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One thousand jaguars (*Panthera onca*) in Bolivia's Chaco? Camera trapping in the Kaa-Iya National Park

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Abstract

This paper reports on efforts to trap jaguars *Panthera onca* on camera in the dry forests of the Kaa-Iya del Gran Chaco National Park in Bolivia. Ad hoc camera trapping provided certain information on jaguar presence and habits, but was limited in application. Activity patterns showed that jaguars are active all day, particularly at one of three sites, with peaks in the morning and evening the more common pattern. Minimum observed home range was variable, with males (up to 65 km^2) occupying more area than females (up to 29 km^2). The authors adapted systematic methodologies first developed to survey tigers in India, based on individually distinctive pelage patterns in tigers and jaguars. Abundance is estimated using capture–recapture statistical analysis, and a sample area defined based on the maximum distance that individual jaguars move during the sample period. The methodology has proved successful for jaguars in dry Chaco forest, population densities of 1/30–45 km^2 and 1/20 km^2 are estimated in the two most extensive landscape systems of Kaa-Iya. The entire 34 400 km^2 protected area is estimated to sustain a population of over 1000 adult and juvenile jaguars, the largest single population of jaguar reported anywhere, and a viable population for long-term jaguar conservation.

Key words: survey, camera trap, landscape species, *Panthera onca*, Chaco

INTRODUCTION

The jaguar *Panthera onca* is the largest felid in the western hemisphere, the top predator in lowland ecosystems, an important figure in many indigenous cultures, and of economic importance as a tourist and sport hunting attraction, though to some degree offset by predation on domestic livestock (Rabinowitz, 1986; Hoogesteijn, Hoogesteijn & Mondolfi, 1993; Hoogesteijn, 2001; Medellín *et al.*, 2002). These attributes have been systematized in the context of the Wildlife Conservation Society's (WCS) Living Landscapes Program, which at several long-term conservation sites has identified jaguars as a landscape species, i.e. species that occupy large home ranges often extending beyond protected area boundaries, that have a significant impact on the structure and function of ecosystems, and that require a diversity of ecosystem types (Coppolillo *et al.*, 2003; Sanderson, Redford, Vedder *et al.*, 2002). Since 1999, WCS has further focused attention on jaguar conservation across their range through a Jaguar Conservation Program (Medellín *et al.*, 2002). One element of this program has been the systematic definition and identification of jaguar conservation units (JCU) as areas where the population of resident jaguars is potentially self-sustaining over the next 100 years (Sanderson, Redford, Chetiewicz *et al.*, 2002).

The primary JCU in the Chaco dry forest geographic region is the Gran Chaco of Bolivia and Paraguay, including the 34 400 km^2 Kaa-Iya del Gran Chaco National Park. One of the justifications for the protection of this enormous area, created in 1995, was its potential over the long-term to maintain wide-ranging and low-density species such as the jaguar and white-lipped peccaries (Taber, Navarro & Arribas, 1997). To focus conservation action accordingly within the Gran Chaco JCU, our principal objective was to know whether the Kaa-Iya National Park protects enough individuals to ensure the long-term survival of this species in the Gran Chaco. Secondary objectives were to describe jaguar behaviour in South American dry forest habitats, to describe the variation in density estimates across landscape systems within the Kaa-Iya National Park, and to compare density estimates from the Chaco with other eco-regions where higher rainfall would presumably coincide with higher jaguar densities: Brazilian Pantanal, Amazonian rainforest, and Belizean rainforest.

Previous field research on jaguar populations has focused on dry and humid forests in Central America, and on Atlantic rainforest and the Brazilian Pantanal in South

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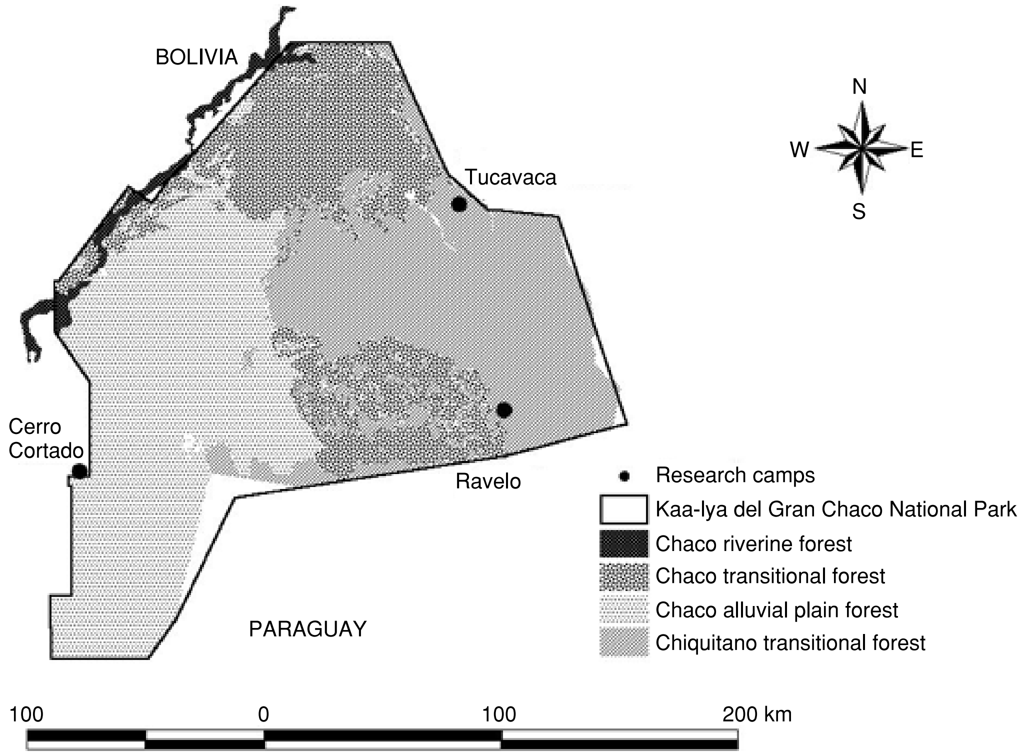

