



More than one way to count a cat: estimation of ocelot population density using frameworks for marked and unmarked species

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Abstract

Camera-traps have become one of the most common tools for studying wildlife abundance and population density. Traditionally, absolute density could be estimated only for species with individual markings, using capture–recapture frameworks. Newer methods allow to estimate density of unmarked species, but these have yet to be thoroughly tested and compared against capture–recapture methods. To make this comparison requires an identifiable species, for which both types of frameworks can be used. Here, we estimate the population density of ocelots (*Leopardus pardalis*) in the Osa peninsula, Costa Rica, comparing methods for marked and unmarked species. We deployed camera-trap grids between 2017 and 2019, identified individuals and determined spatially resolved individual detection histories, station-specific detection frequencies and times to first detection. Estimates obtained with methods for unmarked species (Time-to-Event and Random Encounter Model) varied widely among surveys, from 11 to 169 individuals/100 km², and were significantly different from spatial capture–recapture estimates (28.1 individuals/100 km²). Differences were largely driven by the non-random placement of cameras on human-made trails, which inflated the detection frequency. Maximizing the number of encounters benefits methods based on capture–recapture but is detrimental for methods based on random detections. Our results highlight the incompatibility between surveys designed for capture–recapture analyses, and those that assume random movement of animals. For recently developed unmarked species methods to be used for a larger and more diverse set of species, it is necessary to further test and define the requirements and factors that affect their calculations. This information will ultimately allow for a greater diversity of population and community studies.

Keywords Camera-trapping · Population density · Tropical forests · Population monitoring · Field methods

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Introduction

Abundance is one of the most fundamental parameters studied by ecologists, and a key metric for guiding and assessing the success of conservation strategies. Multiple approaches exist for estimating abundance, but our ability to obtain an accurate estimate varies greatly depending on the species of interest and their characteristics. A unified approach that can provide consistent and comparable abundance estimates for different species and in different contexts is lacking to date. The variety of estimation methods is particularly striking in camera trap studies of terrestrial mammals, where density estimation methods historically have relied on identifying individuals, which is only feasible for a few species where animals can be distinguished based on characteristics such as fur patterns (Borchers and Efford 2008; Karanth et al. 2006; Noss et al. 2012; Satter et al. 2019). Camera-traps have become the tool of choice in wildlife research, and they are especially useful for studying abundance and distribution of elusive and endangered species, as they allow systematic, simultaneous, low-impact sampling of large areas (Burton et al. 2015; Delisle et al. 2021). Given their frequent and widespread use, there is a need for reliable abundance estimation methods for many species, most of which are not individually distinguishable.

Several frameworks have been created or adapted to estimate abundance, or more commonly density, using camera-trap data. Among the most common are Capture-Recapture (CR) and Spatial Capture-Recapture (SCR) methods. Both methods estimate density based on individual detection histories (Delisle et al. 2021), but they use different underlying models; CR uses the number of recaptures to estimate the number of individuals in a survey area, while SCR uses the spatial distribution of recaptures to infer the location and density of home range centers. By calculating density directly, SCR bypasses the need to estimate the size of the survey area, which is one of the main limitations of CR (Borchers and Efford 2008; Efford et al. 2009). Both methods nevertheless require identifying individual animals, which means that in camera-trapping studies they can only be applied to species that naturally have individual markings, such as tigers (Karanth et al. 2006), leopards (Gray and Prum 2012), civets, spotted hyenas, wild dogs (Rich et al. 2019), and jaguars (Noss et al. 2013; Salom-Pérez et al. 2007).

Multiple methods have been developed to estimate the density of unmarked species throughout the last decade, such as the Random Encounter Model (REM) (Rowcliffe et al. 2008), Random Encounter and Stay (REST) (Nakashima et al. 2018), Time-to-Event (TTE), Space-to-Event (STE) and Instantaneous Sampling (IS) methods (Campos-Candela et al. 2018). The basic underlying principle for these methods is that the number of detections of a species increases the more individuals there are in the area around a camera, and/or the faster these individuals are moving (Hutchinson and Waser 2007; Rowcliffe et al. 2008). Therefore, if the speed of a species is known, the density can be back-calculated from the number of detections. These methods typically also assume that animals behave like ideal gases (i.e., constant speed, straight-line movement in a random direction), as this model of movement makes it simple to formalize the expected relationship between density, speed and detections (Campos-Candela et al. 2018; Nakashima et al. 2018; Rowcliffe et al. 2008). Methods for unmarked species have a clear advantage in that there is no need for individual identification, a time-consuming task, that is also prone to error (Johansson et al. 2020). Logistically, they are also more efficient because camera-traps do not need to be set up in pairs, a basic requirement for individual identification (but see Augustine et al. 2018). And perhaps most importantly, using these methods could significantly expand the set of species for which density can

be directly estimated and make it possible to compare densities across species (e.g., among competitors; among predators and their prey).

