Biological Conservation 159 (2013) 375–381

Contents lists available at SciVerse ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

# High jaguar densities and large population sizes in the core habitat of the southwestern Amazon

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ARTICLE INFO

*Article history:*
Received 28 June 2012
Received in revised form 7 December 2012
Accepted 9 December 2012

*Keywords:*
Bayesian analysis
Camera trapping
Madre de Dios
*Panthera onca*
Peru
Spatially explicit capture–recapture model

ABSTRACT

Over 80% of the currently occupied range of the jaguar (*Panthera onca*) lies in the Amazon. However, few density estimates exist for this habitat. Between 2005 and 2010 we carried out six camera trap surveys at three different sites in the department of Madre de Dios in the Peruvian Amazon. We analyzed our data using a Bayesian spatially explicit capture recapture model (SECR) with sex covariates to account for differences in home range size and detection probabilities of male and female jaguars. As several of our camera grids where too small for reliable density estimates, we used estimates for the $\sigma$ parameter from the largest camera grid to correct for the bias. Density estimates for our surveys were similar with an average density of $4.4 \pm 0.7$ jaguar $100\ \text{km}^{-2}$. Both home range size and encounter rates varied significantly between sexes with males having a larger home range and higher encounter rate than females. Our estimated sex ratio was 1:1.5 compared to an observed ratio of 1.9:1. Not accounting for sex would have resulted in an underestimation of the true density. The densities found in this study are among the highest documented and show that the Amazon is indeed a core habitat for the jaguar. We estimate that three jaguar conservation units in our study region (areas defined by experts as having a high conservation priority) could harbor as many as 6000 jaguars (CI: 4278–8142).

## 1. Introduction

The jaguar (*Panthera onca*) has a wide distribution ranging from northern Mexico to northern Argentina, but has disappeared from over 40% of its original range over the last century largely due to habitat loss (Sanderson et al., 2002; Zeller, 2007). It is currently classified as near threatened by the IUCN with populations in Central America and Mexico, the Atlantic forest, the Cerrado of Brazil, the Chaco in northern Argentina and savannas of Venezuela and the Guianas being most threatened (Caso et al., 2008). The Amazon remains the largest continuous block of habitat within the jaguar's range and is considered a stronghold for the species with a very high probability of long term survival (Sanderson et al., 2002; Zeller, 2007). Within the Amazon the upper Amazon tropical lowland moist forest makes up the largest ecoregion, spanning five countries including Brazil, Bolivia, Columbia, Ecuador and Peru.

In Peru the jaguar is found throughout the lowlands of the Amazon basin east of the Andes up to an elevation of about 1500–2000 m and about 23% of its range falls within protected areas (Carrillo-Percastegui and Maffei, in press). During a recent reclassification of the Peruvian red list of threatened species the jaguar was classified as near threatened (Carrillo-Percastegui and Maffei, in press). The major threats to the species are hunting and deforestation due to the expansion of agriculture and a surge of gold mining in the Amazon over the recent years (Swenson et al., 2011). With an increase of cattle ranching and small scale agriculture we also expect more conflicts between jaguar and ranchers with more jaguars being shot as retaliation to livestock loss. While the Peruvian law prohibits any killing of jaguars and all trade with jaguar parts, there is little enforcement and teeth, claws, skin parts and even whole skins are often seen for sale in local markets.

The southern part of the Peruvian Amazon in the department of Madre de Dios still consists of largely continuous forest (Asner et al., 2010). The region includes three protected areas of more than 1 million hectares each: Alto Purus, Manu, and Bauhuja-Sonene National Parks; as well as the Tambopata National Reserve; several large indigenous reserves and a number of private conservation concessions. The landscape connects to Manirupi-Heath Amazonian Wildlife Reserve and Madidi National Park in Bolivia to the east. Based on the large expanse of these forests and the assumed health of jaguar populations in the region, experts defined three jaguar conservation unites (JCUs) of high priority that together cover an area of 138,000 km$^2$, 55,014 km$^2$ of which are within existing protected areas (Zeller, 2007). Despite the importance of the Amazon lowland moist forest as jaguar habitat, only

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http://dx.doi.org/10.1016/j.biocon.2012.12.012

a few studies have been carried out in this ecoregion and as of today no reliable density estimates exist. The goal of our study therefore was to evaluate the density of jaguars in different types of management units in the Madre de Dios basin; government protected areas, a private conservation area, and a forestry concession (one of the first in the Amazon basin to receive FSC certification) in order to obtain a better understanding of their population status across the landscape, and ultimately to estimate the size of the population in the whole region.

Camera traps in combination with capture–recapture models have become the most widely used method for estimating jaguar densities (Maffei et al., 2011; Silver et al., 2004). However, a recent simulation study showed that results can be highly biased when camera grids used are smaller than the home range of the study species (Tobler and Powell, in press; but see Sollmann et al., 2012). Since our surveys were affected by this problem we evaluated a new method of data sharing and borrowing across surveys in combination with spatially explicit capture recapture (SECR) models (Borchers and Efford, 2008; Efford et al., 2009; Royle and Gardner, 2011; Sollmann et al., 2011) in order to obtain unbiased results from three different sites in two of the JCU proposed by Zeller (#75 and #76, 2007) in the south-eastern Peruvian Amazon.

## 2. Materials and methods

### 2.1. Study area

This study was carried out at three different sites in the department of Madre de Dios, Peru (Fig. 1). The first site, the Los Amigos Conservation Concession, is a 1400 km$^2$ private protected area, established in 2001 (12°19′–12°36′S, 70°02′–70°17′W, 200–320 m asl) that is bordered in the south by the Madre de Dios River, in the north and east by forest concessions, and in the west by a large indigenous area that protects uncontacted groups that are living in voluntary isolation. Our second site was located along the Tambopata river in the Bahuaja Sonene National Park, 5 km south of the Malinowsky guard post (12°57′–13°01′S, 69°25′–69°30′W, 200–250 m asl). The third site was within the Espinoza Forestry Concession in the northern part of Madre de Dios south of the Tahuamanu river (11°25′–11°44′S, 69°42′–69°57′W, 300–380 m asl). This forest concession is FSC certified for sustainable management and has been selectively logged since 2003. A network of logging roads has been established that allows access for workers and trucks hauling supplies, logs, and lumber but guarded gates prevent outsiders from using the roads. Hunting at all three sites is prohibited but there is some hunting in surrounding areas. We are not aware of any killing of jaguars within our study areas during the time of our surveys.

