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ESTIMATING PUMA DENSITIES FROM CAMERA TRAPPING ACROSS THREE STUDY SITES: BOLIVIA, ARGENTINA, AND BELIZE

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Estimates of abundance are extremely valuable for species conservation, yet determining abundance for elusive, wide-ranging, carnivores is difficult. We estimated density of pumas using remote cameras across study sites in Bolivia, Argentina, and Belize. We used obvious and subtle markings to identify individual pumas in photographs and conducted double-blind identifications to examine the degree of agreement among investigators. Average agreement on identification between pairs of investigators was nearly 80.0% and 3-way agreement was 72.9%. Identification of pumas as different individuals was uncommon (7.8% pairwise, 0.69% 3-way disagreement) with the remainder described as unidentifiable. Densities of pumas varied consistently from site to site regardless of investigator. Bolivian pumas moved the shortest distances between camera stations and Argentinean pumas the longest, but distances among cameras and area covered by surveys varied among sites. We applied a correction factor to the Bolivian data to account for the small area surveyed and found that, averaged across investigator, Bolivia had significantly more pumas per 100 km^2 (mean $\pm$ *SD*; 6.80 $\pm$ 1.5) than Belize (3.42 $\pm$ 1.3) or Argentina (0.67 $\pm$ 0.2). Numbers of pumas in Argentina match those of low-density North American sites, and those for Belize are consistent with the Pantanal and high-density North American sites. Densities of pumas can be reliably estimated with remote cameras for these sites, and our work presents the 1st density estimates for Central America and for forested environments in South America.

Key words: camera traps, density, individual identification, Neotropics, puma, *Puma concolor*

Although it is likely that numbers of pumas (*Puma concolor*) have declined in recent years because of declines in prey and habitat loss and fragmentation, their status remains unknown over most of their range south of the United States border (Sunquist and Sunquist 2002). There are currently no reliable density estimates, particularly in dense forest habitat, for pumas in Central or South America and no standardized technique for estimating density of pumas. Those density estimates that do exist from its southern range result from radiotelemetry studies, and these methods have a number of limitations including small sample size, unknown number of animals not radio-tagged, and high cost and effort required (Karanth 1999; Karanth and Nichols 1998). Given that habitat loss is considered the most critical threat to populations of pumas (Logan and Sweanor 2001; Medellín et al. 2000), the lack of data on pumas in the Neotropics is particularly troubling because this area is currently experiencing some of the fastest habitat loss on earth. Density estimates are critical to the development of conservation and management plans for the species.

Remotely triggered infrared cameras (camera traps) have been used successfully to estimate densities of elusive predator species such as tigers (*Panthera tigris*—Karanth 1995; Karanth and Nichols 1998; Kawanishi and Sunquist 2004; Linkie et al. 2006; O'Brien et al. 2003), jaguars (*Panthera* onca—Kelly

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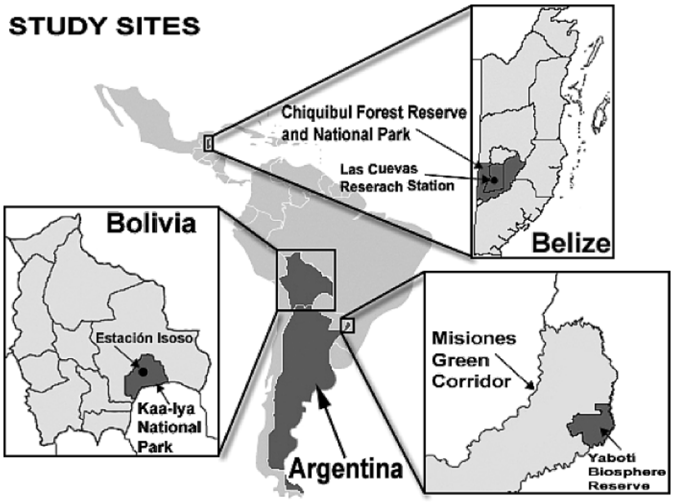

FIG. 1.—Locations of study sites in Bolivia, Argentina, and Belize.

2003; Maffei et al. 2004; Silver et al. 2004; Wallace et al. 2003), ocelots (*Leopardus pardalis*—Di Bitetti et al. 2006; Dillon and Kelly 2007; Maffei et al. 2005; Trolle and Kery 2003), and Geoffroy's cats (*Leopardus geoffroyi*—Cuéllar et al. 2006). This method requires that individual animals be distinguishable in photographs by their natural markings (i.e., stripe and spot patterns). Individual identification is necessary in order to create individual capture histories and perform mark–recapture analysis to estimate abundance. Although this method is relatively straightforward for well-marked species such as tigers and jaguars, there has been considerable debate about whether this technique could be applied to more subtly marked animals such as the puma.

Pumas and jaguars are sympatric throughout most of Central and South America. Therefore, if densities of pumas can be estimated through camera trapping, the numerous studies conducting camera trapping for jaguars likely already have the data in hand to estimate densities of pumas. This makes possible an examination of how densities of pumas vary across numerous habitats in the Neotropics and how they covary with densities of jaguars.

In this study, we assessed the reliability with which pumas can be identified by their individual marks across 3 different camera-trapping study sites in Bolivia, Argentina, and Belize. We conducted double-blind observer identifications, created capture histories based on each investigator's identifications, and used program CAPTURE (Rexstad and Burnham 1991) to estimate abundance of pumas across study sites and by different investigators. We estimated densities of pumas following Karanth and Nichols (1998; see also Silver et al. 2004). We compared our estimates among investigators and sites and to those estimates that existed from other methods and study sites. We also supplied recommendations for applying this technique in future studies.

MATERIALS AND METHODS

Study sites.—Surveys were conducted at study sites in Bolivia, Argentina, and Belize (Fig. 1). Kaa-Iya del Gran Chaco National Park (Taber et al. 1997) is a 34,400-km^2 protected area covering the northern end of the Gran Chaco in Bolivia. This area contains the world's largest remaining area of Chaco dry forest. At 300 m above sea level, the Estación Isoso (18°25′S, 61°46′W) field camp lies within the Chaco plain transitional landscape system on the Bolivia–Brazil gas pipeline, near the western border of Kaa-Iya National Park. The canopy averages 10–15 m, and the thick underbrush is dominated by terrestrial bromeliads and cacti. Annual precipitation averages from 700 to 800 mm and average annual temperature is 25°C. During the 6-month dry season, surface water disappears for extended periods. The nearest human settlement is the Isla Verde ranch and paddy rice farm, 22 km to the west. Some poaching of wildlife took place until security was improved in 2002.