Despite the number of options currently available to estimate density of unmarked species, many studies only calculate relative abundance metrics (Gilbert et al. 2021). This may in part be due to the recency of the methods for unmarked species, the fact that some of these have only been tested in simulations (but see Caravaggi et al. 2016; Loonam et al. 2021), and their technical requirements, such as the need for independent speed estimates (Rowcliffe et al. 2011). It is also not clear that methods for unmarked species can give reliable density estimates that are comparable to more established methods. Previous studies have compared REM with visual census estimates (Caravaggi et al. 2016; Cusack et al. 2015), and REM, TTE and STE have been compared to SCR estimates from fecal samples identified with molecular methods (Loonam et al. 2021). No study, however, has performed similar tests using field data exclusively from camera traps.

We estimated the density of ocelots (*Leopardus pardalis*) in the Osa peninsula, southern Costa Rica. Ocelots have unique spot patterns so traditionally their population density has been estimated using CR (Gonzalez-Maya and Cardenal-Porras 2011; Mosquera et al. 2016), and SCR (Martínez-Hernández et al. 2015; Noss et al. 2012; Penido et al. 2016; Satter et al. 2019), though at least one previous study has used the REM framework (Rowcliffe et al. 2016). The identifiability and relative abundance of ocelots in Osa provides an opportunity to test and compare the performance of multiple frameworks for estimating population density. Here, we compared four methods: SCR, CR, REM and TTE. The latter two have the potential to be used for a more diverse set of study species than capture–recapture frameworks. The REM method is the best known and most developed method of estimation for unmarked species, but experimental results suggest the TTE method could give more precise results closer to SCR estimates (Loonam et al. 2021). We used SCR as a benchmark to compare with the alternative methods (Lucas et al. 2015).

Materials and methods

Study area

We worked in the Osa Peninsula in southern Costa Rica (8°24′14.0″ N, 83°20′12.0″ W). The region is classified as a wet forest life zone characterized by a tropical climate, with high temperatures year-round (annual mean: 27 °C) and heavy rainfall (4000 mm annually) concentrated mostly during the rainy season, from May to November. There is extensive (> 70%) forest cover on the peninsula, mostly inside protected areas where hunting is prohibited and logging is heavily regulated. Forests are surrounded by small towns, roads, pasture, oil palm and timber plantations, which can limit the distribution of large forest-dependent species while benefiting small generalists (Vargas Soto et al. 2021). Wildlife on the peninsula is also relatively isolated from conspecifics on the mainland due to movement barriers set by palm oil plantations and the Inter American Highway (Sánchez-Azofeifa and Daily 2003; Soto-Fournier 2014). We focused on the southern part of the peninsula, between Corcovado National Park and the Matapalo Cape (Fig. 1), which is least affected by humans and harbors some of the best conserved primary forest remnants in the region (Fig. 1; see Whitworth et al. 2018 for a historical description).