The climate in the region is divided into a dry season from June to October and a rainy season from November until May with a mean annual rainfall between 2500 and 3500 mm. Mean annual temperature is 24 °C with a range from 10 to 38 °C.

All three sites are in lowland Amazonian moist forest. Los Amigos and Tambopata contain both *terra firma* and floodplain forest while Espinoza is mainly *terra firme* forest. The floodplain forest in the region is never completely inundated, even at the peak of the rainy season except for a narrow fringe of less than 1 km along the main river.

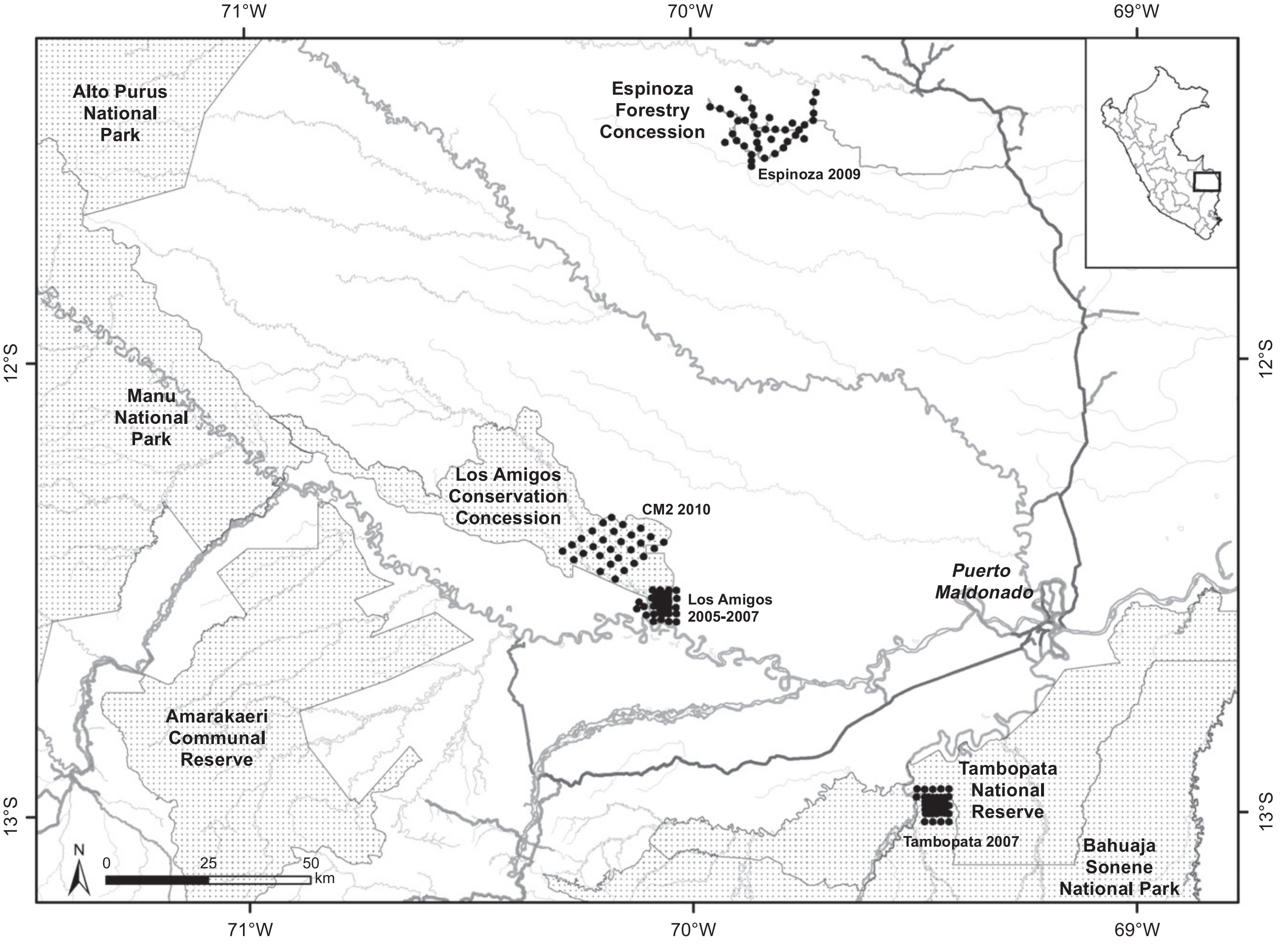

**Fig. 1.** Map showing the location of six camera trap surveys in Madre de Dios, Peru. Shaded areas are protected areas; the dark line shows the interoceanic highway.

### 2.2. Camera trapping

Between 2005 and 2010 we carried out six camera trap surveys designed to estimate jaguar densities (Table 1). At Los Amigos we implemented a total of four surveys on two camera trap grids referred to as Los Amigos 2005–2007 and CM2 2010. There was one survey each in Tambopata (Tambopata 2007) and in the Espinoza forestry concession (Espinoza 2009). Cameras were set on regular grids using existing trails or newly cut trails in Los Amigos 2005–2007 and Tambopata with 1–3 km between stations. At the Espinoza forestry concession cameras were mostly set along existing logging roads. Cameras on the Los Amigos CM2 grid were set in the absence of trails on game trails and in slightly more open spots. All cameras were placed 50 cm above ground and paired cameras were set on each side of the trail. We used Deercam film camera traps and starting in 2009 additionally ScoutGuard SG550 digital cameras traps. All cameras were operating for the whole duration of the surveys except at the CM2 survey were cameras were run in three blocks. Cameras were active 24 h per day, Deercams were checked weekly to replace film and batteries if needed, Scoutguards roughly once a month to change memory cards and replace batteries if necessary.

### 2.3. Data analysis

All data and images were managed in Camera Base 1.4 (Tobler, 2010). For each station we recorded the exact dates when the cameras were operating, considering a station as operational when at least one of the two cameras was working, and for all SECR models (see below) we used the exact number of days each station was active in order to reduce bias caused by camera failure (Foster, 2008). Individual jaguars were identified based on their coat patterns and for the Los Amigos surveys individuals were compared across surveys. If a photo could not be clearly assigned to one individual it was removed from the analysis.

