Perspectives from Ten Years of Jaguar (*Panthera onca*) Camera Trapping in Mesoamerica

Perspectivas de Diez Años de Estudios con Trampas Cámara de Jaguares (*Panthera onca*) en Mesoamérica

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Fecha de recepción: 19 de noviembre de 2010 - Fecha de aceptado: 15 de agosto de 2011

Abstract. Between 2000-2010, the Wildlife Conservation Society's Jaguar Conservation Program (JCP) supported 77 range wide camera trap surveys and 40 surveys in Mesoamerica alone, with density estimates ranging from 0.74 to 11.2 jaguars/100 km². Sampling design varied widely based upon equipment, personnel and budget constraints. The size of the polygon formed by the camera trap stations (i.e., size of trapping area) was highly variable. Another source of sampling variation was the presence of pre-existing trails which have a higher capture rate compared to areas with no trails. The environmental sources of variation included actual high or low jaguar density, based on forest type and protection level. We recommend a minimum of 110 km² camera trap polygons in Central American surveys. If using the program Capture, the effective survey area including a ½ MMDM buffer should be at least 200 km² yet the effective survey area should not be more than twice the camera polygon. The use of digital cameras that take a rapid sequence of photographs will maximize identifications when combined with the application of a scent.

Key words: density, polygon, capture-recapture, scent, digital camera.

Resumen. Entre 2000-2010, el Programa para la Conservación del Jaguar de la Wildlife Conservation Society ha apoyado 77 estudios con trampas cámaras en todo el continente y 40 estudios solo en Mesoamérica, con estimaciones de densidad que van de los 0.74 a 11.2 jaguares/100 km². El diseño de muestreo fue muy variable dependiendo del equipo, personal y presupuesto disponible. El tamaño del polígono formado por las trampas cámaras fue muy variable. Otra fuente de variación fue la presencia de sendas previamente abiertas, las que brindan una posibilidad de captura mayor comparado con áreas sin sendas. Las fuentes de variación ambiental incluyeron densidades poblacionales altas o bajas de jaguares, basados en el tipo de bosque o el nivel de protección. Recomendamos que el polígono formado por las trampas cámaras tenga un mínimo de 110 km² en los estudios Centroamericanos. Si se usa el programa Capture, el área efectiva de muestreo incluyendo el ½ MMDM de borde debe tener al menos 200 km² y el área efectiva de muestreo no debe ser más del doble que el área del polígono. El uso de cámaras digitales que toman una secuencia rápida de fotografías maximiza las identificaciones cuando se combinan con la aplicación de algún atrayente.

Palabras clave: densidad, polígono, captura-recaptura, atrayente, cámara digital.

Introduction

One of the priorities of Wildlife Conservation Society's (WCS) Jaguar Conservation Program (JCP) has been to evaluate the status of individual jaguar populations and to thus inform conservation decisions and actions. In 1999, WCS and the Universidad Nacional Autónoma de México initiated a mapping exercise resulting in maps with the Jaguar Conservation Units (JCUs), areas of key importance for jaguar conservation and expected to contain a population of resident jaguars large enough (at least 50 breeding individuals) to be potentially self-sustaining over the next 100 years (Sanderson *et al.*, 2002).

The exercise included a workshop held in Mexico in 2000, entitled "The Jaguar in the New Millennium" (Medellín *et al.*, 2002). The participating researchers identified 31 JCUs in Central America and Mexico and 60 in South America. Many of these JCUs have since been evaluated with camera trap surveys which provide estimation of jaguar densities, or through numbers of individuals captured, an index of abundance (Maffei *et al.*, 2004; Moreno, 2006; Silveira *et al.*, 2009).

By 2010, the JCP had supported 77 jaguar surveys wholly or in part: 40 in Mesoamerica and 37 in South America. During this first decade, the JCP survey program's emphasis was exploring the proposed JCUs as actual jaguar strongholds and testing the methodology. Because of a series of limitations—logistics, accessibility, time, weather, funds, personnel, equipment—individual researchers conducted surveys that varied greatly in duration, area covered, and spacing and locations of cameras. We review here the JCP-supported surveys conducted in Mesoamerica over the past decade in order to inform future methods for estimating jaguar populations.

Study Area

Most studies cited in this paper were conducted in tropical moist lowland forest (22 studies), from Guatemala to Panama. A small number of surveys were also conducted in montane humid forest (4) and dry forest (1). We have included 27 studies from Central America, of the 40 conducted in total, because these reports provided adequate information on the factors we intended to analyze. Habitat data were obtained from http://www.worldwildlife.org/wildworld/profiles/terrestrial_nt.html and reports of the authors cited in Appendix 1.

Tropical moist lowland forest types represent 64% of the habitat available for jaguars in Mesoamerica. Its climate is tropical humid: annual precipitation is around 1500-3500 mm, reaching more than 4500 mm in certain areas such as Corcovado National Park in Costa Rica (Salom-Perez *et al.*, 2007) and El Darién National Park in Panama (Moreno, 2006). Mean temperatures average 26 °C. Forest canopy reaches 35 m in height. These forests are usually at 0-400 m above sea level, but in some places may extend up to 1000 m. This type of forest was surveyed in Belize, Costa Rica, Guatemala, Honduras, Nicaragua, and Panama.

Tropical moist montane forests usually have altitudinal ranges from 600 to 1800 m, but may extend up to 3000 m. Annual precipitation ranges from 2000 to 4000 mm, but can be as low as 1000 mm. The average temperature can be from 25 °C in the lowest to 5 °C in the highest.

Tropical deciduous forest types are characterized by deciduous trees and a prolonged dry season of 5-8 months with average annual precipitation between 900 and 2000 mm. The average temperature is around 25 °C. This type of forest was surveyed only in Costa Rica (Guanacaste).

Material and Methods

A review of the reports of jaguar camera trapping surveys supported by the JCP Mesoamerica was made in order to: 1) examine variation among studies conducted in similar areas, 2) identify weaknesses in survey methodology and 3) provide recommendations for future improvements in methods which would facilitate cross-site comparisons.

