

SHORT COMMUNICATION

Ocelot (*Felis pardalis*) population densities, activity, and ranging behaviour in the dry forests of eastern Bolivia: data from camera trapping

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In comparison with the Neotropical big cats, jaguar (*Panthera onca* L.) and puma (*Felis concolor* L.), medium and small felids are poorly studied. Furthermore, studying wild felids in forest habitats is extremely difficult using direct methods given that most species are principally nocturnal and secretive (Gittleman 1996). Indirect methods are therefore particularly important, e.g. radio-telemetry (Emmons 1987, 1988; Konecny 1989, Ludlow & Sunquist 1987) or camera trapping (Maffei *et al.* 2002, Trolle & Kéry 2003). Using systematic camera trap surveys, we compare the population density of ocelots (*Felis pardalis* L.) across five Bolivian dry-forest sites with different habitat types and/or annual rainfall regimes (Table 1). We hypothesize that ocelot densities will decline as rainfall declines. In addition, we estimate the population of ocelots in the 34 400-km² Kaa-Iya del Gran Chaco National Park. Finally, we describe and evaluate additional ecological information provided by camera trapping: activity patterns relative to seasonality and moon phase, sex ratios, ranging patterns and relative abundance compared with sympatric felids.

The Kaa-Iya del Gran Chaco National Park protects the northern end of the Gran Chaco ecoregion, with chaco savannas in the park's driest south-west corner, and characteristic dry chaco vegetation with a low forest canopy (4–6 m) and emergents up to 10 m tall, numerous cactus species and terrestrial bromeliads (Navarro & Maldonado 2002). To the north and east, as annual precipitation increases the vegetation grades into chiquitano dry forest, an ecoregion endemic to Bolivia and forming a

transition area between chaco and cerrado (Killeen *et al.* 1998). Transitional chaco-chiquitano dry forests within the Kaa-Iya National Park include a low–medium canopy (12–15 m), with emergents 18–20 m tall (Navarro & Maldonado 2002).

The initial focus of our study was jaguars (Maffei *et al.* 2002, 2004; Silver *et al.* 2004), but pilot studies indicated that we could simultaneously collect valuable data on ocelots. Methods for camera trapping and estimating population densities follow Karanth & Nichols (2002) in addition to the references above. We conducted seven 60-d systematic camera trap surveys, utilizing 16–31 sets of camera traps per survey, at five dry-forest sites (Table 1).

Individual ocelots are relatively easy to distinguish, using black-and-white images, based on rosette and stripe patterns (see also Trolle & Kéry 2003). In the roughly 10% of cases (incomplete photos) where we were unable to positively identify an individual, either matching it with previously identified individuals or confirming that it did not match any of them, we tentatively considered the photos to be repeat observations of previously identified individuals at the same location. While doing so increased the number of recaptures in some cases, we did not consider them to be new individuals, so neither abundance nor buffer estimates changed. In 75–80% of cases across sites, we could confirm sex of the individuals as males present prominent testicles.

We used capture-recapture sampling methods (Otis *et al.* 1978), namely the CAPTURE program (Rexstad & Burnham 1991), to estimate total abundance based on the number of individuals identified (M_{t+1}) and capture frequency statistics, generating estimates of capture probability (p) and population size (N). We considered each day to be a separate sampling occasion, thus surveys

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Table 1. Location and characteristics of systematic camera-trap surveys at the five study sites.

Survey site	Location	Forest type [and landscape system] ^a	Precipitation (mm y ⁻¹)	Survey season	Dates	Trap nights
Guanacos	20°03'S 62°26'W	Chaco woodland on sand dunes [Alluvial plains]	400	dry	December 2003–February 2004	960
Cerro Cortado	19°31'S 62°18'W	Chaco woodland on sandstone outcrops/sands [Alluvial plains]	500	dry wet	April–May 2002 December 2002–January 2003	2280 1680
Tucavaca	18°31'S 60°49'W	Transitional chaco-chiquitano forest [Precambrian shield]	800	wet dry	January–March 2002 April–June 2003	1920 1560
Ravelo	19°17'S 60°37'W	Transitional chaco-chiquitano forest [Precambrian shield]	800	wet dry	February–April 2003 September–November 2003	2160 1320
San Miguelito	17°05'S 61°47'W	Chiquitano forest and transition to chaco forest [plains and shield contact]	1200	dry	September–November 2002	1695

