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Comparing capture–recapture, mark–resight, and spatial mark–resight models for estimating puma densities via camera traps

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Camera-trapping surveys, in combination with traditional capture–recapture or spatially explicit capture–recapture techniques, have become popular for estimating the density of individually identifiable carnivores. When only a portion of the population is uniquely identifiable, traditional and spatial mark–resight models provide a viable alternative. We reanalyzed a data set that used photographic capture–recapture methods to estimate the densities of pumas (*Puma concolor*) across 3 study sites in Belize, Argentina, and Bolivia using newer, more-advanced modeling including spatial and nonspatial mark–resight techniques. Additionally, we assessed how photo identification influenced density estimates by comparing estimates based on capture histories constructed by 3 independent investigators. We estimated the abundances of pumas using mark–resight models in program MARK and then estimated densities ad hoc. We also estimated densities directly using spatial mark–resight models implemented in a Bayesian framework. Puma densities did not vary substantially among observers but estimates generated from the 3 statistical techniques did differ. Density estimates (pumas/100 km^2) from spatial mark–resight models were lower (0.22–7.92) and had increased precision compared to those from nonspatial capture–recapture (0.50–19.35) and mark–resight techniques (0.54–14.70). Our study is the 1st to estimate the density of a population of carnivores, where only a subset of the individuals are naturally marked, using camera-trapping surveys in combination with spatial mark–resight models. The development of spatial mark–resight and spatially explicit capture–recapture techniques creates the potential for using a single camera-trapping array to estimate the density of multiple, sympatric carnivores, including both partially marked and uniquely marked species.

Key words: camera trapping, capture–recapture, density, Neotropics, *Puma concolor*, spatial mark–resight

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Effective conservation depends on accurate knowledge of the distributions and densities of wildlife populations. Camera-trapping surveys, in combination with traditional capture–recapture techniques (Otis et al. 1978; Williams et al. 2002), have been used around the world to estimate the abundance and density of individually identifiable carnivores, including jaguars (*Panthera onca*—Kelly 2003; Maffei et al. 2004; Silver et al. 2004) and tigers (*Panthera tigris*—Karanth and Nichols 1998; Kawanishi and Sunquist 2004). Capture–recapture methods are considered a robust way to estimate demographic parameters of wildlife populations and camera-trapping surveys have become an increasingly common, noninvasive method for sampling wildlife over large areas. Density is generally the parameter of interest because it is needed to compare estimates across space, particularly when comparing sites that have different survey areas. Several limitations, however, constrain traditional photographic capture–recapture techniques. The 1st is that in order to estimate density, we need to know the area from which animals are sampled, which is generally unknown (Royle et al. 2009; O'Brien and Kinnaird 2011). Density is therefore estimated ad hoc, typically by adding a buffer area around the trap array (Wilson and Anderson 1985; Karanth and Nichols 1998; Parmenter et al. 2003). Methods to define the width of that buffer vary; thus, the precise definition of the effective trapping area is generally uncertain (Borchers and Efford 2008; O'Brien and Kinnaird 2011) and density estimates are somewhat arbitrary. A 2nd limitation is that the spatial component of camera-trapping data is not directly incorporated into traditional capture–recapture analyses (Gopalaswamy et al. 2012). The location of camera traps is important because an individual's probability of being photographed depends on the overlap of its home range with the trap array (Efford 2004; Royle et al. 2009). A final limitation of photographic capture–recapture techniques is that the species must be identifiable to the individual level using natural markings, thus restricting sampling to species with unique pelage patterns.

Spatially explicit capture–recapture (SECR) models (Efford 2004; Borchers and Efford 2008; Royle et al. 2009) were developed to address several of the limitations of traditional capture–recapture techniques. In SECR modeling, a hierarchical model is implemented to estimate animal density directly. The probability of being photographed is modeled as a function of the distance between camera-trap locations and an animal's activity center, and density is estimated using a point process model (Efford 2004; Royle et al. 2009). The location of activity centers is unknown, but the spatial coordinates of the traps where individual animals were photographed provide some information about this location (Borchers and Efford 2008; Royle et al. 2009). In practical terms, SECR methods also may be advantageous over nonspatial methods because their performance depends less on the spatial setup of the camera stations (Noss et al. 2012; Sollmann et al. 2012). Thus, with SECR modeling, a standardized trapping design can be used to estimate the density of a single species or multiple, sympatric species (O'Brien and Kinnaird 2011). SECR models, however, still require that all photographed animals be uniquely identifiable.

Mark–resight models (Arnason et al. 1991;White and Shenk 2001; McClintock et al. 2009), on the other hand, provide a viable alternative to spatial and nonspatial capture–recapture techniques when only a subset of the animals is uniquely identifiable either by artificial tagging (e.g., radiocollar or ear tag) or subtle, natural marks (e.g., scars or color patterns on legs). Photographic mark–resight techniques estimate abundance by incorporating photographs of marked (i.e., uniquely identifiable individuals), unmarked (i.e., individuals only identifiable to the species level), and marked but not identifiable individuals (McClintock et al. 2009; McClintock 2012). The last classification occurs when an investigator determines that a photo is of a marked individual but cannot unambiguously identify the individual; this may occur, for example, if a photo only includes part of an animal. Mark–resight techniques assume the subset of marked individuals is representative of the entire population in terms of sighting probabilities (McClintock et al. 2009; McClintock 2012). Mark–resight models also share several of the limitations of traditional capture–recapture techniques, however, including ad hoc estimation of density and not directly incorporating the spatial component of the camera-trapping data.