We compiled information from nine studies in Guatemala, four in Belize, one in Honduras, three in Nicaragua, seven in Costa Rica and three in Panama. Details on these studies are provided in Appendix 1.

The methods for camera trapping at these sites followed the recommendations detailed in Silver (2004). Cameras were set in pairs in order to identify jaguar individuals according to unique spot patterns on each flank. Some surveys used only one brand of commercial camera trap, some used several brands. Contrasts in the performance of camera brands are not evaluated in detail in this paper. Cameras were attached mainly to trees at 30-40 cm high and programmed to function 24 hours/day.

Two ways of setting cameras were used: 1) a single camera trapping period, occupying the complete area to be surveyed, in this case with 20 or more pairs of camera traps; and 2) establishing two grids, deploying the cameras in one grid for half of the study period and then shifting sequentially to the other grid for the second half of the period. Seven studies used these two sequential grids whereas 20 studies surveyed the whole study area as a single block.

Twenty three studies set the camera traps on vehicle roads and trails. In areas lacking roads or trails cameras were set at locations in with signs of jaguar presence, or where researchers predicted jaguars were likely to pass such as narrow valleys and dry stream beds or streams (four surveys). Surveys lasted from 35 to 105 days.

Density estimates are based on methods developed for tigers in India (Karanth and Nichols, 1998): the first step is to estimate abundance from the number of individuals captured and the proportion of recaptures, using the program CAPTURE (Otis *et al*., 1978; White *et al*., 1982), available online at the Patuxent Wildlife Research Center website at http://www.mbr-pwrc.usgs.gov/software/capture.html. The second step is to calculate the area surveyed: the typical way to estimate the sampling area is to calculate the mean maximum distance moved (MMDM) by jaguars in the sample to yield a proxy for home range diameter (Wilson and Anderson, 1985), sum the maximum distances moved by every individual captured in at least two different locations, calculate the average (diameter), divide by two (radius) and apply this value (½ MMDM) as a buffer around the camera traps. The estimation of the sampling area has been one of the most problematic issues for estimating jaguar population density based on camera trap surveys. New approaches termed "spatially explicit capture-recapture" have been developed to address this problem, directly estimating animal density without the need for an independent calculation of the sample area (Efford *et al*., 2004; Borchers and Efford, 2008; Royle *et al.,* 2009, Pallavi-Singh *et al.,* 2010). Researchers had not yet applied spatially explicit capture-recapture analyses to their camera trapping data, and the density estimates reported here are based on the CAPTURE/½ MMDM methodology.

Comparisons were made graphing the variables and comparing the visual results. When possible, a correlation was performed. Variables considered were: maximum distance moved by jaguars photographed in two or more different stations ("station" is understood as a point where one or more camera traps are set), minimum convex polygon formed by the cameras, number of jaguars photographed, jaguar density, number of stations, buffer added to camera stations to obtain the survey area, final survey area and type or road/place where cameras were set.

Results

With the exception of El Salvador, where jaguars have been extirpated (Seymour, 1989), all Mesoamerican countries have JCUs (Marieb, 2006), and estimates of jaguar density have now been generated in each country's main JCUs. Density estimates were highly variable, from 0.74 to 11.2 jaguars/100 km². Inter-survey variation could result either from environmental factors, in which case the density estimates are accurate; or methodological problems, whereby the density estimates are not accurate; or from a combination of both, in which case the clarity of the former is compromised by the latter.

Methodological problems

Methodological factors that can influence estimations of jaguar population densities from camera trap surveys include:

1. Inadequate size of camera trap station polygon.
2. Inaccurate estimates of maximum distance moved (MMDM) in order to calculate the survey area (related to a. above).
3. Proportion of edge / effective survey area vs. camera polygon.
4. Variable efficiency of camera traps in capturing jaguars (e.g., stations along frequented roads/trails might capture more animals than stations with less frequented and habitual travel routes).

We considered the relationship between the size of the camera polygon and MMDM. The size of the camera polygon defines the potential MMDM that can be determined from camera trap records—the survey cannot record movements outside its boundaries. If polygons are sufficiently large this is not a constraint. However, the apparent positive relationship means that the larger the camera polygon, the larger the MMDM potentially measured, and therefore the size of the survey area can directly affect the population density estimate. We observed an increase in MMDM (Figure 1) until the diameter of the camera polygon reached 10-11 km (corr = 0.46), after which MMDM tended to decrease. Based on the graphic results the camera layout should have a diameter exceeding 11 km, therefore covering more than 95 km². Based upon the recommendations for CAPTURE and recent jaguar home range estimates, even larger grids are suggested to avoid sampling a population at the scale of one animal's home range. In Central America, radio-telemetry studies have reported the following home range sizes for jaguars: 10-40 km² in the tropical moist lowland forests of Belize (Rabinowitz and Nottingham, 1986), 32-59 km² in tropical moist lowland forests of Mexico (Ceballos *et al.,* 2002), and 25-65 km² in Mexican deciduous forest (Nuñez *et al*., 2002). These home ranges correspond to minimum diameters of 3.2-8.1 km, assuming they are circular in shape. Small camera polygons are likely to encompass only portions of the home ranges for most individual jaguars

