Chapter 8
Abundance/Density Case Study: Jaguars in the Americas

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8.1 Introduction

Since camera traps were first used to estimate the density of tiger *Panthera tigris* populations in India (Karanth 1995; see also Karanth et al. this volume), this methodology has been widely used to study a variety of species: leopards *Panthera pardus* (Henschel and Ray 2003; Karanth et al. this volume; Kostyria et al. 2003), snow leopards *Panthera uncia* (Jackson et al. 2006), pumas *Puma concolor* (Kelly et al. 2008), ocelots *Leopardus pardalis* (Di Bitetti et al. 2006, 2008; Dillon and Kelly 2007, 2008; Maffei et al. 2005; Trolle and Kéry 2003, 2005), and Geoffroy's cats *Oncifelis geoffroyi* (Cuéllar et al. 2006; Pereira et al. 2006). However, jaguars *Panthera onca* have probably received the most attention with respect to using camera traps to estimate the abundance and density of populations that cover the species' entire Neotropical range (Cullen et al. 2005; Kelly 2003; Maffei et al. 2004b; Miller and Miller 2005; Silver et al. 2004; Soisalo and Cavalcanti 2006). To date, at least 83 different camera trapping efforts have been carried out to survey jaguars, from southern Arizona in the north to northern Argentina in the south. In this chapter, we describe the details of this methodology – summarizing information on survey design and methodologies, results, data manipulation and analyses – and discuss how future surveys can be refined to allow for more robust inferences.

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8.2 Study Sites

The studies have been carried out in 14 countries and 12 major habitat types that range from dry and moist forests to grasslands (Fig. 8.1 and Table 8.1). Most of them were conducted inside designated Jaguar Conservation Units (Sanderson et al. 2002; Zeller 2007). The surveys have covered portions of at least 19 national parks or other protected areas, one Biosphere Reserve, three state or provincial parks, six private reserves, three wildlife sanctuaries or management areas, four indigenous territories, 15 cattle ranches, 11 forestry reserves or concessions, and one private conservation concession (Table 8.1). Additional surveys are underway or planned (for example, by V. Quiroga in the Argentine Chaco, by WCS-Ecuador in Yasuní National Park), the most ambitious of which is Mexico's national jaguar census (CENJAGUAR) to be completed during 2008–2009, with the participation of 18 researchers, and the support of more than 10 institutions led by the Universidad Nacional Autónoma de México (Chávez et al. 2006).

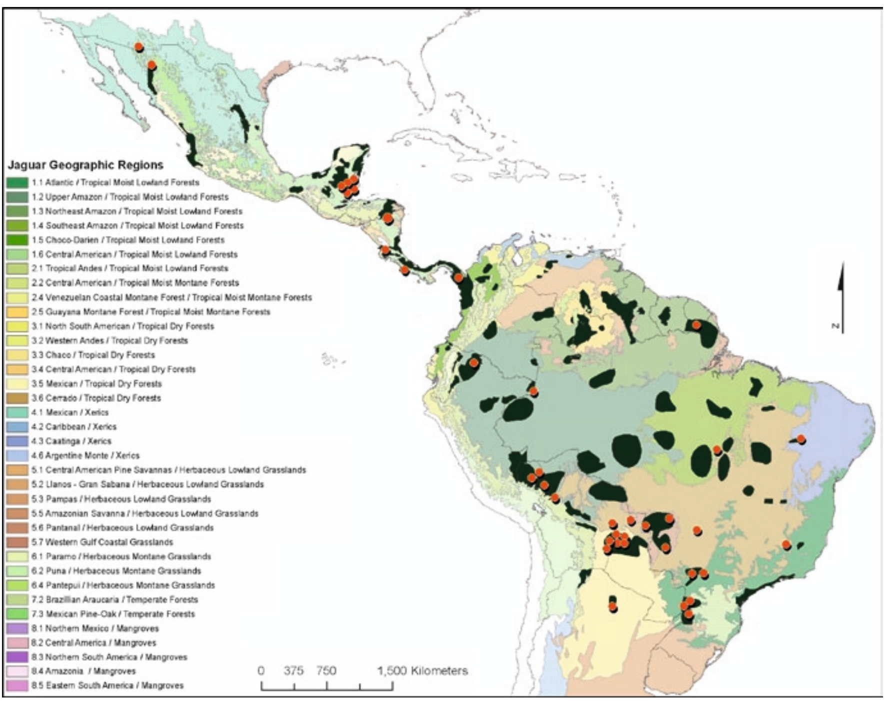

Fig. 8.1 Jaguar Conservation Units and points where systematic jaguar camera trapping surveys have been carried out (map adapted from Zeller 2007). Not all sites are represented at this scale – some single points represent more than one site in Argentina, Belize, Bolivia, Colombia, Costa Rica, and Peru

Table 8.1 Camera trap surveys for jaguars: number of surveys per site, ecoregion and land use

Country	Study site	Surveys	Type of forest-ecoregion	Land use
Argentina	Copo	1	Chaco / tropical dry forests	National Park
Argentina	Impenetrable ChacoAboriginal Reserve	1	Chaco / tropical dry forests	Indigenous Territory
Argentina	Iguazú	2	Atlantic / tropical moist lowland forests	National Park and Forestry Reserve
Argentina	Urugua-í	1	Atlantic / tropical moist lowland forests	Provincial Park and Private Reserve
Argentina	Yabotí	1	Atlantic / tropical moist lowland forests	Forestry Reserve
Belize	Chiquibul	5	Central America / tropical moist lowland and submontane forests	Forest Reserve and National Park
Belize	Cockscomb Basin	6	Central America / tropical moist lowland forests	Wildlife Sanctuary
Belize	Fireburn	1	Central America / tropical moist lowland forests	Private Reserve, Forest Corridor, Mesoamerican Biological Corridor
Belize	Gallon Jug Estate	2	Central America / tropical moist lowland forests	Private protected area
Belize	Rio Bravo	1	Central America / tropical moist lowland forests	Conservation and Management Area
Belize	Mountain Pine Ridge	6	Central American / tropical pine forests	Forest Reserve
Bolivia	Alto Madidi	2	Tropical Andes / tropical moist lowland forests	National Park
Bolivia	Cerro Cortado, Kaa-Iya	2	Chaco / tropical dry forests	National Park and Indigenous communal lands
Bolivia	El Encanto CIMAL	2	Cerrado / tropical dry forests (Chiquitano dry forest)	Certified forestry concession
Bolivia	Estación Isoso, Kaa-Iya	2	Chaco / tropical dry forests (transitional Chaco-Amazon)	National Park
Bolivia	Guanacos, Kaa-Iya	2	Chaco / tropical dry forests (grasslands)	National Park and cattle ranches
Bolivia/ Paraguay	Palmar, Kaa-Iya	2	Chaco / tropical dry forests (transitional Chaco-Chiquitano)	National Park, private reserve, and cattle ranch
Bolivia	Puestos Ganaderos	1	Chaco / tropical dry forests (transitional Chaco-Chiquitano)	Cattle ranches