Fig. 1. Landscape systems and research camps of the Kaa-Iya National Park.

America (Schaller & Crawshaw, 1980; Rabinowitz & Nottingham, 1986; Crawshaw & Quigley, 1991; Aranda, 1998; Medellín *et al.*, 2002). The status of the jaguar in other ecosystems is unknown. Existing information on jaguars for the Chaco is restricted to opportunistic observations and a study of diet based on scats (Taber, Novaro *et al.*, 1997). This paper describes the first efforts to evaluate jaguar populations in South American dry forests, applying camera trap survey methods at three widely separated sites in two distinct landscape systems of the Kaa-Iya National Park to estimate densities and total population for the protected area, to describe jaguar behaviour in the Gran Chaco, as well as to provide baseline information for monitoring, population modelling, and landscape conservation planning.

Study sites

The dry forest vegetation of the Kaa Iya National Park has been described in detail by Navarro & Fuentes (1999), who identify four landscape systems for the protected area (Fig. 1). The riverine Chaco forest landscape system covers $< 2\%$ of the Park's area, while the other three landscape systems each occupy 25–40%. Chaco transitional and Chaco alluvial plain forests are generally low (4–8 m) with emergents (15–20 m), dense and thorny (Taber, Navarro *et al.*, 1997), though Chiquitano transitional and riverine forests are somewhat taller (8–20 m) and have a smoother canopy (Navarro & Fuentes, 1999). Annual temperatures for the entire area average 25–26 °C, while the dry season lasts 4–6 months. Roads into the protected area are scarce, though oil exploration in the early 1970s temporarily opened a network of roads that has since been closed by vegetation. Up to the mid-1980s all three sites were subject to commercial hunting for skins of jaguar, ocelot *Leopardus pardalis* and fox *Pseudalopex gymnocercus* and *Cerdocyon thous*. Our long-term research camps are at three sites (Fig. 1), with *c*. 100 km separating Tucavaca from Ravelo, and 180–200 km separating Cerro Cortado from the other two sites:

(1) *Tucavaca field camp* (18°30.97′S, 60°48.62′W) was established in 2001 on the Bolivia–Brazil gas pipeline, 85 km south of the town of San José de Chiquitos on the north-western side of the Kaa-Iya Park. The vegetation is Chaco–Chiquitano transitional dry forest with scrub patches where the forest was burned roughly 30 years ago, and small patches of palm forest. Annual precipitation averages 800 mm. Existing roads include the gas pipeline itself (30 m-wide right-of-way, with a 3–6 m-wide road to one side or in the centre) and a gravel road north to San José. A square grid of 5-km study trails has been opened, enclosing a 100-km^2 study area centred on the field camp and the gas pipeline. The nearest cattle are over 30 km away and the area has not been hunted since the Park's creation in 1995 (Maffei, Cuéllar & Noss, 2002; Maffei, Cuéllar, Peña *et al.*, 2002).

(2) *Ravelo field camp* (19°17.72′S, 60°37.23′W) was established in 2001 at the military outpost of the same name (manned by 12 soldiers), at the foot of Cerro San Miguel which rises 500 m above the surrounding plain, and 15 km from the Paraguayan border. The vegetation is again Chaco–Chiquitano transitional dry forest with

patches of palm forest. Annual precipitation averages 700 mm. A single road (5 m wide) passes through the area connecting the town of Roboré to the north-east to Paraguay, and 32 km of study trails have been opened. The soldiers keep a herd of 30 cattle but report no predation by jaguar in recent years, and hunting has been prohibited since the creation of the Park (Cuéllar *et al.*, 2003).

(3) Cerro Cortado field camp (19°31′′36′S, 62°18′′ 34′W) was established in 1997 along an overgrown oil prospecting road entering the western side of the Kaa-Iya Park. The vegetation is Chaco alluvial plain forest. Annual precipitation averages 550 mm. A grid of 2-km trails has been opened demarcating a *c.* 64 km^2 study area centred on the field camp and the pre-existing road. The nearest domestic livestock are 20 km away, and the nearest communities 30 km away. Local hunters visit the north-western edge of the sample area in pursuit of armadillos and ungulates, but have not killed jaguar in the past 5 years (Maffei, Barrientos *et al.*, 2002, 2003).

