average radius of a mean home range which is then added onto the outer trap polygon as a buffer width. This new area, the effectively sampled area, is finally used to calculate the density of jaguars in the area, expressed as the number of jaguars/100 km^2. Therefore, a critical factor that ultimately influences density estimates is the buffer width.

This study provided an unique opportunity to examine how different methods to compute a boundary strip width affect jaguar density estimates. In this paper, we present estimates of jaguar density at the study site based on (1) the currently-used MMDM method from camera-trapping photographic captures alone (half of the mean maximum moved distances), (2) the MMDM method from camera-traps alone where the mean maximum distances moved by jaguars were used without being halved (full MMDM) (Parmenter et al., 2003), (3) the "actual MMDM" calculated from the collared cats' maximum moved distances ($n = 6$, 2003 only), and (4) a buffer width calculated using male and female home range sizes derived from the GPS radio-telemetry data.

With the radio-telemetry data, a minimum convex polygon method with 95% of location data for each individual cat was used (Home Range extension for ArcView™). Locations for five males and two females during the same period of the survey (the dry period, from June through October) were used to calculate a mean jaguar home range of 83.45 km^2 (52–176 km^2). We used this area to calculate the buffer width applying $A = \pi r^2$, where A is the estimated area of the mean jaguar home range and r is the buffer width (5.1 km). Although we used information from only 7 individual cats in order to calculate a mean jaguar home range, we are confident this is an accurate representation of jaguar ranges in our study area. The radio-telemetry system we used in this study, based on GPS positions, not only allowed for accurate locations of study animals, but provided coverage over large areas, 24-h a day throughout the year, independent of terrain and weather conditions. This large amount of less biased radio locations, i.e., independent of whether the researcher can reach study animals, allows for an estimation of home ranges that is generally more accurate than an estimation based on traditional telemetry methods.

Only during the 2003 survey were there cats fitted with GPS-telemetry collars, when "actual MMDM" comparisons were conducted. This comparison was carried out only during 2003 as it served to show the same cats had, during the survey, moved much longer distances than reflected by the camera-traps. The "actual MMDM" (or the distance moved by collared cats) produced a buffer which was almost identical to the one calculated from the home range estimated for jaguars at the study site and therefore served to confirm that the "actual" maximum distances moved by cats can be used as a proxy for jaguar home ranges. On the other hand, the mean maximum distances moved by animals as reflected by the cameras alone (not "actual") were shown not to be reliable as a reflection of home range diameter (or of "actual" MMDMs). The problem lies with the MMDM from camera-traps being used to calculate a buffer width, according to the currently-used method based on Wilson and Anderson (1985). In 2004, we did not use information from GPS-collared cats, but the home range and consequently optimal buffer width had already been established at 5.1 km from thousands of locations ($n = 5.600$) in 2003. This buffer width estimated from telemetry can be used in future surveys in this area. Once a home range estimate and its related buffer width had been calculated it did not need to be re-calculated in 2004.

3. Results

The sampling effort of 960 camera-trap-nights (16 traps × 20 days × 3 blocks in 2003 and 16 traps × 60 days in 2004) expended over 20 sampling occasions, resulted in a total of 31 individual jaguars being positively identified in 157 photo captures in 2003, and 25 individual jaguars in 131 photo captures in 2004 (Table 1). No cubs were photographed in 2003 whilst a mother and cub were photographed in the 2004 survey. Capture frequencies ranged from 1 to 22 captures for an individual cat, with a mean of 5.2 captures/individual jaguar.

In the first survey of 2003, model M_b, which allows differences in capture probabilities between newly-caught individuals and animals that were already captured, was selected by CAPTURE as best-fitting for these data. The suggested estimator was *Zippin*, the estimator for M_b. Parameters estimated in this study were population size $(\hat{N})$, estimated at 37 jaguars $(S\hat{E}\hat{N}5.52)$, probability of capture of an unmarked animal on any trapping occasion, $\hat{p} = 0.087$, and the recapture probability of any animal captured at least once, $\hat{c} = 0.167$. The statistical test for population closure in program CAPTURE indicated lack of closure ($z = -2.647$, $P = 0.004$). The best-fitting model for the second survey of 2004 was model M_h, where capture probabilities are heterogeneous for each individual, but are not affected by trap response or time, and the population was estimated at 32 jaguars $(S\hat{E}\hat{N}5.35)$. Program CAPTURE indicated population closure ($z = 0.225$, $P = 0.589$). The areas encompassed by the outer traps were calculated at 165 km^2 (2003) and 110 km^2 (2004). To these areas, we added a buffer width using the described ways to calculate it and the resulting effectively sampled areas and densities are summarised in Table 2.