Spatial mark–resight (SMR) models were recently developed (Chandler and Royle 2013; Sollmann et al. 2013a, 2013b) to address these limitations. SMR techniques are an SECR framework for populations where only some of the individuals can be identified. The main difference between SMR and SECR models is that SMR encounter histories are partially latent because only part of the population is uniquely identifiable (Sollmann et al. 2013a, 2013b).

Spatial mark–resight models, in combination with camera-trapping surveys, offer a promising tool for estimating densities of pumas (*Puma concolor*), an elusive carnivore with uniform, light coloration. Generally, when using photographic records, only a portion of a puma population is unambiguously identifiable to the individual level via scars, ear nicks, and distinctive undercoat marks, thus restricting the use of spatial and nonspatial capture–recapture techniques. Additionally, similar to many large carnivores, pumas generally live at low densities, are nocturnal, and are difficult to observe (Schonewald-Cox et al. 1991; Gros et al. 1996; Mills 1996; Silver et al. 2004; Sollmann et al. 2013b). These characteristics make pumas extremely difficult to physically capture and restrict the use of artificial tagging due to time, budget, and logistical constraints (Potvin et al. 2005). Use of camera traps and the use of natural markings are a time- and cost-effective alternative (Sollmann et al. 2012) because camera traps generally have high detection rates (O'Connell et al. 2006). The challenges associated with monitoring pumas have resulted in their population status remaining relatively unknown throughout most of their range south of the United States (Sunquist and Sunquist 2002). They are perceived, however, to be decreasing in numbers throughout most of their range due to prey loss, habitat loss, and habitat fragmentation (Kelly et al. 2008). A standardized method for estimating puma distributions and densities is needed to monitor these perceived population declines and, if necessary, to enact effective conservation measures.

The overall goal of our study was to reanalyze a data set that used traditional capture–recapture methods to estimate the densities of pumas across 3 study sites in Belize, Argentina, and Bolivia (Kelly et al. 2008), using newer, more advanced modeling including mark–resight and recently developed SMR techniques. Our 3 main objectives were to estimate the abundances and densities of pumas using nonspatial mark–resight models; estimate the densities of pumas using SMR models; and compare density and standard error estimates from capture–recapture (see Kelly et al. 2008), mark–resight, and SMR modeling techniques. A complementary objective was to assess how photo identification influenced density estimates by comparing estimates based on capture histories constructed by 3 independent investigators using the same data sets.

Materials and Methods

Study areas.—We conducted camera-trapping surveys in Belize, Argentina, and Bolivia (see Kelly et al. 2008 for details). In Belize, we deployed camera-trap stations in the Chiquibul Forest Reserve and National Park (1,744 km^2; 16°44′N, 88°59′W), which was the largest managed forest reserve in Belize. The vegetation included broadleaf rain forest, deciduous semievergreen and seasonal forest, and stands of pine in the north. In Argentina, we deployed camera-trap stations in the Yabotí Biosphere Reserve (2,742 km^2; 26°55′S, 54°00′W) in the southeastern portion of the Green Corridor of Misiones Province. The area had a humid subtropical climate and most forests had been logged, thus promoting the invasion of 2 species of bamboo. Lastly, in Bolivia, we deployed camera-trap stations in the Kaa-Iya del Gran Chaco National Park (34,400 km^2; 18°25′S, 61°46′W) located in the northern end of the Gran Chaco. This area included the largest remaining area of Chaco dry forest and the thick underbrush was dominated by bromeliads and cacti.

Camera-trapping surveys and photo classification.—We deployed 17, 42, and 22 camera stations in Belize, Argentina, and Bolivia, respectively, at regular intervals of 2–3 km in a grid across the respective landscapes. At each station, we placed 2 cameras opposite of each other on both sides of the road or trail. We programmed cameras to operate 24 h/day with a camera delay of 30 s to 5 min. The primary sampling intervals lasted from 4 January to 9 April 2003 in Belize, 27 August to 30 November 2005 in Argentina, and 28 October to 24 December 2005 in Bolivia (see Kelly et al. 2008 for details).

We selected 3 investigators and had each investigator classify photographs of pumas from the 3 study sites, unaware of how the others had identified and categorized the photographs. Investigators identified individual pumas by obvious and subtle markings (e.g., kinked tails, scars, ear nicks, tail-tip coloration and shape, or undercoat spot patterns). Each investigator labeled photographs of pumas with either the individual's identification, as marked but not unambiguously identifiable, or unmarked.

Abundances and densities of pumas: capture–recapture models.—Kelly et al. (2008) created capture histories for each investigator at each study site (i.e., 9 capture histories total) and used program CAPTURE (Otis et al. 1978; Rexstad and Burnham 1991) to estimate abundances of pumas across study sites and by different investigators. To determine the size of the areas surveyed, Kelly et al. (2008) buffered each camera-trap location with half of the mean maximum distance moved (½ MMDM—Wilson and Anderson 1985). Kelly et al. (2008) then estimated the densities of pumas by dividing abundance estimates by survey area estimates; standard errors were estimated using the delta method described in Nichols and Karanth (2002).

Abundances and densities of pumas: mark–resight models.—We constructed encounter histories of individual pumas for each of the investigators and each study site (i.e., 9 capture histories in total). When implementing photographic mark–resight models in program MARK (McClintock 2012), encounter histories contained the count of the total number of times an individual was resighted during the primary sampling interval (i.e., primary sampling interval is not divided into multiple sampling occasions). If an individual puma was photographed 6 times during the primary sampling interval, for example, its encounter history was 06. The encounter histories also included an overall count of the number of photographs where pumas were classified as unmarked or as marked but not identifiable. Counts of unmarked individuals are used to inform detection parameters and the proportion of marked but not identifiable photos per known individual is used as a correction factor for the encounter rates of marked individuals. Lastly, we identified the number of marked pumas as unknown. We also constructed a capture history for each study site by combining identifications made by all of the investigators. We labeled a photograph with the individual's identification if all investigators agreed upon the identification. We labeled an individual as marked but not unambiguously identifiable if all investigators identified the photo as a marked individual but did not agree on the individual identification, and finally we labeled an individual as unmarked if ≥ 1 investigator identified the photo as unmarked.