METHODS

Camtrakker® and Trailmaster® active and passive remote camera traps triggered by both heat and motion were used. Initial work at the Cerro Cortado site focused on ungulate species important to local hunters, with direct and indirect observations of jaguar recorded opportunistically. In contrast, work at the Tucavaca site began with a focus on jaguar, recording again direct and indirect observations, but also placing 12 camera traps where jaguars or jaguar signs had been observed (as suggested by Karanth & Nichols, 1998) on newly opened study trails and the gas pipeline in an attempt to record and identify individual animals over an 8 month period. Work at Ravelo also began with a focus on jaguar, recording observations and placing 4–7 camera traps during 6 months in an ad hoc fashion along study trails and at seasonal ponds.

These initial efforts were followed by systematic camera trapping surveys at all 3 sites, representing the 2 largest of the 4 landscape systems, covering 73%, of the Kaa-Iya National Park. The systematic surveys were repeated at 2 of the sites to cover both the wet and dry seasons. These surveys are based on a methodology developed for tiger *Panthera tigris* monitoring in India by Karanth and Nichols (Karanth, 1995; Karanth & Nichols, 1998, 2000) and in Latin America (Maffei, Cuéllar & Noss, 2002; Silver *et al.*, in press). The technique takes advantage of the distinctive individual markings of spotted big cats, identifying individual animals 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). Camera stations are set out with 2 cameras to photograph simultaneously both sides of an animal passing in between them along a trail; 26–34 camera stations were placed 1–2 km apart along all roads and trails in the study areas.

The method seeks to maximize the chances of photographing a jaguar, but we were unable to identify factors that would increase the likelihood of jaguar visitation aside from the trails/roads themselves, which greatly facilitate movement through the dense and thorny vegetation. At all 3 sites existing roads were used as well as trails opened for jaguar surveys and other research purposes. At Cerro Cortado and Ravelo, cameras were also set at salt licks, ponds, and around the edges of a salt pan. Cameras were also spaced to avoid gaps in the sample area large enough to accommodate an adult female jaguar home range. In other words, the camera trap placement should ensure that no adult jaguar within the sample area would have a zero capture probability, and that any animal whose home range overlapped with the survey area would have a capture probability > 0. The spacing among camera stations was calculated by halving the mean distance of 6.4 km moved by a female jaguar at Tucavaca during the pilot study period, and erring on the conservative side with cameras 2–3 km apart. Following the surveys, the sample area at each site was calculated by drawing a buffer around each camera station equivalent to half the mean maximum distance covered by individual animals photographed more than once during the survey period (Wilson & Anderson, 1985). These buffers left no gaps within the sample area.

The camera traps were programmed to take photographs 24 h/day, with a 3-min interval between photos, and to record date and time on each photograph. Because cameras operated continuously for the 60-day survey period, it was assumed that captures by time period reflect jaguar activity patterns in the study areas. After developing the film, individual jaguars were identified in photographs by variations in their spot patterns. Using the software program CAPTURE (Otis *et al.*, 1978; Rexstad & Burnham, 1991), the number of individual animals (adults and juveniles) captured and the frequency of recaptures per individual we analysed to generate an abundance estimate for the sampled area. CAPTURE tests a number of models which differ in their assumed sources of variation in capture probability, including variation among individuals (e.g. based on sex, age, ranging patterns, dominance, activity), variation over the sample period, and responses to having been captured. CAPTURE in turn identifies the model that best fits the dataset in question. Trap-nights were not grouped but rather each trap-night was considered to be a separate sampling occasion. To estimate densities for each study site, the abundance calculated above was divided by the sample area. Finally, a minimum home range was estimated for animals photographed at > 3 locations by measuring the area of the minimum convex polygon connecting the locations (Lynam, Kreetiyutanont & Mather, 2001).

RESULTS

Capture frequencies (2–20/1000 trap-nights, mean 10.1, SE 5.5) were low at all sites. A total of 26 jaguars was identified across all three sites from May 2001 to June 2003 (Table 1): seven females, 12 males, three juveniles, one cub, and three unsexed adults. We observed juveniles

Table 1. Jaguar *Panthera onca* individuals and captures. M, male; F, female; J, juvenile

Tucavaca	T1	T2	T3	T4	T5	T6	T7	T8	T9		
	M	F	M	F	M	M	F	J	?		Total
Ad hoc May–Dec 2001		14[a]	1				3		2		20
Survey I Jan–Mar 2002	11	5	1	2	3	1	1				24
Survey II Apr–Jun 2003		3				4	3	2			12
Cerro Cortado	C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	
	M	M	M	F	M	F	J	M	M	?	Total
Survey I Apr–May 2002	8	3	4	3[b]	1	2	1				22
Survey II Nov ‘02–Jan ‘03				8	6		1	4	5	1	25
Ravelo	R1	R2	R3	R4	R5	R6					
	M	?	M	F	F	J					Total
Ad hoc Feb–Jul 2001				1	2						3
Survey Feb–Mar 2003	1	2	12	4		4					23

[a] Accompanied by one cub on three occasions.
[b] Accompanied by one cub on a single occasion.

at all three sites, representing 15% of the population, in each case a single juvenile per female. Among adults, males outnumbered females 2:1.

Direct observations and pilot trapping

Four adults (two females, one male, one unsexed) and one cub were photographed during the pilot study from May to December 2001 at Tucavaca ($n = 2520$ trap-nights on trails and along the gas pipeline). Also, jaguars were encountered (direct observations) on three occasions during the 8 months of 2001, as well as five times during the 60-day survey period in 2002. During 5 years of continuous field work at Cerro Cortado, jaguars were encountered on only three occasions. At Ravelo during the pilot study from February to July 2001 ($n = 1248$ trap-nights at seasonal ponds and along study trails), three jaguar photographs of two different individuals were obtained.