^a Forest types and landscape systems are described by Navarro & Maldonado (2002).

included 60 sampling periods, and multiple observations of the same individual during a single day to be a single observation. The CAPTURE program tests the data against several capture-recapture models, and recommends the model that best fits the data. Following Otis *et al.* (1978), we assume that $M(o)$ is not appropriate for the species, and use the second-best model when CAPTURE recommends $M(o)$. We did not use the test for closure in the CAPTURE program, because Rexstad & Burnham (1991) indicate that ‘the test has poor power and is seldom capable of properly rejecting the null hypothesis of closure’. Instead, we assumed that the population of ocelots remained closed during the 60-d survey period.

In order to estimate the effective sampled area where the population size (N) was estimated, we measured the mean maximum distance covered by all individuals photographed at two or more locations during the survey period as a proxy for home-range diameter (Karanth & Nichols 2002). We used half the mean maximum distance (w) to buffer each camera trap location (following Silver *et al.* 2004). Animals whose home ranges overlap the buffered area at least partially have a capture probability greater than zero.

We divided the population size estimate by the effective sampled area to estimate population density (individuals km⁻²). In turn, we extrapolated population densities at the four chaco study sites across the entire area covered by similar forests to roughly estimate the total population of ocelots within the Kaa-Iya National Park.

We derived daily activity patterns by summing captures recorded for each hour of the day: the camera traps functioned 24-h a day and the automatic cameras stamped the date and time on each photograph. In turn, we compared them across sites, seasons, and moon

phases. In addition to the rough estimate of home range length provided by the mean maximum distance described above, cumulative observations of individuals at three or more locations provide a rough suggestion of ranging patterns. We present the area of the polygon joining these points as a minimum observed range.

Individual ocelots were photographed as many as 17 times during the cumulative 2-y survey period, though many were recorded only once. Considering all individuals that could be sexed over the entire period, sex ratios varied from site to site: 44% males ($N = 45$) at Tucavaca, 47% males ($N = 19$) at San Miguelito, 50% males ($N = 24$) at Cerro and 65% males ($N = 59$) at Ravelo. Sex ratios did not vary by season except at Tucavaca, where relatively fewer males were observed in the dry season. Across the three Kaa-Iya sites, more individuals of both sexes were identified in the dry season as opposed to the wet season.

We did not observe a single ocelot at Guanacos: this is the driest site and the rainfall may be insufficient for ocelots, while the open chaco grasslands that predominate at the site may not be suitable for the species. From the two surveys at Cerro Cortado (chaco forest) and Tucavaca (transitional chaco-chiquitano forest) respectively, we estimated an average population density of approximately 0.3 ocelots km⁻² at each site (Table 1). Ocelots can be relatively abundant even where rainfall is very low, if forest cover is sufficiently dense and extensive. At Ravelo, transitional chaco-chiquitano forest with a rainfall regime similar to Tucavaca's, the average density of 0.6 ocelots km⁻² is double the estimates for the other two sites. Despite the considerably higher rainfall at San Miguelito (chiquitano forest), average population density appears to be lower than at Ravelo. Together with density estimates from other Neotropical sites, these

