

Salom-Pérez, R., Camillo, E., Sáenz, J. C., and Mora, J. M. (2007). Critical condition of the jaguar *Panthera onca* population in Corcovado National Park, Costa Rica. *Oryx* 41(1): 51-56.

Keywords: 2CR/abundance/camera trap/Corcovado NP/jaguar/*Panthera onca*

Abstract: The jaguar *Panthera onca* is threatened throughout its range and categorized as Near Threatened on the IUCN Red List. To inform conservation of the jaguar population in Corcovado National Park, Costa Rica, population size was estimated using data from a 3-month camera trap study. Individuals were identified from their coat patterns. The resulting density estimate of 6.98 +/- SD 2.36 individuals per 100 km² was lower than expected. The sex ratio was 1.33 males per female, and the minimum home ranges of two males were 25.64 and 6.57 km². Hunting pressure on jaguar and white-lipped peccaries *Tayassu pecari*, the jaguar's main prey in the Park, may be responsible for the low jaguar density as space does not seem to be a limiting factor. The numbers of females may have been underestimated because of sampling bias and therefore the sex ratio obtained in this and similar studies must be interpreted cautiously. Better protection of the corridor that connects the Park with other protected areas is essential to guarantee long-term survival of the jaguar in Costa Rica.

Critical condition of the jaguar *Panthera onca* population in Corcovado National Park, Costa Rica

Roberto Salom-Pérez, Eduardo Carrillo, Joel C. Sáenz and José M. Mora

Abstract The jaguar *Panthera onca* is threatened throughout its range and categorized as Near Threatened on the IUCN Red List. To inform conservation of the jaguar population in Corcovado National Park, Costa Rica, population size was estimated using data from a 3-month camera trap study. Individuals were identified from their coat patterns. The resulting density estimate of $6.98 \pm \text{SD } 2.36$ individuals per 100 km^2 was lower than expected. The sex ratio was 1.33 males per female, and the minimum home ranges of two males were 25.64 and 6.57 km^2 . Hunting pressure on jaguar and white-lipped peccaries *Tayassu pecari*, the jaguar's

main prey in the Park, may be responsible for the low jaguar density as space does not seem to be a limiting factor. The numbers of females may have been underestimated because of sampling bias and therefore the sex ratio obtained in this and similar studies must be interpreted cautiously. Better protection of the corridor that connects the Park with other protected areas is essential to guarantee long-term survival of the jaguar in Costa Rica.

Keywords Abundance, camera traps, Corcovado National Park, Costa Rica, jaguar, *Panthera onca*.

Introduction

Jaguar *Panthera onca*, categorized as Near Threatened on the IUCN Red List (IUCN, 2006), are found throughout the Americas, ranging from northern Mexico to southern Argentina (Seymour, 1989; Sanderson *et al.*, 2002b). There has, however, been a decrease in the number of their prey and increased fragmentation of their natural habitat, and so-called problem jaguars accused of preying on livestock have been killed (Swank & Teer, 1989; Emmons, 1990; Sáenz & Carrillo, 2002; Sanderson *et al.*, 2002b). Only 4% of the most important areas for jaguar are currently being protected effectively (Sanderson *et al.*, 2002b) and Costa Rica is one of the countries where, because of habitat loss and hunting, the jaguar is most threatened (Swank & Teer, 1989; Sanderson *et al.*, 2002a). Although forested areas large enough to support 500 or more jaguars may no longer exist in Central America (Emmons, 1990; Ceballos *et al.*, 2002; Maffei *et al.*, 2004) connections between populations living in distinct areas could help to guarantee the

survival of the species in the long term (Shaffer, 1989; Swank & Teer, 1991).

Camera traps have been used to estimate populations of tiger *Panthera tigris* in India (Karanth & Nichols, 2000; Carbone *et al.*, 2001) and are also now being used with jaguar and other felids in the Neotropics (Trölle & Kéry, 2003; Sarmiento, 2004; Silver *et al.*, 2004). The present study is one of the first investigations in Central America to use this methodology for jaguar. Our objective was to estimate the population size and examine the conservation status of jaguar in Corcovado National Park.