Systematic surveying

The first capture–recapture sampling at Tucavaca ran from 19 January to 20 March 2002 ($n = 1920$ trap-nights). Three of the four adults identified during the pilot period were again photographed during the survey (the cub was seen but not photographed), as well as four additional adult animals (two males, one female, and one unsexed). The second survey ran from 11 April to 11 June 2003, registering three of the adults previously identified (two females, one male) as well as a juvenile animal accompanying female T107. Including the pilot study, one male was observed over 17-months (T106), two males over 2-months (T101 and T105), one male over 3-months (T103), and two females over 24-months (T107 and T102).

At Cerro Cortado between 1 April and 30 May 2002 ($n = 2280$ trap-nights), six adult jaguars (two females, four males) and one juvenile were photographed. During the second survey from 25 November 2002 to 25 January 2003 ($n = 1660$ trap-nights), six adult jaguars (two females, three males, one unsexed) and the same juvenile recorded previously were photographed. Three males and one female present in the first survey were not recorded in the second survey 8 months later, and were replaced by two males and one unsexed individual. During the second survey, the juvenile animal was photographed only once, together with female C104 and male C108.

At Ravelo between 8 February and 8 April 2003 ($n = 2160$ trap-nights), four adult jaguars (two male, one female, and one unsexed), and one juvenile accompanying female R104 were photographed. This female had been recorded during the pilot study 2 years previously, while the other female observed during the pilot study did not appear during the systematic survey.

Activity patterns

Figure 2 presents activity patterns for jaguar obtained from 121 observations at all three sites combined. Jaguars in the Kaa-Iya National Park can be active at any hour of the day. However, diurnal records are concentrated at Tucavaca, whereas crepuscular peaks in the morning (05:00–10:00) and evening (17:00–19:00) are more pronounced at Cerro and Ravelo, with a decline in activity around midnight.

Ranging patterns

From the 2-year study period at Tucavaca, multiple photographs have been accumulated for all nine jaguars,

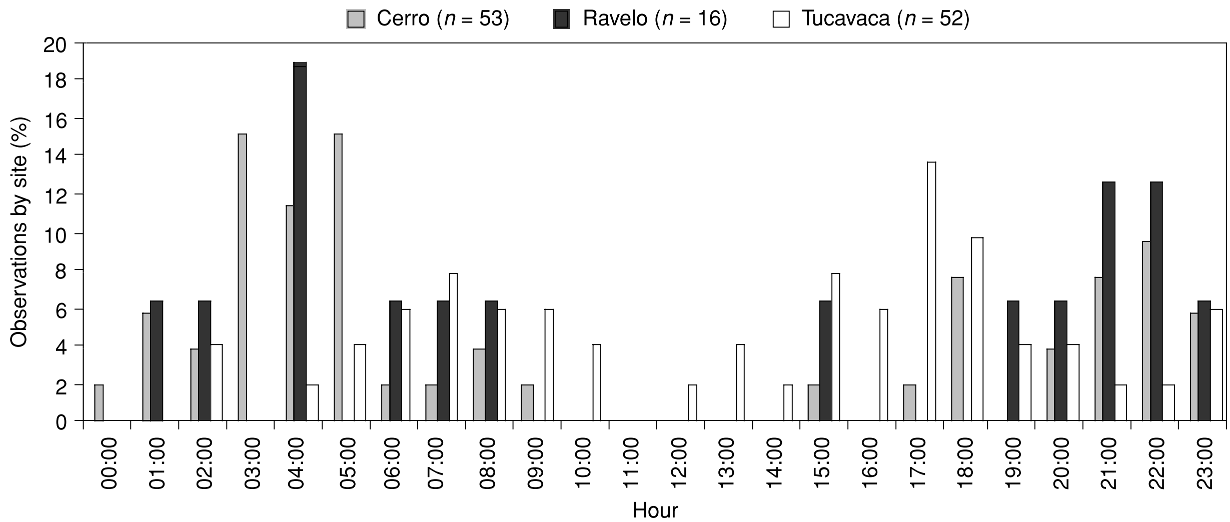

Fig. 2. Activity patterns of jaguars *Panthera onca* in dry forest, Bolivia (proportion of observations by site).

though T109 was photographed twice at a single location. The maximum distance between observations for the other eight animals ranged from 3.3 to 10.8 km (mean 6.4 km, SD 2.86 km). For the three individuals with observations at four or more locations, minimum 'ranges' (minimum convex polygon method) have been estimated: 29 km^2 for female T107 ($n = 8$ locations), 24 km^2 for female T102 ($n = 9$ locations), and 65 km^2 for male T101 ($n = 9$ locations). The observed range of male T101 encompassed the ranges of both females almost entirely (Fig. 3). During a 2-month survey period, two separate camera sets, which each captured three individual jaguars, and another camera set that captured two individual jaguars, were obtained.

From Cerro Cortado over the entire 10-month study, multiple photographs were obtained for nine of the 10 jaguars observed, but again one animal was photographed twice at the same site. The maximum distance between observations for the remaining eight animals ranges from 1.9 to 11.4 km (mean 7.0 km, SD 4.22 km). Minimum observed 'ranges' are smaller than those at Tucavaca: 23 km^2 ($n = 8$ locations) for male C101 and 20 km^2 ($n = 9$ locations) for male C105 (Fig. 4). One photograph shows three jaguars together: female C106, juvenile C107, and male C108.