(continued)

Table 8.1 (continued)

Country	Study site	Surveys	Type of forest-ecoregion	Land use
Bolivia	Ravelo, Kaa-Iya	2	Chaco/tropical dry forests (transitional Chaco-Chiquitano)	National Park
Bolivia	Rio Heath, Madidi	2	Tropical Andes/tropical moist lowland forests, tropical grasslands	National Park
Bolivia	Rios Tuichi and Hondo, Madidi	3	Tropical Andes/tropical moist lowland forest	National Park
Bolivia	San Matias	1	Pantanal/herbaceous lowland grasslands	Cattle ranch and National Integrated Management area
Bolivia	San Miguelito	2	Cerrado/tropical dry forests (Chiquitano dry forest)	Private reserve and cattle ranch
Bolivia	Tucavaca, Kaa-Iya	3	Chaco/tropical dry forests (transitional Chaco-Chiquitano)	National Park
Brazil	Emas National Park, Goiás	1	Cerrado/tropical dry forests	National Park
Brazil	Fazenda Cauaia	1	Cerrado/tropical dry forests	Cattle ranch
Brazil	Fazenda Santa Fé and Cantão State Park, Tocantins	1	Amazon/tropical moist forests – Cerrado/tropical dry forests ecotone	Cattle ranch, State Park
Brazil	Fazenda Sete	2	Pantanal/herbaceous lowland grasslands	Cattle ranch
Brazil	Moro do Diablo	1	Atlantic/tropical moist lowland forest	National Park
Brazil	Serra da Capivara	1	Caatinga/xerics	National Park
Brazil	SESC Pantanal	1	Pantanal/herbaceous lowland grasslands	Private reserve
Brazil	Varzeas do Rio Ivinhema	1	Atlantic/tropical moist lowland forest/varzea	State Park
Colombia	Amacayacu National Park and Ticoya Indigenous Territory	1	Amazon/tropical moist lowland forest	National Park and indigenous territory
Colombia	Calderón river valley	1	Amazon/tropical moist lowland forest	National Forestry Reserve (unprotected) and indigenous territory
Costa Rica	Corcovado	1	Central American/tropical moist lowland forest	National Park

(continued)

Table 8.1 (continued)

Country	Study site	Surveys	Type of forest-ecoregion	Land use
Costa Rica	Golfo Dulce, Golfito	1	Central American/tropical moist lowland forest	Private ranches, Forest Reserve, Wildlife Reserve
Costa Rica	Golfo Dulce	1	Central American/tropical moist lowland forest	Forest reserve
Costa Rica	Santa Rosa, Guanacaste, San Cristobal	3	Central American/tropical dry forest	National Parks and biological corridor
Ecuador	Yasuní and Waorani Ethnic Reserve	2	Amazon/tropical moist lowland forest	National Park and indigenous territory
French Guiana	Counami forest	1	Amazon/tropical moist lowland forest	Unprotected
Guatemala	Carmelita-AFISAP	1	Central America/tropical moist lowland forest	Forestry concessions
Guatemala	La Gloria-Lechugal	1	Central America/tropical moist lowland forest	Forestry concession, multiple use zone
Guatemala	Rio Azul	1	Central America/tropical moist lowland forest	National Park
Guatemala	Tikal	1	Central America/tropical moist lowland forest	National Park
Mexico	Sonora	1	Mexican xerics/tropical thorn scrub	Private Reserve and cattle ranches
Nicaragua	Bosawas	1	Central America/tropical moist lowland forest	Biosphere Reserve
Panama	Darien	2	Central America/tropical moist lowland forest	National Park
Peru	Los Amigos	2	Tropical Andes/tropical moist lowland forest	Conservation concession
Peru	Bahuaja Sonene, Tambopata	1	Tropical Andes/tropical moist lowland forest	National Parks
United States	Southern Arizona	1[a]	Mexican xerics/tropical thorn scrub	National Forest, National Wildlife Refuge, private ranches

[a]McCain and Childs (2008) established a grid system of camera traps to monitor the southern Arizona borderlands continuously from 2001 through 2007.

8.3 Survey Design and Data Analysis

Two approaches have been used to set camera traps for jaguar surveys: (1) placing traps in a single grid for the entire sample period, or (2) shifting traps to a different area within the study period for a length of time equal to the initial sample. The second approach is used when the number of cameras available cannot cover the entire study area in a single sample period. In the second case, the sample period is considered the length of time the camera traps are operable in a single location.

For either of the sampling approaches described, jaguar surveys have followed a systematic survey design that typically follows some defined travel route (Silver et al. 2004; http://savingwildplaces.com/media/file/SilverJaguarCamera-TrappingProtocol.pdf) to accommodate low jaguar densities and capture probabilities high enough to run capture–recapture (CR) models (but see Discussion). In some cases, researchers clear trails specifically for the survey in order to reach inaccessible areas and distribute the camera traps throughout the study area, as well as providing a feature to attract jaguars. Once trails are established, they are routinely cleared to maintain travel routes for jaguars. Figure 8.2 shows a selection of camera trapping grids that take advantage of available roads, trails, and rivers at various survey sites.

Cameras usually are set 30–40 cm above the ground to accommodate the height of the target species. Jaguars can be active day or night, and therefore camera traps are programmed to take pictures 24 h per day. The time delay for activation is usually between 30 s and 5 min, but in places with high traffic of non-target species/objects (e.g., roads with trucks, trails or salt licks with people or wildlife), a longer time delay can be used. We also note that on several occasions different male jaguars have been photographed within 2 min of each other at one camera station (M. Kelly, Virginia Tech University, Blacksburg, VA, unpublished data). In locations with low traffic, camera traps are typically checked only once every 10–14 days, whereas they are checked every two or three days at sites with high traffic, in order to avoid running out of film. Pilot surveys are useful in determining the frequency with which cameras and film need to be checked and replaced, as well as in evaluating the optimum sites for photographing jaguars (Rosas-Rosas 2006). Scents or attractants are not known to be necessary or even effective for increasing capture probabilities, but jaguars are known to occasionally investigate scents. This can result in multiple photographs from different angles, facilitating identification in some cases. In areas with abundant livestock, researchers have protected cameras with fencing that permits wildlife and especially jaguar movement, but keeps livestock away from the cameras (Rosas-Rosas 2006).