The 2,742-km^2 Yabotí Biosphere Reserve is located in the southeastern portion of the Green Corridor of Misiones Province (26°55′S, 54°00′W; 200–600 m above sea level) in the Atlantic Forest of Argentina. The study site has a humid subtropical climate with a mean annual precipitation that usually ranges between 1,700 and 2,300 mm, with no marked dry season (Crespo 1982). Although most of the Yabotí Biosphere Reserve lies within private properties, the core area of the Yabotí Biosphere Reserve is represented by the 316-km^2 Esmeralda Provincial Park, which is relatively inaccessible in relation to other areas within the Yabotí Biosphere Reserve. Seasonality in temperature, day length, and primary productivity is marked, with hot summers and ocassional frosts during the winter months (Crespo 1982; Di Bitetti and Janson 2001). Most forests within the Yabotí Biosphere Reserve have been logged or are currently under heavy logging. Logging promotes the invasion of the forest by 2 species of bamboo (*Merostachys claussenii* and *Chusquea ramossisima*) that preclude forest regeneration (Campanello 2004). By provincial law, the native forest within the Yabotí Biosphere Reserve cannot be converted to other uses, including monoculture forest plantations. Despite special regulations and efforts by the provincial government, poaching and illegal timber harvesting are common and widespread in the private properties of the Yabotí Biosphere Reserve and affect forest structure, in particular by favoring the invasion of the forest by the 2 species of bamboo.

In western Belize, the 1,744-km^2 Chiquibul Forest Reserve and National Park (16°44′N, 88°59′W; 500 m elevation) is the largest managed forest reserve in Belize. With the adjacent Peten region of Guatemala and Mexico, the Cockscomb Basin Wildlife Sanctuary, and the Bladen Nature Reserve, this area forms one of the last large naturally forested tropical areas within Central America (Carr and de Stoll 1999; Penn et al. 2004). Rainfall averages about 1,500 mm/year with a rainy season from June to January (Johnson and Chaffey 1973). The life zone is classified as subtropical moist forest (Holdridge et al. 1971) and vegetation occurs on steep limestone terrain where water availability in the dry season is low. The vegetation is a mosaic of broadleaf tropical moist rain forest, deciduous semievergreen, deciduous seasonal forest, and stands of pine in the north (Wright et al. 1959). The general canopy is at

TABLE 1.—Summary of date of surveys, numbers of camera stations, trap nights, and trap success across study sites.

Study site	Dates of survey	Approximate spacing between camera stations (km)	No. camera stations	Survey length (days)	Total trap nights[a]	Percent (%) puma trap success (capture events per 100 trap nights)	Encounter occasions[b]	MCPs around camera traps (km^2)[c]
Bolivia: Kaa-Iya del Gran Chaco National Park	28 October–24 December 2005	2	22	56	1,232	2.84	15	51.00
Argentina: Yabotí Biosphere Reserve	27 August–30 November 2005	2.5	42	96	1,871	2.41	16	549.19
Belize: Chiquibul Forest Reserve and National Park	4 January–9 April 2003	3	17	95	1,601	3.00	19	109.85

[a] Calculated as number of stations times number of nights minus number of days when stations were nonfunctional because of camera malfunctions.
[b] Number of trapping occasions used in program CAPTURE after collapsing data; for example, for Belize, 95 days were collapsed into nineteen 5-day capture periods.
[c] MCP = minimum convex polygon.

20–30 m. Some blocks of the Chiquibul Forest Reserve have been, and are still being, selectively logged for commercially important species such as mahogany (*Swietenia macrophylla*) on a greater than 40-year rotational basis.

Camera-trapping surveys.—At all study sites we deployed remote cameras arrayed at regular intervals (2–3 km) in a gridlike formation across the landscape following previous protocol for jaguar surveys (Silver et al. 2004) originally pioneered by Karanth (1995) for tigers. Surveys used between 17 and 42 camera stations operational for a 2- to 3-month time period (Table 1). We collapsed daily data in blocks such that 1 encounter occasion consisted of a 4- to 7-day time period depending on the study. We found abundance estimates to be relatively insensitive to period of collapse after 3 days, although capture and recapture rates, and probability of closure did change. We also calculated a minimum convex polygon surrounding camera traps to determine the extent of the area over which cameras were deployed. Two cameras per station were placed opposite each other on both sides of a trail or road. This allowed us to obtain photographs of both flanks of the puma. Studies used a suite of camera brands that included: Camtrakker (CamTrakker, Watkinsville, Georgia), Deer Cam 100 and 200 (Non Typical Inc., Park Falls, Wisconsin); Leaf River Trail Scan model C-1 (Leaf River Outdoor Products, Taylorsville, Mississippi), TrailMAC (Trail Sense Engineering, Middleton, Delaware), Trapacâmera (Trapacâmera, Cidade Universitária, São Paulo, Brazil), Tigrinus (Tigrinus Equipamentos para Pesquisa Ltda., Timbó, Santa Catarina, Brazil), and TrailMaster Active 1550 (Goodson and Associates Inc., Lenexa, Kansas). Cameras were operational 24 h/day with a camera delay of 30 s to 5 min (i.e., the time that the cameras would be ready to take another photograph should another animal pass by). A capture "event" consisted of a record of a puma at 1 or more of the cameras at a station within a 30-min to 1-h time period. We tallied the total number of events and the total number of photographs for pumas and calculated trap success as the number of puma events per 100 trap nights.

Identification of pumas and comparisons among sites and investigators.—To test the accuracy with which each investigator (or investigator team) identified individuals, we duplicated our photographs, exchanged them, and conducted a blind identification test in which the 3 investigators were unaware of how the others had identified and categorized the photographs. Pumas were identified by obvious marks (kinked tails, scars, and ear nicks), by less obvious marks (scars that healed over time [e.g., from botflies], tail-tip coloration, and rings), and by subtle marks (undercoat spot patterns, coloration on the underside of legs, tail carriage, and body shape and carriage; Fig. 2). Each researcher sorted cats into positive identifications, tentative identifications, and not possible to tell (usually an unusable photo because of poor quality).