Study site

The 425 km^2 Corcovado National Park on the Osa Peninsula of the Pacific coast of Costa Rica borders the Guaymí Indigenous Reserve and the Golfo Dulce Forest Reserve. A portion of the latter forms a corridor that connects the Park with Piedras Blancas National Park and Golfito National Wildlife Refuge (Fig. 1). The altitude of the Park is 0–745 m, annual maximum and minimum temperatures for the nearest weather station are 31.7 and 22.1°C, respectively, and mean precipitation is $4,656.5 \pm \text{SD } 43.8$ mm, one of the highest in Costa Rica. The Park has a rich and diverse flora and fauna and a relatively large number of endemic species (Hartshorn, 1983; Soto, 1994; Naranjo, 1995). This and other forests on the Osa Peninsula are the last of the tropical rainforests on the Pacific side of Central America (Hartshorn, 1983).

Roberto Salom-Pérez (Corresponding author) P.O. Box 350-2300, Curridabat, San José, Costa Rica. E-mail robersalom@yahoo.com

Eduardo Carrillo and Joel C. Sáenz Programa Regional en Manejo de Vida Silvestre, Universidad Nacional, P.O. Box 1350-3000 Heredia, Costa Rica.

José M. Mora Escuela de Biología, Universidad de Costa Rica, Costa Rica.

Received 27 September 2005. Revision requested 17 January 2006.

Accepted 7 June 2006.