Surveys are based upon the standard procedures used in CR sampling of closed populations (see Karanth and Nichols 1998; 2002) using cameras in place of live traps, and using the natural markings of the jaguar to recognize individuals and "recaptures" in photographs. The objective of our CR (in this case, photograph/rephotograph) surveys was to estimate the number of individuals within a sample area. In general terms, this estimate is obtained by first estimating capture probability based on the capture histories of individuals that are caught at least once. The number of animals in the sampled area is then estimated by dividing the total number of animals caught by the estimated average probability of catching an animal at least once. The technique does not have to be based on a random sampling of the area, but rather, cameras are set up systematically in a pattern designed to maximize capture probability for all animals in the sampled area (Silver 2004). The method estimates the efficiency of the survey to photograph all the individuals in the survey area. The more jaguars that are photographed, and subsequently the more often they can be rephotographed, the more robust the abundance estimate

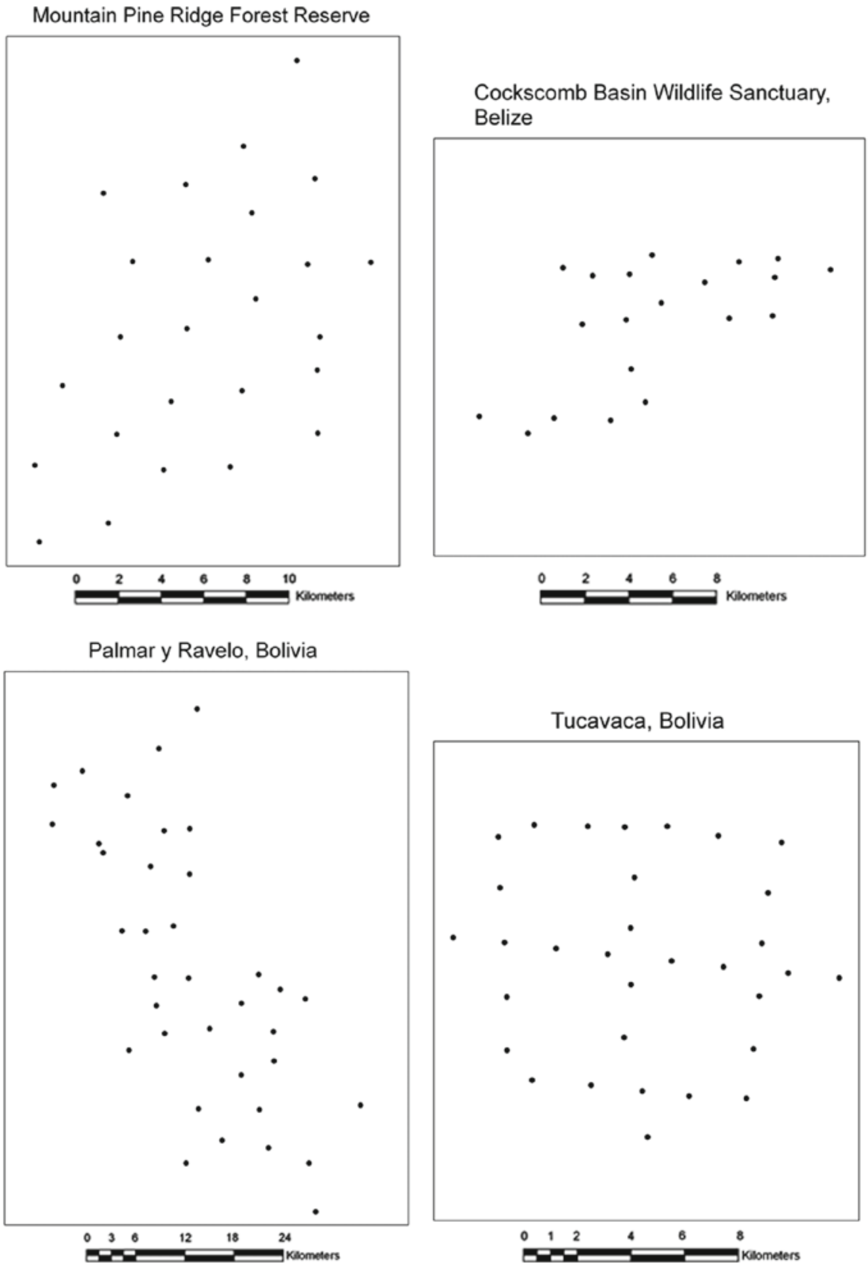

Fig. 8.2 Camera trap placement patterns for jaguar surveys (*dots* camera trap positions)

will be for the study period. With the date and time stamped on the photographs, researchers can measure days or blocks of days as discrete sampling events.

Single CR surveys assume a closed population (i.e., no births, deaths, immigration or emigration of individuals) within the study area during the survey. In reality, few animal populations are actually closed, so in practice researchers try to meet this assumption by limiting the duration of the survey. A short survey length, relative to the lifespan of the animal, decreases the likelihood of violating this assumption. Since jaguars, like tigers, are long-lived, most jaguar surveys follow the convention established by Karanth and Nichols (1998) in using no longer than a 4-month time period to gain photographs to conduct CR and yet still satisfy the assumption of a closed population. Similarly, surveys on African leopards have typically used two to three months (Henschel and Ray 2003). Although there are few life history data available for jaguars, it is reasonable to assume the same duration is satisfactory. Most jaguar surveys have used three months or less as a data collection period. The most commonly used software for estimating jaguar abundance through camera photographs is the program CAPTURE (Otis et al. 1978; White et al. 1982), available online from the Patuxent Wildlife Research Center website (http://www.mbr-pwrc.usgs.gov/software/capture.html). This program uses different models to generate abundance estimates based on the number of individuals captured and the proportion of recaptures. The models differ in their assumed sources of variation in capture probability, including variation among individuals (e.g., sex, age, ranging patterns, dominance, activity), variation over time, behavioral responses to having been captured, and various combinations of these factors. Specifically, the model M(o) indicates that the probability of capture is the same for every animal at every occasion; M(h) incorporates heterogeneity, a unique capture probability for each individual; M(t) is characterized by differences in capture due to time; and M(b) applies where animals have different reaction to the camera traps such as being trap-happy or trap-shy. A series of models also combines the aforementioned factors. The majority of jaguar surveys have used M(h) as the best fitting model based on our knowledge of individual animal behavior and ecology, individuals – especially territorial carnivores – that have different capture probabilities (Karanth and Nichols 1998). Occasionally, however, M(o) may be the model that CAPTURE recommends; but we recommend caution when this is the case. The M(h) model uses the jackknife estimator, which is much more robust than the maximum likelihood estimator that the other models use.

Collapsing data from a long survey into fewer trapping occasions (e.g., a 70-day survey into ten 7-day trapping occasions), increases the capture probability per trapping occasion, and may ameliorate violations of closure. If sampling generates multiple recaptures of multiple individuals, collapsing the number of trapping occasions does not generally affect the abundance estimate and may reduce the standard error of the estimate. CAPTURE uses a discriminant analysis function in its model selection procedure to determine which model best fits the available data. It should be noted that CAPTURE is also a built-in feature of the program MARK (http://welcome.warnercnr.colostate.edu/~gwhite/mark/mark.htm).