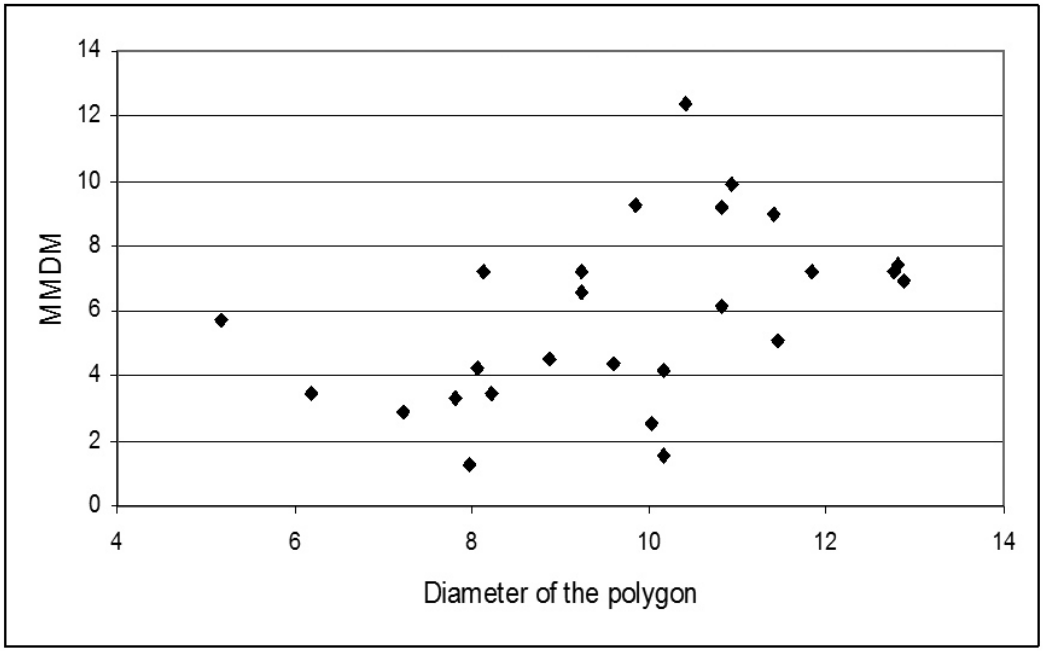

Figure 1. Comparison between Maximum Distance Moved by jaguars photographed in at least two different cameras and the diameter of the camera trap polygon.

photographed (Harmsen, 2008). As a result, observed MMDM will under-estimate home range diameter, and in turn density estimates will be over-estimated.

Another possible source of variation is the number of camera traps. We examined the relation between number of camera traps deployed and the density estimate but found no significant correlation (Figure 2: correlation -0.14). An investigator can use a smaller number of camera traps in two blocks, as suggested by Silver (2004), or survey a single block with 20 or 30 camera trap stations. However, if a small number of cameras translate to small blocks that add up to a small polygon, the survey incurs the problems described regarding MMDM estimation. Multiple blocks

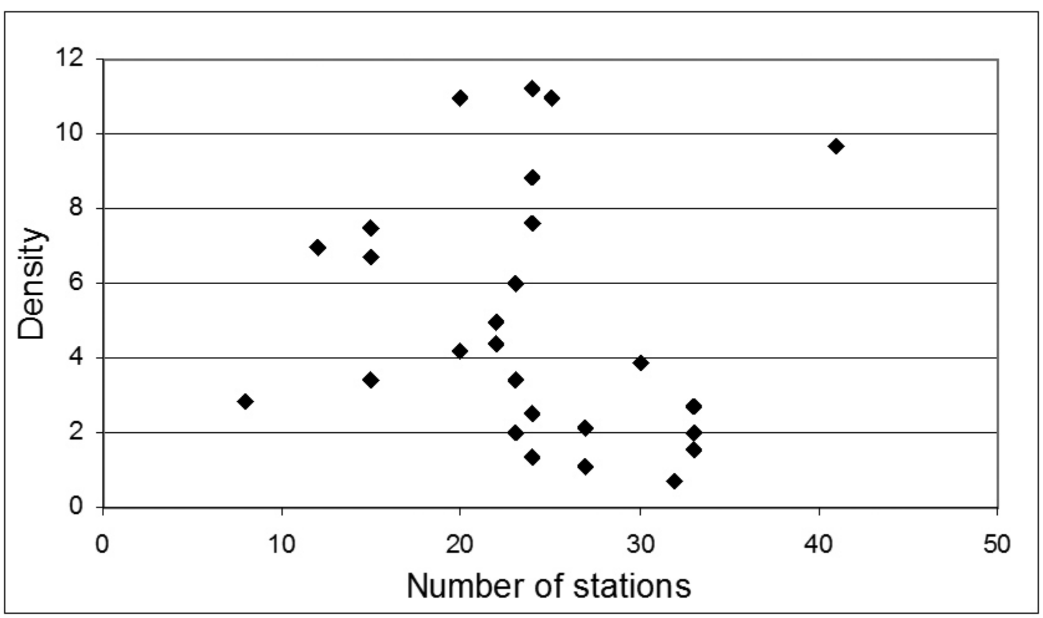

Figure 2. Comparison between jaguar density and number of camera trap stations.

may also reduce the amount of time that cameras are operational in each station, and therefore reduce overall captures and recaptures. Minimum length of time per block (30 versus 45 days) is yet a matter of contention.

We evaluated the percentage increase in the survey area from the minimum convex polygon formed by the camera traps to the final effective survey area including the buffer (Figure 3). In some cases the effective survey area is as much as 5 times the original polygon, meaning that as much as 84% of the effective survey area is outside the area bounded by the cameras. The buffer area in the surveys we reviewed varied from 24-84% of the polygon and averaged 60% across surveys. In 23 of 27 surveys, more than 50% of the effective survey area is outside the camera polygon, where jaguars have lower capture probability. We compared the percentage of increase of the effective survey area over the camera polygon with the density and found an inverse relationship between them (corr = -0.48), suggesting that the larger the proportion of buffer area, the smaller the density estimate. Figure 3 suggests an inflection point where the effective survey area exceeds 150% of the original camera polygon. The more conservative surveys, with an increase ≤150%, had an average camera polygon of 110 km². In order to minimize biased population density estimates resulting from buffer areas relatively large with respect to the camera polygon, we recommend therefore that the minimum camera polygon area for jaguars in Central American lowland tropical forests should be more than 110 km².