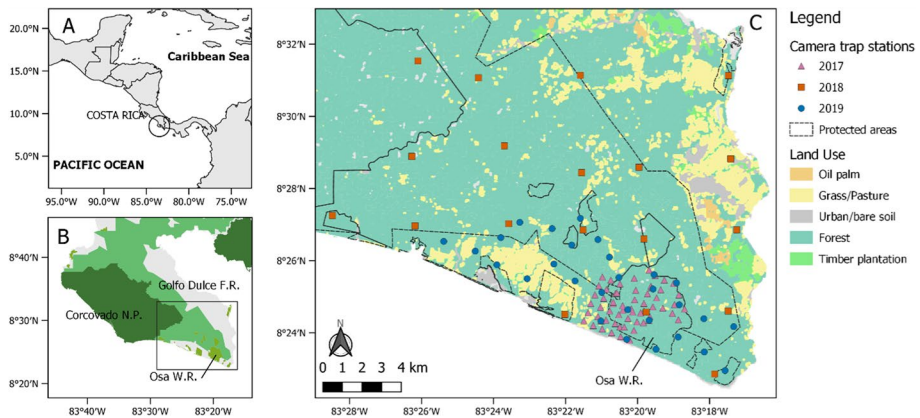


Fig. 1 **A** Map of the survey area in the Osa Peninsula, southern Costa Rica. **B** Protected areas in the region create a corridor between Corcovado National Park and the southern tip of the peninsula, dark green shows the National Parks, lighter green shows the Forest Reserve (F.R.), and the smaller protected areas are Wildlife Refuges (W.R.). **C** Cameras were distributed across different habitat types (see legend) around the Osa Wildlife Refuge in 2017 (purple triangles), as part of a regional study in 2018 (orange squares) and specifically for estimating the density of ocelots in the Matapalo corridor in 2019 (blue circles)

Study species

The ocelot (*Leopardus pardalis*) is the third largest feline found in the Osa region. They are smaller than jaguars (*Panthera onca*) and pumas (*Puma concolor*), but larger than margays (*L. wiedii*) and jaguarundis (*Puma yagouaroundi*). Ocelots are key mesopredators of small mammals, birds and reptiles on the Osa, but their potential isolation from the mainland may make the population vulnerable to perturbations such as habitat loss, hunting, or disease (Salom-Pérez et al. 2007). Ocelot relative abundance has previously been assessed on the Osa using tracks (Tavares-de-Almeida 2003), but density has been estimated only once before in the region, and only inside Corcovado N.P. (Salom-Pérez 2005).

Camera-trapping surveys

We used data from three different camera-trap surveys that had different scopes and designs, all three were within the same region in the southern part of the Osa peninsula, and smaller grids were contained within the survey area of the larger ones. The first was a localized, general study of the terrestrial vertebrate community in and around the Osa Wildlife Refuge (8° 24'12" N, 83° 20'11" W) (Whitworth et al. 2018). This grid was deployed from May to August 2017 in a 500×500 m (0.25 km²) square arrangement. This was a small and dense arrangement intended to study multiple species at the same time—some of which have small home ranges—and estimate their population density with the REM framework, which assumes random spatial sampling. The second grid was a region-wide effort to study the wildlife community in relation to the level of anthropogenic disturbance (Vargas Soto et al. 2021). Camera stations were deployed between February and July of 2018 in a 4×4 km (16 km²) square arrangement and covered the entirety of the Osa Peninsula and part of the adjacent mainland. For our study we used the data from stations

located in our focal area east of Corcovado National Park. The third grid was set up specifically to estimate the density of ocelots using capture–recapture analysis. This grid was deployed between December 2018 and March 2019, and covered a smaller area than the 2018 survey, but with stations closer together, 1500 m apart, in a hexagonal arrangement (Fig. 1). The results from the 2017 and 2018 surveys indicated ocelot home range diameters of about 4 km on average (based on the sigma parameter estimate for the SCR model), so we designed this grid to include multiple stations within each territory. In addition, because felines are known to use human-made trails and non-paved roads to move across their territories (Di Bitetti et al. 2014), we placed the majority of cameras on trails (13/29) or dirt roads (3/29) during the 2019 survey. In 2017, we prioritized a consistent distance across stations, only 11 of 60 cameras were placed on forest trails and none on roads. In 2018, 14 of 18 cameras were placed on forest trails and none on roads.

In 2018 and 2019, all stations had paired cameras to capture both sides of passing animals, whereas the 2017 survey had only one camera per station. For every station, we recorded the coordinates, and whether stations were on or off trail. The survey designs differ in effort, trap spacing, and small-scale placement (on vs. off-trail) and could therefore produce different results using the methods for unmarked species. Considering these differences, we only compared density estimates produced by different methods using data from the same survey. The design used in 2019 should maximize the number of detections. Many detections and, more importantly, many recaptures at different stations should increase the accuracy of the SCR model outputs but it could invalidate the assumptions of the REM and TTE methods regarding random movement. This situation is not uncommon in this type of studies, as researchers often try to estimate the abundance of multiple species using a single study design and doing so may require different density estimation methods.