The second important assumption is that every jaguar inhabiting the survey area has at least some probability of being photographed (i.e., one camera trap within each animal's home range for the duration of the survey). This assumption dictates distance between camera traps and determines the maximum size of an area to be sampled by at least one camera trap. Thus, the estimated minimum home range of a jaguar in the study area ultimately determines the local minimum camera trap density. Ideally, there should be no gaps between camera trap stations large enough to encompass a jaguar's home range. A conservative approach to satisfy this assumption is to adopt the smallest home range estimate documented locally for jaguars. In practice, most jaguar surveys have spaced cameras 2–3 km apart using the smallest home range of 10 km^2 for a female jaguar in Belize (Rabinowitz and Nottingham 1986). This spacing may not be applicable for other areas where jaguars have larger home ranges.

Once we have the abundance estimate, the next step is to calculate the area surveyed. This has been one of the most problematic issues for estimating jaguar population density based on camera trap surveys. The classical way to estimate the sampling area is to calculate the mean maximum distance moved (MMDM) as a proxy for home range diameter (Wilson and Anderson 1984), sum the maximum distances moved by every individual captured in at least two different locations (but see Dillon and Kelly 2007 regarding animals repeatedly captured at one location), calculate the average, diameter, divide by two (radius), and apply this as a buffer around the camera traps. In the scientific literature, the buffer has been applied two ways: as a strip around the polygon formed by connecting the camera trap locations (polygon buffer), or as a circular buffer surrounding each camera trap location (point buffer). The first method is more subjective because different researchers (and software programs) create different polygons depending on the way they connect the camera locations. The second method is not subject to an interpretation of polygon-drawing because it generates the same area surveyed each time and is the one commonly used in jaguar surveys. However, some argue that buffering each camera location individually does not conform to the idea of a single jaguar population being sampled under the "ball-and-urn concept" (White et al. 1982), where individual jaguars represent the "balls" within a single population or "urn." All areas determined by creating circular buffers and dissolving those buffers have resulted in a continuous sampling area. It is important to note, however, that this may not always be the case; for example, when using camera trap data from a jaguar study to estimate buffers for animals with a smaller home range such as the ocelot. The estimation of the buffer, which in turn determines the area effectively sampled, is the weakest link in density estimation. The MMDM can vary widely even between surveys (in the same location); thus, when data are available from multiple surveys in the same location, we can opt to use one half of a cumulative MMDM. This cumulative MMDM averages the maximum distances moved by all individuals across multiple surveys in different years. This increases the sample size and reduces the variance associated with the MMDM, and gives a more precise estimate of the effective sample area (Dillon and Kelly 2007).

However, even this does not improve the estimate of MMDM if the overall sample area is too small relative to the ranging patterns of the individuals.

New approaches are being developed to address the deficiencies in density estimation procedures (Borchers and Efford 2008; Efford et al. 2004; Royle et al. 2009).

8.4 Results

Both the camera trap polygons and the effective survey area (including a ½ MMDM buffer around the camera traps) vary considerably across surveys, from 24–555 km^2 to 54–938 km² respectively (Table 8.2). In the case of private reserves, cattle ranches, and relatively small reserves, the cameras can be distributed across 30–100% of the land use unit: Moro do Diablo National Park and Fazenda Sete ranch in Brazil, San Miguelito Private Reserve in Bolivia, Gallon Jug Estate in Belize. At the opposite extreme is the Kaa-Iya del Gran Chaco National Park, where surveys at six different sites add up to barely 1% of the park's land area. Considering the area effectively surveyed, most surveys cover at least 35% of the land area, again with the exception of the Bolivian parks such as Kaa-Iya where the all surveys total only 4% of the area. Other surveys fall between the two extremes. For example, the largest camera polygons achieved in any study, 550 km^2 at Iguazú and Yabotí, represented 21% of the protected areas in each case. Including the buffer, the effective survey areas in these two studies covered 35% of the protected areas. Density estimations also varied considerably across study areas (Table 8.2): from 0 to >11 individuals per 100 km². Some of the highest density estimates were reported from private properties: a cattle ranch in the Brazilian Pantanal (Soisalo and Cavalcanti 2006) and a private reserve in Belize (Miller and Miller 2005). Another unexpectedly high density estimate comes from forestry concessions that are under heavy pressure from non-timber forest product harvesters and hunters (McNab et al. 2008).

Several surveys using camera traps in specific areas have not photographed jaguars despite documentation of individuals by other means. We can attribute these results to a number of issues: (1) camera failure, (2) low jaguar densities, (3) camera trapping period was not long enough to photograph an individual, and (4) lack of local knowledge about routes jaguars travel combined with a failure to place camera traps in such areas. Problems with density estimation also arise when too few individuals are photographed, without recaptures or with very few recaptures. Nevertheless, these data do comprise a minimum confirmed population based on the number of individuals positively identified. Camera trapping data has been used to calculate a "capture frequency" based on the number of photographs recorded per 100 or 1,000 trap-nights. Overall capture frequency has been found to correlate with abundance of target animals (see O'Brien, Chap. 6), but population density estimates based on individual identification and CR analysis provide the only reliable comparisons across studies and species when measuring abundance

Table 8.2 Capture frequency, population density estimates (average when multiple surveys were conducted at the same location), and survey area

Country	Study site	Reference	Captures per 100 trap nights	Density ± SE (ind/100 km^2)	Effective survey area using ½ MMDM buffer (km^2)	Camera polygon (km^2)	Protected area size (km^2)	% surveyed[c]
Argentina	Copo	1	0	0	–	388	1,140	34
Argentina	Impenetrable Chaco Aboriginal Reserve	39	0	0	–	449	1,500	30
Argentina	Iguazú	2	0.5–1.5	1.12 ± 0.30	576–958	209–555	670–2,594[b]	**31, 21** / 86, 37
Argentina	Urugua-í	2	0.1	0.3[a]	368	81	872	**11** / 42
Argentina	Yabotí	2	0.2	0.2[a]	1,001	549	2,600	**21** / 39
Belize	Cockscomb basin	3,	3.1–8	3.5–11	196–322	80	400	**20** / 40–80
Belize	Chiquibul	3, 6	3.5	7.48 ± 2.74[d]	107–405	89–146	1,670	**5–9** / 6–24
Belize	Fireburn	27	1.2	5.3 ± 1.76	132	55	8 priv res	**100+** / 100+
Belize	Gallon Jug Estate	4	3.3–4.7	10.05 ± 2.47	170–195	130–165	520 ranch	**32** / 38
Belize	Mountain Pine Ridge	35	3.3–7.1	2.32–5.35	302–345	105–140	430	**24–33** / 74–80
Bolivia	Cerro Cortado, Kaa-Iya	7	1.0–2.0	5.24 ± 2.46	137–149	49–52	34,400	**<1** / <1
Bolivia	El Encanto	8	0.4	5.66 ± 2.33	106	36	876 concession	**4** / 12
Bolivia	Estación Isoso, Kaa-Iya	9	2.2–3.2	2.91 ± 0.33	153–158	48–51	34,400	**<1** / <1
Bolivia	Guanacos, Kaa-Iya	10	1.1–2.9	2.28 ± 0.66	191–243	49–62	34,400	**<1** / <1
Bolivia/Paraguay	Palmar, Kaa-Iya	9, 25	2.4–2.9	1.13 ± 0.13	230–1,068	71–434	34,400	**1** / 3
Bolivia	Puestos Ganaderos	32	0	0	–	217	270	**80**
Bolivia	Ravelo, Kaa-Iya	12	1.2–1.5	1.92 ± 0.76	309–319	100	34,400	**<1** / <1
Bolivia	Rios Tuichi and Hondo, Madidi	3	0.9	2.84 ± 1.78	458	200	15,000 lowlands	**1** / 3
Bolivia	San Matias	13	0	0	–	125	29,200	**<1**
Bolivia	San Miguelito	14	1.2–3.2	4.23 ± 1.43	54–142	24–53	24 priv res, 600 ranch	**100** / 100priv res, **9** / 24 ranch