We used the zero-truncated Poisson–log-normal mark–resight model in program MARK because marked individuals could not have all-zero encounter histories (i.e., had to be photographed ≥ 1 time to be known—McClintock et al. 2009; McClintock 2012). Because we only had 1 primary sampling interval, we used the closed resighting model, which included 3 parameters: intercept for mean resighting rate (α), individual heterogeneity (σ), and number of unmarked individuals in the population (U). For each of the countries, and for each investigator separately and combined, we ran 1 model where the parameters were constant and 1 model with $\sigma = 0$ to test for individual heterogeneity. We evaluated the candidate models using Akaike's information criterion corrected for small sample size (AIC_c—Burnham and Anderson 2002) and used the top-ranked model to derive an estimate of total population size (N) and overall mean resighting rate (λ).

We estimated the size of the surveyed area in each country using capture histories created by the investigators separately and combined; we only used data from individually identifiable pumas that were detected at ≥ 2 camera stations. We used ½ MMDM as a buffer radius around each camera-trap location (Wilson and Anderson 1985). We dissolved ½ MMDM buffers and calculated total surveyed area (km^2) in ArcGIS version 10.0 (Environmental Systems Research Institute, Inc. 2012).

We used ½ MMDM as the buffer radius so that our estimates would be comparable to those of Kelly et al. (2008). We divided estimates of the number of pumas by the corresponding estimate of the total survey area to obtain country- and investigator-specific estimates of puma density. Analogous to capture–recapture techniques, we calculated standard errors for the density estimates following the delta method.

Densities of pumas: SMR models.—We collapsed daily camera-trapping data into blocks such that 1 encounter occasion consisted of a 5-day sampling period. We collapsed the data in this manner because photographic detections of pumas were sparse and we wanted to avoid estimated detection rates close to 0, because this can sometimes lead to estimation problems. We then created capture histories for each investigator separately and combined at each study site (i.e., 12 capture histories in total). For photographs of individually identifiable pumas, capture histories included the individual identification, camera-trap station identification, and encounter occasion. For photographs of unmarked pumas, capture histories included an accumulated count of the number of times unmarked pumas were photographed at each camera-trap station during each encounter occasion. For photographs of marked but unidentifiable pumas, capture histories included a total count (across stations and encounter occasions). We also created an input file with the Universal Transverse Mercator coordinates of each camera-trap station as well as data on the number of days each camera-trap station was active during each encounter occasion (i.e., accounting for malfunctions or cameras set up and taken down on different days).

We implemented SMR models using the software R version 2.15.1 (R Development Core Team 2012). Similar to SECR models, we assumed each individual i had an activity center, s_i, and that all of the activity centers were distributed uniformly across the state space S (Royle et al. 2009). The state space is an area large enough to include the activity centers of all animals potentially exposed to trapping. To define S, we used a 27-km buffer in Belize, a 27-km buffer in Argentina, and a 10-km buffer in Bolivia from the outermost coordinates of the trapping grids. This resulted in an area for S of 5,002, 7,029, and 957 km^2 in Belize, Argentina, and Bolivia, respectively. We used a smaller buffer in Bolivia because puma movement in Bolivia was more restricted, which was likely an artifact of the camera-trapping grid being much smaller in Bolivia (51 km^2) than the grids in Belize (110 km^2) and Argentina (549 km^2—Kelly et al. 2008).

For the marked pumas, we assumed they were a random sample from the population of pumas in the state space. This assumption is problematic when relying on artificial marks, but should be valid when using natural marks, as in the present study (Sollmann et al. 2013b; Royle et al. 2014). We further assumed that the number of photographs of puma i at camera station j during encounter occasion k, y_{ijk}, was a Poisson random variable with mean encounter rate λ_{ijk}. We modeled the mean encounter rate using a half-normal decreasing function of the distance from trap j to the individual's activity center, dependent on λ_0 (i.e., encounter rate for a hypothetical camera trap located on s_i) and τ (i.e., scale parameter of this half-normal function, which is related to animal movement—Royle et al. 2009). The scale parameter is generally represented by σ; we changed the symbol to τ to avoid confusion with the traditional mark–resight models where σ represents individual heterogeneity. We assumed that λ_0 and τ were constant across encounter occasions.

For photographs of marked but unidentifiable pumas (e.g., photo only included the front half of a puma), we assumed that the inability to identify marked individuals occurred at random throughout the population and space (Sollmann et al. 2013a). To incorporate these photos, we estimated the probability of correctly identifying a photo of a marked puma. We assumed the sum of all correctly identified photos of marked individuals was a binomial random variable with sample size equal to the total number of records of marked individuals, and probability c (Sollmann et al. 2013a). For marked pumas, we then multiplied λ_0 by c to account for the fact that we observed incomplete individual encounter histories (Sollmann et al. 2013a).

