The use of camera traps for estimating jaguar *Panthera onca* abundance and density using capture/recapture analysis

Scott C. Silver, Linde E. T. Ostro, Laura K. Marsh, Leonardo Maffei, Andrew J. Noss, Marcella J. Kelly, Robert B. Wallace, Humberto Gómez and Guido Ayala

Abstract Across their range jaguars *Panthera onca* are important conservation icons for several reasons: their important role in ecosystems as top carnivores, their cultural and economic value, and their potential conflicts with livestock. However, jaguars have historically been difficult to monitor. This paper outlines the first application of a systematic camera trapping methodology for abundance estimation of jaguars. The methodology was initially developed to estimate tiger abundance in India. We used a grid of camera traps deployed for 2 months, identified individual animals from their pelage patterns, and estimated population abundance using capture-recapture statistical models. We applied this methodology in a total of five study sites in the Mayan rainforest of Belize, the Chaco dry forest of Bolivia, and the Amazonian rainforest of Bolivia. Densities were 2.4–8.8 adult individuals per 100 km^2, based on 7–11 observed animals, 16–37 combined 'captures' and 'recaptures', 486–2,280 trap nights, and sample areas of 107–458 km^2. The sampling technique will be used to continue long-term monitoring of jaguar populations at the same sites, to compare with further sites, and to develop population models. This method is currently the only systematic population survey technique for jaguars, and has the potential to be applied to other species with individually recognizable markings.

Keywords Amazonia, Belize, Bolivia, camera traps, census, Chaco, *Panthera onca.*

Introduction

The jaguar *Panthera onca*, categorized as Near Threatened on the IUCN Red List (IUCN, 2003), is the largest felid in the western hemisphere and the third largest felid worldwide. Jaguars are distributed from northern Mexico to Argentina and inhabit areas in the arid scrublands of northern Mexico, the moist tropical forests of Central and South America, and the grasslands of the Pantanal in Brazil. The jaguar is a landscape species (i.e. occupying large home ranges that often extend beyond protected area boundaries, having a significant impact on the structure and function of ecosystems, and requiring a diversity of ecosystem types; Coppolillo *et al.*, in press; Sanderson *et al.*, 2002a). Jaguars are currently threatened by the effects of habitat destruction and fragmentation, illegal hunting and prey depletion. The current estimated known range of the jaguar is thought to be <50% of its range in 1900, although 70% of the area within their current range is thought to have a high probability of being able to support their long-term survival (Sanderson *et al.*, 2002b).

Like many other large felids, jaguars are difficult to monitor because of their cryptic nature, large home range sizes, and low population densities. Recent efforts to develop a range-wide approach to jaguar conservation (Sanderson *et al.*, 2002b) brought to light a lack of population data for the species. Despite more than three decades of field research on jaguars, few studies have estimated jaguar populations. Where estimates have been made, they are usually based upon assumptions about the occurrence and home range sizes of a few individuals (Schaller & Crawshaw, 1980; Rabinowitz & Nottingham, 1986; Crawshaw & Quigley, 1991; Aranda, 1998). To achieve conservation objectives that adequately protect jaguar populations, conservation planners need accurate estimates of densities across a variety of habitats.

In an effort to provide a population monitoring technique that can be used throughout the jaguars' range, we adapted a method first developed and implemented

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by Karanth & Nichols (Karanth, 1995; Karanth & Nichols, 1998, 2000, 2002) to monitor tiger *Panthera tigris* populations in India. The technique takes advantage of distinctive individual markings through photographs taken with remote camera stations, and applies the theoretical framework of mark/recapture models to estimate population abundance (Otis *et al.*, 1978; Nichols, 1992).

Study sites

Surveys were carried out at a total of five study sites, two in Belize and three in Bolivia (Fig. 1). In Belize the two sites were in the broadleaf tropical moist rainforest of the 5,000 km^2 Maya Mountain complex. Cockscomb Basin Wildlife Sanctuary is a 400 km^2 area on the eastern slope of the Maya Mountains in south-central Belize, Central America, located 15 km from the Caribbean Sea and with elevations of 50–1,120 m (Kamstra, 1987). The survey was undertaken in a comparatively flat area, with 75% of the area below 200 m (Kamstra, 1987). The Sanctuary has a mixture of evergreen and semi-evergreen broadleaf tropical forest (Kamstra, 1987), consisting primarily of various stages of disturbed and secondary growth. Silver (1997) and Ostro (1998) provide an extensive description of the study area. Trails were cut during the 3 months prior to the camera trapping in February 2002. The 1,775 km^2 Chiquibul Forest Reserve at an altitude of 500 m on the western side of the Maya Mountain Divide lies within the Chiquibul National Park. The vegetation is a mosaic of deciduous semi-evergreen, deciduous seasonal forest, with stands of pine *Pinus carribea* in the northern sector (Wright *et al*., 1959). Some blocks of the Chiquibul Forest Reserve have been, and are still being, selectively logged for commercially important species such as mahogany *Swietenia macrophylla*, cedar *Cedrela odorata*, and pine on a >40 year rotational basis. The Las Cuevas Research Station is the only permanent settlement in the forest. Rainfall averages *c*. 1,500 mm per year with the rainy season from June to January. Study trails were opened specifically for camera trapping in the more remote areas of the reserve in January 2002, with the survey following immediately after.