The 3 data sets were then compared to determine number of exact matches between investigators across sites. Some investigators classified some photos as unusable whereas others did not. Therefore we discarded events (unusable events) only when all 3 investigators agreed they were unusable because of poor quality. We then calculated percentage of exact matches by dividing the number of events with exact and tentative matches by the total number of usable events. In the same fashion, we also calculated the number and percentage of events where all 3 investigators agreed on identifications. Finally, we examined the number and percentage of complete disagreements between pairwise investigators and among all 3 investigators.

Abundance of pumas.—Each investigator constructed 3 capture histories for the pumas at their own site based on their own identification of pumas and those of the other 2 investigators based on the identifications provided by the others. These capture–recapture histories were then analyzed using program CAPTURE (Otis et al. 1978; Rexstad and Burnham 1991; White et al. 1982) to estimate sizes of populations of pumas. To determine the size of the area surveyed, the mean of the maximum distance moved between cameras was calculated for each puma capture history and half this distance was used (½ MMDM) as the buffer radius around each camera trap location (Dice 1938; Wilson and Anderson 1985). Buffers were dissolved and total area calculated in ArcView (ESRI 1999) using X-tools or Spatial Analyst. The number of pumas from each survey was then divided by the total survey area to obtain density of pumas. This estimation method has been detailed extensively in other camera-trapping publications and our study follows those methods closely (Di Bitetti et al. 2006; Karanth 1995; Karanth and Nichols 1998; Kelly 2003; Maffei et al. 2004, 2005; Silver et al. 2004). There is considerable debate concerning whether the ½ MMDM truly reflects animal

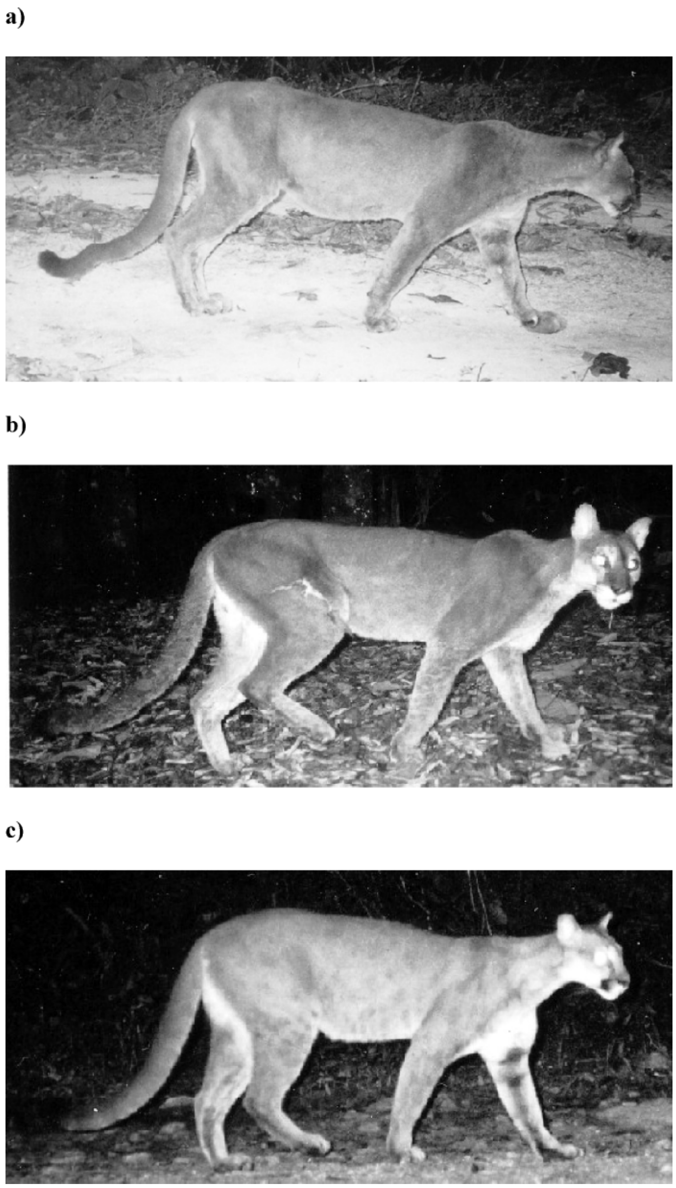

Fig. 2.—Identification of pumas (*Puma concolor*) was done by careful scrutiny of photographs for a and b) obvious characters such as kinked tailed and scars to c) more subtle characteristics such as undercoat spot patterns, smaller scars (not pictured), spot patterns on the underside of the legs, and body and tail shape and carriage.

movement and home range and whether it should be used to buffer camera traps. We did not address this concern in our study, but it is addressed by others (A. G. Dillon and M. J. Kelly, in litt.; Maffei and Noss 2008; Soisalo and Cavalcanti 2006). We focused on whether densities of pumas could be reliably estimated with current methodology.

Movement and density of pumas.—Because number of pumas is not a continuous variable and may not be normally distributed, we used a 2-way nonparametric test, the Scheirer–Ray–Hare extension of the Kruskal–Wallis test (Sokal and Rohlf 1995), to determine if the numbers of pumas identified and the estimate of population size obtained varied among investigators and among sites. Because different investigators may have identified pumas differently, the estimates of distances moved (½ MMDM) may change. Therefore, we used 2-factor analysis of variance (ANOVA) to determine whether the ½ MMDM estimates varied more between investigators within sites than across sites. Because we were interested in all pairwise comparisons between sites, we then used a Tukey–Kramer honestly significant difference post hoc test for differences between site means to further investigate whether pumas moved more at 1 site than another.

Density estimates result from a combination of the estimate of population size and buffers calculated. We calculated standard errors on density estimates following Nichols and Karanth (2002). We used 2-factor ANOVA, this time on the log-transformed density estimates (because of nonnormality) to determine whether densities of pumas varied among investigators and sites. We again used a Tukey–Kramer honestly significant difference post hoc test to determine if 1 site had significantly more pumas than any other. Significance level for all ANOVAs was set at an alpha of 0.05, and paired *t*-tests were adjusted to an alpha level of 0.01667 using the Bonferroni correction for multiple comparisons (i.e., alpha/3 for 3 comparisons).