We estimated the number of marked and unmarked pumas using data augmentation (Royle and Dorazio 2012). For the unmarked pumas, encounter histories are latent (all we observed were accumulated counts of unmarked individuals) and thus, essentially, missing data (Sollmann et al. 2013a). Following Sollmann et al. (2013a), we adopted a Bayesian framework and used Metropolis-within-Gibbs Markov chain Monte Carlo sampling to update missing data using their full conditional distribution. For each investigator separately and combined, and for each study site, we ran 3 chains of the Metropolis-within-Gibbs sampler with 200,000 iterations each, discarding 10,000 iterations as burn-in. We checked for chain convergence by calculating the Gelman–Rubin statistic R-hat (Gelman et al. 2004) using the R package coda (Plummer et al. 2006); values < 1.1 indicated chain convergence. We report results as posterior mean with standard error (defined as the standard deviation of the posterior distribution of a parameter) and 2.5 and 97.5 percentiles, which represent the Bayesian equivalent to a confidence interval. For density estimates we report the mode over the mean because simulations have shown the mode to be less biased than the mean with low sample sizes (Chandler and Royle 2013; Sollmann et al. 2013b).

Comparing density estimates among investigators and modeling techniques.—When comparing density estimates among investigators and among modeling techniques, we considered estimates to be different if the 95% confidence intervals (95% *CI*s) did not overlap.

Results

Camera-trapping surveys and photo classification.—The durations of the camera-trapping surveys were 95 days in Belize, 96 days in Argentina, and 56 days in Bolivia. We photographed pumas 48, 65, and 35 times, which translated to 3.00, 2.41, and 2.84 photographs of pumas per 100 trap nights in Belize, Argentina, and Bolivia, respectively (Kelly et al. 2008).

The majority of photographs of pumas were labeled with an individual identification (Table 1). When classifications among the 3 investigators were combined, the number of photographs labeled with an individual identification decreased and the number of photographs labeled as marked but not identifiable or unmarked increased (Table 1). Investigator 3 was generally the most conservative (i.e., classifying more photos as marked but not identifiable or unmarked) and investigator 2 was generally the least conservative (Table 1).

Abundances and densities of pumas: capture–recapture models.—Estimates of puma abundance from capture–recapture models ranged from 6 to 18 and density of pumas per 100 km^2 ranged from 0.5 to 19 (Fig. 1; Kelly et al. 2008).

Abundances and densities of pumas: mark–resight models.—Models that allowed for individual heterogeneity had the most support (i.e., lower AIC_c values) when using capture histories constructed by each investigator separately (Table 2). Conversely, when using the combined capture histories, models without individual heterogeneity had the most support (Table 2). We used the top-ranked models to estimate abundance and density for each study population. Estimates of abundance were greatest in Bolivia and smallest in Argentina (Table 2). In each case, values estimated by the mark–resight models were lower than those estimated using capture–recapture models.

Half of the mean maximum distance moved among cameras by individual pumas, calculated using capture histories constructed by each investigator separately and combined, were considerably higher in Belize and Argentina (5–9 km) as compared to Bolivia (2 km [Table 3]). In turn, densities of pumas per 100 km^2 were several times lower (0.5–2.0) in Belize and Argentina, versus in Bolivia (Table 3).

Densities of pumas: SMR models.—Capture histories created for SMR models had 19, 19, and 12 five-day encounter occasions in Belize, Argentina, and Bolivia, respectively. Estimates of density were again much lower in Belize and Argentina (0.2–1 pumas/100 km^2) than in Bolivia (3–8 pumas/100 km^2 [Table 4]). Estimates of baseline encounter rates (λ_0) were higher in Belize and Argentina than it was in Bolivia, and a photo of a marked puma was more likely to be identified (c) in Argentina and Bolivia than in Belize (Table 4). The posterior mean for τ (i.e., scale parameter) was higher in Belize and Argentina than it was in Bolivia (Table 4). All parallel Markov chains appeared to converge (Gelman–Rubin statistic R-hat for all parameters < 1.1).

Comparing density estimates among investigators and modeling techniques.—Density estimates among the investigators were similar (i.e., overlapping 95% *CI*s [Fig. 1]). Density estimates from capture–recapture models were generally the highest and density estimates from SMR models were generally the lowest (Fig. 1). However, when comparing 95% *CI*s we found no support that estimates generated from the 3 types of models were different (i.e., overlapping 95% *CI*s) with the exception of Belize, where estimates from investigators 1 and 2 were lower when generated from SMR models (Fig. 1). The 95% *CI*s were generally the largest when using capture–recapture models and the smallest when using SMR models (Fig. 1).

Table 1.—The number of pumas (*Puma concolor*) identified to the individual level (n*) and the total numbers of puma photographs that were labeled as individually identifiable, marked but not unambiguously identifiable, and unmarked. Classifications were made by 3 independent investigators, separately and combined.

	n*	Individually identifiable	Marked but not identifiable	Unmarked
Belize				
Investigator 1	8	42	6	0
Investigator 2	11	42	4	2
Investigator 3	11	40	1	7
Combined	6	27	13	8
Argentina				
Investigator 1	6	53	2	10
Investigator 2	6	60	0	5
Investigator 3	7	58	2	5
Combined	5	47	8	10
Bolivia				
Investigator 1	11	32	0	2
Investigator 2	13	33	1	0
Investigator 3	14	32	0	2
Combined	11	30	2	2

Discussion

Estimating the densities of large carnivores is challenging because they are generally wide ranging, elusive, and occur at low densities. The task is particularly challenging with species that have uniform coloration (e.g., pumas) because individuals often cannot be identified by distinct pelage patterns, thus limiting the use of photographic capture–recapture (Otis et al. 1978; Karanth and Nichols 1998) and recently developed SECR techniques (Borchers and Efford 2008; Royle et al. 2009). We reanalyzed a camera-trapping data set that used traditional capture–recapture methods to estimate the densities of pumas across 3 study sites in Belize, Argentina, and Bolivia (Kelly et al. 2008), using mark–resight and SMR techniques. We showed that standardized camera trapping, in combination with SMR techniques, is a feasible method for obtaining robust demographic estimates for pumas across their geographic range.