Data analysis

We organized the photos from each camera, extracted their metadata (date/time) and determined the number of days each station was functional using the *camtrapR* package (Niedballa et al. 2016). We used four different methods to estimate the population density of ocelots: traditional capture–recapture (CR), and Spatial Capture–Recapture (SCR), which require the identification of individuals, and the Random Encounter Model (REM) and Time-To-Event (TTE) methods, which only require the identification of species, but not individual identity. We identified individual ocelots based on their spot pattern, and determined their sex based on the visible presence or absence of testes. Photos were compared manually, and identification was based on matching the shape, size, and position of at least five spots on the side of the animals. If only the head was visible, stripes along the neck were used. When only one side of the animal was available, individuals were considered distinct unless they could be matched using the same side. The identification was updated each year as new photographs became available, particularly when photographs of both sides at the same station were obtained. A single observer identified all individuals. To test the reliability of the identification, a second observer identified a random subset of 30% of the images (33/184). Pictures that were classified differently were reviewed together to decide a consensus identity. There were few instances (<5%) of disagreement between observers. Some ocelots could not be individually identified and were only included in the REM and TTE calculations. All analyses were run in R 3.6 (R Core Team 2020).

Spatially explicit capture–recapture

Spatially explicit capture–recapture (Borchers et al. 2014) assumes each individual has a defined home range and that individuals spend more time near its center. The SCR model estimates the most likely density of home range centers, given a spatially resolved detection history and a detection function that decreases with distance from the center. We used the *secr* package (Borchers and Efford 2008; Efford et al. 2009) to obtain individual detection histories and to estimate population density using maximum likelihood. The detection history indicates whether an individual i was detected (1) or not (0) at station j during occasion k . The sampling period for each survey was divided into one-week long distinct occasions for the detection history. To include sex differences in detection parameters, we used hybrid mixture models, with a fixed effect of sex and a random effect for individuals of unknown sex (Gardner et al. 2010). We included the camera placement as a binary station covariate indicating whether cameras were on or off trails. We used a half-normal detection function for all models. Alternative detection functions (hazard rate, exponential) produced virtually identical parameter estimates.

Capture recapture

Closed population capture–recapture methods estimate the number of animals in the study area based on the number of recaptures of previously detected individuals, i.e., the individual detection histories. The abundance is then divided by the sampling area to calculate population density. We used the detection history determined for the SCR analysis, and estimated the number of individuals using the closed population estimators in the *secr* package (Efford 2020). We accounted for heterogeneous detection probability among individuals, and used the jackknife method for parameter estimation (Burnham and Overton 1978). The definition of the sampling area is a source of conflict and uncertainty in the density estimation literature. Studies of felines with defined home ranges, like ocelots, assume that the mean maximum distance moved (MMDM) represents either the mean radius or the mean diameter of an individual home range, and calculate the sampling area using the full MMDM or 1/2 MMDM as a buffer distance around sampling stations. Density estimates obtained with MMDM are more conservative and empirical studies have found it to be closer to the values obtained with SCR (Dillon and Kelly 2008; Noss et al. 2012), so we used this distance to calculate our effective sampling area. Given the different grid designs, we estimated the density separately for each survey using survey-specific MMDM values.

Random Encounter Model

The Random Encounter Model (REM) was proposed as a way for estimating the density of species where individuals cannot be distinguished. The method uses the species' detection frequency and movement speed, along with the camera's detection distance and angle, to estimate density (Rowcliffe et al. 2008): higher encounter rates between moving individuals and stationary cameras are expected when there are more individuals in the area, when individuals move faster, and for cameras with larger detection zones. Assuming that individuals move like ideal gases around a station (i.e., in straight lines with constant speed), density can be estimated as

$$D = \frac{n}{rvp} \quad (1)$$

where n is the number of independent detections, \bar{v} is the mean movement rate of the species, and t is the station deployment time. We estimated the mean movement rate, \bar{v} , of ocelots in the Osa as the product of their expected mean speed and their observed activity rate (i.e., the proportion of the day when animals were active). We used the mean speed estimated previously for moving ocelots in Barro Colorado Island, Panama (Rowcliffe et al. 2016), and determined the activity rate by fitting a von Mises kernel distribution to the time-of-capture data from our study (Rowcliffe et al. 2014) using the *activity* package in R (Rowcliffe 2019). The parameter p in Eq. 1 is the mean profile width of a camera's detection zone, calculated from the camera's detection radius, r , and detection angle, θ (Rowcliffe et al. 2008):

$$p = \frac{r(2+\theta)}{\pi} \quad (2)$$

We calculated the detection angle, θ , and distance, r , of our cameras for ocelots following the adapted distance sampling method described by Rowcliffe et al. (2011). Briefly, we fit detection probability functions to the estimated distances and angles from the camera for each ocelot detection; the detection distance/angle is the value for which the probability of detection is 0.5.