From Ravelo, over the entire 25-month study, multiple photographs were obtained for five of six observed jaguars, but one was photographed twice at a single location. The maximum distance between observations for the remaining four animals ranges from 2.0 to 16.5 km (mean 7.9 km, SD 6.13 km). Minimum observed 'ranges' are 44 km^2 ($n = 6$ locations) for male R103 and 10 km^2 ($n = 4$ locations) for female R104 (Fig. 5).

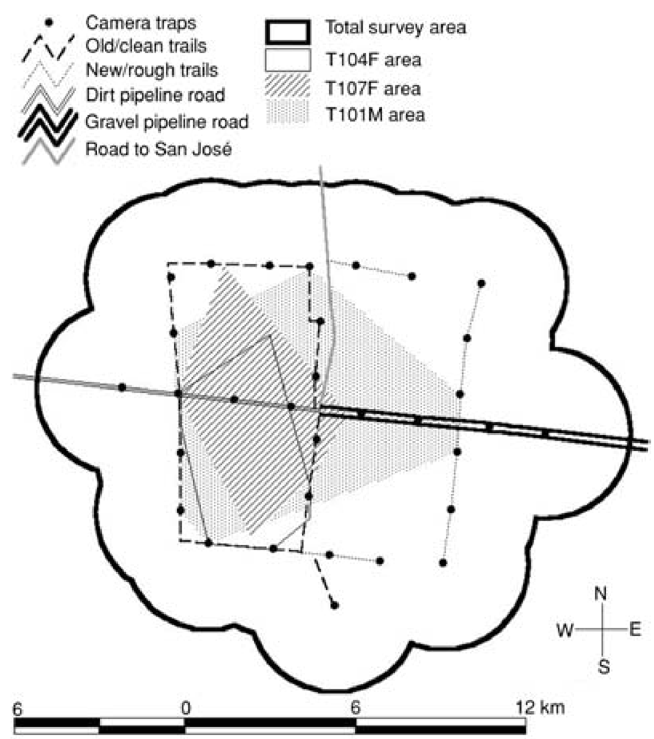

Fig. 3. Camera trap surveys and cumulative observed jaguar *Panthera onca* 'ranges' at Tucavaca I.

Capture rates and type of trail

The type of trail/road apparently affects capture rates (Table 2), with the old and relatively clean trails registering more captures at Tucavaca (G-test = 10.9, d.f. = 4, $P < 0.05$). Two jaguars together were only photographed once, on the wide gravel pipeline road in Tucavaca. At the other two sites, the road registered relatively more captures than the trails (Cerro Cortado: G-test = 26.3, d.f. = 3, $p > 0.001$; Ravelo: G-test = 33.7, d.f. = 3, $P < 0.001$). Few jaguar records were collected at ponds, salt licks or salt pans.

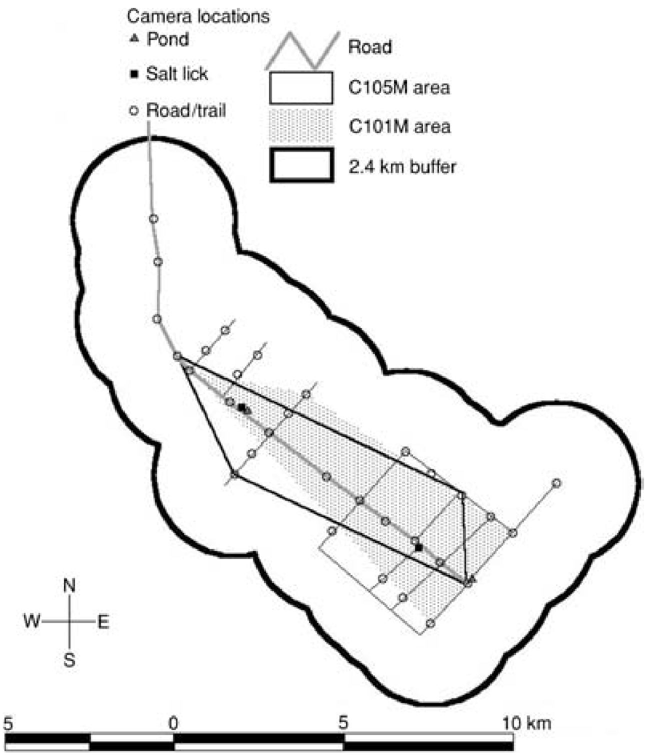

Fig. 4. Camera trap surveys and cumulative observed jaguar *Panthera onca* ‘ranges’ at Cerro Cortado I.