Density estimates from SMR models were lower than those from nonspatial (i.e., capture–recapture and mark–resight) techniques. Similar results have been found when comparing SECR models to nonspatial models, suggesting that statistical techniques relying on ad hoc estimation of density (i.e., using estimates of ½ MMDM to estimate survey areas) may result in overestimates (Gerber et al. 2012; Noss et al. 2012; Blanc et al. 2013), likely because they do not fully account for animal movement off the sampling grid. We also found that precision improved when employing mark–resight models, spatial or

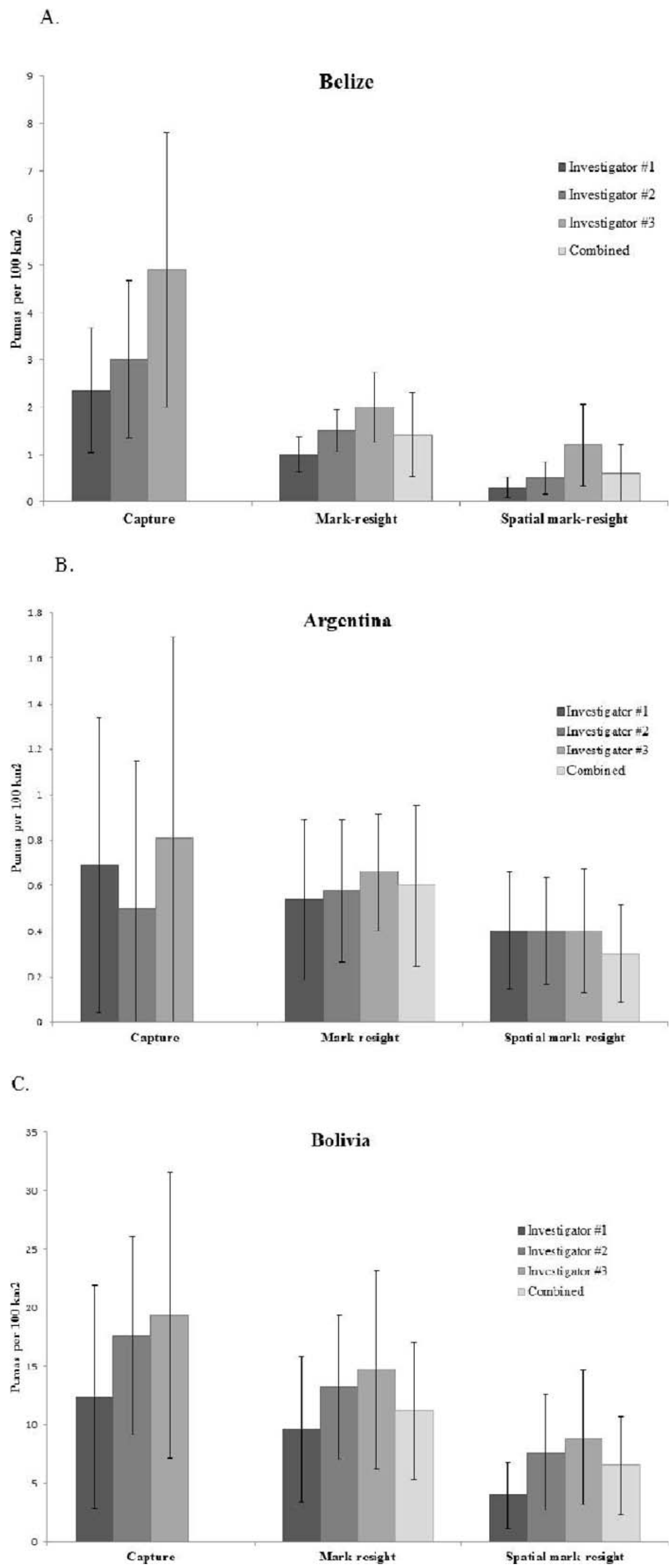

FIG. 1.—Estimated density of pumas (*Puma concolor*), and the associated 95% confidence intervals, generated from camera-trapping surveys in A) Belize, B) Argentina, and C) Bolivia. Estimates were generated from capture histories constructed by 3 independent investigators from the same data sets, and for mark–resight models from the 3 investigators combined.

nonspatial, likely because these models used data from marked, unmarked, and marked but not identifiable pumas, whereas the capture–recapture models only used data from the individually identifiable pumas. Discarding photographs from marked but unidentifiable and unmarked pumas resulted in a substantial loss of data (Table 1), particularly because data sets were sparse to begin with. Similarly, simulations showed that in a SMR framework, parameter estimates based on marked and unmarked individuals were less biased and more precise than parameter estimates based on marked individuals only (Royle et al. 2014).

Estimates of puma density from SMR techniques were the lowest; however, estimates among the 3 statistical techniques were generally comparable (i.e., overlapping 95% *CI*s). This was the result of all density estimates having relatively large standard errors. Standard error estimates were likely large because of our limited data sets, which included a small number of naturally marked pumas, a limited amount of resighting data, and in 1 case a small camera-trapping array. In Bolivia, for example, we had an average of 2.6 resighting events per puma and the minimum convex polygon around the camera traps was 51 km^2 (Kelly et al. 2008). Camera stations that are spaced too widely can result in few spatial recaptures and cause SMR (or SECR) models to perform poorly (Sollmann et al. 2012; Chandler and Royle 2013). Because cameras were spaced on average 2.5 km apart, which was less than or approximately equal to our estimate of τ, we attributed our limited number of resighting events to pumas being rare and elusive, which is also reflected in low estimates of baseline encounter probability (spatial models) and detection probability (nonspatial models). Regardless of statistical technique, results followed the same trends with highest density estimates for Bolivia, intermediate for Belize, and lowest for Argentina.