We analyzed the data using various SECR models (Borchers and Efford, 2008; Efford et al., 2009; Royle and Gardner, 2011; Sollmann et al., 2011). SECR models use the spatial information of the capture–recapture data to estimate the distribution of animals in space and their density. They assume that animals have fixed home ranges that are approximately circular and that the encounter rate declines with distance from the home range center following a specific detection function. The most commonly used detection function is the half-normal function which has two parameters: the encounter rate at the home range center $\lambda_0$, and the scale parameter $\sigma$ which describes how the encounter rate decreases with increasing distance from the home range center and is related to the home range radius. As with all closed capture–recapture models they assume a closed population for the duration of the study. The models can be fitted in a maximum-likelihood framework (Borchers and Efford, 2008; Efford et al., 2009) or a Bayesian framework using data augmentation (Royle and Gardner, 2011; Royle and Young, 2008).

Based on results from a simulation study (Tobler and Powell, in press) we assumed that the $\sigma$ parameter of the SECR models was underestimated for all of our small grids. At the same time the simulations showed that density estimates for small grids can be corrected by using the "correct" value for $\sigma$ (Tobler and Powell, in press). We therefore used estimates for this parameter from our most robust survey (Espinoza 2009) for all other surveys.

Previous work has shown that home range size and movement patterns can vary between male and female jaguars and that including these covariates can improve density estimates (Sollmann et al., 2011). We created a SECR model that included sex as a covariate both for $\sigma$ and $\lambda_0$ while still using the $\sigma$ estimate from the largest survey. We implemented all SECR models in a Bayesian framework using WinBUGS (Gilks et al., 1994) run through the package R2WinBUGS (Sturtz et al., 2005) in R 2.14 (R Development Core Team 2011). Models were adapted from models by Sollmann et al. (2011) and Tobler et al. (in press). Estimates for $\sigma$ were included in the model as fixed values obtained from the Espinoza 2009 survey. For each Bayesian model we ran three Markov Chain Monte Carlo (MCMC) chains with 40,000 iterations, 20,000 burn-in iterations, and a thinning rate of 20 to reduce auto-correlations.

## 3. Results

We photographed a total of 67 jaguars across all six surveys of which 40 were males, 21 females, and 6 of unknown sex. Nine individuals at Los Amigos were captured during multiple surveys, most in consecutive years but one female was captured in 2005 and 2010 and one male in 2006 and 2010. The maximum number of individuals captured at one single camera station was 5.

As expected we found large differences in density estimates produced by the different methods (Table 2). For estimates using the spatial parameters $\sigma$ from each survey, a grid size effect can be seen, resulting in higher estimates for surveys with smaller grids. Using $\sigma$ from the Espinoza 2009 survey for all surveys removed the grid effect resulting in more similar density estimates except for two surveys with very low detection probabilities where we assumed the densities were overestimated by the SECR models (Fig. 2). Based on extensive fieldwork in the region we have no reason to believe that densities are much higher in Tambopata or that densities decreased drastically between 2005 and 2006 at Los Amigos. Confidence intervals for density estimates for the final SECR model increased with lower detection probabilities and decreased with greater survey effort (Table 3, Fig. 2). The mean density across all surveys (excluding the 2 with low detection probabilities; Los Amigos 2005 and Tambopata 2007) calculated by the final model was 4.4 ± 0.7 ind. 100 km$^2$ (CI: 3.1–5.9).

When estimating values for $\sigma$ and $\lambda_0$ for each sex independently we found that females had smaller home ranges ($\sigma = 2.53$ km, HR = 130 km$^2$) than males ($\sigma = 3.85$ km, HR = 283 km$^2$) and a lower encounter rate. The probability of a random individual being a female was estimated as 0.6 (CI: 0.46–0.73), translating into a sex ratio of about 1:1.5.

**Table 1**
Data for six camera trap surveys carried out in the Peruvian Amazon. The camera grid area was calculated by a minimum convex polygon around the camera stations.

| Survey name | Start date | End date | Stations | Camera days | Grid area (km$^2$) |
|---|---|---|---|---|---|
| Los Amigos 2005 | 12.09.2005 | 13.11.2005 | 24 | 1478 | 56 |
| Los Amigos 2006 | 14.08.2006 | 17.10.2006 | 40 | 2509 | 56 |
| Los Amigos 2007 | 02.09.2007 | 09.11.2007 | 40 | 2510 | 56 |
| Malinowsky 2007 | 03.04.2007 | 09.06.2007 | 43 | 2585 | 52 |
| Espinoza 2009 | 18.10.2009 | 06.03.2010 | 38 | 3460 | 250 |
| CM2 2010 | 22.03.2010 | 15.12.2010 | 30 | 3131 | 196 |

**Table 2**
Comparison of jaguar density estimates for six camera trap surveys in the Peruvian Amazon based on three different methods. SECR: model run for each survey independently; SECR shared: model with $\sigma$ shared across surveys; SECR fixed with sex: model with sex covariate for $\sigma$ and $\lambda_0$ and $\sigma$ set to the value of the largest survey (Espinoza 2009). $N$: number of individuals photographed, freq.: number of photographs/1000 camera days, $\sigma$: scale parameter (m), $\lambda_0$: encounter rate, and $D$: density (individuals 100 km$^{-2}$).

| Survey | N | Freq. | SECR | | SECR shared | | SECR fixed with sex | |
|---|---|---|---|---|---|---|---|---|
| | | | σ | D | σ | D | σ[a] | D |
| Los Amigos 2005 | 10 | 9.5 | 1293 | 12.2 ± 3.0 | 3294 | 8.8 ± 3.0 | 3848/2526 | 9.0 ± 3.0 |
| Los Amigos 2006 | 10 | 14.8 | 3582 | 3.3 ± 1.7 | 3294 | 3.7 ± 1.2 | 3848/2526 | 4.5 ± 1.4 |
| Los Amigos 2007 | 11 | 19.5 | 2965 | 3.9 ± 1.5 | 3294 | 3.4 ± 1.1 | 3848/2526 | 4.0 ± 1.3 |
| Malinowsky 2007 | 7 | 4.6 | 1318 | 12.0 ± 4.3 | 3294 | 6.1 ± 2.9 | 3848/2526 | 7.1 ± 2.8 |
| Espinoza 2009 | 27 | 30.1 | 3621 | 3.7 ± 0.7 | 3294 | 4.1 ± 0.8 | 3848/2526 | 4.9 ± 1.0 |
| CM2 2010 | 12 | 5.8 | 3424 | 4.3 ± 1.7 | 3294 | 4.7 ± 1.8 | 3848/2526 | 4.3 ± 1.6 |

[a] For males and females respectively.