High population density estimates may result from the small area covered by camera grids, given that ranges tend to overlap (Rabinowitz and Nothingham, 1986, Maffei *et al.*, 2004) and therefore several individuals can be photographed in a small area (Maffei and Noss, 2008). In addition, excessively small survey areas, particularly for wide-ranging animals such as jaguars, may under-estimate MMDM if the maximum possible observed distance (the diameter of the camera polygon) is less than the diameter of individual home ranges. We compared the effective survey area (including the buffer) to the density estimate and found that there is also a negative correlation: the larger the survey area, the lower the density (Figure 4). Although there is only a weak correlation (-0.47), we observed that when the effective survey area approaches 200 to 300 km², the density curve begins to stabilize. We recommend that effective survey areas should cover at least 200 km² to avoid overestimation of the density.

A related methodological issue is the number of captures and recaptures recommended by authors of

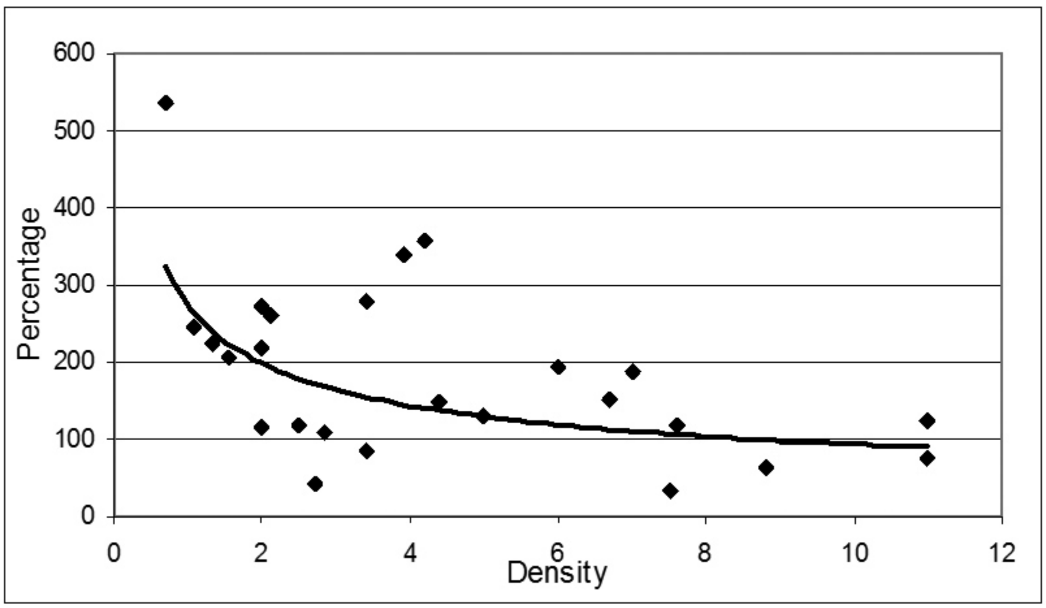

Figure 3. Comparison between jaguar density and the percentage of the effective survey area that results from adding the buffer around each camera station.

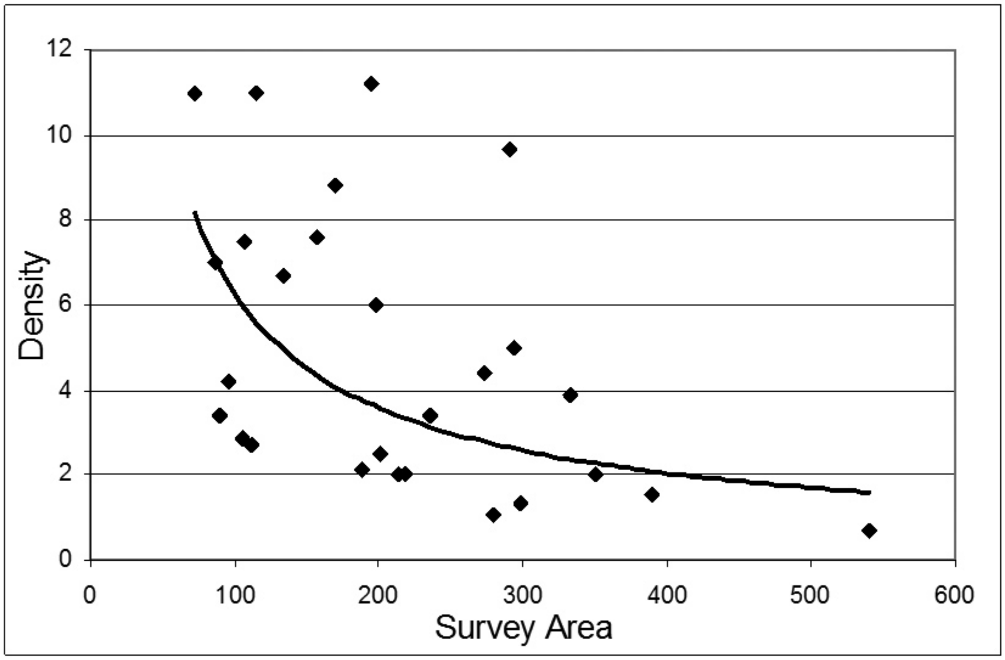

Figure 4. Comparison between jaguar density and effective survey area (including buffer around camera trap stations) in Mesoamerican studies.

capture-recapture analyses. For example, White *et al.* (1982), developing the method for small mammals, recommend a minimum of 75-100 individuals, 20 recaptures, and a capture probability of 0.30. In camera trap surveys for jaguars, between 2 and 27 individuals have been identified (Appendix 1), but most surveys are recording less than 10 individuals. The number of individuals can be increased by enlarging the camera trap polygon, but this is not always logistically feasible, and detecting 75-100 individuals is impossible in practical terms. Caution is nonetheless warranted for the density estimates generated by extremely small samples.

It is known that wild cats like to use human trails (Emmons and Feer, 1997), so capture probabilities also may decline if roads / trails are not available, in turn lowering population density estimates. Where roads/trails are lacking, cameras are set in alternative locations, for example streams. However, since many forests are full of streams, jaguars have more travel route options. Surveys without trails appear to have a lower probability of capturing jaguars (Figure 5). When larger more conspicuous trails cannot be used because the risk of theft, setting the cameras along secondary trails may also reduce the probability of capture and result in lower density estimates (Harmsen, 2008).