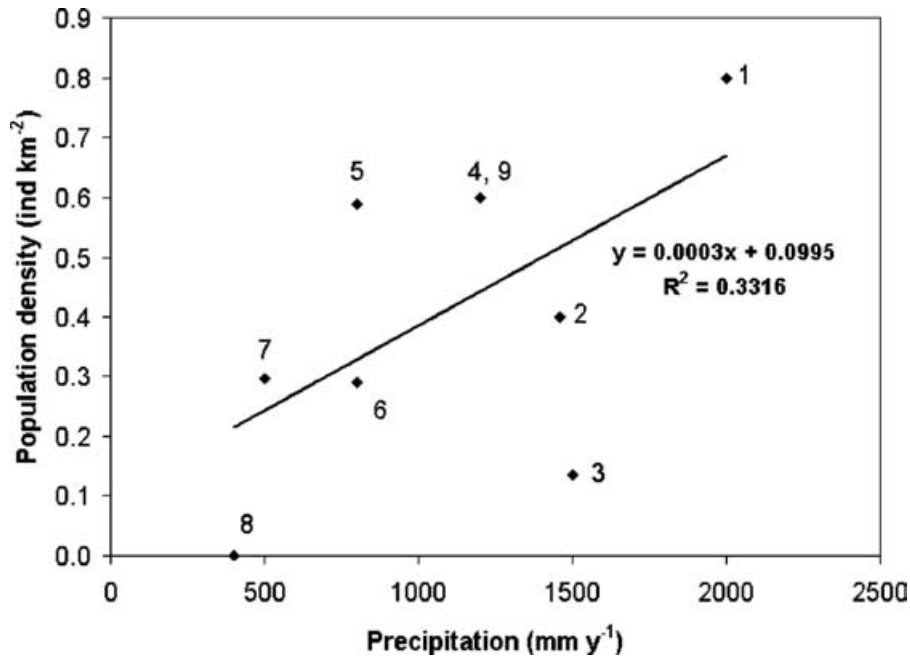


Figure 1. Ocelot population densities and annual precipitation. Data from telemetry studies at Manu National Park, Peru (1, Emmons 1988) and Llanos, Venezuela (2, Ludlow & Sunquist 1987). Data from camera trapping studies in Chiquibul National Park, Belize (3, M. J. Kelly, unpublished); Pantanal, Brazil (4, Trolle & Kéry 2003); Kaa Iya National Park, Bolivia (5–8, this study); and San Miguelito Private Reserve, Bolivia (9, this study).

estimates contribute to a weak pattern of higher ocelot densities with increasing precipitation: Pearson's correlation coefficient = 0.576, $N = 9$, $df = 7$, $P = 0.10$ (Figure 1). Across these sites, the Venezuelan llanos and Belize rain-forest sites have unexpectedly low population densities. Considering only the five Bolivian dry forest sites, the relationship is stronger: Pearson's correlation coefficient = 0.826, $N = 5$, $df = 3$, $P = 0.07$.

We estimate the total population of ocelots for the Kaa-Iya National Park to exceed 10 000 adult animals (range = 9300–11 300), assuming an average population density of 0.3 ocelots km^{-2} based on our surveys of four sites in landscape systems that extend over 25 300 km^2 of the protected area. One extensive landscape system remains to be surveyed, chaco transitional forest covering 8600 km^2 in Kaa-Iya, whereas chaco riverine and chaco savannas each cover less than 500 km^2 . The absence of ocelots in the latter habitat (Guanacos) does not greatly affect the population estimate for the protected area. We prefer to extrapolate from the relatively low density estimates at Tucavaca and Cerro, rather than the higher Ravelo estimate (0.6 ocelots km^{-2}), in order to err on the conservative side.

Ocelots exhibited strongly nocturnal behaviour across all sites, with 89% of records at night, and activity peaking at 21 h (Figure 2). These results are consistent with data from telemetry research at tropical moist forest and savanna sites elsewhere in South America (Emmons 1988, Emmons *et al.* 1989, Konecny 1989, Ludlow & Sunquist 1987). The highest frequency of day-time

photographs (Ravelo) did not exceed 21%. Ocelot activity did not vary significantly with lunar phase or by season, though we did not survey during the coldest months (June–July).

We recorded cumulative observations at three or more locations for 22 animals: three at Cerro Cortado, 13 at Tucavaca, and six at San Miguelito. The average minimum observed range was 3.0 km^2 (range = 0.2–13.2 km^2 , $SD = 3.5$). Maximum distances observed during the survey periods range from 0.3–8.6 km across sites, with males (mean = 2.76 km, $SD = 1.42$, $N = 24$) apparently ranging further than females (mean = 2.24 km, $SD = 1.60$, $N = 24$). Average mean maximum distances appear to be higher in the dry season (1.34–1.44 km) compared with the wet season (1.02–1.34 km) at each of the three sites where two surveys were conducted, suggesting that ocelots tend to range more widely in the dry season.