(continued)

Table 8.2 (continued)

Country	Study site	Reference	Captures per 100 trap nights	Density ± SE (ind/100 km²)	Effective survey area using ½ MMDM buffer (km²)	Camera polygon (km²)	Protected area size (km²)	% surveyed[c]
Bolivia	Tucavaca, Kaa-Iya	15	0.8–1.3	3.41 ± 1.21	125–272	49–130	34,400	**<1** / <1
Brazil	Emas National Park	28	4.56	2.00	500[f]	–[e]	1,320	**38**
Brazil	Fazenda Cauaia	26	0	0	–	16	17 ranch	**94**
Brazil	Fazenda Santa Fé	29	4.02	2.59 ± 1.03	425	80	570[g]	**14** / 75
Brazil	Fazenda Sete	16	13.6–16.4	11.0 ± 1.73	274–360	110–165	460 ranch	**36** / 78
Brazil	Moro do Diablo	17	3.0	2.22 ± 1.33	300	330	370	**89** / 81
Brazil	Serra da Capivara	37	6.5	2.67 ± 1.06	524	157	1,291	**41** / 12
Brazil	SESC Pantanal	18	0	0	–	54	1,063 priv res	**5**
Colombia	Amacayacu	22	0.56	4.2	120	32	2,930 park, 1,406 indig territory	**1** / 4 park,**2** / 9 indig territory
Colombia	Calderón river valley	34	0.62	2.5	242	70	–	–
Costa Rica	Corcovado	19	1.9	6.98 ± 2.36	86	29	425	**7** / 20
Costa Rica	Golfo Dulce / Golfito	38	0.5	2 ± 1.49	218	102	630	**16** / 35
Costa Rica	Golfo Dulce	30	0	0	–	24	617	**4**
Costa Rica	San Cristobal	20	1.1	6.7	60	134	40 biol corridor	**100** / 100 biol corridor
Ecuador	Yasuní-Waorani	36	0.3	1.38 ± 0.60	218	94	9,820	**<1** / 2
Guatemala	Carmelita-AFISAP	33	3.1	11.28 ± 3.51	115	51	1,056	**5** / 11
Guatemala	La Gloria-Lechugal	34	1.5	1.54 ± 0.85	390	128	911	**14** / 43
Guatemala	Rio Azul	5	2.9	10.5	95	50	1,169	**4** / 8
Guatemala	Tikal	21	5.9	6.63 ± 2.46	121	39	575	**7** / 21
Mexico	Sonora	23	0.9	1.0 ± 1.30	140	100	400	**25** / 35
Nicaragua	Bosawas	24	0.3	3.7	127	52	19,928	**<1** / <1

Panama	Darien	11	0.8	1.8–4.4	213–274	67–110	5,790	**1–2** / 4–6
Peru	Los Amigos	31	1.0–1.6	9.6 ± 2.35	130–141	56	1,460	4 / 10
Peru	Bahuaja-Sonene, Tambopata	31	0.5	11.4 ± 19.8	105	52	13,830	**<1** / <1

[a]Density estimates from observed individuals only

[b]Combined area of National Parks in Brazil and Argentina and San Jorge Forest Reserve

[c]Figure in bold is camera polygon as proportion of protected area, other figure is effective survey area as proportion of protected area

[d]Densities declining since the high of this first survey

[e]Does not apply, as cameras were placed along a trap line

[f]Only 30% of the total area was considered suitable jaguar habitat

[g]Total ranch area, including 200 km^2 permanent pasture, and over 50% deciduous forest

References: 1, Denapole (2007); 2, Paviolo et al. (2008); 3, Silver et al. (2004); 4, Miller (2005); 5, Miller and Miller (2005); 6, Kelly (2003); 7, Maffei et al. (2003); 8, Arispe et al. (2007); 9, Romero-Muñoz (2008); 10, Cuéllar et al. (2004); 11, Moreno (2006); 12, Cuéllar et al. (2003); 13, Maffei (2005); 14, Arispe et al. (2005); 15, Maffei et al. (2004a); 16, Soisalo and Cavalcanti (2006); 17, Cullen et al. (2005); 18, Trolle and Kéry (2005); 19, Salom-Pérez et al. (2007); 20, Amit (2007); 21, García et al. (2006); 22, Payan (2008); 23, Rosas-Rosas (2006); 24, Polisar (2006); 25, Montaño et al. (2007); 26, Trolle et al. (2007); 27, Miller (2006); 28, Silveira (2004); 29, L. Silveira and N.M. Negrões (Jaguar Conservation Fund/Instituto Onça-Pintada, Mineiros, Brazil) (unpublished data); 30, Carrillo et al. (2007); 31, S. Carrillo-Percastegui, M. Tobler and G. Powell (unpublished data); 32, Arispe et al. (2006); 33, McNab et al. (2008); 34, Moreira et al. (2007); 35, M. Kelly, Virginia Tech University, Blacksburg, VA (unpublished data); 36, S. Espinosa, University of Florida, Gainesville, FL (unpublished data); 37, Silveira et al. (2009); 38, Bustamante (2008); 39, V. Quiroga (CONICET, Mendoza, Argentina) (unpublished data).