Spatial mark–resight models address many of the limitations of traditional capture–recapture and mark–resight models but they still include 2 potentially problematic assumptions: marked individuals are a random sample from the study population, both demographically and spatially; and if marked individuals are not always identified to the individual level, failure to identify marked individuals occurs at random in space and time and throughout the population (White and Shenk 2001; McClintock et al. 2009; Sollmann et al. 2013a). The 1st assumption may have been violated if, for some reason, our naturally marked pumas had a higher probability of being photographed. This may have occurred, for example, if males, on average, were more likely to be marked than females (e.g., via scars) and were more active than females, thus increasing their probability of being photographed. This could be addressed explicitly within the model if animals could be sexed. It also is possible that we violated the 2nd assumption because some of the pumas had more obvious, easy to identify natural markings than others. In the future, it may be possible to directly address this potential bias in the model by allowing different markings (i.e., subtly versus obviously marked pumas) to have different identification rates. Similarly, if habitat conditions at the camera stations influenced puma

TABLE 2.—Candidate models to estimate the abundance (N) and overall mean resighting rate (λ) of pumas (*Puma concolor*) sampled in Belize, Argentina, and Bolivia. Abundance was estimated using photographic mark–resight analysis (program MARK) and capture histories constructed by 3 investigators. AIC_c = Akaike's information criterion with small sample size; ΔAIC_c = differences in AIC_c; Log(l) = maximized log-likelihood; K = number of estimable parameters; ω_i = Akaike weights; $n*$ = total number of marked pumas resighted.

	Model definition[a]	AIC_c	ΔAIC_c	Log(l)	K	ω_i	$n*$	N (SE)	λ (SE)
Belize									
Investigator 1	$\alpha(.)\sigma(.)U(.)$	45.97	0.00	39.97	2	1.00	8	8.1 (0.05)	5.9 (1.11)
	$\alpha(.)\sigma(0)U(.)$	61.52	15.55	58.94	1	0.00		8.0 (0.04)	6.0 (0.82)
Investigator 2	$\alpha(.)\sigma(.)U(.)$	58.29	0.00	49.29	3	1.00	11	12.6 (1.36)	2.5 (0.86)
	$\alpha(.)\sigma(0)U(.)$	80.52	22.23	75.19	2	0.00		11.6 (0.33)	4.1 (0.61)
Investigator 3	$\alpha(.)\sigma(.)U(.)$	60.48	0.00	51.48	3	1.00	11	12.2 (1.32)	3.6 (1.02)
	$\alpha(.)\sigma(0)U(.)$	69.45	8.97	64.12	2	0.00		13.1 (0.84)	3.6 (0.59)
Combined	$\alpha(.)\sigma(0)U(.)$	46.75	0.00	39.75	2	0.56	6	7.2 (0.46)	7.7 (0.90)
	$\alpha(.)\sigma(.)U(.)$	47.27	0.51	33.27	3	0.44		7.1 (0.88)	6.4 (1.59)
Argentina									
Investigator 1	$\alpha(.)\sigma(.)U(.)$	56.90	0.00	42.90	3	1.00	6	6.6 (0.66)	8.2 (1.69)
	$\alpha(.)\sigma(0)U(.)$	68.14	11.24	61.14	2	0.00		7.0 (0.36)	9.2 (1.21)
Investigator 2	$\alpha(.)\sigma(.)U(.)$	56.03	0.00	42.03	3	0.94	6	6.3 (0.27)	9.8 (2.16)
	$\alpha(.)\sigma(0)U(.)$	61.32	5.29	54.32	2	0.06		6.5 (0.21)	10.0 (1.29)
Investigator 3	$\alpha(.)\sigma(.)U(.)$	57.28	0.00	45.28	3	0.96	7	7.3 (0.34)	8.9 (2.06)
	$\alpha(.)\sigma(0)U(.)$	63.85	6.57	57.45	2	0.04		7.5 (0.25)	8.6 (1.09)
Combined	$\alpha(.)\sigma(0)U(.)$	52.70	0.00	44.70	2	0.62	5	5.9 (0.29)	11.0 (1.36)
	$\alpha(.)\sigma(.)U(.)$	53.71	1.01	35.71	3	0.38		5.7 (0.52)	10.8 (2.30)
Bolivia									
Investigator 1	$\alpha(.)\sigma(.)U(.)$	53.57	0.00	44.57	3	0.79	11	12.3 (1.26)	2.7 (0.92)
	$\alpha(.)\sigma(0)U(.)$	56.25	2.68	50.92	2	0.21		12.7 (0.82)	2.7 (0.53)
Investigator 2	$\alpha(.)\sigma(.)U(.)$	54.27	0.00	45.87	3	0.59	13	14.8 (1.46)	2.2 (0.73)
	$\alpha(.)\sigma(0)U(.)$	54.97	0.70	49.88	2	0.41		14.7 (0.84)	2.4 (0.46)
Investigator 3	$\alpha(.)\sigma(.)U(.)$	54.37	0.00	46.19	3	0.78	14	16.9 (2.35)	1.9 (0.69)
	$\alpha(.)\sigma(0)U(.)$	56.85	2.47	51.85	2	0.22		17.0 (1.37)	2.0 (0.43)
Combined	$\alpha(.)\sigma(0)U(.)$	51.54	0.00	46.20	2	0.57	11	12.9 (0.91)	2.7 (0.53)
	$\alpha(.)\sigma(.)U(.)$	52.13	0.59	43.13	3	0.43		12.8 (1.49)	2.5 (0.81)

[a] α = mean resighting rate; σ = individual heterogeneity level; U = number of unmarked individuals; (.) = parameter constant; (0) = parameter set to 0.

identification then c could be modeled as a function of habitat covariates (Sollmann et al. 2013b).