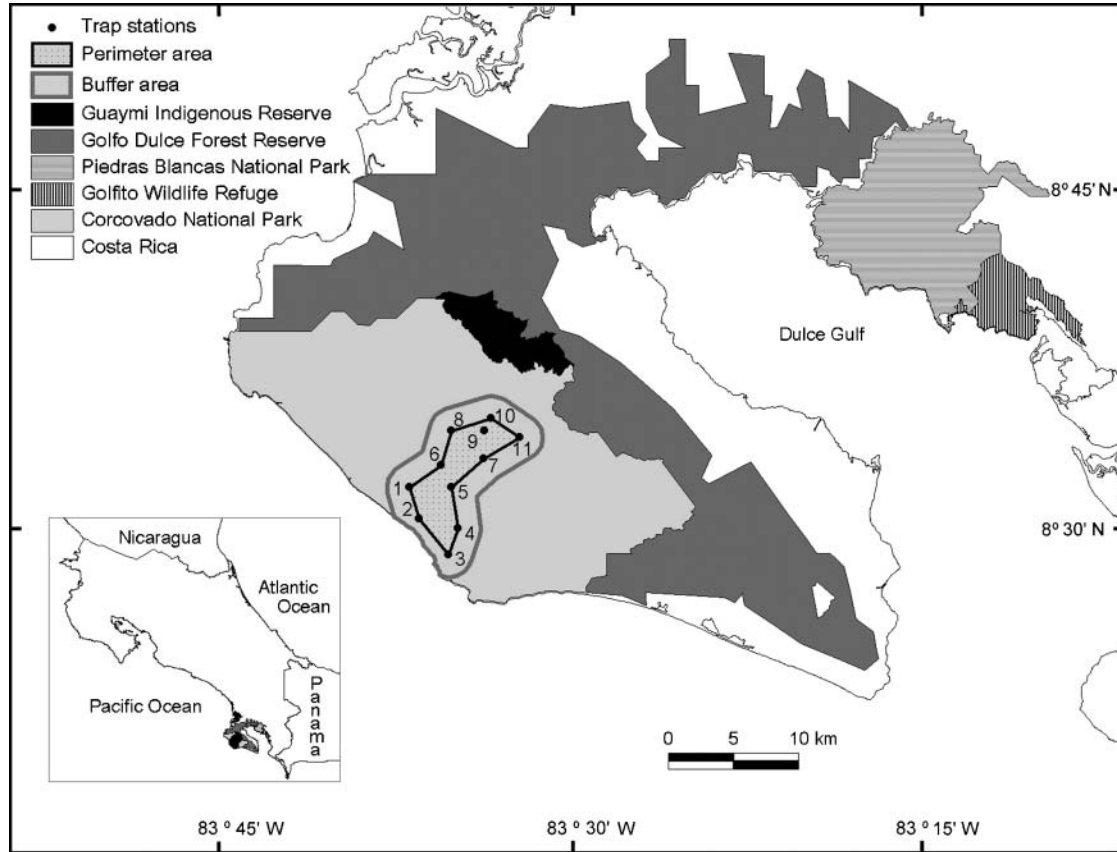


Fig. 1 Protected areas of the Osa Peninsula, Costa Rica, with perimeter and buffer areas (see text for details) and location of the camera-trap stations (numbered) used to estimate the jaguar population within Corcovado National Park (in light grey). The inset shows the location of the Osa Peninsula in Costa Rica.

Methods

A pilot project was carried out in Corcovado National Park from August 2002 to January 2003 with five camera trap stations, each with two cameras sensitive to heat and motion (CamTrakker, Watkinsville, USA). The data from this was not used to determine jaguar population size but was used for other calculations (as explained below). For the full study 12 trap stations, each also with two cameras, were run from 19 January to 18 April 2003. Because of robbery or failure of the cameras we were only able to use the information from 11 stations. We divided the trap stations into two blocks to be able to use only the days in which all trap stations were active continuously in each block. Block 1 consisted of traps 1–6 (data collected 21 January–22 February) and Block 2 of traps 7–11 (data collected 23 February–27 March).

Based on a previous radio telemetry study the minimum home range for a female jaguar in the Park is 12 km² (Carrillo, 2000) and therefore we placed at least one trap station in every 12 km² circular area to ensure that all individuals had a probability >0.0 of being photographed. The two cameras at each trap were

focused at the same spot but not at each other, to avoid flash interference, and were 0.5 m above the ground and 2–4 m from the centre of the trail. The cameras were active 24 hours per day and the minimum interval between photographic events was set to 25 minutes.

Trap stations were located in areas where signs of felid or other mammal activity had been observed (based on photos from the pilot project, faeces and tracks). The cameras were checked *c.* every 15 days to change film and ensure they were functioning correctly. Every photograph obtained of a jaguar in a sampling occasion is equivalent to one capture. Photos of the same individual in successive sampling occasions were considered recaptures. Individuals were identified by their fur pattern, which is unique to each jaguar (Silver *et al.*, 2004).

The area covered by the study was calculated by drawing a polygon, which we refer to as the perimeter area, whose vertices were formed by the outermost trap stations. A buffer area was added to the polygon in the form of a band to determine the total area covered by the study (Fig. 1). The width of this band was half of the

Table 1 Maximum distance moved (MDM) by 10 jaguars in Corcovado National Park. These distances were used in the calculation of the total area covered by the study (see text for further details).

Jaguar	MDM (km)	Gender	Source
jm1	3.17	Male	This study
jm2	5.21	Male	This study
jm3	3.81	Male	This study
jh1	0	Female	This study
rjm1	3.1	Male	Radio telemetry (E. Carrillo, unpubl. data)
rjm2	5.2	Male	Radio telemetry (E. Carrillo, unpubl. data)
rjh1	2.8	Female	Radio telemetry (E. Carrillo, unpubl. data)
rjh2	3.7	Female	Radio telemetry (E. Carrillo, unpubl. data)
rjh3	3.3	Female	Radio telemetry (E. Carrillo, unpubl. data)
rjh4	4.5	Female	Radio telemetry (E. Carrillo, unpubl. data)

mean maximum distance moved (MMDM) by individuals photographed more than once during the 3-month study period (Wilson & Anderson, 1985; Karanth & Nichols, 1998). To improve the calculation of MMDM we also used the maximum distance moved by six jaguars monitored in the Park with radio telemetry during January–March of 1996–98 (E. Carrillo, unpubl. data; Table 1).