For cats with at least 3 captures, camera-trap data provided information on their minimum home ranges. For male and female jaguars, home-range sizes obtained from the camera-trapping data reflected only a small fraction (8.1% and 9.3%, respectively) of the area used by the same collared individuals. For 11 males captured, minimum ranges reflected by the traps ranged from 2.0 to 28.4 km^2, with a mean of 9.5 km^2, whilst the minimum range obtained from the telemetry ($n = 4$) ranged from 65.1 to 176 km^2, with a mean of 116.5 km^2. The female minimum ranges obtained from the camera-trap data ($n = 4$) ranged from 0.5 to 17.6 km^2 with a mean of 5.6 km^2, whilst the minimum ranges obtained from the telemetry ranged from 52 to 65.1 km^2 ($n = 2$).

4. Discussion

We successfully tested the suitability of camera-trap capture–recapture sampling methods combined with telemetry technology for monitoring the status of jaguars in an open wet grassland habitat of the Pantanal, a high-conflict landscape considered important for the long-term survival of the species. Although camera-trapping was an expensive method, where only a small proportion of pictures taken provided information on jaguars, it was a quick and efficient tool to obtain an estimate of the jaguar population at the study site. There are still certain limitations and possible biases related to the method, however, which have been discussed elsewhere (Karanth and Nichols, 2002; Soisalo, 2004).

4.1. *Population closure*

A possible limitation of the method as used here to estimate cat densities is the assumption of population closure. A

Table 1 – Results of camera-trap surveys conducted at Fazenda Sete, Pantanal, during dry seasons of 2003 and 2004

Survey year	Number of individual jaguars	Male	Female	Unknown	Sex ratio, M:F	CAPTURE abundance[c]	SE	95% Confidence interval
2003[a]	31	15	10	6	1.5:1	37	±5.52	33–59
2004[b]	25	12	10	3	1.2:1	32	±5.35	27–51

a Program CAPTURE indicated model M_b as best-fitting for these data.
b Program CAPTURE indicated model M_h as best-fitting for these data.
c Absolute number of individuals as computed by program CAPTURE.

Table 2 – Effectively sampled areas calculated from camera-trap and GPS-telemetry data and their resulting jaguar density estimates

Survey year	Sampled area size (km^2) – outer trap polygon	Method used for buffer width calculation	Buffer width (km)	Effective sampled area (km^2)	Resulting density estimate (jaguars/100 km^2)
2003	165	*Camera-traps*			
		MMDM	3.0	360	10.3 ± 1.53
		Full MMDM	6.0	653	5.7 ± 0.84
		GPS telemetry			
		Actual MMDM	5.2	568	6.5 ± 0.97
		Home range	5.1	557	6.6 ± 0.99
2004	110	*Camera-traps*			
		MMDM	2.9	274	11.7 ± 1.94
		Full MMDM	5.8	554	5.8 ± 0.97
		GPS telemetry			
		Home range	5.1	476	6.7 ± 1.13

critical assumption of closed models is that the animals are not moving in or out of the area and there are no births or deaths, i.e., the population remains constant in size and composition throughout the period of investigation (White et al., 1982). It is difficult, if not impossible, to ascertain closure of a biological population, especially in a non-controlled situation, as even within a short one-hour sampling period for example, a death or immigration, could in reality occur. It has been verified in controlled situations that closure can be shown to be violated even when it is known not to have been, and vice-versa (White et al., 1982). Even when a population is in fact closed the test might be reacting to the behavioural change in capture probabilities which might seem like recruitment, for example (White et al., 1982). The CAPTURE test in this study indicated lack of closure in 2003, probably because sometimes this result in the test can represent certain patterns of variation in capture probability that mimic lack of closure; in this case it may have been the number of animals caught only once ($n = 9$). When model M_b is selected, as was in 2003, the test for closure in program CAPTURE is unable to distinguish failure of closure from any behavioural change in capture probabilities. Closure can only be tested when it is assumed that the underlying model is M_o or M_h. (Otis et al., 1978; White et al., 1982). As these closure tests are poor, we, as researchers, must do what we can to ensure that the assumption of closure is met. The best one can do is to conduct the sampling in a short period relating to the life history of the study animal, as was done in our study and previously described in Section 2.