Mark–resight models also assume there is no loss or misidentification of marks (McClintock et al. 2009). Estimates of puma density were, to some degree, dependent on the investigator who classified the photos, which suggests that this assumption was possibly violated. In our study, pumas were identified to the individual level using obvious (e.g., scar or ear nick) and subtle (e.g., undercoat spot pattern or body shape and carriage) natural marks; thus, correctly identifying pumas required extreme attention to detail. An investigator seeking to be cautious would have been more inclined to classify a photo as unmarked or marked but not identifiable. Alternatively, an investigator who was extremely confident in his or her ability to distinguish individuals may not have classified any photos as unmarked. Both of these alternatives could bias model results. When using traditional mark–resight models, the classification of photos has a 2-fold impact on estimates of density, influencing both the estimates of abundance and effective survey area (i.e., ½ MMDM). Differences among investigator classifications for the Belize data set, for example, resulted in estimates of abundance varying by 3 pumas (8 versus 11, an 38% increase) and estimates of the survey area by 231 km^2 (611 versus 842, a 38% increase). When using SMR models, the classification of photos influences the inferred locations of

TABLE 3.—Estimated density of pumas (*Puma concolor*) in Belize, Argentina, and Bolivia from 3 independent investigators. Density was estimated post hoc using abundance estimates from a photographic mark–resight (program MARK) analysis, and effective survey areas were estimated using half the mean maximum distance moved (½ MMDM).

	½ MMDM (km)	Effective survey area (km^2)	Density (SE) per 100 km^2
Belize			
Investigator 1	8.70	808	1.00 (0.19)
Investigator 2	8.99	842	1.50 (0.23)
Investigator 3	6.92	611	2.00 (0.38)
Combined	5.92	506	1.42 (0.45)
Argentina			
Investigator 1	7.04	1,215	0.54 (0.18)
Investigator 2	6.20	1,092	0.58 (0.16)
Investigator 3	6.35	1,114	0.66 (0.13)
Combined	5.46	986	0.60 (0.18)
Bolivia			
Investigator 1	2.07	128	9.61 (3.17)
Investigator 2	1.79	112	13.21 (3.13)
Investigator 3	1.85	115	14.70 (4.32)
Combined	1.85	115	11.22 (3.01)

Table 4.—Summary statistics (mean; *SE*; mode; and 2.5, 50, and 97.5 percentiles of posterior distribution) of parameter estimates from a spatial mark–resight model incorporating photographic captures of pumas (*Puma concolor*) from camera-trapping surveys conducted in Belize, Argentina, and Bolivia. Capture histories were constructed by 3 independent investigators. Baseline trap encounter rates (λ_0) were standardized to 5-day encounter occasions; λ_0 and c, the probability of identifying a picture of a marked puma, were constant across encounter occasions; τ = scale parameter related to animal movement; N = number of activity centers in the state space; D = density (pumas/100 km^2).

	Investigator 1					Investigator 2					Investigator 3					Combined				
	$\bar{X}$ (*SE*)	Mode	2.5%	50%	97.5%	$\bar{X}$ (*SE*)	Mode	2.5%	50%	97.5%	$\bar{X}$ (*SE*)	Mode	2.5%	50%	97.5%	$\bar{X}$ (*SE*)	Mode	2.5%	50%	97.5%
Belize																				
τ	8.8 (1.62)	8.2	6.3	8.6	12.6	10.1 (1.64)	9.7	7.3	10.0	13.8	6.1 (1.13)	5.7	4.4	6.0	8.8	7.6 (1.77)	6.8	5.0	7.4	11.8
λ_0	1.1 (1.17)	0.2	0.1	0.6	4.3	0.1 (0.13)	0.1	0.1	0.1	0.4	0.2 (0.13)	0.1	0.1	0.2	0.5	0.2 (0.19)	0.1	0.1	0.2	0.7
c	0.9 (0.05)	0.9	0.8	0.9	1.0	0.9 (0.03)	1.0	0.9	0.9	1.0	1.0 (0.03)	1.0	0.9	1.0	1.0	0.7 (0.07)	0.7	0.5	0.7	0.8
N	14.8 (5.62)	11.0	8.0	13.0	29.0	26.1 (8.49)	22.0	15.0	24.0	47.0	59.4 (22.3)	51.0	25.0	56.0	111.0	30.2 (15.34)	22.0	10.0	27.0	68.0
D	0.3 (0.11)	0.2	0.2	0.3	0.6	0.5 (0.17)	0.4	0.3	0.5	0.9	1.2 (0.44)	1.0	0.5	1.1	2.2	0.6 (0.31)	0.4	0.2	0.5	1.4
Argentina																				
τ	8.6 (1.43)	8.1	6.4	8.3	12.0	8.2 (1.27)	7.7	6.4	8.0	11.3	8.2 (1.59)	7.5	6.0	7.9	12.4	9.1 (1.81)	8.3	6.6	8.8	13.8
λ_0	0.1 (0.02)	0.1	0.1	0.1	0.2	0.1 (0.02)	0.1	0.1	0.1	0.2	0.1 (0.03)	0.1	0.1	0.1	0.2	0.1 (0.04)	0.1	0.1	0.1	0.2
c	0.9 (0.03)	1.0	0.9	1.0	1.0	1.0 (0.00)	1.0	1.0	1.0	1.0	1.0 (0.03)	1.0	0.9	1.0	1.0	0.8 (0.05)	0.8	0.7	0.8	0.9
N	25.5 (8.94)	22.0	12.0	24.0	46.0	24.9 (8.40)	22.0	12.0	24.0	44.0	27.9 (9.90)	24.0	12.0	27.0	51.0	20.4 (8.04)	17.0	8.0	19.0	39.0
D	0.4 (0.13)	0.3	0.2	0.3	0.7	0.4 (0.12)	0.3	0.2	0.3	0.6	0.4 (0.14)	0.3	0.2	0.4	0.7	0.3 (0.11)	0.2	0.1	0.3	0.6
Bolivia																				
τ	3.1 (0.53)	2.9	2.3	3.0	4.3	2.1 (0.38)	2.0	1.5	2.1	3.0	2.3 (0.44)	2.1	1.6	2.2	3.3	2.2 (0.41)	2.0	1.6	2.2	3.2
λ_0	0.1 (0.06)	0.1	0.0	0.1	0.2	0.1 (0.03)	0.1	0.0	0.1	0.2	0.1 (0.02)	0.0	0.0	0.1	0.1	0.1 (0.05)	0.1	0.0	0.1	0.2
c	1.0 (0.00)	1.0	1.0	1.0	1.0	0.9 (0.04)	1.0	0.9	1.0	1.0	1.0 (0.00)	1.0	1.0	1.0	1.0	0.9 (0.05)	0.9	0.8	0.9	1.0
N	38.0 (13.8)	31.0	18.0	36.0	71.0	72.8 (24.2)	67.0	34.0	70.0	128.0	85.0 (28.1)	73.0	38.0	82.0	147.0	62.4 (20.4)	54.0	28.0	60.0	105.0
D	4.0 (1.44)	3.2	1.9	3.8	7.4	7.6 (2.53)	6.9	3.6	7.3	13.4	8.9 (2.94)	7.9	4.0	8.6	15.4	6.5 (2.13)	5.7	2.9	6.3	11.0