To estimate the jaguar population and the average probability of a capture per sampling occasion (\hat{P}) we used the software *CAPTURE* (Otis *et al.*, 1978; Rexstad & Burnham, 1991; Karanth & Nichols, 1998). One of the assumptions of *CAPTURE* is that the study population is closed, i.e. individuals do not enter or leave the area. We considered the study period of 3 months short enough to be certain that this assumption held. Nevertheless, *CAPTURE* also tests for closure. Every sampling occasion was set to 3 days. Because of differences in mobility between male and female and between adult and juvenile jaguar it cannot be assumed that there is no variation in the probability of capture of individuals. We therefore used the heterogeneity estimator in *CAPTURE*. The population estimate and the size of the study area were used to calculate jaguar density.

To determine the sex ratio, activity patterns, and the minimum home range of jaguar we used data from this 3-month study, the pilot project, and a parallel study of sea turtle predation by jaguar carried out within the limits of the study area (September 2002–June 2003; Salom-Pérez, 2005). Minimum home ranges were estimated as the minimum convex polygon. To calculate the perimeter and buffer areas we used the geographical information system *ArcView v. 3.2* (ESRI, Redlands, California). Distances between trap stations were obtained using a global positioning system.

Results

Average distance between consecutive trap stations was $2.75 \pm \text{SD } 0.67$ km (range 1.10 – 3.64 km), i.e. there was

no area >10.41 km² without a camera (mean of one camera per 7.82 km²; Fig. 1). In a total of 363 trap nights four individual jaguars were photographed (Table 2). The total number of captures (including recaptures) used for the population estimate was seven, and \hat{P} was 0.11. The closure test of *CAPTURE* indicated that the population was closed ($z = 2.13$, $P = 0.98$) and the population estimate was $6.0 \pm \text{SE } 1.96$ individuals (95% confidence interval 5–14). All four jaguars photographed were recaptured during the 3-month study period (Table 2). The MMDM used to calculate the buffer area was $3.48 \pm \text{SD } 0.47$ km. The total area (perimeter area of 29.46 km² + buffer area of 56.55 km²) studied was 86.02

Table 2 Camera-trap capture history of jaguars in Corcovado National Park, 2002–2003.

Jaguar ¹	Date	Time	Trap station ²
Jm1	8/9/2002	0.35	Pilot study 5
Jm1	3/10/2002	23.38	Pilot study 4
<i>Jm1</i>	23/2/2003	7.49	10
<i>Jm1</i>	25/3/2003	4.20	10
Jm1	6/4/2003	17.42	8
Jm2	13/9/2002	22.38	Pilot study 1
<i>Jm2</i>	26/1/2003	8.14	4
<i>Jm2</i>	4/2/2003	2.52	1
<i>Jm2</i>	14/2/2003	23.42	4
Jm2	18/4/2003	4.24	4
Jm2	18/4/2003	5.31	3
<i>Jm3</i>	14/3/2003	1.57	7
Jm3	9/4/2003	15.07	10
Jm4	22/8/2002	19.55	Pilot study 3
<i>Jh1</i>	8/3/2003	10.58	8
Jh1	18/4/2003	9.19	8
Jh2	14–16/10/2002		Turtle study 3
Jh2	10/11/2002	21.44	Turtle study 5
Jh3	2/9/2002		Turtle study 2

¹Only the records in italics were used for the population estimate (see text for further details).

²In this study (see numbered locations in Fig. 1) and in an earlier pilot study and a study of jaguar predation of turtles (see text for details)

\pm SD 7.75 km² (Fig. 1), giving a jaguar density of 6.98 \pm SD 2.36 individuals per 100 km².

In the pilot project and the parallel study of jaguar predation on turtles two additional female (jh2 and jh3) and one juvenile male (jm4) jaguar were photographed (Table 2). The total of seven jaguars therefore gave a 1.33 male/female sex ratio. Of the 17 photographs in which the time could be clearly determined, 11 (64.7%) were during the night (18.00–6.00) and the others (35.3%) during the day (6.00–18.00; Table 2). Mean home range could only be determined for the two jaguars, both males (jm1 and jm2), that were photographed at >two trap stations: 25.64 km² (jm1, 6 captures) and 6.57 km² (jm2, 6 captures).