Two of the sites in Bolivia were in the tropical dry forest of the 35,000 km^2 Kaa-Iya del Gran Chaco National Park. Tucavaca field camp on the north-eastern side of the Kaa Iya National Park lies on the Bolivia-Brazil gas pipeline, 85 km south of the town of San José de Chiquitos. The vegetation is transitional (to Chacoan) Chiquitano dry forest, with scrub patches resulting from burns *c*. 30 years ago. Annual averages for temperature and precipitation are 26° C and 800 mm, respectively. Existing roads consist of the gas pipeline (a 30 m wide right-of-way, with a 3–6 m wide road to one side or in the centre) built in 1998, the road north to San José, open since 1998, and an overgrown road south to Paraguay. In 2001, one year before the survey described here, we opened a grid of study trails that includes four squares each measuring 5 × 5 km, centred on the field camp lying at the intersection of the gas pipeline with the San José road. Cerro Cortado field camp is located on the south-western side of the Kaa-Iya del Gran Chaco National Park. The vegetation is xeric Chacoan forest. Annual averages for temperature and precipitation are 26° C and 550 mm, respectively (Montes de Oca, 1997). In 1997 we reopened an overgrown road to Paraguay and a grid of trails extending 2–4 km on either side along 14 km of the road. These trails were used during the survey in 2002.

The third site in Bolivia was an Amazonian rainforest site in the Madidi National Park and Natural Area of Integrated Management. The region is characterized by

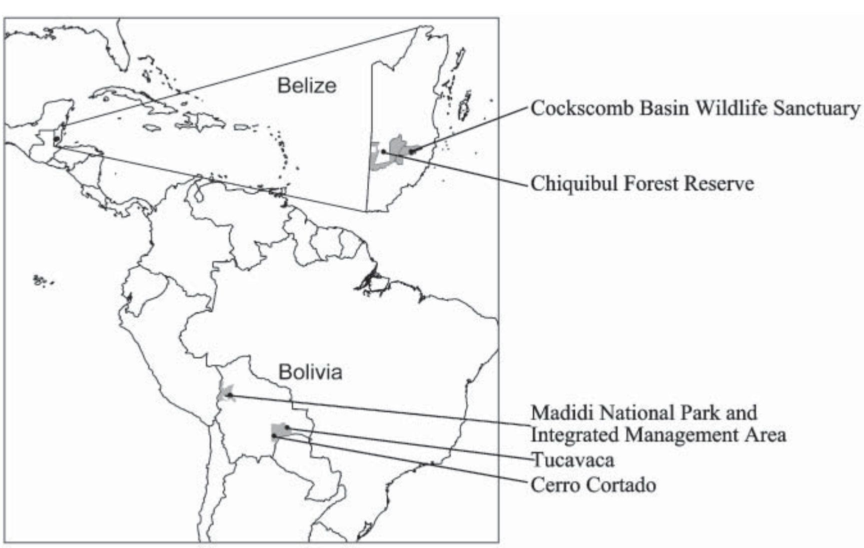

Fig. 1 Locations of the study sites in Cockscomb Basin Wildlife Sanctuary and Chiquibul Forest Reserve, Belize, and Madidi National Park and Kaa-Iya Del Gran Chaco National Park (KINP), Bolivia.

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a marked dry season between April and November and a mean annual precipitation of 2,230 mm. This forest is characterized by a relatively open canopy and a large proportion of palms of the genera *Scheelea*, *Astrocaryum*, *Socratea* and *Jessenia*. For 8 years before the creation of the Madidi protected area in 1995 the area was exploited for high-value commercial timber species. The camp was situated at Pacaysal on the Tuichi River and at Marihui on the Hondo River. Cameras were placed during the dry season on beaches along the Tuichi and Hondo rivers and several smaller tributaries, as well as on a grid of trails established between 2001 and 2002 immediately prior to and during the survey.