Our Bolivian site had a smaller area surveyed than the other sites. It has been suggested that surveying small areas captures the edges of many home ranges and artificially inflates density estimates (Maffei and Noss 2008). As a guideline, Maffei and Noss (2008) suggest a survey area of 3–4 times the average home-range size of the target species. Although our sites in Argentina and Belize most likely meet these requirements, the Bolivian site does not. Because of this concern, we used a correction factor for the densities of pumas in Bolivia based on recently available data on densities of jaguars from a nearby site with 3 small areas surveyed in Bolivia and from a much larger area survey that encompassed all 3 small survey areas (A. J. Noss, in litt.). Assuming no bias in the way densities of jaguars versus those of pumas are calculated via camera traps, and assuming similar ranging patterns, densities of pumas should decline by a similar ratio as density of jaguars when survey area is increased. We multiplied this "density ratio" for jaguars (i.e., density of jaguars in large area divided by density of jaguars in small area) by our density of pumas for the small area, to correct for the small area surveyed.

Results

Camera-trapping surveys.—Surveys lasted between 56 and 96 days (1,232–1,871 trap nights), trap success for pumas ranged from 2.41 to 3.00 capture events per 100 trap nights, and minimum convex polygons surrounding traps ranged from 51.00 to 549.19 km^2 (Table 1). Number of puma events ranged from 35 to 48 and included 48–69 photographs of pumas (Table 2). Although quality of some photos made them too poor to use because of lighting, angle, or capture of only part of an animal in the photograph, on average this represented a very small percentage of the total number of events (4.66%) or photos (4.47%; Table 2). In addition, we found that many poor-quality images could be assigned because the visible portion of the animal had a characteristic mark such as a scar

TABLE 2.—Summary of number of and percentage of unusable capture events and photographs of pumas (*Puma concolor*).

Study site	No. puma capture events	No. photos in events	No. (%) unusable events[a]	No. (%) unusable photos[a]
Bolivia: Kaa-Iya del Gran Chaco National Park	35	48	1 (2.86)	2 (4.17)
Argentina: Yabotí Biosphere Reserve	65	97	5 (11.11)	6 (9.23)
Belize: Chiquibul Forest Reserve and National Park	48	69	0 (0.00%)	0 (0.00%)

[a] Agreed upon as unusable by all 3 investigators or investigator teams.

or tail kink. We therefore found no real relationship between quality of photos and ability to assign identifications to pumas.

Identification of pumas and comparisons among sites and investigators.—The average agreement on identifications of pumas between pairs of investigators was high, at 79.3% across all sites (Fig. 3a). Belizean pumas were more difficult to identify and had the lowest average pairwise agreement at 68.1%, whereas Bolivian pumas were more easily identifiable at 87.3% average agreement between pairs of investigators. Average agreement between all 3 investigators across sites was slightly lower at 72.9% than average pairwise agreement.

Disagreement on identification between investigators was not simply the remainder of all cases other than agreement because some investigators classified pumas as unidentifiable whereas others did not and instances when pumas were considered unidentifiable were not included as agreements or disagreements. Only if a puma event was classified by all 3 investigators as unidentifiable was it discarded. Disagreement between investigators, when investigators identified pumas as different individuals, was uncommon at only 7.8% between investigators across sites (Fig. 3b) with the lowest disagreement occurring for Argentinean pumas (4.7%) and the highest for Belizean pumas (13.9%). Three-way disagreement (e.g., 3 unique pumas identified) was almost nonexistent at an average of 0.69% (range 0–2.1%).

Abundance of pumas.—The number of pumas identified by investigators ranged from 6 to 14 and varied significantly among study sites ($H = 6.424$, $d.f. = 2$, $P < 0.05$) but not among investigators ($H = 1.303$, $d.f. = 2$, $P > 0.05$; Table 3; Fig. 4). Although differences among investigators were not statistically significant, investigator 3 had a tendency to identify more pumas (splitter) than investigator 1 (lumper) across sites. We identified fewer pumas in Argentina (mean ± *SD*; 6.67 ± 1.16, $n = 3$) than Bolivia (12.67 ± 1.53, $n = 3$) or Belize (10.00 ± 1.73, $n = 3$).

Model selection in program CAPTURE always resulted in either the null model M(o), or the heterogeneity model M(h) as the most appropriate model (Table 3). We used M(h) for our final estimates of population size because this seemed to reflect puma behavior more appropriately than a constant probability of capture, M(o). In 1 case, however, we used the more conservative M(o) estimate of abundance because of large inconsistencies in the M(h) estimate over several runs of the model. Estimates of population size ranged from 6 to 18 animals