Estimating the position of observed animals with respect to the camera usually requires comparing against landmarks visible in the photograph that have been measured in the field (Rowcliffe et al. 2011). These measurements were not made in our surveys, so we used an ad-hoc method based on basic trigonometry instead. In a photograph, the horizontal distance from the middle of the frame (in pixels) is proportional to the tangent of the angle θ with respect to the camera's line of sight. The relationship between the horizontal distance from the middle of the photograph p_x , the photograph resolution w , the camera's field-of-vision φ , and the angle θ is given by:

$$\frac{p_x}{\frac{w}{2}} = \frac{\tan \theta}{\tan \frac{\varphi}{2}} \quad (3)$$

$$\theta = \arctan \frac{2p_x \tan \frac{\varphi}{2}}{w} \quad (4)$$

Similarly, the distance d from the camera is given by

$$d = \frac{p_r}{\sin(\theta)}, \quad (5)$$

where p_r is the real-world distance corresponding to p_x , calculated as

$$p_r = \frac{l_r p_x}{l_x},$$

where l_r is the real length of a reference object visible in the photograph, and l_x is its length in pixels. In this case, we used the head of ocelots as a reference object, which measures roughly $l_r = 16$ cm (Murray and Gardner 1997).

We estimated the mean density and 95% confidence intervals by bootstrapping the per-station detections data 1000 times and applying Eq. 1. We estimated three density values per year, one with all the data, and two with the data separated by location of cameras (on- and off-trail).

Table 1 Camera-trap grid designs used to estimate population density of ocelots in the Osa peninsula, Costa Rica, with multiple estimation frameworks

Grid	Deployment period	Trap nights	Number of stations (double stations)	Arrangement	Mean spacing (m)
2017	May–August 2017	6114	60 (0)	Square	430
2018	February–July 2018	2049	19 (19)	Square	3555
2019	December 2018–April 2019	4050	29 (25)	Hexagonal	1301

Time-to-event method

Like the REM, the Time-to-event (TTE) method (Moeller et al. 2018) aims to estimate density from camera trap observations assuming that animal movement can be reasonably approximated by the ideal gas model. Instead of detection frequency, however, the TTE method is based on the time until the first detection of a species, which is expected to decrease with higher densities and faster speeds. If individuals are homogeneously distributed around stations, the time until first detection should follow an exponential distribution:

$$TTE \sim \exp(\lambda)$$

where λ is the number of individuals per sampling area. We use one-hour intervals as the sampling time units. The sampling area is then the area surveyed by a single station in an hour, calculated as the profile length p (as derived for the REM, Eq. 2) multiplied by the mean distance travelled by an individual in one hour (the daily travel distance derived for the REM divided by 24 h). To obtain a distribution of TTE, we divided the sampling time into one-week occasions and determined a TTE for each occasion. We used maximum likelihood to estimate λ , and the delta method to estimate a confidence interval (Moeller et al. 2018). For species at low density, most occasions will have no detections. These empty occasions are right-censored, i.e., they are assigned a likelihood value equal to the likelihood that detection may occur past the occasion length (Moeller et al. 2018). We obtained estimates for each survey separately.

Results

There were 60 single-camera stations in 2017 deployed for 101 (SD 15.6) days on average, for a total effort of 6079 trap-days. In 2018, there were 19 stations deployed for 109 (SD 11.8) days, for a total effort of 2068 trap-days. Finally, in 2019 we deployed 29 stations for 75.7 (SD 19.4) days on average, for a total effort of 2196 trap-days. We recorded 184 independent ocelot detections, most of them during the 2019 survey (Table 1; Fig. 2). Very few stations (18.3%, 11/60) were on trails in 2017, whereas three quarters (73.6%, 14/19) in 2018 and more than half (55.2%, 16/29) in 2019 were on trails or dirt roads. Accordingly, only one quarter (25%, 15/60) of the stations detected ocelots in 2017, unlike the following years where there were detections at over 60% of stations (2018: 63.2%, 12/19; 2019: 72.4%, 21/29). Stations with detections recorded on average one detection every ten weeks in 2017 (mean frequency: 0.11/week), one per month in 2018 (0.23/week), and one every other week in 2019 (0.52/week).