Methods

Mark-recapture methods assume individuals can be identified to determine whether they have been 'captured' and 'recaptured'. Because individual jaguars are easily identified by variation in their rosettes (Plate 1), photographs from camera traps facilitate this analytical technique (Wallace *et al.*, in press). Another assumption of the method is that of demographic closure of the sample population. The model assumes no births, deaths or migration during the sample period. Karanth & Nichols (1998, 2000) used 3-month sample periods to ensure demographic closure for tigers. Our studies took place over *c.* 2 months.

The final major assumption of the model is that no jaguars within the sampled area have a zero probability of being captured. The smallest conservatively estimated home range size for jaguar is 10 km^2 for a female jaguar in a Central American tropical forest habitat (Rabinowitz & Nottingham, 1986). With no data from the dry forest Chaco sites in Bolivia, we assumed home ranges in the Chaco to be roughly twice as large (20 km^2) for a female jaguar. Consequently, we placed cameras such that no areas without cameras greater than 10 km^2 (rainforest in Belize and Bolivia) or 20 km^2 (dry Chaco forest in Bolivia) existed within the sample area.

The camera stations were located to maximize the number of jaguar captures, while covering as large an area as possible to maximize the number of individuals photographed. In most cases cameras were placed in areas where there was evidence of jaguar in the form of tracks, scrapes or past sightings. However, to satisfy the assumption that all animals have at least some probability of being photographed, camera stations were established in areas with little or no jaguar sign when necessary. The camera stations were placed within 100 m of pre-selected coordinates on human trails, game trails, stream beds, and open and overgrown logging roads with signs of jaguar or their prey. Where necessary, new

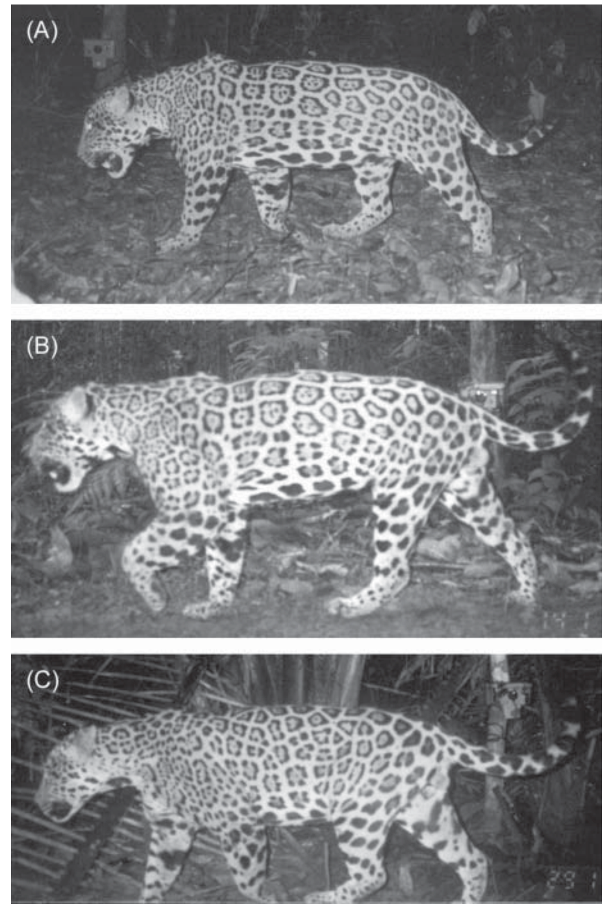

Plate 1 Two individual jaguars caught by phototraps. (A) and (B) show male jaguar M00-1; examination of the rosettes show them to be identical in shape and location on the animal. (C) shows a different jaguar male (M00-5); the rosettes are clearly different in shape and location from M00-1.

trails were cut to establish stations in more remote areas. At the Chiquibul site two separate but adjacent grids of nine camera stations each were established and run sequentially, each for 27 days for a total of 54 days.

At the Bolivian Chaco sites, because of the lack of obvious stream beds and game trails, we sited most camera trap stations on a grid of research trails. The exceptions were set at salt licks and seasonal ponds. At the Amazonian site in Bolivia there were no roads and camera traps were therefore placed along the beaches of rivers and streams, and on a number of trails cut for the purpose. At the Madidi site, two separate but adjacent grids of 32–34 camera stations were established and run sequentially.