Except for Guanacos, the ocelot is the most abundant felid at our dry-forest sites (Table 2), between 5–15 times more abundant than the second species, the puma. The number of photographs alone, or an abundance index derived from observations and total trap nights, is not a reliable indicator of relative abundance among species. For example, at Cerro Cortado, although we obtained more photographs of pumas than of ocelots, the population density of the latter is considerably higher given the smaller buffer (and corresponding survey area), combined with the number of individuals identified (30 ocelots versus 12 pumas). The low number of photographs of

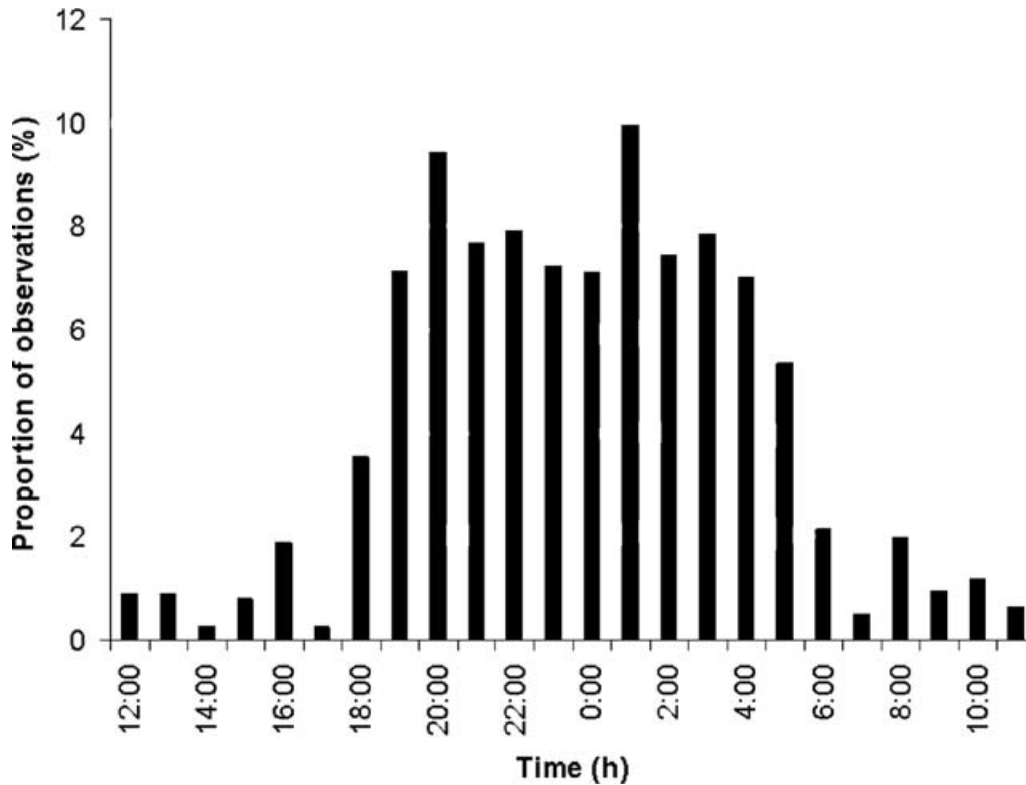


Figure 2. Ocelot activity patterns in the Kaa-Iya del Gran Chaco National Park and San Miguelito Private Reserve (per cent of observations by hour).

the other sympatric small cats (*Felis wiedii* Schinz, *F. yagouaroundi* E. Geoffroy, and *F. geoffroyi* d'Orbigny & Gervais) are insufficient to estimate population density.

The camera trap surveys and camera spacing were designed for jaguars rather than ocelots. The smaller distances covered by ocelots resulted in smaller buffers, and the buffers in turn described discontinuous effectively sampled areas at both Ravelo and Tucavaca, though not at Cerro or San Miguelito. However, in defining the sampled area, we chose not to draw a polygon around the

outermost cameras and buffer that polygon (as described by Karanth & Nichols 2002, Trolle & Kéry 2003), because doing so can include 'holes' within the sampled area that encompass an entire home range, resulting in a zero capture probability for the resident animal. Our discontinuous sampled areas included no such holes, but did increase the edge effect where capture probabilities will approach zero. By buffering camera locations rather than the polygon we have reduced the effective sampled area, and in turn increased the density estimate.