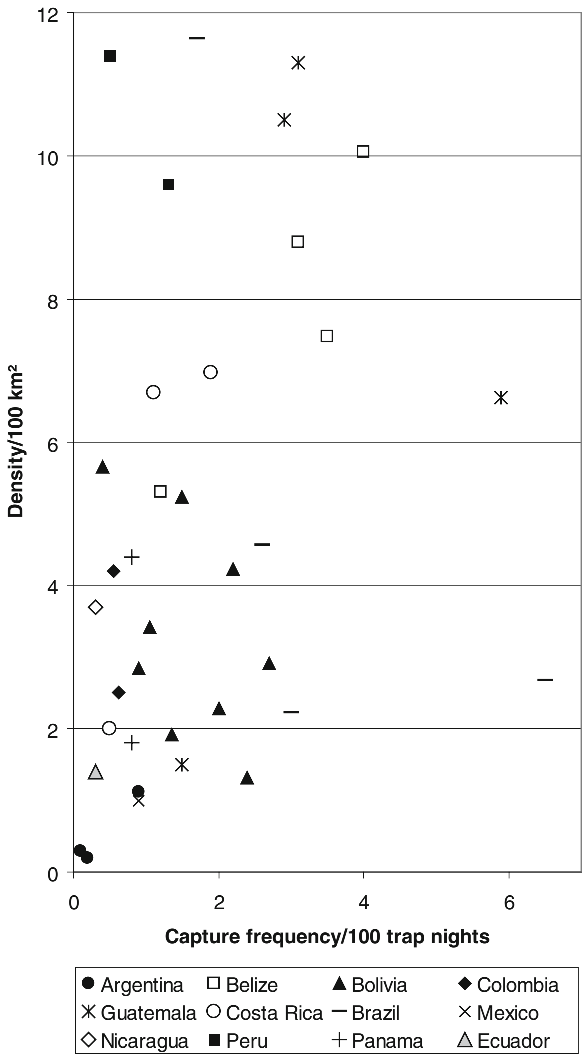

Fig. 8.3 Jaguar population density estimates relative to capture frequency (excluding the Fazende Sete site, Brazil, with a capture frequency of 13–16 photographs per 100 trap nights and a population density of 11 individuals per 100 km^2)

or density. Using capture frequency as an index of abundance, therefore, remains controversial (Carbone et al. 2001, 2002; Jennelle et al. 2002). Figure 8.3 confirms that population density and capture frequency do not correlate across sites: the sites with the highest capture frequencies in Belize and Bolivia are not the same as the sites with the highest population densities. The Atlantic forest site, Moro do Diablo, in Brazil has a capture frequency as high as the Belize/Guatemala moist forest sites, but a considerably lower population density in the range of the dry forest sites in Bolivia. Furthermore, excluded from Fig. 8.3 is the case of the Fazenda Sete in the Brazilian Pantanal. This area had this area recorded an average capture frequency of 15 photographs per 100 trap nights across two surveys, a figure >2.5 times the next highest capture frequency recorded anywhere. However, the population density was similar to the highest Belize estimate (Table 8.2).

Sex ratios also vary across camera trap surveys (Table 8.3), but most surveys have recorded more males than females: from 3:2 (Maffei et al. 2004a, Soisalo and

Table 8.3 Adult sex ratios by jaguar survey site (cumulative where multiple surveys conducted), and locations where cubs/juveniles were photographed

Study (reference)	Males	Females	Unsexed	Cubs/ juveniles
Argentina Iguazú (Paviolo et al. 2008)	4	6	0	Yes
Argentina Urugua-í (Paviolo et al. 2008)	1	0	0	
Argentina Yabotí (Paviolo et al. 2008)	1	0	0	
Belize Chiquibul (M. Kelly [Virginia Tech University, Blacksburg, VA] unpublished data)	15	6	0	Yes
Belize Cockscomb (Silver et al. 2004)	9	0	2	
Belize Fireburn (Miller 2006)	3	0	2	
Belize Gallon Jug (Miller and Miller 2005)	9	7	4	
Belize Mountain Pine Ridge (M. Kelly [Virginia Tech University, Blacksburg, VA] unpublished data)	14	7	0	Yes
Bolivia Cerro Cortado (Maffei et al. 2003)	6	2	1	Yes
Bolivia CIMAL (Arispe and Venegas [WCS/Fundación para la Conservacion del Bosque Chiquitano, Santa Cruz, Bolivia], unpublished data)	2	4	0	Yes
Bolivia El Encanto (Arispe et al. 2007)	4	0	0	
Bolivia Estación Isoso (Romero-Muñoz 2008)	4	1	0	Yes
Bolivia Guanacos (Cuéllar et al. 2004)	2	2	2	Yes
Bolivia Palmar (Romero-Muñoz 2008; Montaño et al. 2007)	7	2	0	
Bolivia Ravelo (Cuéllar et al. 2003)	5	2	0	Yes
Bolivia Río Tuichi/Río Hondo (Silver et al. 2004)	5	3	1	Yes
Bolivia San Miguelito (Arispe et al. 2005; Rumiz et al. 2003)	5	5	1	Yes
Bolivia Tucavaca (Maffei et al. 2004a)	5	3	1	Yes
Brazil ENP (Silveira 2004)	2	1	5	
Brazil Fazenda Santa Fé and Cantão State Park (L. Silveira and N.M. Negrões [Jaguar Conservation Fund/Instituto Onça-Pintada, Mineiros, Brazil], unpublished data)	6	0	2	
Brazil Fazenda Sete (Soisalo and Cavalcanti 2006)	15	10	6	Yes
Brazil Moro do Diablo (Cullen et al. 2005)	2	3	1	Yes
Brazil Serra da Capivara (Astete 2008)	6	4	3	Yes
Colombia Amacayacu (Payan 2008)	3	1	0	

(continued)

Table 8.3 (continued)

Study (reference)	Males	Females	Unsexed	Cubs/ juveniles
Colombia Calderón river valley (Payan 2008)	2	1	1	
Costa Rica Corcovado (Salom-Pérez et al. 2007)	3	1	0	
Costa Rica Corcovada buffer zone (Bustamante 2008)	4	0	0	
Costa Rica San Cristobal (Amit 2007)	0	3	1	
Ecuador Yasuní-Waorani (S. Espinosa [University of Florida, Gainesville, FL], unpublished data)	3	0	0	
Guatemala Carmelita-AFISAP (McNab et al. 2008)	7	3	0	
Guatemala La Gloria-Lechugal (Moreira et al. 2007)	4	2	0	
Guatemala Río Azul (Miller and Miller 2005)	6	0	1	
Guatemala Tikal (García et al. 2006)	3	1	3	
Mexico Sonora (Rosas-Rosas 2006)	4	1	0	Yes
Nicaragua Bosawas (Polisar 2006)	3	0	1	
Panama Darien (Moreno 2006)	1	3	0	
Peru Los Amigos (S. Carrillo-Percastegui, M. Tobler and G. Powell [Arizona State University, Tucson, AZ], unpublished data)	6	3	1	
Peru Bahuaja-Sonene, Tambopata (S. Carrillo-Percastegui, M. Tobler and G. Powell [Arizona State University, Tucson, AZ], unpublished data)	5	1	1	
United States (McCain and Childs 2008)	4	0	0	