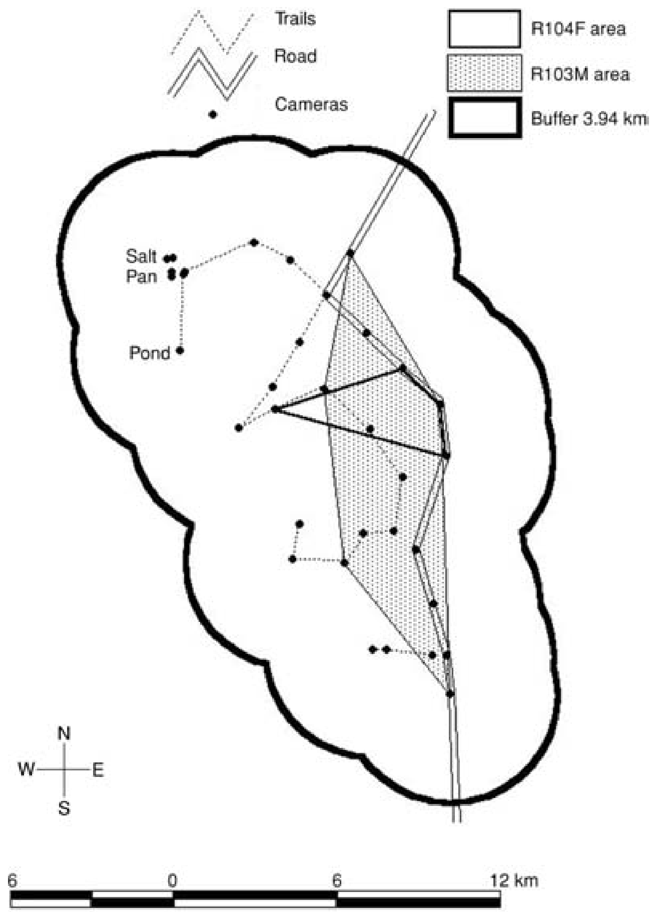

Fig. 5. Camera trap surveys and cumulative observed jaguar *Panthera onca* ‘ranges’ at Ravelo.

Jaguar densities

Despite the large number of cameras deployed, each day was considered to be a separate sampling occasion ($n = 59$–61 per survey), and capture probabilities were extremely low: $0.03 < P < 0.05$. As a result, CAPTURE generally indicated that the data were ill-suited for analysis. However, the program recommended either the null model M(o), assuming no variation in capture probability among individual jaguars, or the jackknife estimator and heterogeneity model M(h), which assumes variation in capture probability among individual (e.g. based on sex, age, ranging patterns, dominance, activity, etc.). Following Karanth & Nichols (1998), Table 3 presents the abundance estimates using the heterogeneity model because it more appropriately reflects biological reality. Table 3 also presents the buffer estimated from

Table 2. Cumulative jaguar *Panthera onca* captures by type of trail/road during systematic surveys

Type of trail/road	Trap nights	Captures	Captures/ 1000 trap-nights	Individuals	Individuals/ 1000 trap-nights
Tucavaca I + II					
Old/clean	2040	28	13	8	4
Pipeline/dirt	600	6	10	4	7
New/rough	600	2	3	1	2
Pipeline/gravel	240	0	0	0	0
Cerro Cortado I + II					
Road	1380	42	30	5	7
Trails	1980	13	7	4	4
Salt licks/ponds	340	1	3	1	4
Ravelo					
Road	590	16	27	5	8
Trails	986	5	5	5	5
Salt pan/pond	584	0	0	0	0

Table 3. Jaguar *Panthera onca* density (individuals/100 km^2) estimates

	Captures/ 1000 trap-nights	Capture probability	Abundance[a]	Buffer (km)	Area (km^2)	Density	SE
Tucavaca I	12.5	0.04	7	3.00	272	2.57	± 0.77
Tucavaca II	7.8	0.04	4	2.30	128	3.10	± 0.97
Cerro Cortado I	10.1	0.03	7	2.41	137	5.11	± 2.10
Cerro Cortado II	19.9	0.05	8	2.81	149	5.37	± 1.79
Ravelo	9.7	0.04	7	3.94	309	2.27	± 0.89

[a] Abundance is estimated by CAPTURE using M(h) model, assuming heterogeneity in capture probability among individuals.

the mean maximum distance observed for each particular survey period, the total survey area, and the resulting density. The standard error is calculated from the variances in the abundance estimate and the sample area estimate, respectively, as described in Karanth & Nichols (1998, 2002). Considering the standard error, only the Ravelo and Cerro II density estimates are statistically different.

Tucavaca

The two intermediate density estimates come from Tucavaca. For the first survey, the camera-traps covered an area of *c.* 130 km^2 around the 5 × 5 km grid of study trails. For the second survey at this site, several trails were added in a 1 × 1 km grid for an ocelot telemetry study, and concentrated the camera traps in the western portion (55 km^2) of the study area. Despite the smaller area covered by the second survey, and the smaller number of jaguars observed, the density estimate is consistent with the previous estimate. If the same buffer were used for both surveys, the resulting density estimates would be even closer.

Cerro Cortado

During the first survey, cameras were distributed over 59 km^2 of study trails, whereas in the second survey fewer cameras covered 49 km^2. The highest density estimates came from Cerro Cortado, and were not simply a product of the relatively small survey area, because the Tucavaca II camera distribution covered a similar area. The results from the two surveys were similar despite the change in the identity of the jaguars observed from one survey to the next: four individuals ‘left’ the sample area, and three new animals ‘entered.’ Contrary to the Tucavaca example above, using the same buffer for the two surveys would increase the variation among the two density estimates.

Ravelo

The camera traps were distributed over an area of 102 km^2. The lowest density estimate comes from Ravelo, and is a factor principally of the buffer distance, which is the largest of any survey. The large buffer in turn results from the observed distance of 16.5 km covered by male R103, the largest distance recorded at any site. A buffer closer to that for the other sites would result in a density estimate equal to or surpassing those from Tucavaca.