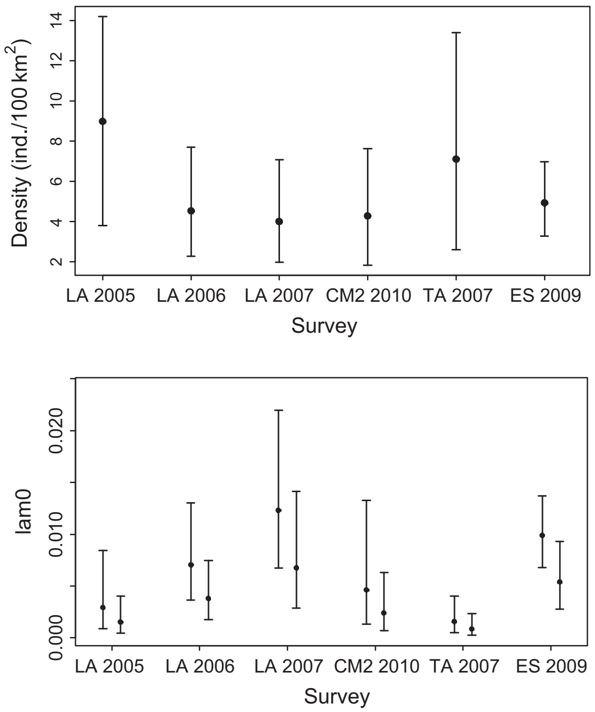

**Fig. 2.** Jaguar densities and encounter rates estimated by a spatially explicit capture–recapture (SECR) model for six camera trap surveys in south-eastern Peru. Bars show the confidence interval and the two bars for each survey in the second graph show encounter rates for males and females respectively.

## 4. Discussion

### 4.1. Jaguar density

This study is the second and most extensive study of jaguar densities in the southwestern Amazon (Silver et al., 2004). Collecting data from several sites in the same region and in one case over multiple years allowed us to assess variation among sites and to improve estimates by sharing parameters across years. Once corrected for methodological issues (see below) density estimates were very similar across sites, indicating that they should be representative for the region. Our average density of 4.4 ± 0.7 jaguar 100 km$^{-2}$ was much higher than that calculated for the Tuichi Valley the Madidi National Park (2.8 ± 1.75 ind. 100 km$^{-2}$, Silver et al., 2004), which is adjacent to our study region, even though the density estimate for the Madidi site was calculated with ½ MMDM which is more likely to result in a positive bias. Wallace et al. (2003) speculated that the low density of jaguars in the Tuichi Valley could be related to extensive hunting for skins in the 1970s and 1980s or to a relatively low abundance of prey species caused by hunting between 1987 and 1995. Furthermore, a short sampling period and cameras placed off trails or on fresh trails could have led to low encounter rates and an underestimation of the true density.

With respect to comparisons of densities in other ecoregions, our average density is much higher than the estimate of 0.29 jaguar 100 km$^{-2}$ from the Emas National Park in the Brazilian Cerrado obtained with a SECR model using sex covariates (Sollmann et al. 2011). Given that Emas is largely isolated and the landscape surrounding it has been seriously degraded by agriculture and cattle ranching, jaguar populations in Emas are depressed and thus not comparable to the largely intact sites we worked in. The same concern of human impact is likely to be relevant for the Iguazu moist forest of northern Argentina which had a density of only 0.49–0.93 jaguars 100 km$^{-2}$ (Paviolo et al., 2008). Silveira et al's (2010) recent estimate of a density of 1.28 jaguars 100 km$^{-2}$ in the Caatinga of north-eastern Brazil represents a dry forest habitat with low prey densities. Densities from the transitional Chaco-Chiquitano forest in Bolivia ranged from 0.46 to 0.99 jaguar 100 km$^{-2}$ when calculated with a SECR model (Noss et al., 2012). Only estimates of 5.8–6.0 jaguar 100 km$^{-2}$ from the Pantanal of Brazil (Soisalo and Cavalcanti, 2006) are similar and even higher than the results from Madre de Dios. Much higher estimates of 8–10 jaguars 100 km$^{-2}$ were reported by several studies (Harmsen, 2006; Miller, 2005; Silver et al., 2004), however, all of them used ½ MMDM and relatively small camera polygons which tends to greatly overestimated densities (Tobler and Powell, in press).

### 4.2. Comparison of methods and bias correction

Density estimates for different models varied both within and among the different surveys, with densities ranging from 3.3 to 12.2 ind. 100 km$^{-2}$. The results from our field data confirm findings of a simulation studies (Tobler and Powell, in press): low detection probabilities lead to a low precision of the estimate, especially for small grids; not accounting for differences in detection probabilities and movements by sex leads to an underestimation of density; and density estimates from small camera grids can be corrected by using $\sigma$ estimates from a large grid. The SECR models were less sensitive to grid size than the MMDM-based models (Supplement B) producing similar estimates for $\sigma$ for four of our surveys. Applying $\sigma$ from the largest survey to all surveys reduced the variability among them and improved our estimates. Still, two surveys that had both small grid sizes and low detection probabilities yield what appear to be very large estimates with very large confidence intervals. We believe these are outliers caused by poor data and thus eliminated them from the comparisons.

### 4.3. Sex-specific detection and home range size

Most camera trap surveys of jaguar report a sex ratio biased towards males with a mean observed sex ratio for all studies listed in

**Table 3**
Parameter estimated by a spatially explicit capture–recapture model for six jaguar surveys in the Peruvian Amazon. $\sigma$: Distance parameter, $\lambda_0$: encounter rate, $D$: density, and $\pi$: sex ratio.