Cavalcanti 2006) to 4:1 (Kelly 2003, Wallace et al. 2003) and up to 9:0 (no animals positively identified as females, Silver et al. 2004). One exception is in the Darien, and two others in Atlantic forest: Iguazú and Moro do Diablo National Parks. In the latter two cases, the protected areas are islands of forest surrounded by heavily transformed landscapes and may provide breeding refuges for jaguars. Most radio telemetry studies report that males have larger home ranges than females (Crawshaw 1995; Cullen et al. 2005; Rabinowitz and Nottingham 1986; Scognamillo et al. 2002, 2003; Soisalo and Cavalcanti 2006), so we would assume that more females than males are present in any given area where there is a resident breeding population. However, males may have a higher capture probability because of larger home ranges that are presumably include relatively more cameras. In addition, males tend to walk more than females (Rabinowitz and Nottingham 1986) and use human trails/roads (where camera traps are almost always set) more than females (Salom-Pérez et al. 2007). Both radio telemetry and camera trapping studies suggest that multiple males and females overlap in their ranging patterns. Sites where females and cubs are present clearly represent conservation priorities. On the other hand, the failure to photograph females does not mean that they are absent from an area, but only that such areas should be evaluated more carefully to determine whether they function principally as corridors or dispersal areas, and whether they potentially represent population sinks.

Finally, the camera trap methodology can provide considerable information about jaguars besides density estimation (see other chapters of this volume), including activity patterns, reproduction data (number of cubs, seasonality) and information on prey

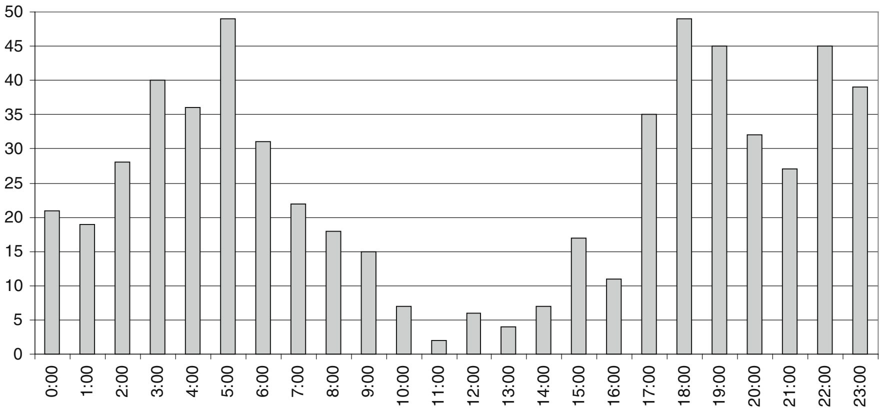

Fig. 8.4 Sample activity patterns for jaguars based on camera trapping records from Bolivia dry forest sites ($N = 605$ records)

(species present, relative abundance from capture frequency, activity patterns). Figure 8.4 presents jaguar activity budgets derived from camera trapping records at a sample of survey sites. Camera trap photos suggest that jaguars can be active at any time of day, but are principally crepuscular-nocturnal in their habits. Cubs are occasionally photographed (single cubs only in the Chiquibul in Belize; and Cerro Cortado, Guanacos, Tucavaca in Bolivia), and juvenile animals occur in the company of their mothers more frequently (a pair of juveniles together in the Chiquibul in Belize and Cerro Cortado in Bolivia; single juveniles only in Estación Isoso, Ravelo, San Miguelito, Tucavaca in Bolivia). This type of information provides preliminary information on reproductive patterns: one to two cubs born during the rainy season, December–May in Chaco dry forests, and maternal care until the juveniles approach adult size.

Conducting multiple surveys at the same site can validate density estimates, ranging patterns, and document rough turn-over rates of individuals within specific populations. For example, Table 8.4 suggests which individuals may be resident (females T2 and T4, males T5 and T6) vs. transient (possibly males T1, T3, T10, and T9 [unknown sex]). This information must be viewed in context, however, because alternatively, the latter group could have been photographed at the edge of their ranges, thereby incorrectly categorizing as transients resident individuals whose ranges overlap minimally with the camera layout. For example, the cub of female T2 and the juvenile offspring of female T7 were not subsequently photographed, suggesting that they dispersed outside the survey area if they survived. Karanth et al. (2006) go much further to estimate rate of change, survival, recruitment, temporary emigration, etc., based on 12 years of data. Though jaguar researchers have not estimated these rates to date, the longest running surveys are currently six years and these estimates should be possible in the near future. Camera trap surveys have also documented transboundary movements of jaguars between the United States and Mexico (McCain and Childs 2008), between Argentina and Brazil (Paviolo et al. 2006), and between Bolivia and

Table 8.4 Turn-over of individual jaguars according to multiple camera trap surveys at Tucavaca, Kaa-Iya del Gran Chaco National Park (Maffei et al. 2004a)

	T1	T2	T2	T3	T4	T5	T6	T7	T8	T9	T10	
	M	F	Cub	M	F	M	M	F	J	?	M	Total
Preliminary May–Dec, 2001		14	2	1				3		2		20
Survey I Jan–Mar, 2002	11	5		1	2	3	1	1				24
Survey II Apr–Jun, 2003		3					4	3	2			12
Survey III Mar–May, 2004						8	2	1			3	14

Paraguay (Romero-Muñoz et al. 2007). Such information is invaluable for promoting international conservation efforts.

8.5 Discussion

Another approach when there are too few detections to calculate abundance or when grid trapping is not possible is to use detection-non detection data at each camera site to model detection probabilities and the proportion of area occupied (MacKenzie and Kendall 2002; MacKenzie et al. 2003, MacKenzie et al. 2006, see O'Connell and Bailey, Chap. 11). In this way, detection-nondetection data (often referred to as presence-absence) data can be used as a surrogate for abundance for cryptic or low density species. The underlying logic is that changes in the proportion of occupied sites will be correlated with changes in the population size, provided sites are defined at an appropriate spatial scale (MacKenzie 2005; MacKenzie et al. 2006). So far, this approach has not yet been applied to jaguars, but holds promise for future studies.

Although new camera trapping techniques are developing that use random camera placement, combined with information on species' day range, to address spatial variability (Rowcliffe et al. 2008), random placement is unrealistic for most jaguar field studies because capture probabilities would be impossibly low. Given that capture probability is already low even in studies that target jagaurs (~2 per 100 trap nights), the increased effort required to obtain captures using random placement is probably not realistic. The study approach for jaguars – systematic, regularly-spaced, traps set to target jaguars (i.e., on roads, trails, games trails, riverbeds, etc.) – violates the random placement of traps which has proven to be necessary to generate unbiased estimates as in the gas model approach of Rowcliffe et al. (2008). However, increasing the capture probability is also necessary to obtain enough recaptures to conduct CR surveys. Perhaps a compromise approach of random placement with directed sampling will be fruitful. Alternatively, the approach of Borchers and Efford (2008) used capture locations to estimate animal locations and spatially referenced capture probabilities. With this technique, density is evaluated in a maximum likelihood framework, based on spatial and temporal co-variates. This approach has not yet been applied to jaguars.