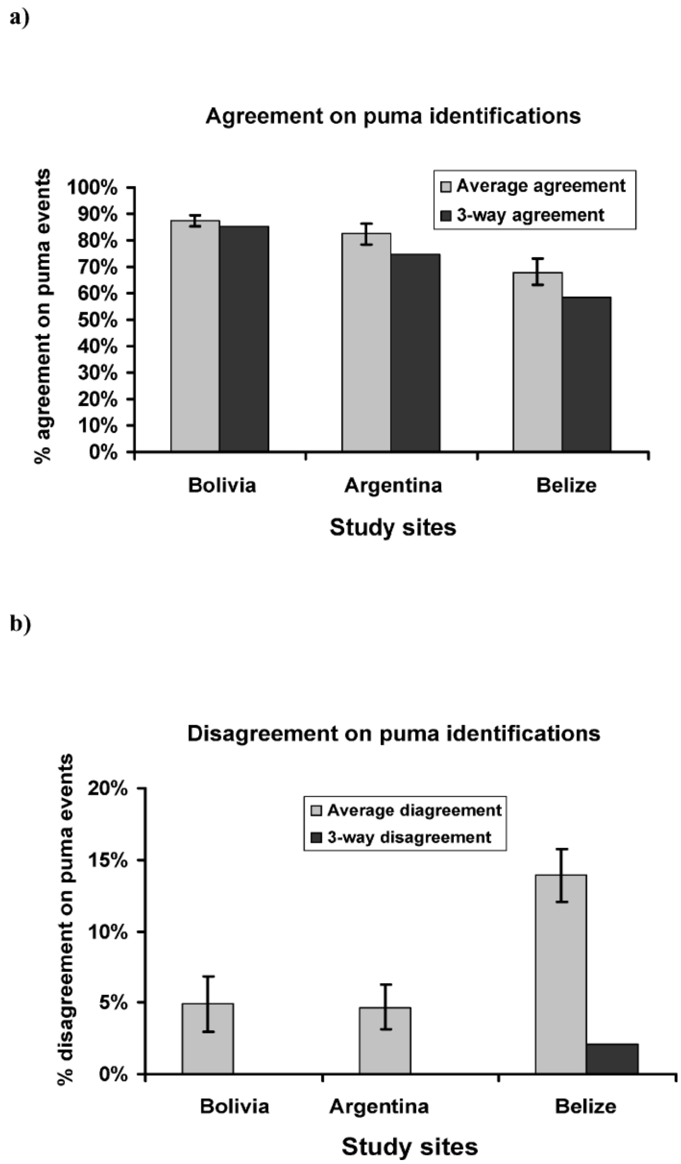

FIG. 3.—a) Average agreement on identification of pumas (including tentative agreements) between pairs of investigators (e.g., investigator 1 to 2, 1 to 3, and 2 to 3) within each study site, and b) average disagreement, which included cases when investigators identified a puma as 2 different individuals but did not include cases when investigators classified events as unusable and did not make an identification.

across study sites and for all model runs except 1, we could not reject the null hypothesis of population closure (Table 3). It should be noted that there are no truly suitable tests for the assumption of closure (Rexstad and Burnham 1991), but the length of our survey was short relative to the life span of the animal, which is logically consistent with population closure. Number of pumas estimated did not vary significantly among investigators ($H = 1.6497$, $d.f. = 2$, $P > 0.05$), but did vary significantly (marginally) among sites ($H = 5.8531$, $d.f. = 2$, $0.06 > P > 0.05$).

Movement and densities of pumas.—Movement of pumas among camera stations varied significantly among sites regardless of investigator (2-way ANOVA; effect of site: $F = 43.5901$, $d.f. = 2, 4$, $P = 0.0019$; effect of investigator: $F =$

TABLE 3.—Numbers of pumas (*Puma concolor*) identified by different investigators across sites and resulting estimates of population size, effective survey area, and estimates of density.

Study site	No. individuals identified	No. captures + recaptures	Model selection[a] M(o)	Model selection[a] M(h)	Population size estimate M(h)	*SE*	Capture probability	Closure test *Z*-score	Closure test *P*-value	Closure test ½ MMDM (km)	Effective survey area (km^2)	Density (*SE*) per 100 km^2[b]
Bolivia												
Investigator 1	11	25	0.97	1	13	3.16	0.113	−0.003	0.499	2.04	105	12.38 (4.85)
Investigator 2	13	27	0.93	1	16	3.48	0.104	−0.7	0.242	1.7	93	17.58 (4.29)
Investigator 3	14	27	0.92	1	18[c]	3.03	0.095	−0.675	0.25	1.74	91	19.35 (6.24)
Argentina												
Investigator 1	6	22	1	0.88	8	2.01	0.172	−0.18	0.429	6.64	1,154	0.69 (0.33)
Investigator 2	6	26	1	0.82	6	0.88	0.271	−1.15	0.125	6.99	1,204	0.50 (0.33)
Investigator 3	8	28	1	0.89	10	2.01	0.175	−1.071	0.142	7.23	1,240	0.81 (0.45)
Belize												
Investigator 1	8	33	0.95	1	10	2.05	0.144	−2.378	0.087	5.83	426	2.35 (0.67)
Investigator 2	11	34	0.9	1	13	3.24	0.114	−1.507	0.066	5.89	431	3.01 (0.85)
Investigator 3	11	27	1	0.95	14	3.48	0.102	−1.773	0.038	4.07	285	4.91 (1.48)

[a] M(o) = the null model, constant capture probability; M(h) = the heterogeneity model, heterogeneous capture probabilities for each individual.
[b] For Bolivia, these densities estimates are before the correction factors for small area surveyed were applied.
[c] For this estimate only we used the more conservative M(o) model because of inconsistencies in the M(h) model over several model runs.

0.5367, *d.f.* = 2, 4, *P* = 0.6216; Table 3; Fig. 5). Post hoc comparisons for all pairs using the Tukey–Kramer honestly significant difference method indicated that movement by pumas (as measured by mean maximum distances among camera captures) was significantly different among sites. Pumas in Bolivia moved significantly shorter distances than pumas in Argentina and those for Belize were intermediate (mean ½ MMDM ± *SD*, *n* = 3; Bolivia: 1.827 ± 0.186 km; Belize: 5.263 ± 1.034 km; Argentina: 6.953 ± 0.297 km).

Densities of pumas per 100 km^2 determined by different investigators were similar within each site and ranged from 0.50 to 0.81 for Argentina, 2.35 to 4.91 for Belize, and 5.13 to 8.01 for Bolivia (after applying the least conservative [i.e., strongest impact of 3] correction factor of 0.414 to densities of pumas in Bolivia; Fig. 6). Densities varied significantly across sites but not among investigators (2-way ANOVA on log-transformed density estimates; effect of site: $F = 94.232$, *d.f.* = 2, 4, $P = 0.0004$; effect of investigator: $F = 3.679$, *d.f.* = 2, 4, $P = 0.124$). Post hoc comparisons for all pairs using the Tukey–Kramer honestly significant difference method (using the log-transformed density estimates in a 1-way ANOVA) indicated that Bolivia had significantly higher densities of pumas, at an average (± *SE*) of 6.80 ± 1.50 pumas/100 km^2 than either Argentina (0.67 ± 0.16 pumas/100 km^2) or Belize (3.42 ± 1.33 pumas/100 km^2) and the density estimates for Belize where statistically higher than those of Argentina. No single investigator had consistently higher or lower densities estimates than another across sites.