Discussion

Although we only photographed four jaguars during the 3 months of the study we know that there were at least three more jaguars present (Table 2). In Bolivia Wallace *et al.* (2003) and Maffei *et al.* (2004) also captured different individuals while performing consecutive studies in the same area within <1 year. It is possible that several jaguars share an area but at different times. Presumably they detect other individuals by the presence of faeces or other sign and move to other parts of their home ranges (Rabinowitz & Nottingham, 1986). The occurrence of a localized resource (marine turtles) that are relatively easy to predate could explain this convergence of home ranges, at least for jaguars captured near the beach.

The density of jaguar calculated in this study (6.98 \pm SD 2.36 per 100 km²) is higher than that reported in a number of other localities in South America and Mexico (0.45–5.23 per 100 km²; Schaller & Crawshaw, 1980; Quigley & Schaller, 1988; Aranda, 1991; Núñez *et al.*, 2002; Wallace *et al.*, 2003; Maffei *et al.*, 2004; Silver *et al.*, 2004), but similar to that determined from a 3-year radio telemetry study of jaguar in Calakmul, Mexico (Ceballos *et al.*, 2002), and similar to or less than that determined from camera-trap studies (Silver *et al.*, 2004) in Cerro Cortado, Bolivia (5.11 \pm 2.10 per 100 km²) and in two sites in Belize (8.80 \pm 2.25 per 100 km² and 7.48 \pm 2.74 per 100 km²). The jaguar density in Corcovado National Park was, however, lower than we expected. It was previously thought that, because of the abundance of prey and high habitat quality, the Park had the highest density of jaguar in Costa Rica, and that the density was greater than that found in Belize (E. Carrillo, pers. obs.). As our study only encompassed 20% of the Park it is possible that we underestimated density. However, the similarity of the maximum distance moved by jaguars monitored with radio telemetry (E. Carrillo, unpubl. data) and in this camera-trap study suggest that the

movement patterns reported here, and hence our estimate of density, are relatively accurate.

As an individual jaguar's range is usually not exclusive (e.g. male jaguar jm1 shared his home range with male jm3 and female jh4) it is likely that Corcovado National Park could accommodate a greater density than that estimated (Schaller & Crawshaw, 1980; Quigley & Schaller, 1988; Núñez *et al.*, 2002; Maffei *et al.*, 2004). As space does not appear to be a limiting factor it is possible that food supply is limiting jaguar density in the Park. This is supported by the fact that in the past few years hunting has caused a considerable decrease in the numbers of white-lipped peccaries *Tayassu pecari*, the primary prey of the jaguar in the Park (E. Carrillo, unpubl. data; Chinchilla, 1994; Carrillo, 2000). Jaguar activity depends mainly on the prey being hunted (Carrillo, 2000) and as c. 65% of the jaguar photographs were taken during the night this suggests they were probably searching for alternative, nocturnal prey such as marine turtles.

The limitations of our data do not allow us to confidently extrapolate our density estimate to the whole of Corcovado National Park. However, if jaguar occur at a similar density throughout the Park the total population would be c. 30 individuals, and even if the Park could support the maximum density reported for the species in Central America (8.80 \pm 2.25 per 100 km²; Silver *et al.*, 2004) it would contain no more than 50 jaguars. If this population is reproductively isolated its survival is threatened as it probably does not contain sufficient individuals for a minimum viable population (Eizirik *et al.*, 2002). However, jaguars killed in areas surrounding the Park and individuals photographed in the corridor that connects the Park with Piedras Blancas National Park and Golfito National Wildlife Refuge (E. Carrillo, unpubl. data), are evidence that there is probably movement of jaguars between the Park and other protected areas. This indicates the importance of upgrading the management level of Golfo Dulce Forest Reserve, or at least a part of it, because a National Park in Costa Rica provides better protection to large and medium size mammals than that given by a Forest Reserve (Carrillo *et al.*, 2000).