4.2. *Model selection*

For the 2003 survey, model M_b, an estimator which assumes that capture probabilities vary by behavioural response to capture, was identified as the most appropriate model; the CAPTURE test suggested there may have been a behavioural response in the jaguars. It is assumed in this model that capture probability differs for animals that have, or have not, been caught previously. The results of this test indicated that the cats had a 9% chance of being caught the first time, but this probability increased to 17% for recaptures. At first, this might seem that the jaguars could have become “trap-happy”, a term used to indicate that the likelihood of a cat returning to a particular trap is increased (White et al., 1982). This is the case when there is a positive response to trapping resulting from a favourable first-capture experience, for example when using bait or lure. In this study, we believe these animals were not “trap-happy”, as there were no rewards (no bait or lure was used) on returning to a trap. Instead, these results appear to reflect our choices of trap locations made by incorporating the telemetry dataset available (Cavalcanti, unpublished data), and not having to rely solely on sign. There was a better chance of capturing the animals, not because of a behavioural change where they returned to the trap more often, but because we succeeded in placing the traps in several spots shown to be regularly used by cats. This increased the probability of recapturing individual jaguars as they returned to use their habitual trails or roads. This high recapture rate suggests that we must have identified several established travel routes within the study site.

In 2004, as in most jaguar (Wallace et al., 2003; Maffei et al., 2004; Silver et al., 2004) and tiger camera-trapping surveys (Karanth and Nichols, 1998, 2000; Karanth et al., 2001; Kawanishi, 2002; Kawanishi and Sunquist, 2004), the model chosen as best-fitting was model M_h. This model allows variation in capture probability among individuals, but the probability of each individual being recaptured remains the same throughout the sampling period. This difference in the choice of best-fitting models by program CAPTURE for the same population may have been a reflection of the different sampling designs used in 2003 and 2004. Although in our study both models produced the same density estimates, future studies should consider differences in sampling design and how they influence model selection.

4.3. *Combining two techniques to estimate population size*

In tiger (Karanth, 1995; Karanth and Nichols, 1998, 2000; Karanth et al., 2001, 2004) and other jaguar (Wallace et al., 2003; Maffei et al., 2004; Silver et al., 2004) camera-trapping surveys, trap locations were based solely on evidence of sign (tracks, scrapes or past sightings) and/or trails in the forest thought by local people to be used by cats. Karanth and Nichols (2000) point out how a "*better choice of sites would yield higher capture probabilities. A higher proportion of the animals in the area may then be caught, and the resulting estimates of population size derived would be statistically more precise*." Since this design is the first to use GPS-based telemetry to enhance the choice of optimal sites for camera-trap placement and, consequently, increase capture probabilities, it may be fair to assume that a high proportion of the jaguar population in the area was probably captured. If we apply mark-recapture concepts to the radio-collared cat population at the ranch in 2003, out of a total known population of six collared cats, all six (100%) were captured by the camera-traps. If we look at the abundances estimated by program CAPTURE for both years (37 in 2003 and 32 in 2004, Table 1) our cameras photographed a high proportion (84% and 78%, respectively) of the population. Karanth and Nichols (2002) used an index of tiger density based on a trapping rate as the mean number of tiger pictures per 100 trap nights. Our surveys produced a high mean index of 15.1 jaguars/100 trap nights. These results support the argument that we had a very high encounter rate and are likely to have captured a high proportion of the population. Therefore the combination of the two techniques used, which optimised trap site selection, may have produced a more accurate representation of the true jaguar population at the study site.