Population

Based on our surveys at the three sites, it is estimated that there is one jaguar per 30–45 km^2 in the Chiquitano transitional forest landscape system, which covers *c.* 11 500 km^2 and 33% of the Kaa-Iya protected area (minimum 250 jaguars total), and one jaguar per 20 km^2 in Chaco alluvial plain landscape system, which covers around 13 800 km^2 and 40% of the protected area (690 jaguars total). The other two landscape systems (covering 9100 km^2 and 27% of Kaa-Iya) have not yet been surveyed, but because rainfall and vegetation are intermediate between the other two landscape systems, it is assumed that jaguar densities will be similar to those recorded in the neighbouring landscape systems, at least one jaguar per 45 km^2 and 200 jaguars in total. Summing these figures, a minimum population for Kaa-Iya is roughly estimated as 1000 jaguars.

DISCUSSION

In concordance with Karanth & Nichols’ (1998) observations, work at the three Chaco sites demonstrates that neither ad hoc camera trapping nor direct observations of jaguars coincide with jaguar density estimates from systematic surveys. Ad hoc camera trapping can provide preliminary information on the presence of jaguars at a given site as well as confirming use of particular locations by jaguars. In most surveys, species density was positively correlated with the number of photographs recorded, and capture frequency may serve as an index of relative abundance (Carbone *et al.*, 2001). However, it is important to note that the capture frequencies even in systematic surveys do not always translate reliably into species density (Jennelle, Runge & MacKenzie, 2002). For example, the second Cerro Cortado survey produced 81 photographs of eight individual pumas *Puma concolor vs* 62 photographs of 18 individual ocelots. Including the differing buffer sizes and the abundances of the two species estimated in Capture, ocelot densities were estimated to be over three times puma densities, despite the higher capture frequency for the latter species (Maffei, Barrientos *et al.*, 2003). Several factors contribute to confound the relationship between capture frequency and density across sites: locations for camera placement, availability and condition of roads and trails, weather, season, camera failure, buffer estimation, etc. Although other methods are currently being developed for the identification of individual jaguars from tracks as well as from DNA analysis of scats, currently the camera trapping methodology described above is the only statistically robust method for estimating populations of jaguars.

The method is expensive, taking into account the cost of camera traps ($300–450/camera), film and batteries ($10/camera/survey), the large number of traps required, and investments in trails where road or river networks do not exist. However, radio-telemetry, an alternative method that has been used to estimate jaguar densities, is also costly in terms of radio-collars, capture equipment and effort, and data collection effort. It is also an invasive methodology that can pose a serious risk to both the subject animals and to researchers, and at least a year of research effort is required to determine home ranges. In contrast, systematic camera trapping is non-invasive, and produces a statistically rigorous density estimate within only 2 or 3 months of trapping (Karanth & Nichols, 1998).

As expected, the highest Kaa-Iya density estimate is below those resulting from surveys using the same methodology in rainforest national parks of Belize (7.5–8.8/100 km^2) and at a small private reserve in Bolivia's Chiquitano dry forest (11.1/100 km^2) (Rumiz *et al.*, 2003; Silver *et al.*, in press). Surprisingly, however, the lowest Kaa-Iya density estimate is comparable to that recorded from Amazonian rainforest in Bolivia's Madidi National Park (2.8/100 km^2) (Silver *et al.*, in press). Likewise, our density estimates suggest that Transitional Chiquitano dry forest may support lower jaguar densities, but Chacoan dry forest higher jaguar densities, than the nearby Brazilian Pantanal. Schaller & Crawshaw (1980) found one individual per 25 km^2 in a habitat where cattle (an important prey item for jaguars living on ranches) are abundant, reaching 8.8 cows per km^2. In contrast, the most abundant ungulate in Kaa-Iya is the much smaller (17 kg) grey brocket deer *Mazama gouazoubira* at 10–12/km^2 (Noss, Cuéllar & Ayala, in press).

Jaguar densities in the dry forests of the immense Kaa-Iya are much lower than those attained by tigers in India's comparatively small 'island' protected areas (Karanth & Nichols, 2000; Carbone *et al.*, 2001). Prey availability at these sites is much higher, with several large and abundant game species producing an exceptional prey biomass exceeding 4400 kg/km^2: chital *Axis axis* (weight ~ 70 kg; biomass ~ 2730 kg/km^2), sambar *Cervus unicolor* (weight ~ 185 kg; biomass ~ 1165 kg/km^2), munjac *Muntiacus muntjak* (weight 21 kg; biomass ~ 67 kg/km^2) and wild pig *Sus scrofa* (weight ~ 200 kg; biomass ~ 460 kg/km^2). In contrast, the most important prey (based on preliminary examination of scats) of jaguars in Kaa Iya are much smaller and less abundant for a prey biomass around 430 kg/km^2: grey brocket deer (weight ~ 17 kg; biomass ~ 204 kg/km^2; Noss, 2000; Noss, Cuéllar, Barrientos *et al.*, in press), tortoises *Geochelone carbonaria* (weight ~ 6 kg; biomass ~ 100 kg/km^2; unpubl. data), tapir *Tapirus terrestris* (weight ~ 150 kg; biomass ~ 35–75 kg/km^2; Ayala, 2003; Noss, Cuéllar, Barrientos *et al.*, 2003), and collared peccary *Tayassu tajacu* (weight ~ 22 kg; biomass ~ 55 kg/km^2; Miserendino, 2002). Although tigers weigh twice as much as jaguars, the prey biomass available for tigers is roughly 10 times higher, and it seems that large felid density is proportional to prey availability.