| Parameter | Mean | SD | 2.5% | Median | 97.5% |
|---|---|---|---|---|---|
| $\sigma$ Male[a] (km) | 3.85 | 0.43 | 3.13 | 3.80 | 4.77 |
| $\sigma$ Female[a] (km) | 2.53 | 0.72 | 1.58 | 2.39 | 4.30 |
| HR male[b] (km$^2$) | 283 | 65 | 185 | 273 | 428 |
| HR female[b] (km$^2$) | 130 | 90 | 47 | 108 | 347 |
| $\pi$ | 0.60 | 0.07 | 0.46 | 0.60 | 0.73 |
| $\lambda_0$ Male LA 05 (photographs day$^{-1}$) | 0.0029 | 0.0020 | 0.0009 | 0.0024 | 0.0084 |
| $\lambda_0$ Female LA 05 (photographs day$^{-1}$) | 0.0015 | 0.0010 | 0.0005 | 0.0013 | 0.0040 |
| $\lambda_0$ Male LA 06 (photographs day$^{-1}$) | 0.0071 | 0.0024 | 0.0036 | 0.0066 | 0.01306 |
| $\lambda_0$ Female LA 06 (photographs day$^{-1}$) | 0.0038 | 0.0015 | 0.0018 | 0.0035 | 0.00754 |
| $\lambda_0$ Male LA 07 (photographs day$^{-1}$) | 0.0123 | 0.0042 | 0.0068 | 0.0114 | 0.0220 |
| $\lambda_0$ Female LA 07 (photographs day$^{-1}$) | 0.0067 | 0.0030 | 0.0029 | 0.0062 | 0.0141 |
| $\lambda_0$ Male CM2 10 (photographs day$^{-1}$) | 0.0046 | 0.0033 | 0.0013 | 0.0037 | 0.0133 |
| $\lambda_0$ Female CM2 10 (photographs day$^{-1}$) | 0.0024 | 0.0015 | 0.0007 | 0.0020 | 0.0063 |
| $\lambda_0$ Male TA 07 (photographs day$^{-1}$) | 0.0016 | 0.0011 | 0.0005 | 0.0013 | 0.0040 |
| $\lambda_0$ Female TA 07 (photographs day$^{-1}$) | 0.0009 | 0.0006 | 0.0002 | 0.0007 | 0.0024 |
| $\lambda_0$ Male ES 09 (photographs day$^{-1}$) | 0.0099 | 0.0017 | 0.0068 | 0.0098 | 0.0137 |
| $\lambda_0$ Female ES 09 (photographs day$^{-1}$) | 0.0054 | 0.0017 | 0.0028 | 0.0052 | 0.0093 |
| D LA 05 (individuals 100 km$^{-2}$) | 9.0 | 3.0 | 3.9 | 9.0 | 14.2 |
| D LA 06 (individuals 100 km$^{-2}$) | 4.5 | 1.4 | 2.3 | 4.3 | 7.7 |
| D LA 07 (individuals 100 km$^{-2}$) | 4.0 | 1.3 | 1.8 | 3.8 | 7.0 |
| D CM2 10 (individuals 100 km$^{-2}$) | 4.3 | 1.6 | 1.8 | 4.1 | 7.6 |
| D TA 07 (individuals 100 km$^{-2}$) | 7.1 | 2.8 | 2.6 | 6.7 | 13.4 |
| D ES 09 (individuals 100 km$^{-2}$) | 4.9 | 1.0 | 3.2 | 4.8 | 7.0 |
| D average[c] (individuals 100 km$^{-2}$) | 4.4 | 0.7 | 3.1 | 4.4 | 5.9 |

[a] Estimated based on data from the ES 09 survey and applied to all other surveys.

[b] Based on the 95% probability interval of circular bivariate normal distribution with a radius of 2.45 * $\sigma$.

[c] Excluding LA 05 and TA 07.

Maffei et al. (2011) of 2.16:1, which is very close to our observed sex ratio for all surveys combined of 1.9:1. When we include sex covariates in our SECR model to correct for sex specific movement and encounter rates our predicted sex ratio was 1:1.5, showing that the observed bias towards males is mainly caused by larger home ranges and higher detection probabilities and that there are actually more females than males. The observed sex ratio at birth for jaguar in captivity is 1:1 (male:female:unknown = 533:529:152, $N = 1214$) according to the jaguar studbook (S. Johnson, persona. com.), but a higher proportion of adult females is common among large cats and can be explained by a lower survival of males due to intraspecific conflicts and a higher mortality during dispersal (Balme and Hunter, 2004; Goodrich et al., 2008; Logan and Sweanor, 2001). It seems that raw sex ratios for jaguars obtained from camera traps are highly biased and need to be corrected in order to be meaningful.

Our final model including the sex covariates indicates that males have about 2.2 times larger home ranges than females. This is consistent with data from telemetry studies; male home ranges in the Pantanal of Brazil were about 2.5 times larger than female home range (Cavalcanti and Gese, 2009), male home ranges in the Atlantic Forest of Brazil were three times the size of female home ranges (Cullen, 2006), in the wet forest of Mexico male home ranges were about three times larger than female home ranges (Conde et al., 2010). If we assume a circular 95% home range based on our $\sigma$ estimates, mean male home range size would be 283 km$^2$ and females would have a home range of 130 km$^2$. This seems fairly accurate when compared to telemetry data from the same region (WWF/SDZG unpubl. data). While with 280 km$^2$ the 95% kernel home range for the 2 month period was very close to the SECR estimate, the home range for the 4 months of the survey would likely be larger. On the other hand, the 2-month range was very elongated, a shape that has been shown to lead to negatively biased estimates (Ivan, 2011). How these factors impact our density estimates is unclear, but it is possible that even our largest grid was too small and our density estimates are still biased high.

While the SECR model does oversimplify reality in that it assumes a circular bivariate normal home range model and it is not clear yet how realistic home range estimates from these models are, our results indicate that the models are able to show biological differences between sexes which in turn helps to improve density estimates.

### 4.4. Sampling, trails, and detection probabilities

Our data suggest that the age of trails had an influence on detection probabilities of jaguars. At Los Amigos a large part of the trail network used for the camera trap surveys was established in 2005. After this we see a constant increase in encounter rates in subsequent years. Tambopata, where trails were also cut right before the survey, and CM2, where cameras were set without trails, had similarly low encounter rates, whereas Espinoza, where established logging roads were used had high encounter rates. This agrees with other studies; Sollmann et al. (2011) showed that cameras on roads in Brazil had a 10 times higher encounter rate compared to cameras off-road, and Harmsen et al. (2010) showed that encounter rates for jaguar in Belize increased with trail width and age. The use of existing trails and dirt roads for jaguar survey can therefore significantly increase encounter rates and improve density estimates. While it has been argued that placing cameras on trails and roads can lead to biased estimates due to different individual preferences for these features (Foster and Harmsen, 2012), we believe that the gain in data greatly outweighs the potential bias introduced, especially if detection probability is being modeled by sex. Alternatively a subset of the cameras could be placed on trails and the other subset off trails and the difference in capture probability could be modeled explicitly (Sollmann et al., 2011).