Amongst the jaguar population studies using camera-trap surveys in Central and South America (Wallace et al., 2003; Maffei et al., 2004; Silver et al., 2004), the highest number of jaguars photographed at any one site was in this study ($n = 31$ in 2003 and $n = 25$ in 2004). In addition to lacking complementary information from radio-telemetry, these other surveys took place in forested areas with no cattle presence. The number of animals captured ranged from 7 to 11 individuals in areas ranging from 117 to 458 km^2. This disparity in numbers of animals photographed may be due not only to the different methods used, but also to several factors, such as differences in habitat, prey availability, and cattle density. In the Pantanal, domestic cattle are abundant, readily-available prey items that comprise an important part of the jaguar's diet (de Almeida, 1990; Schaller, 1983; Hoogesteijn and Mondolfi, 1992; Quigley and Crawshaw, 1992; Cavalcanti, unpublished data). In addition, the availability of native prey in the Pantanal is also higher than in forested areas (Hoogesteijn and Mondolfi, 1992). With a higher density of prey, both wild and domestic, a higher density of predators in the area is not surprising.

The combination of techniques used in this study provided a sound basis for analysing how sample area size calculations can affect density estimates. Density calculations are driven by two components: the abundance estimate and the size of the sampled area. A crucial factor during camera-trapping capture–recapture surveys, therefore, is the buffer calculation used to produce the "effectively sampled area". It ultimately influences final density estimates. As tiger and jaguar camera-trapping surveys mentioned herein have been using the previously-described MMDM method for this calculation, this was a good opportunity to examine how the density estimate obtained using this method compared to that obtained using GPS-telemetry data to compute a boundary strip.

4.4. *Density estimates derived from MMDM method and GPS-telemetry compared*

The incorporation of thousands of GPS radio-telemetry locations to compute a buffer width, produced considerably larger effectively sampled areas (Fig. 2) and, consequently, lower density estimates when compared to smaller areas and higher densities derived from the MMDM method as used in other large cat studies (Karanth and Nichols, 1998, 2000; Karanth et al., 2001, 2004; Wallace et al., 2003; Maffei et al., 2004; Silver et al., 2004). These results suggest that the MMDM method consistently overestimated the density of jaguars at the site over two yearly surveys (Table 2), suggesting that other studies using this method might also be overestimating large-cat densities. This difference in our study is expressed as a ratio of 1.56 (2003) and 1.74 (2004) between the estimates based on MMDM calculations from camera-traps alone and telemetry-based calculations. If the density at this site were reported using the same methods used elsewhere (Karanth and Nichols, 1998, 2000; Karanth et al., 2001, 2004; Wallace et al., 2003; Maffei et al., 2004; Silver et al., 2004), the resulting densities of 10.3–11.7 jaguars/100 km^2, based on radio-telemetry comparisons, might be overestimating the population by as much as 74%. We believe this to be a worryingly-high level of error when it comes to making management decisions based on population estimates.

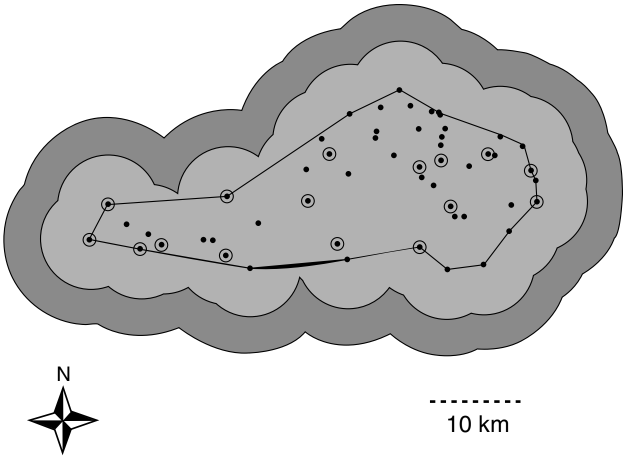

Fig. 2 – Survey map showing camera-trap locations for 2003 and 2004, outer trap polygon and the effectively sampled area sizes (2003) calculated using two different methods to calculate a buffer width. •, Camera-trap stations 2003; ◉, camera-trap stations 2004; –•–, outer traps polygon (area = 165 km^2); ■, effectively sampled area with buffer calculated from jaguars' MMDM, or camera-trap information alone (area = 360 km^2); ■, effectively sampled area with buffer calculated from GPS-telemetry, or the jaguars' "actual" MMDM (area = 568 km^2). Home range calculations from telemetry produced a very similar resulting area of 557 km^2.