An underlying problem for all jaguar camera trap surveys is that we do not actually know the true densities of the target population and therefore cannot judge whether we are underestimating or overestimating true densities. Calibrating the camera trapping technique would require conducting a camera survey in an area with known densities. This may be possible for other animals such as lions *Panthera leo* where all study animals in an area are known (C. Packer [University of Minnesota] pers. comm.), but it is unlikely to be the case for any area in the jaguar's range.

The systematic camera trapping methodology was originally developed for tigers in India, where many protected areas are relatively small islands and where surveys can cover large proportions or even all of the area, and where the target species may have difficulty moving outside the protected area. Similar conditions may exist for jaguars in parts of their range, for example in much of Central America and in Atlantic forest patches in Brazil. However, in many other landscapes and particularly in South America, we are often surveying only tiny portions of vast protected areas or potential habitat, exceeding 10,000 km^2, through which jaguars can move freely beyond the boundaries of a 100–500 km^2 camera trap survey. The density estimate is then crucial because it provides information on the status of the species within this wider landscape. However, it should only be used tentatively and cautiously to extrapolate and estimate total populations (Maffei et al. 2004b) for wider protected areas or regions. Carnivore densities may vary significantly even under natural conditions with no or minimal human interventions (Karanth et al. 2004; Sunquist et al. 1999).

Density estimates are extremely sensitive to the calculation of the effective survey area, which depends on the size of the buffer surrounding traps. Camera trap spacing, total survey area, and degree of concordance between home range radius and ½ MMDM from cameras have arisen as three important factors impacting density estimation (Dillon and Kelly 2007; 2008). Increased camera spacing can lead to decreases in density estimates because MMDM increases (Dillon and Kelly 2007). Maffei and Noss (2008) suggest that MMDM may not be an appropriate proxy for home range diameter when camera survey areas are small compared to home range areas of the target species because the small area leads to an underestimate of maximum distance moved. While the use of ½ MMDM as a proxy for home range radius has a long history in the literature (Dice 1938) and has performed well in simulation studies (Wilson and Anderson 1985), its use has recently been called into question. Parmenter et al. (2003) found that small numbers of capture locations produce severe underestimates of home range size and movement distances. Most jaguar studies use 30 or fewer camera stations, undoubtedly a small number of capture locations. And while Parmenter et al. (2003) found that using the full rather than the ½ MMDM performed very well empirically in their small mammal studies, they caution against using MMDM at all due to the large number of underlying assumptions about animal movement. They instead suggest substituting known movement distances derived from radio telemetry.

A few studies have done this. Soisalo and Cavalcanti (2006), who followed jaguars with radio collars simultaneously with camera trapping efforts in the Pantanal, found that distances moved with radio collars were as much as twice the distance estimated with camera traps. Based upon comparisons between the ranging behavior of the collared jaguar and their MMDM, they recommended using the full MMDM to buffer camera locations rather than ½ MMDM (following Parmenter et al. 2003). Recent research on ocelots with simultaneous camera trapping and radio telemetry has proven equivocal with one study finding similar results to Soisalo and Cavalcanti (2006) (Dillon and Kelly 2008) and the other finding ½ MMDM a good proxy for home range radius (Maffei and Noss 2008). Habitat types were different in the two ocelot studies pointing to flexibility in wild cat movements patterns from one subpopulation to another.

In order for the MMDM to be an accurate characterization of ranging patterns in surveyed jaguar populations (and therefore an accurate tool in estimating the effective sample area), the camera trapping grid must be large enough to account for the long distances the jaguars are likely to travel during the survey. Obviously, having camera trap arrays with cameras spread only 15 km apart will not allow an accurate ranging characterization of animals that travel > 15 km. Thus, investigators designing camera trap surveys need to make some a priori assumptions about the minimum dimensions of a camera trap grids.

In Central America, radio telemetry studies have reported the following home range sizes for jaguars: 10–40 km^2 in the tropical moist lowland forests of Belize (Rabinowitz and Nottingham 1986), 32–59 km^2 in tropical moist lowland forests of Mexico (Ceballos et al. 2002), and 25–65 km^2 in Mexican dry forests (Núñez et al. 2002). Applying the recommendation that camera trap surveys encompass at least four average home ranges of the target species (Maffei and Noss 2008), jaguar surveys in Central America should, at a minimum, cover areas in the range of 100–180 km^2. Several of the Belize surveys have met this requirement, as well as the San Cristobal survey in Costa Rica and the second Darien survey in Panama (Table 8.2). The low population densities and wide ranging patterns of jaguars in the Mexico–USA border region require that even extensive areas be surveyed (McCain and Childs 2008).

In South America, average home ranges are considerably larger than in Central America: 52–176 km^2 in Pantanal grasslands (Crawshaw and Quigley 1991; Soisalo and Cavalcanti 2006), 43–177 km^2 in Atlantic tropical moist lowland forest (Crawshaw 1995; Cullen et al. 2005), 48–130 km^2 in Venezuelan Llanos grasslands (Scognamillo et al. 2002, 2003), and 69–1,200 km^2 in the Chaco (McBride et al. 2004, 2005; Romero-Muñoz et al. 2007). Again, applying the tentative rule suggested by Maffei and Noss (2008), jaguar surveys in South America should ensure that cameras cover a minimum of 500–600 km^2. The Yabotí and second Iguazú surveys (Argentina – Paviolo et al. 2008) do so, each covering around 550 km^2, which is equivalent to 21% of the protected area in each case. The Moro do Diablo study (Brazil) comes close to doing so, coincidentally also covering 90% of the island protected area, and with telemetry information to confirm the camera trap density estimation (Cullen et al. 2005). The second Palmar survey in Bolivia also comes close to doing so, but covers barely 3% of the immense Kaa-Iya National Park (Montaño et al. 2007).

We recommend that density estimates from camera trapping surveys, particularly when they cover only small portions of vast protected areas or potential jaguar habitat, be treated only as preliminary until the methodology can be tested further by conducting camera trap surveys with cameras spread ≥ 500 km^2. If it is logistically impossible to insure that the area covered by the camera traps include at least four average home range areas, we suggest that density estimates for jaguar populations be interpreted with great care. In addition, radio telemetry studies are needed to determine daily home ranges across similar habitats and regions that can be used as a substitute for ½ MMDM to estimate the effective area sampled by camera traps. We also recommend the development of a more theoretically sound approach, based on modeling, to estimate effective survey area.

Finally, compared to tiger surveys published in the literature, jaguar surveys have generated relatively small samples sizes (Table 8.3). Given the generally low population densities of jaguars across their range, future research should emphasize larger survey areas to confirm whether density estimates are consistent with larger sample sizes.

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