In three separate surveys in Guatemala's Maya Biosphere Reserve we compared jaguar detections in matched pairs of Reconyx RM45 digital camera traps programmed to take a sequence of ten photographs without delay, and Leaf River film units. The pattern of detection was 2:1 in favor of the digital camera traps (81:43, G = 0.1, P = 0.752). While these surveys compared only one type of digital camera with one type of film camera, and are thus limited in inference, they do suggest that digital camera traps programmed to take a rapid sequence of photographs may be more effective at capturing what passes in front of units, and thus are more likely to provide photographs which allow identifications.

Environmental factors

When the methodology is successful, accurate estimates of jaguar population densities can allow the examination of across-site variation resulting from intrinsic productivity of the habitat and status of the prey base. High density estimations then can reflect real high jaguar abundance, for example preferred jaguar habitats, in areas with high degrees of effective protection, and low densities can indicate the inverse. Reducing the variation in the methodology is necessary to better evaluate the effectiveness of the JCUs in protecting jaguar populations.

Most density surveys in Central America were conducted in tropical moist forest (22 cited in this publication) and densities reported were between 0.7 and

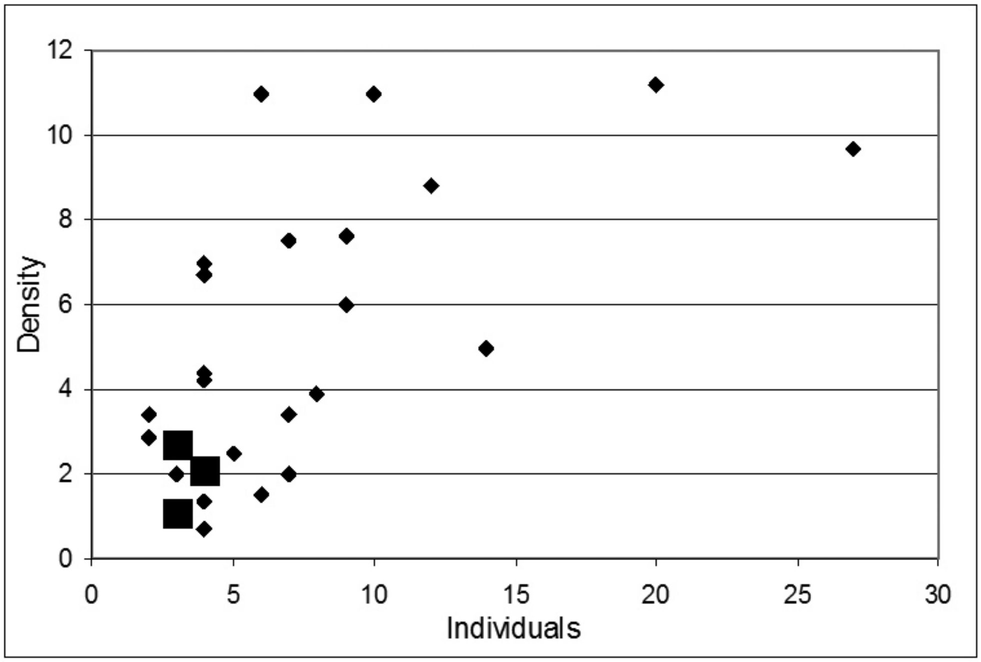

Figure 5. Comparison between jaguar individuals photographed and jaguar density obtained. Squares are the surveys with no trails available and cameras set in the middle of the forest.

11.2 individuals/100 km² (Novak, 2003; Miller, 2005), for an average of 5.19. In comparison, density estimates from tropical montane forest ranged from 1.34 to 6.7 individuals/100 km², and averaged 3.61; while the single density estimate from deciduous forest is 2.85. These results suggest that tropical moist forest is the preferred habitat for jaguars in Central America, but all three forest types support jaguar populations.

Most of the jaguar surveys were made within protected areas. Surveys in national parks (n = 17; range 0.7-11.2) had an average density of 6.3 (±3.4) inds/100 km², while multiple use zones in biosphere reserves (where hunting by residents and some natural resource extraction was permitted; n = 9; range: 1-11) had an average of 3.2 (±2.9) inds/100 km². Although the difference is not statistically significant ($x^2 = 1.65$; df = 1; $P<0.05$), the sample results suggest that effectively-defended national parks favor higher densities of jaguars. Clearly this will not be the case when legal status does not reflect correspondingly effective protection as in the case of some national parks in which unauthorized activities and security risks make surveys impossible. Conversely, some biosphere reserves or community managed areas may achieve high densities of jaguars when conservation measures are effectively implemented. Adequate in-field institutional presence and compliance with protected/managed area objectives are key.

Jaguar Conservation Units are defined as areas of sufficient extent, prey availability, and habitat quality to support a jaguar population for at least the next 100 years (Sanderson *et al.*, 2002; Marieb, 2006). Jaguar Conservation Units are assumed to contain at least 50 breeding individuals. All surveys have been conducted within JCUs, so we cannot compare density estimates inside and outside of JCUs. However, we found no significant relation (corr = 0.15 $p = 0.7$) between the size of JCU and jaguar density. Assuming an average density of 3 jaguars/100 km², 2000 km² of well-conserved forest are needed to have a population of at least 50 jaguars.

Factors that can affect jaguar population density but often cannot be compared because of sparse data include the following:

1. Levels of direct human-induced mortality of jaguars.
2. Inherent habitat quality in terms of primary and secondary production.
3. Depletion of native prey from inherent productive potential through over-hunting.
4. Differences in detectability of males and females. In this review, males were recorded more than females, an average of 3 males per 2 females, although the difference is not statistically significant: $x^2 = 0.33$; $p>0.1$. In some station locations females might have

avoided the specific areas with camera traps: 12 surveys registered more males than females with a ratio of 2♂:1♀, while in only four surveys females were more abundant than males, but in a ratio of 2♂:5♀.