Camera-trapping renders a biased representation of the movement of the animals, while the information from GPS radio-telemetry is a more accurate representation of their movements and, consequently, of the size of the effectively sampled area, crucial in calculating the final density. Our radio-telemetry data showed that the animals had, in fact, moved linear distances, which were almost twice as long as the distances reflected by the maximum distances shown by traps, illustrating the fact that the effectively sampled area, and the manner in which it is being calculated, is problematic. The "actual MMDM" from telemetry provided an almost identical estimate to the actual home range sizes (6.5 and 6.6 jaguars/100 km^2 in 2003 and 2004) but the estimates using camera-trap MMDM alone were not similar (10.3 jaguars and 11.7 jaguars/100 km^2, respectively), and might inflate animal densities when used to calculate the effectively sampled area (Table 2). Although tiger and jaguar surveys herein mentioned have been using the MMDM method as described, Parmenter et al. (2003) used another version which includes the full MMDM values in the buffer calculation. When the mean maximum distances moved by all animals was not halved and a "full MMDM" value was used to calculate a buffer for our surveys, it produced a slightly lower (5.7 and 5.8 jaguars/100 km^2, in 2003 and 2004) but much closer density estimate to that calculated using telemetry (Table 2).

Minimum home ranges obtained from camera-trapping during a short sampling period were found to be highly unrepresentative of true home ranges. Areas used by jaguars, as reflected by the camera-traps, represented only 8–9% of the true ranges as shown by the GPS-telemetry. We recommend that data from camera-trapping surveys alone should not be used to estimate large cat home ranges.

From our five-year experience conducting research at the study site and this new body of information, we suggest that the density estimates of 6.5–6.7 jaguars/100 km^2 are more biologically accurate than the estimates of 10.3–11.7 jaguars/100 km^2 obtained from camera-trap MMDM calculations (see Table 2). This discrepancy becomes of great relevance within a conservation management framework. To illustrate this, we extrapolated these numbers to different-sized areas. If, for example, within an area of 100 km^2, we overestimate a jaguar population by 3.8–5 individuals (2003–2004 results), in an area the size of the Pantanal (140,000 km^2), we would be overestimating the population by 5.320–7.000 individual jaguars.

Any extrapolation of these density results outside the study area boundaries would be unwise as there are differences in vegetation cover, land-use and hunting levels outside the ranch and throughout the Pantanal, and was only used here to illustrate the problem. An extrapolation at this stage could give an incorrect idea about numbers of jaguars throughout the area. Additional surveys should be conducted at different sites in the region to begin to understand jaguar distribution on a larger-scale in the Pantanal.

Karanth et al. (2004) believe "*that given the large number of camera-trap surveys now being conducted across the world*...*there is room for improvement in the survey design and analytical protocols used in many cases*". Although we agree this method is currently the most successful available tool to survey individually identifiable big cats systematically, a serious problem has been brought to light, relating to the conversion of an abundance estimate into a density estimate. The combination of these two powerful techniques has shown that we need to reconsider how we calculate effectively sampled areas for jaguars. The original model used for small mammals to formulate the calculation in this method (Wilson and Anderson, 1985) might work well with smaller mammals but it does not seem to hold when it comes to applying these notions to far-ranging large cats such as jaguars.

We urge researchers to exercise the utmost caution when reporting densities using the MMDM method for calculations to derive the size of an effectively sampled area. We suggest existing studies of the same species and their known home ranges might be useful additional references when deciding the size of the buffer width, rather than using the MMDM from camera-traps alone. However, only studies conducted in the same type of habitat should be considered. Parmenter et al. (2003) compared estimates of boundary strips based on different methods and found that the use of the full MMDM to calculate effective trapping area provided the most accurate density estimate. In our study, although the full MMDM did not produce an identical result to that obtained from telemetry, and in comparison underestimated the population by 14%, this would have been a much safer estimate than the MMDM method (one-half the maximum distances moved) which produced overestimates of up to 74%. We believe this question should continue to be addressed and further studies of this kind should be able to produce a calibration function, which can be recommended for future camera-trapping capture–recapture population estimate calculations.

An important benchmark has been established from which to begin a long-term monitoring programme of a jaguar population. The study was conducted at a privately-owned cattle ranch and the results presented in this paper highlight the importance of this particular site for conservation. As more than 95% of the Pantanal is privately-owned (Quigley and Crawshaw, 1992; Swarts, 2000), jaguar conservation programmes will need to work closely with landowners who will be sympathetic to the plight of the jaguar on their land if this cat is to survive in this wetland habitat, one of its last strongholds.