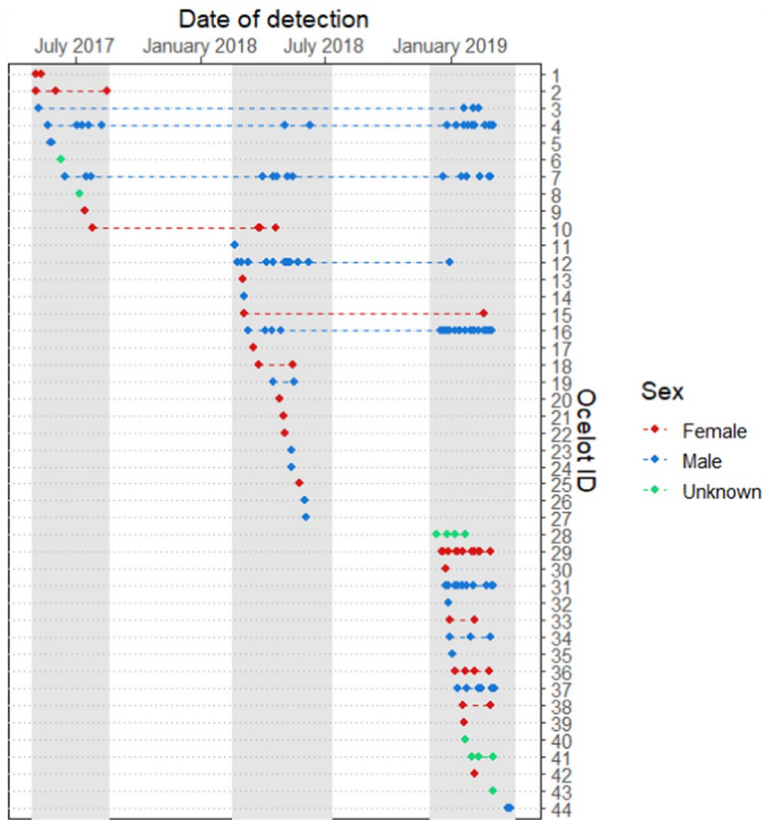


Fig. 2 Individual detection histories of ocelots in the Osa peninsula, southern Costa Rica. Each row represents an individual, each point represents a detection, and dashed lines connect the first and last detections for every individual to indicate continuous presence in the area. Shaded areas show the duration of surveys conducted in 2017, 2018, and 2019

We were able to assign an individual identity to most detections, but with varying success across years. In 2017, when we had a single camera per station, 15% (4/27) of records could not be positively identified, compared to 2% in 2019 (2/115), and 0% in 2018. We identified 44 individual ocelots overall, roughly half of which (23) were recaptured at least once over the three-year period. Only seven, however, were detected during more than one survey. Only two individuals, both males, were detected in all three surveys (Fig. 2). The 2019 survey was specifically designed for ocelots, it produced the most detections, and captured the most individuals. This grid also had more recaptures, more than 78% of detections were recaptures, compared to about 50% for the 2017 and 2018 grids (Table 2).

Spatially explicit capture–recapture

We estimated densities between 28.1 (CI 18.7–42.2) in 2019 and 52.7 (CI 26.3–105.6) ind/100 km² in 2017 using the SCR method (Tables 3, 4). The most accurate results should be those from the 2019 grid, which had the most recaptures, and has the narrowest confidence interval. We estimated a higher density for the 2017 and 2018 grids but there is

Table 2 Summary of survey scope and detections of ocelots for camera-trap surveys between 2017 and 2019 in the Osa peninsula, Costa Rica

Year	Survey area (km ²)	Stations	Station spacing (m)	Arrangement	Detections (recaptures)	Individuals (recaptured) ^a	Mean (median) recaptures per individual
2017	27.7	60	430	Square	27 (13)	10 (6)	1.5 (1)
2018	95.0	19	3555	Square	42 (22)	20 (7)	1.1 (0)
2019	88.9	29	1301	Hexagonal	115 (90)	23 (14)	3.8 (1.5)