## 5. Conclusion

### 5.1. Data analysis

By using a SECR model with sex covariates many of the problems outlined by Foster and Harmsen (2012) can be addressed. SECR models can use the exact number of days each camera station was operating, avoiding bias caused by camera failure. Including sex covariates can significantly improve density estimates and can show biologically important differences in movement patterns and detection probabilities between the two sexes. Sharing parameters across surveys can help reduce grid size induced biases for small surveys, improve parameter estimates by increasing the amount of available data, and make data more comparable when different survey designs were used. While SECR models are a great improvement over the MMDM-based methods, they still do require an appropriate survey design that generates enough data for reliable density estimates; small survey area and low capture rates will result in inaccurate density estimations. Increasing the survey area not only results in more accurate estimates of $\sigma$, it also increases the number of individuals caught allowing for models with more covariates and more accurate parameter estimates. Placing cameras on established trails and roads helps increasing encounter rates and improve density estimates. Our data show that low encounter rates together with small gird sizes can result in highly biased density estimates. We therefore urge caution when applying these models (or any other model used to estimate density) to sparse datasets.

### *5.2. Status of jaguar in south-eastern Peru*

Our findings support Sanderson et al.'s (2002) conclusion that the Amazon is a core habitat for jaguars supporting large connected populations of the species. The densities found for undisturbed populations in the Peruvian Amazon are on the high end of published densities, surpassed only by densities in the Pantanal. The available data for the species in South America show two general trends, lower densities in drier areas (Caatinga, Cerrado, Chaco) and in areas with a high human impact (Emas and Iguazú) and higher densities in wetter habitats with high prey densities (Amazon, Pantanal). Our density estimates did not vary much between the two areas of the Los Amigos Conservation Concession and the Espinoza Forestry Concession further north, indicating that they represent an average density for unhunted areas in the region. While we do not have estimates on prey densities for our sites, our camera trap data show that all sites have an intact large mammal fauna with healthy populations of large ungulates (Tobler et al., 2008, 2009, unpubl. data). Our findings also suggest that well managed forestry concessions may support jaguar densities that are similar to those of conservation areas as long as no hunting is permitted. The low impact, low volume harvest of timber as well as the construction of a limited network of logging roads seems to have no impact on jaguars and they are frequently observed to use the roads as travel routes. The key to the protection of the large mammal fauna in these logging concessions is a complete prohibition of hunting as well as a strict access control that prevents outside persons to enter the concession.

When extrapolating our densities to the major conservation units in the MDD basin (JCU 74: Alto Purus, JCU 75: Manu, and Jcu 76: Bahuaja-Sonenen and Madidi National Parks) that together cover 138,000 km$^2$ of lowland forest (based on data from Zeller (2007), we find that they could support a population of about 6000 jaguars (CI: 4278–8142) of which 2500 (CI: 1705–3245) would be within protected areas. Even when considering the large confidence intervals and some uncertainty in the status of the species outside protected areas, our results show that the southwestern Amazon potentially supports a large population of the species with a high probability of long-terms survival.

## Acknowledgements

We would like to thank the Gordon and Betty Moore Foundation and the Blue Moon Foundation for the generous funding of this research through grants to WWF and the Botanical Research Institute of Texas (BRIT). The following people are thanked for their help with the camera trapping: Mario Alvites, Ruben Aviana, Angel Balarezo, Rufo Bustamante, Darío Cruz, Dario Cruz Junior, Alberto Escudero, Rene Escudero, Ernesto Gamarra, Marlon Guerrra, Lucas Huaymana, Javier Huinga, Renata Leite Pitman, Rafael Mares, Armando Mendoza, Emeterio Nuñoncca, Juan Racua, Jhin Pierr Solis and Vicente Vilca. We are grateful to the WWF Areas management team, Karim Ledesma, Cinthya Verastegui, Arnaldo Marquez, and Carmen Garate as well as the BRIT AABP team, especially John Janovec, Keri McNew, and Amanda Neill, for their support. We would like to thank the DGFFS (INRENA) for continuously granting us permission to carry out this research in Peru, as well as the Amazon Conservation Association for logistical support at Los Amigos and the Bahuaja Sonene Park Administration for their help in the Tambopata area. We would like to thank Victor Espinoza, Elisabeth Espinoza and Victor Leoni Espinoza from the Maderas Cocama y Aserradero Espinoza concessions for allowing us to setup a survey in their concessions and for providing us with great logistical support. We are grateful to Beth Gardner and Andy Royle for advice with the SECR models in WinBUGS and thank two anonymous reviewers for valuable comments that helped improve the manuscript.

## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2012.12.012.

## References

Asner, G.P., Powell, G.V.N., Mascaro, J., Knapp, D.E., Clark, J.K., Jacobson, J., Kennedy-Bowdoin, T., Balaji, A., Paez-Acosta, G., Victoria, E., Secada, L., Valqui, M., Hughes, R.F., 2010. High-resolution forest carbon stocks and emissions in the Amazon. Proc. Nat. Acad. Sci. 107, 16738–16742.

Balme, G., Hunter, L., 2004. Mortality in a protected leopard population, phinda private game reserve, South Africa: a population in decline? Ecol. J. 6, 1–6.

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

Carrillo-Percastegui, S.E., Maffei, L., in press. Estado de la conservación del jaguar en Perú, In El jaguar en el Siglo XXI: La Perspectiva Continental. eds R.A. Medellín, C. Chávez, A.d.l. Torre, H. Zarza, G. Ceballos.

Caso, A., Lopez-Gonzalez, C., Payan, E., Eizirik, E., de Oliveira, T., Leite-Pitman, R., Kelly, M., Valderrama, C., 2008. Panthera onca, In IUCN 2011. IUCN Red List of Threatened Species. Version 2011.1, <www.iucnredlist.org>.

Cavalcanti, S.M.C., Gese, E.M., 2009. Spatial ecology and social interactions of jaguars (*Panthera onca*) in the Southern Pantanal, Brazil. J. Mammal. 90, 935–945.

Conde, D.A., Colchero, F., Zarza, H., Christensen Jr, N.L., Sexton, J.O., Manterola, C., Chávez, C., Rivera, A., Azuara, D., Ceballos, G., 2010. Sex matters: modeling male and female habitat differences for jaguar conservation. Biol. Conserv. 143, 1980–1988.

Cullen, L., 2006. Jaguars as landscape detectives for the conservation of Atlantic Forest in Brazil. In: Durrell Institute of Conservation and Ecology (DICE). p. 192. Univerity of Kent, Canterbury, UK.