Conclusions

The camera-trap surveys conducted between 2000-2010 in Mesoamerica supported wholly or partially by the JCP, were often exploratory in nature. They confirmed the presence of jaguars in the three principal forest types surveyed, and suggest relatively higher densities in tropical moist forests as compared to tropical montane forests.

In addition to variation in procedures across surveys—duration, area covered, camera location, the problems with CAPTURE/½ MMDM as a method for estimating population density, in particular the estimation of the effective survey area, requires that many of the results published to date must be treated as preliminary.

For comparative purposes, we have analyzed data from the Gran Chaco in Bolivia with camera trap polygons ranging from 48-434 km², and using three analytical programs, CAPTURE with ½ MMDM, maximum likelihood spatially explicit capture recapture (ML SECR, program DENSITY, Efford *et al.,* 2004), and a Bayesian Markov-Chain Monte Carlo (MCMC) SECR (program SPACECAP, Pallavi-Singh *et al.,* 2010). The constraints imposed by small polygons with wide-ranging animals are obvious. The example of a jaguar in a 434 km² survey grid crossing the entire area, a straight-line distance of 34 km (Romero-Muñoz, 2007) is reminder of the need for adequate sized sample areas despite the associated labor and cost. Density estimates using either of the SECR models are lower than those using CAPTURE ½ MMDM, with the MCMC model generating lower density estimates (though differences are not statistically significant) than the ML model across most Kaa-Iya surveys. We recommend analyzing camera trap data with the new SECR models in order to qualify density estimates using Capture ½ MMDM.

In order to reach the goal of comparable accurate and unbiased density estimates we need to go beyond the recommendations of Silver (2004) distinguish between exploratory surveys and those intended for density estimates; and aim for an adequate combination of large grid, quality cameras, and more uniform capture efficacy so that across-site comparisons of jaguar abundance are more plausible.

For future jaguar surveys in Central American forests, we therefore recommend that the polygon formed by the camera traps should cover a minimum of 110 km², based roughly on home ranges reported in telemetry studies. If CAPTURE/½ MMDM will be used to estimate population density, the effective survey area should be at least 200 km², but the effective survey area should not be more than twice the polygon area in order to avoid over-estimation of population density from an excessively large buffer area. A survey can be done with a limited number of cameras, shifting the cameras to two or three grids within a two-three month period and if the overall grid is more than 110 km². Ideal spacing between cameras would be between 2 and 3 km. This is intended to maximize recaptures of each individual (ensuring multiple cameras within each individual's home range) to strengthen the capture-recapture analysis. A minimum of 45 camera stations is required to cover a polygon of 110 km² at 2 km and 20 stations at 3 km spacing. All evidence urges grids no smaller.

We also recommend using existing trails when they are available as well as opening trails prior to the survey period where none exist and waiting some months until jaguars and wildlife in general get used to these. This may entail considerable labor costs in some sites, but more uniform methods will benefit comparisons. Comparisons of surveys made with cameras set in trails/roads versus surveys that had to set cameras somewhere else needs to be made with caution.

The effort and costs in conducting field surveys is considerable and it is important that the camera traps perform as efficiently as possible. We have found that digital camera traps capable of recording a rapid sequence of photographs and the standardized application on a local attractant (e.g., Calvin Klein's Obsession for Men) can both cause the jaguars to linger in front of the camera, and maximize the opportunities for adequate photographs to identify the individuals.

One of the primary motivations of the JCP supported surveys has been to evaluate the performance of the JCU in adequately protecting cats. Recording additional information, even if of a qualitative nature -on prey base, incursions, and other measures of the area's efficacy in protecting jaguar- may be useful in guiding management efforts. While an unbiased and accurate estimate of abundance is the loftiest and rightful goal of a well-executed survey, surveys are one of our tools that inform a combination of activities intended to ensure the survival of jaguars in the study area.

Finally, a fundamental issue for a successful camera trapping project is employ and train local people to participate in the surveys. Aside from reducing equipment losses and other security risks, the inclusion of the community in our research—particularly where these local people have rights and responsibilities over the conservation area and its resources—is the best guarantee of long-term jaguar conservation.

Acknowledgments

We would like to thank the Liz Claiborne and Art Ortenberg Foundation, Jaguar Motor Cars, the US Department of State, The Nature Conservancy, the US Agency for International Development and Panthera Foundation for their financial support to the WCS Jaguar Conservation Program and to the researchers whose surveys are analyzed in this paper. We are grateful for the support that the Central American Commission for Environment and Development provided in endorsing the Mesoamerican Biological Corridor and studies of the jaguar populations within it. Special thanks to Alan Rabinowitz, Scott Silver and Linde Ostro for their contributions to the WCS jaguar survey program. We are grateful to the Institute of Ecology of the National University of Mexico for hosting opportunities for range wide exchanges in 1999 and 2009.

Literature Cited

Alfaro, L. D. 2007. Estimación de la población de jaguares (*Panthera onca*) en el Parque Nacional Santa Rosa y Parque Nacional Guanacaste del Área de Conservación Guanacaste, Costa Rica. M. Sc. Thesis. Universidad Nacional, Costa Rica.

Amit, R. R. 2007. Densidad de jaguares (*Panthera onca*), en el Sector San Cristóbal del Área de Conservación Guanacaste, Costa Rica. Undergraduate thesis. Universidad Nacional, Heredia, Costa Rica.

Borchers, D. L. and M. G. Efford. 2008. Spatially explicit maximum likelihood methods for capture–recapture studies. Biometrics 64: 377-385.

Bustamante, H. A. 2008. Densidad y uso de hábitat por los felinos en la parte sureste del área de amortiguamiento del Parque Nacional Corcovado, Península del Osa, Costa Rica. M. Sc. Thesis, Universidad Nacional, Heredia, Costa Rica.