^aWe include in this count only individuals that could be positively identified, i.e., excluding records with inconclusive identification

Table 3 Estimated parameter values for a spatially explicit capture–recapture model of ocelots in the Osa Peninsula show the difference between the detection of males vs. females, and between stations on or off-trail

Survey year	Parameter	Estimate ^a (95% CI)
2017	Density	– 5.25 (– 5.96 : – 4.53)
	Base detection probability	– 7.59 (– 8.91 : – 6.27)
	Effect of male	0.88 (– 0.49 : 2.26)
	Effect of position on trail	1.84 (0.98 : 2.7)
2018	Density	– 5.43 (– 6.31 : – 4.56)
	Base detection probability	– 6.21 (– 8.08 : – 4.35)
	Effect of male	1.72 (0.29 : 3.14)
	Effect of position on trail	0.84 (– 0.56 : 2.24)
2019	Density	– 5.87 (– 6.29 : – 5.46)
	Base detection probability	– 5.9 (– 6.66 : – 5.13)
	Effect of male	0.71 (0.12 : 1.3)
	Effect of position on trail	2.06 (1.41 : 2.72)

Data were obtained through three distinct camera-trapping grids

^aUntransformed coefficients

Bold text indicates 95% CI that do not include 0

significant uncertainty around the estimates, and the confidence intervals include the 2019 estimate. There was no significant deviation from a 1:1 sex ratio, but the detection parameters indicate a higher detection probability for males, and on trails (Table 3).

Capture–recapture

The traditional capture–recapture analysis estimated 12.9 (95% CI 10.5–28.4), 36.6 (26.3–63.5), and 42.7 (30.2–77.1) individuals in the 2017, 2018 and 2019 surveys, respectively. We estimated MMDM of 2079 m in 2017, 1256 m in 2018 and 2532 m in 2019. The resulting effective sampling area varied more than twofold, between 43.3 km² in 2017 and 108.1 km² in 2019, but the estimated density was similar across survey years: 29.8

Table 4 Population density estimates for ocelots (*Leopardus pardalis*) in the Osa peninsula, Costa Rica

Grid	Data subset	SCR	CR	REM	TTE
2017	All	52.7 (26.3–105.6)	29.8 (24.2–65.5)	11.6 (6.4–19.6)	12.1 (7.2–17.1)
	Off trail			6.6 (2.9–11.1)	5.7 (2.0–9.5)
	On trail			44.0 (14.7–78.0)	42.7 (18.5–66.8)
2018	All	43.7 (18.6–102.9)	41.4 (29.8–71.9)	64 (25.9–112.1)	66.0 (46.1–86.0)
	Off trail			21.4 (0–64.9)	22.0 (0.4–43.5)
	On trail			81.3 (33.5–145.8)	86.1 (58.7–113.5)
2019	All	28.1 (18.7–42.2)	39.5 (27.9–71.4)	164 (89.5–367.6)	164.1 (133.8–194.4)
	Off trail			35.5 (14.8–56.6)	37.9 (16.5–59.4)
	On trail			368.7 (175.2–716.9)	289.7 (232.7–346.8)

Density was estimated using different methods: capture–recapture (CR), spatial capture recapture (SCR), random encounter model (REM) and time-to-event (TTE). Data come from three camera-trapping surveys with different scopes and designs. The 2019 grid was designed specifically for ocelots, the others were general terrestrial mammal surveys

(24.1–65.5) individuals/100 km² in 2017, 41.4 (29.8–71.9) individuals/100 km² in 2018, and 39.5 (27.9–71.4) individuals/100 km² in 2019 (Table 4).

Random Encounter Model

There was significant variation in REM density estimates among years and between stations placed on versus off trails. Survey-specific density estimates ranged from 11.6 ind/100 km² in 2017, to 164.0 ind/100 km² in 2019 (Table 4). Using only the data from stations off trail gives more consistent REM estimates.