As in other camera-trap studies of jaguar a greater number of males were captured than females (Wallace *et al.*, 2003; Silver *et al.*, 2004). The number of females could, however, have been underestimated because females have smaller territories and move less than the males, and therefore have fewer opportunities to be captured. In addition, females are known to be more timid than males and are more likely to avoid walking on man-made trails; six of the 12 trap stations were located on man-made trails. Two females were photographed on the beach preying on turtles (jh2 and jh3, on

two and one occasions, respectively) and one was photographed on a game trail (jh1, on two occasions), but none of these individuals were photographed on man-made trails.

The use of camera traps allows the calculation of more accurate population estimates of felids and other animals than earlier methods based on indirect signs (Mondolfi & Hoogesteijn, 1991; Smallwood & Fitzhugh, 1993; Cutler & Swann, 1999; Grigione *et al.*, 1999; Silveira *et al.*, 2003; Trölle & Kéry, 2003). Radio telemetry has also been used to obtain data on home range size and densities but, in addition to being expensive, has problems related to topography, forest cover, data collection and animal health (because of capture and sedation; Rabinowitz & Nottingham, 1986; Mondolfi & Hoogesteijn, 1991; Carrillo *et al.*, 2000). However, cameras are expensive (USD 90–400 per camera, plus the price of the film and developing), must be checked frequently, may be stolen, and may malfunction, especially in extremely humid conditions (R. Salom-Pérez, pers. obs.; Maffei *et al.*, 2004; Silver *et al.*, 2004).

Our results emphasize the need to safeguard corridors that connect protected areas in Costa Rica. Such protection could include the possibility of modifying the management categories of such prioritized areas. In addition, more rigorous control of hunting and an increase in environmental education in the communities neighbouring the protected areas are required. Currently, RS-P, EC and others from various state universities and the National Institute of Biodiversity are carrying out investigations to facilitate delineation of the corridor between Corcovado and Piedras National Parks. Other governmental and non-governmental organizations are resolving matters regarding land possession, providing environmental education, and supporting sustainable development programmes for the area.

Acknowledgments

We thank Scott Silver for his guidance and valuable comments. In addition we thank Daniela Araya, Juan de Dios Valdez, Alexander Gómez, Alfonso Chamorro, Carolina Orta, Nereyda Estrada, Marcela Fernández, Rebeca Chaverri, Martin Zeilbauer, Coral Pacheco, Eduardo Toral, Franklin Castañeda, Charles Foerester, Rausel Sarmiento and the 14th promotion of PRMVS-UNA for their invaluable help and companionship in the field, the staff at Corcovado National Park for their support and for sharing their facilities, Jose Pablo Carvajal for his assistance with the maps, and Meg Harper for translating this document. We thank the Wildlife Conservation Society, Corcovado National Park, the University of Costa Rica and the National

University of Costa Rica for their support, and Gerardo Umaña, Marcella Kelly and an anonymous reviewer for their comments.

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Biographical sketches

This study was a part of Roberto Salom-Pérez's MSc thesis at the University of Costa Rica, which included a population estimate for ocelots and investigation of the predator/prey relationship between jaguars and marine turtles. This research was also part of the Jaguar Conservation Program (JCP) of the Wildlife Conservation Society, which began in 1999 with the objective of reversing jaguar decline throughout its range. Eduardo Carrillo is a professor at the Wildlife and Management Institute (IMVS) of the National University in Costa Rica and the coordinator for the JCP of Mesoamerica. As part of the JCP Roberto Salom-Pérez and Eduardo Carrillo are now carrying out a camera-trap based investigation to help delineate the corridor in Golfo Dulce Forest Reserve, using spider monkey *Ateles geoffroyi* and large felids as key species. José M. Mora is a professor at the University of Costa Rica and has carried out research focused on mammals and reptiles. Joel C. Sáenz is the director of IMVS and carries out research on habitat fragmentation.