Efford, M.G., Dawson, D.K., Borchers, D.L., 2009. Population density estimated from locations of individuals on a passive detector array. Ecology 90, 2676–2682.

Foster, R., 2008. The ecology of jaguars (*Panthera onca*) in a human-influenced landscape, p. 358. University of Southampton, Southampton, UK.

Foster, R.J., Harmsen, B.J., 2012. A critique of density estimation from camera-trap data. J. Wildl. Manag. 76, 224–236.

Gilks, W.R., Thomas, A., Spiegelhalter, D.J., 1994. A Language and program for complex Bayesian modeling. Statistician 43, 169–177.

Goodrich, J.M., Kerley, L.L., Smirnov, E.N., Miquelle, D.G., McDonald, L., Quigley, H.B., Hornocker, M.G., McDonald, T., 2008. Survival rates and causes of mortality of Amur tigers on and near the Sikhote-Alin Biosphere Zapovednik. J. Zool. 276, 323–329.

Harmsen, B.J., 2006. The use of camera traps for estimating abundance and studying the ecology of jaguars (*Panthera onca*). In: School of Biological Sciences. p. 286. University of Southampton, Southampton, UK.

Harmsen, B.J., Foster, R.J., Silver, S., Ostro, L., Doncaster, C.P., 2010. Differential use of trails by forest mammals and the implications for camera-trap studies: a case study from Belize. Biotropica 42, 126–133.

Ivan, J.S., 2011. Density, demography, and seasonal movements of snowshoe hares in central Colorado. In: Fish, Wildlife and Conservation Biology. p. 154. Colorado State University, Fort Collins, Colorado.

Logan, K.A., Sweanor, L.L., 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington, DC.

Maffei, L., Noss, A.J., Silver, S.C., Kelly, M.J., 2011. Abundance/Density Case Study: Jaguars in the Americas. In: O'Connell, A.F., Nichol, J.D., Karanth, K.U. (Eds.), Camera Traps in Animal Ecology: Methods and Analyses. Springer, New York, pp. 163–190.

Miller, C.M., 2005. Jaguar density in Gallon Jug Estate, Belize, p. 24. Wildlife Conservation Society, Gallon Jug, Belize.

Noss, A.J., Gardner, B., Maffei, L., Cuéllar, E., Montaño, R., Romero-Muñoz, A., Sollman, R., O'Connell, A.F., 2012. Comparison of density estimation methods for mammal populations with camera traps in the Kaa-Iya del Gran Chaco landscape. Animal Conservation, n/a–n/a.

Paviolo, A., de Angelo, C.D., Di Blanco, Y.E., Di Bitetti, M.S., 2008. Jaguar *Panthera onca* population decline in the upper Parana Atlantic forest of Argentina and Brazil. Oryx 42, 554–561.

R Development Core Team, 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Royle, J.A., Gardner, B., 2011. Hierarchical Spatial Capture–Recapture Models for Estimating Density from Trapping Arrays. In: O'Connell, A.F., Nichol, J.D., Karanth, K.U. (Eds.), Camera Traps in Animal Ecology: Methods and Analyses. Springer, New York, pp. 163–190.

Royle, J.A., Young, K.V., 2008. A hierarchical model for spatial capture–recapture data. Ecology 89, 2281–2289.

Sanderson, E.W., Redford, K.H., Chetkiewicz, C.L.B., Medellin, R.A., Rabinowitz, A.R., Robinson, J.G., Taber, A.B., 2002. Planning to save a species: the jaguar as a model. Conserv. Biol. 16, 58–72.

Silveira, L., Jácomo, A.T.A., Astete, S., Sollmann, R., Tôrres, N.M., Furtado, M.M., Marinho-Filho, J., 2010. Density of the near threatened jaguar *Panthera onca* in the caatinga of north-eastern Brazil. Oryx 44, 104–109.

Silver, S.C., Ostro, L.E.T., Marsh, L.K., Maffei, L., Kelly, A.M.J., Wallace, R.B., Gómez, H., Ayala, G., 2004. The use of camera traps for estimating jaguar *Panthera onca* abundance and density using capture/recapture analysis. Oryx 38, 148–154.

Soisalo, M.K., Cavalcanti, S.M.C., 2006. Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture–recapture sampling in combination with GPS radio-telemetry. Biol. Conserv. 129, 487–496.

Sollmann, R., Furtado, M.M., Gardner, B., Hofer, H., Jácomo, A.T.A., Tôrres, N.M., Silveira, L., 2011. Improving density estimates for elusive carnivores: accounting for sex-specific detection and movements using spatial capture–recapture models for jaguars in central Brazil. Biol. Conserv. 144, 1017–1024.

Sollmann, R., Gardner, B., Belant, J.L., 2012. How Does Spatial Study Design Influence Density Estimates from Spatial Capture-Recapture Models? PLoS ONE 7, e34575.

Sturtz, S., Ligges, U., Gelman, A., 2005. R2WinBUGS: a package for running WinBUGS from R. J. Stat. Softw. 12, 1–16.

Swenson, J.J., Carter, C.E., Domec, J.C., Delgado, C.I., 2011. Gold mining in the Peruvian Amazon: global prices, deforestation, and Mercury Imports. PLoS ONE 6.

Tobler, M.W., 2010. Camera Base Version 1.4. Botanical Research Institute of Texas.

Tobler, M.W., Carrillo-Percastegui, S.E., Pitman, R.L., Mares, R., Powell, G., 2008. An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals. Anim. Conserv. 11, 169–178.

Tobler, M.W., Carrillo-Percastegui, S.E., Powell, G., 2009. Habitat use, activity patterns and use of mineral licks by five species of ungulate in south-eastern Peru. J. Trop. Ecol. 25, 261–270.

Tobler, M.W., Hibert, F., Debeir, L., Richard-Hansen, C., in press. Density and sustainable harvest estimates for the lowland tapir (*Tapirus terrestris*) in the Amazon of French Guiana. Oryx.

Tobler, M.W., Powell, G.V.N., in press. Estimating jaguar densities with camera traps: problems with current designs and recommendations for future studies. Biol. Conser.

Wallace, R.B., Gomez, H., Ayala, G., Espinoza, F., 2003. Camera trapping for jaguar (*Panthera onca*) in the Tuichi Valley, Bolivia. J. Neotropical Mammology 10, 133–139.