Acknowledgements

Camera-trapping was funded by A. Zarzur, J. Poyry, H. Ehrnrooth, N. Kuzbari, B.D.Turner and M. Soisalo. British Airways Assisting Conservation, the British Ecological Society, Fujifilm UK and the Specialist – SP, also contributed towards the project. Radio-telemetry was funded by Utah State University, Wildlife Conservation Society (WCS), Sociedade Civil Mamirauá (SCM), National Scientific and Technological Development – Brazil (CNPq), and Conservation, Food and Health Foundation. We thank Mr. and Mrs. Israel Klabin for their enthusiastic support of our work and permission to conduct this research on their land. We are immensely grateful to K. Ullas Karanth who, at the conception stages of the study, was of great assistance in explaining his pioneering method and suggesting alternative sampling designs. In the field we thank E. Vilalba, M. Bassani, F. Cavalcanti, T. Micheletti, M. Perilli, S. Romeiro, J. da Silva and T. Lee for their invaluable assistance. The Centro de Conservação do Pantanal Research Centre run by Fundação Brasileira para o Desenvolvimento Sustentável, WCS and SCM provided a base from where these studies were conducted. We thank D.J. Chivers, E. Gese, A. Noss and C. Thompson for their constructive comments on the draft. M. Conner provided insight into model selection within program CAPTURE. Permission to conduct animal procedures was granted by the Brazilian government through the Brazilian Institute of Environment and Natural Renewable Resources (IBAMA).

REFERENCES

Alho, C.J., Lacher, T.E., Gonçalves, H.C., 1988. Environmental degradation in the Pantanal ecosystem. Bioscience 38, 164–171.

de Almeida, A., 1990. Jaguar Hunting in the Mato Grosso and Bolivia. Safari Press, CA, USA.

Carbone, C., Christie, S., Conforti, K., Coulson, T., Franklin, N., Ginsberg, J.R., Griffiths, M., Holden, J., Kawanishi, K., Kinnaird, M., Laidlaw, R., Lynam, A., Macdonald, D.W., Martyr, D., McDougal, C., Nath, L., O'Brien, T., Seidensticker, J., Smith, D.J.L., Sunquist, M., Tilson, R., Wan Shahruddin, W.N., 2001. The use of photographic rates to estimate densities of tigers and other cryptic mammals. Anim. Conserv. 4, 75–79.

Ceballos, G., Chavez, C., Rivera, A., Manterola, C., Wall, B., 2002. Tamaño poblacional y conservación del jaguar en la reserva de la biosefera Calakmul, Campeche, México. In: El Jaguar en el nuevo milenio. Ediciones Científicas Universitárias, Universidad Nacional Autónoma de México/Wildlife Conservation Society, New York, pp. 403–417.

Conforti, V.A., de Azevedo, F.C.C., 2003. Local perceptions of jaguars (*Panthera onca*) and pumas (*Puma concolor*) in the Iguaçu National Park area, South Brazil. Biol. Conserv. 111, 215–221.

Crawshaw, P.G., Quigley, H.B., 1984. A ecologia do jaguar ou onça pintada no Pantanal. Relatório entregue ao Instituto Brasileiro de Desenvolvimento Florestal (IBDF)/DN (Brasilia), p. 110.

Crawshaw, P.G., Quigley, H.B., 1991. Jaguar spacing, activity and habitat use in a seasonally flooded environment in Brazil. J. Zool. Lond. 223, 357–370.

Hoogesteijn, R., Mondolfi, E., 1992. The Jaguar. Armitano Publishers, Venezuela.

Fortney, R.H., 2000. Cattle Grazing and Sustainable Plant Diversity in the Pantanal: What Do We Know? What Do We Need to Know? The Pantanal of Brazil, Bolivia and Paraguay. Hudson Mac Arthur Publishers.

Franklin, N., Bastoni, S., Siswomartono, D., Manansang, J., Tilson, R., 1999. Last of the Indonesian tigers: a cause for optimism. In: Seidensticker, J., Christie, S., Jackson, P. (Eds.), Riding the Tiger: Tiger Conservation in Human-dominated Landscapes. Cambridge University Press, Cambridge, UK, pp. 130–147.