Four other felids are sympatric with jaguars at each of the three sites: puma *Puma concolor*, ocelot, Geoffroy's cat *Oncifelis geoffroyi*, and jaguarundi *Herpailurus yaguarondi*. Preliminary analyses using the same capture–recapture methodology with camera trap photographs suggest puma densities of 2.9–7.2/100 km^2 across the three sites, similar to or higher than densities of jaguar, while ocelots (25–67/100 km^2) are much more abundant than either of the big cats. Few photographs were obtained of either Geoffroy's cat or jaguarundi across the sites and densities for these species cannot be estimated (Maffei, Barrientos *et al.*, 2002, 2003; Maffei, Cuéllar & Noss, 2002; Maffei, Cuéllar, Peña *et al.*, 2002; Cuéllar *et al.*, 2003).

Jaguar activity peaks were found to be crepuscular, similar to the data reported by Rabinowitz & Nottingham (1986). This behaviour is probably related to the activity patterns of some of their principal prey: brocket deer *Mazama* spp. and peccaries *Tayassu* spp. are also most active in the first hours of the morning and in the evening (Barrientos & Maffei, 2000; Miserendino, 2002).

Camera trapping observations suggest that one male jaguar home range could contain the ranges of two or more females, and evidence was also found suggesting range overlaps among females as well as among males, as reported by Rabinowitz & Nottingham (1986). Our observed minimum range estimates over 2–25 months are similar to estimates made by Schaller & Crawshaw (1980), although camera trapping records represent a small number (< 25) of observations. In addition, camera trapping records are geographically restricted, to sample areas of 49–130 km^2 at our three sites, with no information on where the animals might range outside the sample area. The changes in individuals recorded and shifts in observed ranges over time suggest that actual home ranges may be considerably larger, perhaps stretching well outside the boundaries of the Kaa-Iya National Park. Only telemetry can provide complete and detailed information on individual home ranges, and this methodology would provide a useful complement to camera trapping to guide interventions on behalf of jaguar conservation.

The surveys were conducted at three of the most accessible areas of the Kaa-Iya National Park, where jaguar populations presumably would have been harmed the most by commercial hunting through the mid-1980s and by opportunistic hunting since that time. Apart from six ranch properties within its boundaries (total head of cattle 2000 in an area of 20 000 ha), the Kaa-Iya National Park is uninhabited and subject to only infrequent hunting as the few access points along its borders are protected by park guards. Therefore we are confident that the jaguar densities calculated from the three surveys can be extrapolated to the entire Kaa-Iya protected area, suggesting that it harbours a population of over 1000 adult and juvenile jaguars, of which roughly 15% would be juvenile animals.

Redford & Robinson (1991) estimated an area of 5486 km^2 to maintain a population of 500 jaguars at a density of one animal/10 km^2, with 500–650 individuals frequently cited figure for a minimum viable population to avoid the loss of genetic heterozygosity from inbreeding and genetic drift (Franklin, 1980; Soulé, 1980; Eizirik, Indrusiak & Johnson, 2002). Despite the lower jaguar population densities in the Chaco, given the enormous size of the Kaa-Iya National Park (without considering additional areas within the larger Gran Chaco Jaguar Conservation Unit), and the estimated densities at three widely separated sites in two different landscape systems with repeated surveys at two of the sites over a 2-year period, it seems that Kaa-Iya's jaguar population well exceeds any minimum viable population estimates. The Kaa-Iya population also exceeds any other published figures (Medellín *et al.*, 2002). We conclude that the jaguar population of the Kaa-Iya National Park is one of the fittest to be found, and can indeed be self-sustaining for the next 100 years.

However, rather than encouraging complacency, our results challenge us to redouble efforts to ensure the long-term conservation of the biological treasure that is Kaa-Iya, one the world's last great wild places. In particular, our complementary research and actions are focusing on the following themes that derive from the camera trapping results presented above:

(1) Does the Kaa-Iya National Park represent a source for dispersing jaguars into neighbouring rangelands (Quigley & Crawshaw, 2002)? If so, what is the scale of jaguar predation on livestock and of ranchers killing jaguars in these area, and how can such conflicts be reduced (Hoogesteijn *et al.*, 1993; Hoogesteijn, 2001)?

(2) Do jaguars, with individual ranges, which may extend outside the Kaa-Iya National Park and which overlap with the ranges of other jaguars as well as other felids, constitute a vector for disease transmission among domestic and wild carnivores (see Fiorello, Deem & Noss, 2002)?

(3) What is the status of jaguars in rangelands and fragmented agricultural landscapes surrounding the Kaa-Iya National Park, and the potential of private reserves to conserve jaguars and other wildlife in these areas (see Rumiz *et al.*, 2003)?

(4) Does the conservation of a landscape species like the jaguar ensure that biodiversity in general in the Gran Chaco landscape is being conserved (Sanderson, Redford, Vedder *et al.*, 2002)?

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