DISCUSSION

Estimates of abundance for pumas are rare, and yet they are extremely valuable for species conservation because they allow

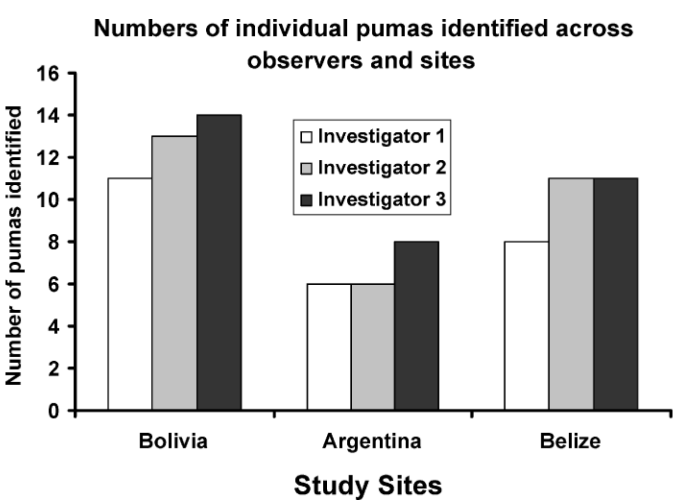

FIG. 4.—Numbers of pumas (*Puma concolor*) identified by investigators varied among study sites.

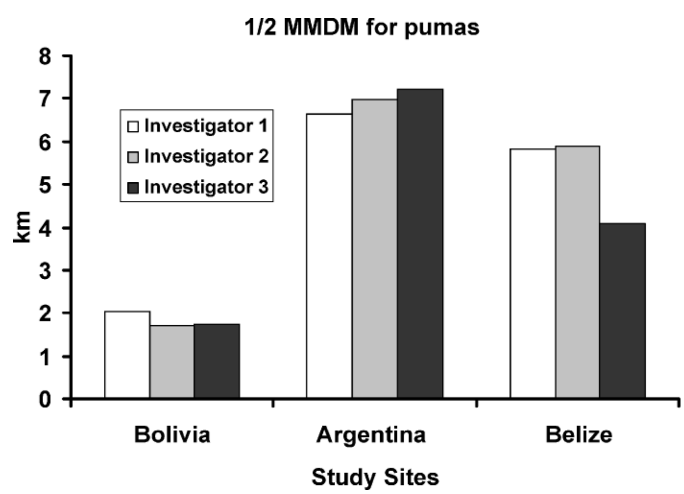

FIG. 5.—Movements of pumas (measured as half the mean maximum distance moved by individual pumas between camera stations) varied among study sites.

us to determine population trajectories or trends over time. Our study demonstrated that densities of pumas can be reliably estimated through remote camera surveys. Our results are similar to the findings of Jacobson et al. (1997), who reliably identified individual white-tailed deer (by antler shape and pattern) in remote camera surveys. Although there were some differences in the identifications of pumas made by different investigators, these differences did not translate into significant differences in density estimates within each site because standard errors overlapped between all investigators. Most pumas were identifiable, especially if both cameras captured images and full-body and tail photos were obtained from both sides. Pairwise disagreements were rare, at an average of only 7.8% and primarily occurred when partial photographs were obtained (i.e., animal was too close or moved too quickly past camera), when only 1 camera was triggered, or when photographed animals were too far away. In future studies these discrepancies can be reduced even further by careful placement and maintenance of cameras. For example, Belizean pumas were difficult to identify in this study because animals were often photographed from a distance of 8–10 m. This led to very few photographs of pumas being discarded (because they were whole-animal photos), yet there were more identification discrepancies for the Belizean site because of the difficulties in seeing subtle marks in photos taken at these distances. In Belize, cameras were placed along old logging roads, some of which were very wide. In the future, camera sites can be sought with passages that funnel animals closer to the cameras but not so close that partial photographs are obtained, which was often the case in Argentina. We suggest a distance of approximately 3 m to obtain high-quality photos, but this may depend on the camera trap model, because some models have longer delays after detection before firing and these should be placed at a farther distance ($\geq$3 m). In addition, zooming in, or blowing up, photographs to a larger size can facilitate identification.

Identifying pumas through photographs is tedious work requiring extreme attention to detail that only some investigators possess. Therefore, we suggest that within study sites, 2 or 3 investigators conduct blind identifications as in our study and compare results to check for disagreements. As a guide, our disagreement level was less than 10%, and our agreement level was nearly 80%, with another 10% falling into the gray area where 1 investigator did not assign an identification. One of the investigators in our study also had a tendency to split (versus lump) questionable identifications into new animals. Therefore, our results suggest that observer bias should be evaluated and monitored. Even so, observer bias in our study did not result in significant differences in abundance estimates. Simulating random identification of questionable animals is not necessarily appropriate because identifications may not be random. For example, a questionable animal that does not have a tail kink should not be randomly assigned to an animal that does. Therefore, differences in estimates resulting from lumping (assigning an identification based on the most likely possibility) and splitting (assigning the identification to a new animal) likely give the widest range of possibilities. We suggest other studies follow this model.

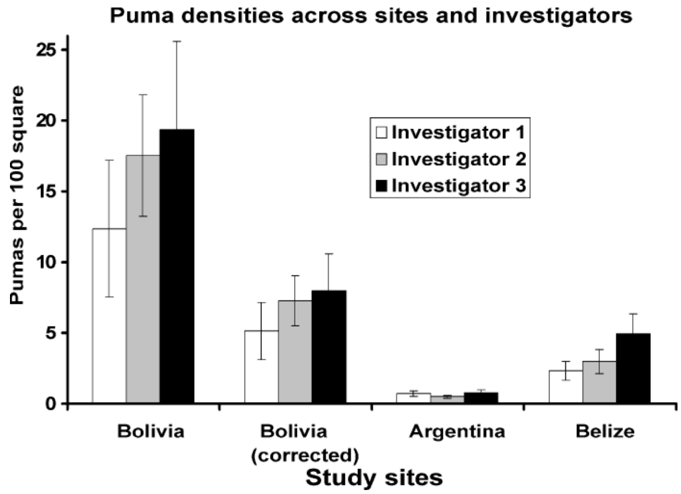

Fig. 6.—Density of pumas (*Puma concolor*) varied significantly among sites regardless of investigator. The corrected values for Bolivia are adjusted for the small area surveyed (see text for explanation of correction factor).