Karanth, K.U., 1995. Estimating tiger *Panthera tigris* populations from camera-trap data using capture–recapture models. Biol. Conserv. 71, 333–338.

Karanth, K.U., Nichols, J.D., 1998. Estimation of tiger densities in India using photographic captures and recaptures. Ecology 79 (8), 2852–2862.

Karanth, K.U., Nichols, J.D., 2000. Ecological Status and Conservation of Tigers in India. Final Technical Report to the Division of International Conservation, US Fish and Wildlife Service, Washington DC and Wildlife Conservation Society, New York. Centre for Wildlife Studies, Bangalore, India.

Karanth, K.U., Nichols, J.D., 2002. Monitoring Tigers and Their Prey: A Manual for Researchers, Managers and Conservationists in Tropical Asia. Centre for Wildlife Studies, Bangalore.

Karanth, K.U., Bhargav, P., Kumar, S., 2001. Karnataka Tiger conservation Project. Final Report to Save the Tiger Fund – National Fish and Wildlife Foundation, Exxon Mobil Corporation and other donors. Wildlife Conservation Society, International Programs, Bronx, NY 10460-1099.

Karanth, K.U., Chundawat, R.S., Nichols, J.D., Kumar, N.S., 2004. Estimation of tiger densities in the tropical dry forests of Panna, Central India, using photographic capture–recapture sampling. Anim. Conserv. 7, 285–290.

Kawanishi, K., 2002. Population status of tigers (*Panthera tigris*) in a primary rainforest of Peninsular Malaysia. Ph.D. Dissertation, University of Florida, Gainsville.

Kawanishi, K., Sunquist, M.E., 2004. Conservation status of tigers in a primary rainforest of Peninsular Malaysia. Biol. Conserv. 120, 329–344.

Luna, L.E., Amaringo, P., 1999. Ayahuasca Visions: The Religious Iconography of a Peruvian Shaman. North Atlantic Books, USA.

Maffei, L., Cuellar, E., Noss, A.J., 2004. One thousand jaguars (*Panthera onca*) in Bolivia's Chaco? Camera-trapping in the Kaa-Iya National Park. J. Zool. 262 (3), 295–304.

Nuñez, R., Miller, B., Lindzey, F., 2002. Ecología del jaguar en la reserva de la biosfera Chamela-Cuixmala, Jalisco, México. In: El Jaguar en el nuevo milenio. Ediciones Científicas Universitárias, Universidad Nacional Autónoma de México/ Wildlife Conservation Society, New York, pp. 107–126.

O'Brien, T.G., Kinnaird, M.F., Wibisono, H.T., 2003. Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. Anim. Conserv. 6, 131–139.

Otis, D.L., Burnham, K.P., White, G.C., Anderson, D.R., 1978. Statistical inference from the capture data on closed animal populations. Wildlife Monogr. 62, 1–135.

Parmenter, R.R., Yates, T.L., Anderson, D.R., Burnham, K.P., Dunnun, J.L., Franklin, A.B., Friggens, M.T., Lubow, B.C., Miller, M., Olson, G.S., Parmenter, C.A., Pollard, J., Rextad, E., Shenk, T.M., Stanley, T.R., White, G.C., 2003. Small-mammal density estimation: a field comparison of grid-based vs. web-based density estimators. Ecol. Monogr. 73, 1–26.

Polisar, J., Maxit, I., Scognamillo, D., Farrell, L., Sunquist, M.E., Eisenberg, J.F., 2003. Jaguars, pumas, their prey base, and cattle ranching: ecological interpretations of a management problem. Biol. Conserv. 109, 297–310.

Prance, G.T., Schaller, G.B., 1982. Preliminary study of some vegetation types of the Pantanal, Mato Grosso, Brazil. Brittonia 34, 228–251.

Quigley, H.B., Crawshaw, P.G., 1992. A conservation plan for the jaguar *Panthera onca* in the Pantanal region of Brazil. Biol. Conserv. 61, 149–157.

Rabinowitz, A.R., 1986. Jaguar predation on domestic livestock in Belize. Wildlife Soc. Bull. 14, 170–174.

Rabinowitz, A., Nottingham, B., 1986. Ecology and behaviour of the jaguar (*Panthera onca*) in Belize, Central America. J. Zool. Lond. (A) 210, 149–159.