At all sites we set up two cameras, one on either side of the trail, stream or beach, to ensure that pictures were taken of both sides of any jaguars that passed by (allowing positive identification of individuals despite asymmetric coat patterns) and to ensure redundancy in case of camera failure. In Belize, the Cockscomb survey used Camtrakker camera traps triggered by heat and motion sensors, while in the Chiquibul site and at the Bolivia sites we used a combination of Camtrakker and Trailmaster camera traps, with the latter triggered by disturbance of an infra-red beam. Cameras were positioned opposite each other, 30–60 cm above the ground, at least 1 m off the trail where we expected the jaguar to pass, and faced slightly down the trail to prevent mutual interference, but set to fire simultaneously. Cameras functioned continuously for a period of 29–61 days, with rolls of 36-print, 400 ASA (Belize and Bolivian Amazon) or 100 ASA (Bolivian Chaco) 35 mm film. Each station recorded the date and time of day of each photograph. Each camera station was checked approximately every 12–14 days (Belize) or 3–5 days (Bolivia) to ensure that they still functioned and to change film as necessary.

Individual jaguars were identified by variations in their pelage patterns. The number of photographed and re-photographed animals was analysed using the software CAPTURE (Otis *et al.*, 1978; White *et al.*, 1982; Rexstad & Burnham, 1991). This programme uses a number of different models to generate abundance estimates for the sampled area, based on the number of individual animals captured and the frequency of recaptures. These models differ in their assumed sources of variation in capture probability, including variation among individuals, over time, as a result of having been captured, and various combination of these. CAPTURE also has a model selection function that analyses the data set to determine which model and which estimator best fits the data in question. Finally, CAPTURE computes a closure test statistic to test the closed population assumption for each data set.

Density estimates were generated by dividing jaguar abundance by the effective sample area. The effective sample area included a circular buffer around each camera trap site, whose radius was half the mean maximum distance among multiple captures of individual jaguars during the sample period (Wilson & Anderson, 1985).

Results

All sampling was conducted over a continuous 2-month period, with a variable number of camera stations and trap nights at each site (Table 1). The number of individuals identified at each site varied from 7 to 11, and the number of total captures and recaptures varied from 16 to 37 (Table 2). The largest mean maximum distance between recaptures of individuals was in the Tuichi/Hondo basin at Madidi in Bolivia (n = 4 animals recaptured), and the smallest was in the Chiquibul Forest Reserve (n = 4 animals recaptured) site (Table 3).

Table 1 Characteristics of sample effort for each camera trap survey site.

Study site	Dates (2002)	Days	Camera stations	Trap nights
Cockscomb, Belize	4 Feb.–4 Apr.	59	20	1,180
Chiquibul, Belize	12 Jan.–20 Mar.	54[1]	18[2]	486
Tucavaca, Bolivia	19 Jan.–20 Mar.	60	18	1,080
Cerro Cortado, Bolivia	1 Apr.–30 May	60	38	2,280
Madidi, Bolivia	25 June–1 Sep.	56[3]	66	1,848

[1]Two adjacent grids each with nine stations were run for 27 days each for a total of 54 days. The second grid was run directly after the first with a short break in between while cameras were moved from grid 1 to grid 2.
[2]Although 18 stations were established, three were eliminated in the final analysis due to double camera failures in the field.
[3]Two adjacent grids, one with 32 stations and another with 34 stations, were run sequentially for 28 days each for a total of 56 days. A break of 13 days was required to remove stations and then reset at the second site.

Closure test results indicated that there was no violation of the closed population assumption (Table 3). Density estimates for each site based on analysis using CAPTURE varied from 2.8 to 8.8 individuals per 100 km^2, and the effective area sampled ranged from 107 to 458 km^2 (Table 3). For all sites we have presented the results of the jackknife population model M(h). This model incorporates variable probabilities of the capture of individual jaguars, and of the available models it is the one we consider to be most reflective of the biological reality (c.f. Karanth and Nichols, 1998, for a discussion of the merits of various models). Resulting density estimates for jaguars ranged from a low of 1 per 40 km^2 in the Tuichi/Hondo to a high of 1 per 11 km^2 in Belize's Cockscomb Basin Wildlife Sanctuary.

Discussion

This is the first use of the photographic capture/recapture sampling technique for estimating abundance of jaguars. The technique provides a statistically robust estimate grounded in mark/recapture analysis that can be used in both tropical moist and tropical dry forest ecosystems to determine jaguar densities within a short period of time. Confirming the previous research with tigers, this study demonstrates the viability of the method for estimating densities of individually recognizable species that have been traditionally difficult to study because of cryptic habitats, large home ranges, and low population densities. Additional species in the Neotropics that could be monitored using this method include the other spotted felids such as ocelot *Leopardus pardalis*, margay *Leopardus wiedii*, and Geoffroy's cat *Oncifelis geoffroyi*.