Ceballos, G., C. Chávez, A. Rivera, C. Manterola and B. Wall. 2002. Tamaño poblacional y conservación del jaguar en la Reserva de la Biosfera Calakmul, Campeche, México. *In*: Medellín, R. A., C. Equihua, C. L. B. Chetkiewicz, P. G. Crawshaw Jr., A. Rabinowitz, K. H. Redford, J. G. Robinson, E. W. Sanderson and A. B. Taber (eds.). El jaguar en el nuevo milenio. Fondo de Cultura Económica, Universidad Nacional Autónoma de México and Wildlife Conservation Society. pp. 403-417.

Díaz-Santos, F., J. Polisar, L. Maffei, G. García, A. Amador and L. Mullenso. 2007. Estudio de densidad de jaguares en la parte alta de la cuenca del río Lakus, Bosawas, Atlántico Norte de Nicaragua. Technical Report for Wildlife Conservation Society, Bronx, NY.

Díaz-Santos, F. G., F. Díaz, L. Maffei, J. E. Miranda, M. A. Urbina, M. Urbina and H. Jarquín. 2009. Densidad de jaguares en el sector suroeste de la reserva Indio-Maíz, Río San Juan, Nicaragua. Technical Report for Wildlife Conservation Society, Bronx, NY.

Efford, M. G., D. K. Dawson and C. S. Robbins. 2004. DENSITY: software for analyzing capture-recapture data from passive detector arrays. Animal Biodiversity and Conservation 27: 217-228.

Emmons, L. H. and F. Feer. 1997. Neotropical rainforest mammals. A field guide. University of Chicago Press. Chicago and London.

García, A. R., R. B. McNab, J. S. Soto, J. Radachowsky, J. Moreira, C. Estrada, V. Méndez, D. Juárez, T. Dubón, M. Córdova, F. Córdova, F. Oliva, G. Tut, K. Tut, E. González, E. Muñoz, L. Morales and L. Flores. 2006. Los jaguares del corazón del Parque Nacional Tikal, Petén, Guatemala. Asociación Balám and Wildlife Conservation Society, Flores, Petén, Guatemala.

González-Maya, J. F., J. Mata-Lorenzen, E. Navarro-Arquez, A. Benítez and J. Schipper. 2008. Conservation assessment of jaguar (*Panthera onca*) and their prey in the Talamanca Mountains, Costa Rica. Technical Report for Wildlife Conservation Society, Bronx, NY.

González-Maya, J. F., K. Rojas-Jiménez, J. Cardenal, A. Mattey, D. Corrales and E. Nájera. 2009. Jaguar (*Panthera onca*) density estimation in Cordillera Talamanca, Costa Rica. Technical Report for Wildlife Conservation Society, Bronx, NY.

Harmsen, B. J. 2008. The use of camera traps for estimating abundance and studying the ecology of jaguars (*Panthera onca*). Ph. D. dissertation. University of Southampton, Southampton, UK.

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

Kelly, M. J. 2003. Jaguar monitoring in the Chiquibul Forest, Belize. Caribbean Geography 13(1): 19-32.

Marieb, K. 2006. Jaguars in the New Millennium Data Set Update: The State of the Jaguar in 2006. Report for Wildlife Conservation Society-Jaguar Conservation Program. Wildlife Conservation Society, New York.

Maffei, L., E. Cuéllar and A. Noss. 2004. One thousand jaguars (*Panthera onca*) in Bolivia's Chaco? Camera trapping in the Kaa Iya National Park. Journal of Zoology, London 262: 295-304.

Maffei, L. and A. Noss. 2008. How small is too small? Camera trap survey areas and density estimates for Ocelots in the Bolivian Chaco. Biotropica 40(1): 71-75.

McNab, R. B., J. Moreira, R. García, G. Ponce, V. Méndez, M. Córdova, F. Córdova, G. Ical, I. García, A. Vanegas, E. Zepeda, H. Tut and R. Monzón. 2008. Densidad de jaguares en la Concesión Comunitaria de Carmelita y Asociación Forestal Integral San Andrés Petén, Reserva de la Biosfera Maya. Technical Report. Wildlife Conservation Society, Flores, Guatemala.

Medellín, R. A., C. Equihua, C. B. Chetkiewicz, P. G. Crawshaw Jr., A. Rabinowitz, K. H. Redford, J. G. Robinson, E. W. Sanderson and A. B. Taber. 2002. El jaguar en el nuevo milenio: una evaluación de su estado, detección de prioridades y recomendaciones para la conservación de los jaguares en América. Fondo de Cultura Económica, Universidad Nacional Autónoma de México and Wildlife Conservation Society.

Medellín, R. A., A. de la Torre and B. K. Tavera. 2008. Jaguar camera trap surveys at Montes Azules Biosphere Reserve, Chiapas, Mexico. Technical Report for Wildlife Conservation Society, Bronx, NY.

Miller, C. M. 2005. Jaguar density in Gallon Jug Estate, Belize. Technical Report for Wildlife Conservation Society, Bronx, NY.

Miller, C. M. and B. Miller. 2005. Jaguar density in La Selva Maya. Technical Report for Wildlife Conservation Society, Bronx, NY.

Moreira, J., R. B. McNab, D. Thornton, R. García, V. Méndez, A. Vanegas, G. Ical, E. Zepeda, R. Senturión, I. García, J. Cruz, G. Asij, G. Ponce, J. Radachowsky and M. Córdova. 2007. The comparative abundance of jaguars in La Gloria-El Lechugal, Multiple Use Zone, Maya Biosphere Reserve, Guatemala. Wildlife Conservation Society, Flores, Guatemala.

Moreira, J., R. B. McNab, R. García, V. Méndez, G. Ponce-Santizo, M. Córdova, S. Tun, T. Caal and J. Corado. 2008. Densidad de jaguares en el Biotopo Protegido Dos Lagunas, Parque Nacional Mirador Río Azul, Petén, Guatemala. Wildlife Conservation Society, Flores, Guatemala.