activity centers and in turn, λ_0 and τ. This resulted in estimates of density varying by 5 pumas/100 km^2 (4 versus 9 pumas/100 km^2, a 125% increase) in Bolivia. Similar to Kelly et al. (2008), we suggest that 2 or 3 investigators conduct blind identifications of puma photographs so results can be compared to check for disagreements. Disagreements can be categorized as marked, but unidentifiable. This is perhaps conservative, but a better approach than using single investigator opinions. In this way, capture histories can build on the combined investigator approach to create 1 set of final input data.

Knowledge of the densities of wildlife populations is crucial to their management and conservation. Herein, we present advancements in modeling techniques that go beyond traditional, problematic capture–recapture techniques and result in more precise density estimates. Our study is the 1st to estimate the density of a population of carnivores, where only a subset of the individuals are naturally marked, using camera-trapping surveys in combination with SMR models. This method is ideal for uniformly colored, elusive carnivores with some naturally distinguishing marks, because it does not require the physical capture of individuals nor does it require the species to be completely individually identifiable. The development of SMR and SECR techniques creates the potential for using a single camera-trapping array to estimate the density of multiple, sympatric carnivores because both techniques are less sensitive to the spatial setup of the camera stations than are traditional nonspatial methods (Noss et al. 2012; Sollmann et al. 2012). The density of individually identifiable carnivore species can be estimated using SECR techniques and the density of carnivore species where only a portion of the population is individually identifiable can be estimated using SMR techniques. For species where no animals can be identified to the individual level, the methods of Chandler and Royle (2013) may be applied. Developing monitoring programs that address the densities of multiple, sympatric species will result in considerable savings in time and money when compared to single-species approaches (O'Brien and Kinnaird 2011).

Resumen

Los relevamientos con trampas-cámara en combinación con modelos tradicionales o espacialmente explícitos de captura–recaptura, se han convertido en metodologías muy utilizadas para estimar la densidad de carnívoros que pueden ser identificados individualmente. Cuando sólo una porción de la población puede ser identificada inequívocamente, los modelos de marcado–revisualización tradicionales y espacialmente explícitos proveen una alternativa viable. Reanalizamos un conjunto de datos, que se utilizó para estimar la densidad de pumas (*Puma concolor*) mediante el método fotográfico de captura–recaptura en 3 sitios de estudio en Belice, Argentina y Bolivia, utilizando modelos más novedosos y avanzados incluyendo técnicas de marcado–revisualización tradicionales y espacialmente explicitas. Adicionalmente, evaluamos cómo la identificación de fotografías influyó en las estimaciones de densidad, comparando estimaciones basadas en las historias de captura construidas por 3 investigadores independientes. Estimamos la abundancia de pumas usando modelos de marcado–revisualización en el programa MARK y luego estimamos las densidades ad hoc. También estimamos densidades usando modelos espaciales de marcado–revisualización espacialmente explícitos implementados en un marco Bayesiano. La densidad de pumas no varió sustancialmente entre observadores, pero las estimaciones generadas mediante los 3 modelos estadísticos fueron diferentes. Las densidades de pumas (pumas/100 km^2) de modelos de marcado–revisualización espacialmente explícitos fueron más bajas (0.22–7.92) y aumentaron en precisión comparadas con aquellas de captura–recaptura (0.50–19.35) y técnicas de marcado–revisualización no espacialmente explícitos (0.54–14.70). Nuestro estudio es el primero en estimar la densidad mediante la utilización de datos de trampas-cámara en combinación con modelos marcado–revisualización espacialmente explícitos de una población de carnívoros donde sólo un subconjunto de individuos está marcado naturalmente. El desarrollo de técnicas de marcado–revisualización y captura–recaptura espacialmente explícitos ofrece la oportunidad de utilizar un mismo diseño de trampas-cámara para estimar la densidad de múltiples carnívoros simpátricos, incluyendo especies parcial o totalmente identificables individualmente.

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