Rexstad, E., Burnham, K.P., 1991. User's Guide for Interactive Program CAPTURE Abundance Estimation of Closed Population Animal Populations. Colorado State University, Fort Collins, CO, USA.

Sanderson, E.W., Chetkiewicz, C.-L.B., Rabinowitz, A., Redford, K.H., Robinson, J.G., Taber, A.B., 1999a. Un análisis geográfico del estado de conservación y distribuición de los jaguares a través de su área de distribuición. In: Medellín, R.A., Equihua, C., Chetkiewicz, C.-L.B., Crawshaw, P.G., Jr.Jr., Rabinowitz, A., Redford, K.H., Robinson, J.G., Sanderson, E.W., Taber, A.B. (Eds.), El Jaguar en el Nuevo Milenio. Ediciones Científicas

Universitárias, Universidad Nacional Autónoma de México/ Wildlife Conservation Society, New York, pp. 551–600.

Sanderson, E.W., Chetkiewicz, C.-L.B., Rabinowitz, A., Redford, K.H., Robinson, J.G., Taber, A.B., 1999b. Prioridades geográficas para la conservación del jaguar. In: Medellín, R.A., Equihua, C., Chetkiewicz, C.-L.B., Crawshaw, P.G., Jr.Jr., Rabinowitz, A., Redford, K.H., Robinson, J.G., Sanderson, E.W., Taber, A.B. (Eds.), El Jaguar en el Nuevo Milenio. Ediciones Científicas Universitárias, Universidad Nacional Autónoma de México/ Wildlife Conservation Society, New York, pp. 601–627.

Saunders, N.J., 1998. Icons of Power: Feline Symbolism in the Americas. Routledge, London.

Schaller, G.B., 1983. Mammals and their biomass on a Brazilian ranch. Arq. Zoo. São Paulo 31 (1), 1–36.

Schaller, G.B., Crawshaw, P.G., 1980. Movement patterns of jaguar. Biotropica 12, 161–168.

Seymour, K.L., 1989. *Panthera onca*. Mammal. Species 340, 1–9.

Siemel, S., 1953. Tigrero! Ace Books. A.A. Wyn Inc., New York.

Silver, S.C., Ostro, L.E.T., Marsh, L.K., Maffei, L., Noss, A.J., Kelly, M.J., Wallace, R.B., Gomez, H., Crespo, G.A., 2004. The use of camera traps for estimating jaguar (*Panthera onca*) abundance and density using capture/recapture analysis. Oryx 38 (2), 148–154.

Smith, J.L.D., Tunhikorn, S., Tanhan, S., Simcharoen, S., Kanchanasaka, B., 1999. Metapopulation structure of tigers in Thailand. In: Seidensticker, J., Christie, S., Jackson, P. (Eds.), Riding the Tiger: Tiger Conservation in Human-dominated Landscapes. Cambridge University Press, Cambridge, UK, pp. 166–175.

Soisalo, M.K., 2004. Estimating jaguar (*Panthera onca*) densities usingi camera-trap capture–recapture surveys in a southern Pantanal ranch, Brazil. M.Phil. Dissertation, Wildlife Research Group, University of Cambridge, UK.

Sunquist, M.E., Sunquist, F.C., 2002. Wild Cats of the World. The University of Chicago Press, Chicago, USA.

Swarts, F.A., 2000."The Pantanal in the 21st Century: For the Planet's Largest Wetland, an Uncertain Future" in The Pantanal of Brazil, Bolivia and Paraguay. Hudson Mac Arthur 2000. Waterland Research Institute.

Wallace, R.B., Gomez, H., Ayala, G., Espinoza, F., 2003. Camera trapping for jaguar (*Panthera onca*) in the Tuichi Valley, Bolivia. Mastozoologia Neotropical/J. Neotrop. Mammal. 10 (1), 133–139.

White, G.C., Anderson, D.R., Burnham, K.P., Otis, D.L., 1982. Capture–recapture and removal methods for sampling closed populations. Los Alamos National Laboratory Publication LA 8787 NERP, Los Alamos, NM, USA.

Wilson, K.R., Anderson, D.R., 1985. Evaluation of two density estimators of small mammal population size. J. Mammal. 66, 13–21.