Zeller, K., 2007. Jaguars in the New Millennium Data Base Update: The State of the Jaguar in 2006, p. 82. Wildlife Conservation Society-Jaguar Conservation Program, New York, NY.

## Appendix A. Supplementary material

WinBUGS model for a spatially explicit capture-recapture model with fixed $\sigma$ and data sharing across multiple surveys.

```
model {

  for(t in 1:T){
    psi[t]~dunif(0, 1)
  }

  #sex ratio
  pi~dunif(0, 1)

  #base encounter rate
  lambase~dnorm(0.0,0.10E-6)I(-15,15)

  #sex covariate
  lamsex[1]<-0 #reference class
  lamsex[2]~dnorm(0.0,0.10E-6)I(-15,15) #sex-specific lam0

  #session covariate
  for(t in 2:T){
    lamt[t]~dnorm(0.0,0.10E-6)I(-15,15)
  }
  lamt[1]<-0

  #sigma fixed
  sigmabase<-1.3509
  sigmasex[1]<-0
  sigmasex[2]<--0.4393

  for(t in 1:T){      #loop over all surveys
    S[t]<-(xu[t]-xl[t])*(yu[t]-yl[t])  #study area size

    for (i in 1:M){     #loop over all individuals
      sex[i,t]~dbern(pi)
      sex2[i,t]<-sex[i,t] + 1

      z[i,t]~dbern(psi[t])   #individual included or not
```

```
      SX[i,t]~dunif(xl[t], xu[t])  #individual HR center X
      SY[i,t]~dunif(yl[t], yu[t])  #individual HR center Y

      log(sigma[i,t])<-sigmabase + sigmasex[sex2[i,t]]
      sigma2[i,t]<-2*sigma[i,t]*sigma[i,t]

      for(j in 1:J) {  #loop over all traps
        D2[i,j,t] <- pow(SX[i,t]-trapmat[j,1], 2) + pow(SY[i,t]-trapmat[j,2],2) #distance from camera to HR center

        log(lam0[i,j,t])<-lambase + lamt[t] + lamsex[sex2[i,t]]

        Eo[i,j,t] <- lam0[i,j,t]*exp(-D2[i,j,t]/sigma2[i,t]) #encounter rate at trap site
        log(pmean[i,j,t])<-log(K[j,t]) + log(Eo[i,j,t]) #encounter rate over all occasions (K)
        tmp[i,j,t]<-pmean[i,j,t]*z[i,t]
        y[i,j,t]~dpois(tmp[i,j,t])
      }
    }
  }

  for(t in 1:T){
    N[t]<-sum(z[1:M,t])
    D[t]<-N[t]/S[t]
  }
}
```

## Appendix B. Densities estimated with MMDM-based methods.

### Methods

For comparison purposes we analyzed the data using different classic mean maximum distance moved (MMDM) based estimates (Karanth and Nichols 1998). For all estimates we used the Mh that incorporates heterogeneity in the capture probability (Otis et al. 1978). We used three different buffers for estimating the effective trapping area (ETA): 1) ½ MMDM estimated for each survey independently, 2) the full MMDM estimated for each survey independently, and 3) the MMDM from the largest survey (Espinoza 2009) that was applied to all other surveys. Calculations for all the MMDM based models were carried out using functions in the secr package (Efford 2011) in R (R Development Core Team 2011).

### Results

For estimates using the MMDM from each survey, a grid size effect can be seen, resulting in higher estimates for surveys with smaller grids. A buffer of ½ MMDM produced very high density estimates while using the full MMDM as a buffer resulted in estimates closer to the SECR models. Using the MMDM from the Espinoza 2009 survey for all surveys removed the grid effect resulting in more similar density estimates for all surveys.

### Discussion

A buffer of a full MMDM performs better than ½ MMDM, which tends to greatly overestimate density, and density estimates from small camera grids can be corrected by using MMDM or σ estimates from a large grid. Independent MMDM estimates were clearly related to grid size making comparisons across surveys misleading.

### References

Efford, M.G., 2011. secr: Spatially Explicit Capture-Recapture Models. R package version 2.1.0.

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

Otis, D.L., Burnham, K.P., White, G.C., Anderson, D.R., 1978. Statistical inference from capture data on closed animal populations. Wildlife Monograph 62.

R Development Core Team, 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Table 1: Comparison of Jaguar density estimates for six camera trap surveys in the Peruvian Amazon based on six different methods. N: number of individuals photographed, Freq.: number of photographs/1000 camera days, $\sigma$: scale parameter (m), $\lambda_0$: encounter rate, D: density (individuals 100 km$^{-2}$), MMDM: Mean Maximum Distance Move (m).

| | Grid area | | | Mh 1/2 MMDM | | Mh full MMDM | | Mh fixed MMDM | | SECR fixed with sex | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Survey | (km$^2$) | N | Freq. | Buffer | *D* | Buffer | *D* | Buffer | *D* | $\sigma^a$ | *D* |
| Los Amigos 2005 | 56 | 10 | 9.5 | 1994 | 12.0 | 3987 | 6.7 | 7569 | 3.3 ± 1.1 | 3848/2526 | 9.0 ± 3.0 |
| Los Amigos 2006 | 56 | 10 | 14.8 | 2261 | 8.5 ± 1.9 | 4521 | 4.6 ± 1.2 | 7569 | 2.5 ± 0.7 | 3848/2526 | 4.5 ± 1.4 |
| Los Amigos 2007 | 56 | 11 | 19.5 | 1872 | 11.3 ± 2.6 | 3744 | 6.4 ± 1.8 | 7569 | 3.0 ± 0.8 | 3848/2526 | 4.0 ± 1.3 |
| Malinowsky 2007 | 52 | 7 | 4.6 | 1578 | 8.8 ± 3.9 | 3155 | 5.2 ± 1.8 | 7569 | 2.0 ± 0.9 | 3848/2526 | 7.1 ± 2.8 |
| Espinoza 2009 | 250 | 27 | 30.1 | 3785 | 7.1 ± 1.3 | 7569 | 3.8 ± 0.8 | 7569 | 3.8 ± 0.8 | 3848/2526 | 4.9 ± 1.0 |
| CM2 2010 | 196 | 12 | 5.8 | 2702 | 5.2 ± 1.5 | 5403 | 3.1 ± 1.1 | 7569 | 2.3 ± 0.7 | 3848/2526 | 4.3 ± 1.6 |

[a] for males and females respectively.