Despite the discrepancies in identification of pumas in our study, the dramatic difference in densities of pumas among the sites was clear. Bolivia had a much higher density of pumas than the other sites even after correction for the small area surveyed. The Bolivian site was the driest of the 3 and although pumas live in a wide variety of habitats, there is evidence suggesting that pumas can tolerate drier conditions (Noss et al. 2006) or that they avoid wetter areas used by sympatric jaguars (Emmons 1987; Schaller and Crawshaw 1980). There also is evidence that pumas favor dense understory for stalking cover (Logan and Irwin 1985; Seidensticker et al. 1973) and the tropical dry forest scrubland of the Chaco contains ample thick understory. However, the Yabotí Biosphere Reserve and the Chiquibul also have very dense understories and it may be that pumas can tolerate a more open canopy and an understory that may be thick, but with higher visibility through the thorny scrub, than is afforded in the typical ''jungle'' understory.

It is unclear why densities of pumas in Argentina are lower than those in Belize. Both sites consisted of similar dense, subtropical forests. It is likely that poaching and illegal timber extraction in Argentina have a strong impact on pumas in the area, lowering their numbers. Densities of ocelots and jaguars also are very low at the Yabotí Biosphere Reserve compared to other study sites in the Neotropics and even within Misiones Province (Di Bitetti et al., in press; A. Paviolo et al., in litt.), indicating that the area may be depauperate in many species.

For comparison, the lowest recorded density of pumas comes from an intensive survey and telemetry study conducted in southern Utah where numbers of pumas ranged from 0.3 to 0.5 pumas/100 km^2 (Hemker et al. 1984) and remained relatively constant at 0.37 pumas/100 km^2 for 9 years (Lindzey et al. 1994). In Idaho, the average minimum density was 0.77 pumas/100 km^2 and only went at high as 1.04 pumas/100 km^2 during 11 years of surveys (Laundré and Clark 2003). Anderson's (1983) summary of North American puma population studies revealed that the highest estimate was 4.9 individuals/100 km^2

as of the time of their review. Smallwood (1997) claimed that some studies have reported up to 13 pumas/100 km^2, but implied that these high densities may result from too small a survey area and were potentially unreliable.

Aside from the Chaco, the only other density estimates for pumas in South America are from Patagonia, Chile, and the Brazilian Pantanal. However, these estimates are primarily derived from radiotelemetry studies with small sample sizes rather than mark–recapture studies. Patagonia was similar to the Chaco with high densities of pumas at 7 pumas/100 km^2 (Iriarte et al. 1991) and possibly much higher ($\sim$30 pumas/100 km^2) in a peninsular area (Franklin et al. 1999). Crawshaw and Quigley (in litt.; cited in Nowell and Jackson 1996) estimated density at 4.4 pumas/100 km^2 for the Pantanal, similar to a preliminary estimate of 3 pumas/100 km^2 from camera trapping (Trolle et al. 2007). There are no estimates of density of pumas from forested environments in South America and no estimates from any habitat in Central America. Compared to North America, the puma remains relatively unstudied in the Neotropics, with only a handful of studies focusing primarily on food habits and diet (Aranda and Sanchez-Cordero 1996; Crawshaw and Quigley 2002; de Oliveira 2002; Emmons 1987; Iriarte et al. 1990; Novack et al. 2005; Taber et al. 1997; Yanez et al. 1986), spatial distribution and home range (Rabinowitz and Nottingham 1986; Schaller and Crawshaw 1980; Scognamillo et al. 2003), or both.

We provided the 1st density estimates of pumas for Central America and from a forested environment in South America. We advise that future studies follow Maffei and Noss (2008) and standardize distance between cameras as well as cover an area that encompasses at least 4 times the average home-range size of the study animals. In addition, across the survey area, spacing of cameras should seek to maximize capture probability, with 2 or more cameras per average home-range area. We also provided a protocol and recommendations for estimating puma densities reliably from remote cameras studies (Appendix I). Our study revealed that Bolivia had the highest densities of pumas, whereas Belize had intermediate densities similar to those from the Pantanal and the highest North American densities, and Argentina had low numbers of pumas most similar to those of the long-term studies in Idaho and Utah, the lowest densities recorded. Given that there are currently numerous studies in the Neotropics conducting camera trapping for jaguars, our technique could be used to estimate densities of pumas in many other locations across the geographic range of pumas. This would greatly expand our knowledge of the population status of pumas in the Neotropics and allow examination of how densities of pumas covary with those of jaguars across their ranges. These data are valuable for conservation, especially as habitat continues to shrink and become more fragmented, potentially heightening competition between these top predators.

Resumen

Las estimaciones de abundancia son muy valiosas para la conservación de especies, sin embargo, es difícil determinar la abundancia poblacional para carnívoros elusivos y con áreas de acción extensas. Estimamos la densidad poblacional de pumas utilizando cámaras remotas en Bolivia, Argentina, y Belice. Usamos marcas obvias y sutiles para identificar los individuos en las fotografías, y realizamos pruebas doble-ciegas de identificación para determinar la concordancia entre investigadores. El promedio de concordancia entre pares de investigadores fue de casi el 80%, y la concordancia entre 3 investigadores fue de 72.9%. La identificación de pumas como individuos diferentes fue poco común (7.8% entre pares, 0.69% desacuerdo entre 3), con los demás casos asignados a individuos no-identificables. Las densidades poblaciones de pumas variaron de manera consistente de un sitio a otro sin importar el investigador. Los pumas en Bolivia tuvieron las menores distancias de desplazamiento entre estaciones mientras que los pumas en Argentina las mayores distancias, pero las distancias entre estaciones y las áreas cubiertas por los muestreos no fueron consistentes entre sitios. Aplicamos un factor de corrección a los datos de Bolivia para tomar en cuenta la reducida área de muestreo y encontramos que, usando el promedio de los investigadores, Bolivia registró un número significativamente más alto de pumas cada 100 km^2 (promedio $\pm$ *DE*; 6.80 $\pm$ 1.5) que Belice (3.42 $\pm$ 1.3) o Argentina (0.67 $\pm$ 0.2). La densidad de pumas en Argentina es similar a la de sitios de Norteamérica con densidad baja, mientras que las densidades en Belice son consistentes con las densidades del Pantanal y de sitios de alta densidad en Norteamérica. Las densidades poblacionales de pumas se pueden estimar de manera confiable en estos sitios utilizando cámaras remotas, y nuestro trabajo presenta las primeras estimaciones de densidad para Centroamérica y para ambientes de bosque en Sudamérica.

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Appendix I

Protocol to identify individual pumas with camera-trap photography for density estimation.