Table 2 Jaguar captures and recaptures by study site, with estimated capture probability ($\hat{p}$) per sampling occasion under the jackknife model of variable probability of capture (M(h)).

Study site	Total captures + recaptures	Individuals	Individuals recaptured	Male	Female	Unknown sex	$\hat{p}$
Cockscomb, Belize	37	11	6	9	0	2	0.04
Chiquibul, Belize	17	7	4	4	1	2	0.07
Tucavaca, Bolivia	22	7	4	3	3	1	0.05
Cerro Cortado, Bolivia	22	7	5	3	3	1	0.03
Madidi, Bolivia	16	9	4	5	3	1	0.04

Table 3 Results of closure test for the closed population assumption, and abundance and density estimates for each study site using the jackknife population model M(h), in which capture probabilities vary by animal because of differences in sex, age, social dominance, and activity level.

Study site	Abundance ±SE	95% confidence interval	Closure Test		Sample area (km^2)	Buffer: 1/2MMDM* (km) ± SE	Density (per 100 km^2) ± SE
			z	P			
Cockscomb, Belize	14 ± 3.57	12–30	–0.93	0.18	159	1.95 ± 1.18	8.80 ± 2.25
Chiquibul, Belize	8 ± 2.51	8–19	–1.03	0.15	107	1.55 ± 0.81	7.48 ± 2.74
Tucavaca, Bolivia	7 ± 2.63	7–20	–0.43	0.34	272	2.99 ± 0.89	3.93 ± 1.30
Cerro Cortado, Bolivia	8 ± 3.01	8–25	–0.27	0.40	137	2.41 ± 1.12	5.11 ± 2.10
Madidi, Bolivia	13 ± 8.16	10–57	–0.22	0.41	458	3.55 ± 1.40	2.84 ± 1.78

*MMDM, Mean maximum distance moved by individuals photographed on separate capture occasions.

The number of camera traps, sample period, and sample area necessary to generate an abundance estimate varies amongst sites and are a function of jaguar abundance. A minimum number of individuals must be photographed/re-photographed for CAPTURE to generate an abundance estimate, although with a smaller data set the number of individuals identified still provides a minimum population abundance estimate (Wallace *et al.*, in press). With a sufficiently high density of subject animals, a small number of camera trap sites functioning for a short period of time may produce sufficient observations to generate an abundance estimate. Likewise a low-density population can be sampled if sufficient camera traps are used and there is logistical support to operate them. The only limitation is that the sample period should not be so long as to violate the assumption of demographic closure of the sample population. Where existing roads or river beds are scarce, as in Bolivia's Kaa-Iya del Gran Chaco National Park, opening study trails several months before sampling can result in successful abundance and density estimates. Jaguars, like other carnivores, soon begin to use these trails, and camera traps can be placed along them.

We successfully deployed the technique under a variety of habitat conditions different from that of previous work on tigers (Karanth & Nichols, 1998, 2002). Each of the five study sites exhibited differences in road and trail density, types and levels of human disturbance, as well as vegetative, topographic, and meteorological differences. Four of the sites deployed the camera trap design without use of motor vehicles. Each site represents substantially different challenges for using the sampling technique, and resulted in major differences in capture probability (Table 2).

The limitations to the technique need to be considered. At a current price of several hundred dollars per camera trap, sampling a jaguar population represents a substantial financial investment in equipment. Using fewer cameras in a systematic rotation can reduce equipment costs, but requires substantially more effort. In areas with considerable human activity, cameras are also subject to theft and vandalism. Topographical challenges also exist. Opening trails, where roads or rivers do not exist, may not be recommended in areas where such trails would facilitate and encourage illegal activities such as hunting or logging within study areas. Trained field assistance must be available throughout the sampling period to monitor all camera trap sites so that film can be collected and changed as necessary, and any damaged, tampered with, or malfunctioning cameras can be removed and replaced.

The photographic capture/recapture sampling technique provides a valuable tool for formulating global and local jaguar conservation strategies. With population data, conservation managers can begin to make decisions based upon sound principles of small population management. Estimates of carrying capacities, population sizes, and population trends provide important information for ensuring that sufficient areas are available for minimum viable population sizes. Density estimates from multiple sites and habitat types will provide better estimates of global jaguar populations, and scientific data to justify support for existing protected areas as well as the creation of new protected areas for jaguar. Repeated camera trap density estimates from the long-term sites described in this study will facilitate population monitoring and the development of population models for jaguar conservation programmes.

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Biographical sketches

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