Table 2. Ocelot population densities from camera trap surveys in the dry forest of Santa Cruz. Photos: Number of independent ocelot photos during the entire survey. Individuals: Number of individuals identified during each survey. w: Buffer equivalent to half the mean maximum distance covered by animals observed at more than one location during the survey. A: Effective survey area estimated from the buffered camera trap locations. Model: model that best fits the results selected by the program. M(h) is heterogeneity model using jackknife estimator and assuming heterogeneity in capture probability among individual ocelots, M(o) is null model using null estimator and assuming no variation in capture probability among individuals, M(b) is behaviour model using constant probability removal estimator and assuming behavioural variation in capture probability among individuals. N: Abundance estimated by the CAPTURE software. D: Abundance divided by effective sampled area. P: capture probability.

Survey	Photos	Individuals	w (m)	A (km ²)	Model	N ± SE	D ± SE (individuals km ⁻²)	P
Guanacos (dry)	0							
Cerro Cortado (dry)	65	25	1440	99	M(h)	30 ± 4.53	0.34 ± 0.04	0.03
Cerro Cortado (wet)	53	18	1340	80	M(h)	20 ± 3.35	0.25 ± 0.03	0.05
Tucavaca (dry)	61	18	1340	80	M(b)	20 ± 2.84	0.24 ± 0.03	0.03
Tucavaca (wet)	82	34	1140	84	M(o)	39 ± 3.11	0.34 ± 0.02	0.03
Ravelo (dry)	91	42	1440	117	M(h)	61 ± 11.3	0.52 ± 0.05	0.02
Ravelo (wet)	102	40	1015	98	M(h)	56 ± 6.67	0.66 ± 0.07	0.03
San Miguelito (dry)	71	23	1350	52	M(h)	29 ± 4.25	0.56 ± 0.07	0.04

T1 Table 3. Camera trap records and densities of sympatric felids at five dry-forest sites. D = density (individuals per 100 km²), with D* an average of the two surveys conducted at each site.

Species	Guanacos			Cerro Cortado			Tucavaca			Ravelo			San Miguelito		
	N	%	D	N	%	D*	N	%	D*	N	%	D*	N	%	D
<i>Felis pardalis</i>	0	0	–	127	35	30	355	68	30	102	71	60	71	58	56
<i>F. concolor</i>	18	60	6.8	142	39	6.2	82	16	2.9	16	11	3.7	13	10.5	15.0
<i>Panthera onca</i>	11	37	2.1	56	16	5.2	58	11	2.8	21	15	2.3	21	17	11.1
<i>F. yagouaroundi</i>	0	0	–	12	3	–	18	3	–	2	1.5	–	10	8	–
<i>F. geoffroyi</i>	1	3	–	24	7	–	10	2	–	2	1.5	–	2	1.5	–
<i>F. wiedii</i>	0	0	–	0	0	–	0	0	–	0	0	–	6	5	–

During the second Tucavaca survey, we simultaneously surveyed a 5 × 10-km area with 2–3-km camera spacing and an inlaid 2 × 4-km area with 1-km camera spacing. Considering only those ocelots recorded in the inlaid area, we defined a continuous effective survey area in which the density estimate (0.21 ocelots km⁻², 7 individuals) did not differ significantly from the density estimate (0.24 ocelots km⁻², 18 individuals) associated with the larger discontinuous survey area. Therefore, while research design should strive for continuous survey areas in order to minimize edge effects and increase the precision of density estimates, our observations suggest that density estimates from discontinuous survey areas are valid.

These differences across sites, as well as the significant differences between seasons within sites, merit further study focusing on resource availability. It is not clear, for example, why density estimates for the chaco forest site should be higher in the dry season, when resources are presumably more scarce, and contrary to the pattern observed at both transitional chaco-chiquitano forest sites. At San Miguelito, we surveyed 22 km² of private reserve within a 400-km² ranch. Whereas the population density suggests that the reserve could support only 11 individuals, we do not know how the animals may use agricultural areas surrounding forest fragments: we identified 23 individual ocelots and CAPTURE estimates an abundance of 29 individuals for the area. A radio-telemetry study of ocelots currently underway at Tucavaca will provide an independent density estimate for comparative purposes. It will also confirm several preliminary results presented above: activity patterns, seasonal shifts in ranging behaviour, home-range areas and diameters for males versus females, and in turn the validity of mean maximum distance as a proxy for home-range diameter in density estimation from camera trap surveys.

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