Moreira, J., R. McNab, R. García, G. Ponce-Santizo, M. Mérida, V. Méndez, M. Córdova, G. Ruano, K. Tut, Tut, F. Córdova, E. Muñoz, E. González, J. Cholom and A. Xol. 2009. Abundancia y densidad de jaguares en el Parque Nacional Laguna del Tigre-Corredor Biológico Central. Reserva de la Biosfera Maya. Informe Interno Wildlife Conservation Society-Programa para Guatemala.

Moreira, J., R. García, R. McNab, G. Ponce-Santizo, M. Mérida, V. Méndez, G. Ruano, M. Córdova, F. Córdova, Y. López, E. Castellanos, R. Lima and M. Burgos. 2009. Abundancia de jaguares en las Concesiones del bloque de Melchor de Mencos, Reserva de la Biosfera Maya. Informe Interno Wildlife Conservation Society-Programa para Guatemala.

Moreira, J., R. García, R. McNab, G. Ruano, G. Ponce-Santizo, M. Mérida, K. Tut, P. Díaz, E. González, M. Córdova., E. Centeno, C. López, A. Vanegas, Y. Vanegas, F. Córdova, J. Kay, G. Polanco, and M. Barnes. 2010. Abundancia y densidad de jaguares en el oeste del Parque Nacional Mirador Río Azul, Reserva de la Biosfera Maya. Informe Interno Wildlife Conservation Society-Programa para Guatemala.

Moreno, R. S. 2006. Parámetros poblaciones y aspectos ecológicos de los felinos y sus presas en Cana, Parque Nacional Darien, Panamá. M. Sc. Thesis. Universidad Nacional, Heredia, Costa Rica.

Moreno, R. S. and A. Bustamante. 2007. Estatus del jaguar (*Panthera onca*), otros felinos y sus presas, utilizando cámaras trampa en la región del Alto Chagres, Panamá. Technical Report for Wildlife Conservation Society, Bronx, NY.

Novak, A. J. 2003. Impacts of subsistence hunting on the foraging ecology of jaguar and puma in the Maya Biosphere Reserve, Guatemala. M. Sc. Thesis. University of Florida, USA.

Nuñez, R., B. Miller and F. Lindzey. 2002. Ecología del jaguar en la Reserva de la Biósfera Chamela-Cuixmala, Jalisco, México. *In*: Medellín, R. A., C. Equihua, C. B. Chetkiewicz, P. G. Crawshaw Jr., A. Rabinowitz, K. H. Redford, J. G. Robinson, E. W. Sanderson and A. B. Taber. (eds.). El jaguar en el nuevo milenio: una evaluación de su estado, detección de prioridades y recomendaciones para la conservación de los jaguares en América. Fondo de Cultura Económica, Universidad Nacional Autónoma de México and Wildlife Conservation Society. México. pp. 107-126.

Otis, D. L., K. P. Burnham, G. C. White and D. R. Anderson. 1978. Statistical inference from capture data on closed populations. Wildlife Monographs 62: 1-135.

Pallavi-Singh, A. M. G., A. J. Royle, N. S. Kumar and K. U. Karanth. 2010. SPACECAP: a program to estimate animal abundance and density using Bayesian spatially-explicit capture-recapture models. WCS-India program, Centre for Wildlife Studies, Bangalore, India. Version 1.0.

Polisar, J. 2006. Jaguares, presas y gente en Territorios Indígenas Mayangna Sauni Bu, Reserva Biosfera BOSAWAS. The Nature Conservancy, United States Agency for International Development, Managua, Nicaragua.

Portillo, H. O., J. Hernández, T. Manzanares, T. Manzanares Jr., S. Lacut and R. Lacut. 2008. Estimating jaguar population using traps camera in one hundred square kilometers in Rus Rus La Mosquitia, Honduras. Technical Report for Wildlife Conservation Society, Bronx, NY.

Rabinowitz, A. R. and B. G. Nottingham. 1986. Ecology and behavior of the Jaguar (*Panthera onca*) in Belize, Central America. Journal of Zoology, London 210: 149-159.

Romero-Muñoz, A., A. J. Noss, L. Maffei and R. M. Montaño. 2007. Binational population of jaguars confirmed by camera-trapping in the American Gran Chaco. Cat News 46: 24-25.

Royle, J. A., J. D. Nichols, K. U. Karanth and A. M. Gopalaswamy. 2009. A hierarchical model for estimating density in camera-trap studies. Journal of Applied Ecology 46(1): 118-127.

Ruano, G., J. Moreira, R. García, R. McNab, F. Córdova, G. Ponce-Santizo, M. Mérida and N. Solís. 2010. Abundancia y densidad de jaguares en el Parque Nacional Mirador-Río Azul, Reserva de la Biosfera Maya. Informe Interno Wildlife Conservation Society-Programa para Guatemala.

Salom-Pérez, R., E. Carrillo, J. C. Sáenz and J. M. Mora. 2007. Critical condition of the jaguar *Panthera onca* in Corcovado National Park, Costa Rica. Oryx 41(1): 1-7.

Sanderson, E. W., K. H. Redford, C. B. Chetkiewicz, R. A. Medellín, A. R. Rabinowitz, J. G. Robinson and A. B. Taber. 2002. Planning to save a species: the jaguar as a model. Conservation Biology 16(1): 58-72.

Seymour, K .L. 1989. *Panthera onca*. Mammalian Species 340: 1-9.

Silveira, L., A. T. A. Jácomo, S. Astete, R. Solmann, N. M. Tôrres, M. M. Furtado and J. Marinho-Filho. 2009. Density of the near threatened jaguar *Panthera onca* in the Caatinga for north-eastern Brazil. Oryx 44(1): 104-109.

Silver, S. 2004. Assessing jaguar abundance using remotely triggered cameras. JCP – Wildlife Conservation Society.

White, G. C., D. R. Anderson, K. P. Burnham and D. L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. New Mexico: Los Alamos National Laboratory.

Wilson, K. R. and D. R. Anderson. 1985. Evaluation of two density estimators of small mammal population size. Journal of Mammalogy 66: 13-21.