In the field.—Deploying the camera traps in the field can be done in the same way as currently done to survey for jaguars, namely paired camera traps by the side of roads, trails, or where the animal is expected to walk through, installed 30–40 cm above the ground, and programmed to be active 24 h/day. If you also are targeting smaller animals such as ocelots, we suggest putting cameras at the lower height. Cameras should be set at a distance of 2–3 m from the spot where the animal is expected to pass. As with jaguars, camera traps should be set 2–3 km apart and we recommend that the polygon formed by all the cameras be at least 50 km^2. If home ranges for pumas in the study area are known, then the camera-trap survey should seek to encompass a minimum area 4 times greater than the average annual home range (Maffei and Noss 2008). If home-range data are not available, researchers should conduct a preliminary survey and adjust (usually increase) the sampled area if individual animals are recaptured at stations located at the opposite extremes of the sampled area or if the home range (minimum convex polygon) of an animal covers >30% of the sampled area. Cameras should be deployed in the field for no more than 3 months to fulfill the condition that the population be closed during the survey period.

In the laboratory.—

1. Photographs of pumas must be as clear as possible, printed in color on matte photographic paper at least 10 × 15 cm. In cases where the animal is relatively far from the camera, the laboratory should enlarge the animal itself rather than developing the entire negative. The laboratory also can adjust the contrast and brightness in order to clarify any markings that individual pumas may have.
2. Every photograph should be labeled with the location, date, and time information before starting to identify individuals. Multiple photos of the same individual by the same pair of cameras should be grouped 1st.
3. To identify individuals the animals that have clear and distinctive marks (a large recent scar on the body, an injured eye, a torn ear, a twisted or kinked tail, etc.) should be separated 1st. We have found the most useful characteristics to be the following:

   — Wounds or scars: in some cases fresh wounds are visible (on shoulders, flanks, face, or legs) that, over time, heal but often leave evident scars that serve to confirm the identity of the individual. Injured eyes also are detectable in camera-trap photographs. When using wounds or scars to identify animals it is important to take into account the chronological order of the photographs because the scars fade rapidly or may be absent in the 1st pictures of the animal.

   — Lingering juvenile spotting on the body: the sharp patterns of spots or blotches on cubs linger into adulthood in some cases, faded or more subtle, but constant within a 2- to 3-month survey period.

   — Tail kinks, end tuft, and white markings: pumas may present recognizable kinks in their tails, with the tip bent or curled markedly up or down; the size and coloration of the tail tuft also varies; and finally, the underside of the tail may be a uniform color or present white patches. When walking calmly, the overall shape and form of the tail remains consistent.

   — Sex can often be determined from the photographs, with the testicles of males especially apparent.

Additional subtle characteristics may help to sort the remaining photos, but are generally more difficult to detect, are more variable in camera-trap photographs, or both:

— Patterns of spotting: the inner forearms as well as hind limbs present variable patterns of dark markings on lighter fur; pumas also may present marks or color patterns on their necks.

— Ear nicks, tears, and markings: some animals present tears or notches in 1 or both ears, whereas the white markings on the back of the ears also vary across individuals.

— Overall coat color, body structure, and head shape: coat color may vary from light to dark (although color will be affected by natural or artificial lighting and by any adjustments made in the photo printing process), body structure from relatively heavy to thin (independent of whether the animal has recently eaten), and head shape and size relative to ear size.

Because identifying characteristics can be somewhat subjective, we recommend that at least 2 persons (with experience in camera trapping and examining photographs) independently and without communication with the other observer, classify all the photos and compare results. After this point it is useful to discuss any differences in order to reach a consensus. Each observer may detect different characteristics; therefore, working together helps to ensure that a larger number of identifying characteristics are considered. Practice also is required to train the eye to focus on the determining characteristics rather than less reliable markers. Finally, identification of pumas involves an ability to solve puzzles where the visibility of the marks may vary according to body position, camera angle, lighting conditions, and so on. The relatively small number of individuals present at each site also aids identification, because fewer distinguishing characteristics are required to distinguish few individuals. Multiple photos of the same animal under different conditions and from different angles also assist in confirming the identification of poor-quality photographs.

It is important to recognize that, in contrast to jaguars and ocelots, it is unlikely that photographs of pumas from camera-trapping efforts over long time periods or across different years can be classified. Several characteristics are not permanent: scars can heal definitively and disappear, spots in the inner part of the legs can fade with time, the shape of the body can change with seasonal condition or reproductive status, and so on. Within a survey, however, pumas are highly identifiable.

Quality of photos can be improved in the field by situating the cameras appropriately in relation to the location where the puma is likely to pass: at a distance of 2–3 m. If cameras are too close only partial body photos are acquired, the photos may be out of focus or washed out by the flash, or both. If cameras are too far away the animals are small relative to the negative frame, and the flash may not illuminate the animal sufficiently. Position cameras perpendicular to the point where the animal is expected to pass (identification is more difficult in photos where the animal is angled toward or away from the camera). Choose sites that provide a natural funnel or create a funnel with downed vegetation or debris that directs the animal into a position in front of the camera. Quality of photos also can be improved in the laboratory during the printing process, as described above.

Identifications also can be improved if photos are acquired of both sides of the animal as it passes, that is, if each of the paired cameras functions properly. Thus, a larger set of characteristics visible on each side of any new animal can be compared with those from previously identified individuals. The tail is particularly useful as an identifying characteristic because kinks and the size and shape of the end tuft look similar from either side of the animal, thus it can help in cases when only a single photo is acquired. This makes it especially important to check cameras frequently for proper function in the field. We recommend checking cameras every 10 days, if possible.

For conservation purposes, conservative estimates of abundance are preferable, therefore we recommend "lumping" rather than "splitting" in cases when photos are difficult to assign. Poor-quality photos can be discarded from the analysis outright, but if they are included then they should be assigned tentatively to already-identified individuals as possible recaptures rather than proposed as new individuals. Increasing the number of individuals identified will increase the estimate of population density, whereas increasing the number of recaptures of a smaller set of individuals will often not significantly affect the abundance estimated. Generally the majority of photos will be relatively easy to assign to a small number of individuals, but a small number of photos will be difficult to assign. Additional photos should be checked 1 by 1 against all the previously identified individuals, and only classified as a new individual if 2 or more key characteristics differ.