We estimated the detection distance of our cameras for ocelots in our study areas as 3.89 m (95% CI 3.43–4.19 m), and the detection angle as 35.2° (95% CI 25.4–46.6°). The best model for effective detection distance was obtained using a nonmonotonic hazard rate detection function, where animals are less likely to be detected if they are far away or pass too close to the camera. For the detection angle, the frequency of detections did not decrease but stayed relatively constant regardless of how far animals were away from the center of the detection zone when photographed. To accommodate this frequency distribution, we fit a half-normal detection function with two cosine expansion terms to the angle of detection data, as suggested by Rowcliffe et al. (2011). Ocelots in our study were most active at night, with peaks after dusk, before dawn and at midnight. The estimated daily activity rate was 0.47; multiplying by 0.279 m/s (the mean speed of moving ocelots calculated in Barro Colorado) we obtained a daily travel distance of 11.33 km/day.

Time-to-event

Like the REM method, there was large variation among TTE estimates from different surveys. We estimated a density of 12.1 (95% CI 7.15–17.1) individuals/100 km² in 2017, 66.0 (46.1–86.0) individuals/100 km² in 2018, and 164.1 (133.8–194.4) individuals/100 km² in 2019. Density estimates varied substantially less among years when only the data from off-trail stations were used (range 5.7–38.0 individuals/100 km²; Table 4).

Comparison across methods

The methods that are based on species capture frequency—REM and TTE—performed similarly, the difference among their point estimates was less than 10% for the first two grids, the largest difference was 21.4% for the density calculated only with stations on trails in 2019 (Table 4). In that case both methods produced unrealistically high values, due to inflated detection frequencies. Using only the data from stations off-trails produced consistently lower estimates, but also varied substantially across years, from 6–7 ind/100 km² in 2017 to 35–38 ind/100 km² in 2019 (Table 4).

The methods based on individual detection histories (SCR and CR) did not perform consistently across surveys; the mean estimates were similar in 2018, around 40 ind/100 km², but the CR estimate was 43% lower than the SCR in 2017, and 40% higher in 2019. There was also no evident pattern between REM and TTE estimates compared to SCR estimated, in some cases producing higher and in some cases lower estimates. In 2017, REM and TTE estimates using all the data and only the off-trail data were significantly lower than SCR and CR estimates (based on CI overlap). In 2018, REM and TTE yielded mean density estimates roughly 45% higher than SCR using all the data, and around 50% lower with only the off-trail data. There is, however, no statistical support for these differences as there is substantial overlap between the CIs. Finally, in 2019, REM and TTE using off-trail data produced estimates around 30% higher than SCR, but the difference is not statistically significant. Using all the data or the on-trail data only did give significantly higher estimates than SCR in 2019, but these estimates are not realistic.

The most similar estimates were SCR compared with CR in 2018 (2.3% difference), SCR compared with REM and TTE for stations on trail in 2017 (16.5% and 19.1% difference, respectively), and for stations off trail in 2019 (16.3% and 24.3% difference). The most similar estimates for a single survey were produced in 2019, when comparing SCR, CR, and estimates from off-trail stations for REM and TTE. The CR confidence interval consistently overlapped with SCR estimates. (Table 4).

Discussion

Recent years have seen a rise in the number of frameworks and methods to estimate population density using data from camera-trap captures, for both marked and unmarked species (Moeller et al. 2018; Nakashima et al. 2018; Ramsey et al. 2015). The latter, however, have still to gain popularity of use, in part due to a lack of field testing and confidence in reported values. Here, we tested two methods for estimating the density of unmarked species, Time-to-event (TTE) and Random Encounter Model (REM), against Capture–Recapture methods, the current standard in the field for marked species. Our analysis shows that the same data can produce very different density estimates, which highlights the lingering need for a unified approach that is truly comparable across studies and for different species. Methods for unmarked species have specific assumptions about animal movement with respect to the camera-trap (Rowcliffe et al. 2013) and are therefore greatly affected by study design. Nonetheless, these methods present new opportunities for including more species in abundance studies, and we expect that they will be used more frequently as the factors that affect their estimations are further clarified.

We estimated an ocelot population density of 28.1 individuals/100 km² in the Osa Peninsula, using the spatial capture–recapture method with the data from 2019, when

our survey was specifically designed for estimating density of ocelots. Traditional capture–recapture gave similar point estimates (within 20% of the SCR estimate). These values are comparable to the highest densities reported globally using SCR, from Bolivia (Noss et al. 2012). Density in the Osa is higher than similar habitats in a reserve in the Central Amazon (Gomes da Rocha et al. 2016), and four times higher than those observed in disturbed environments in Mexico (de la Torre et al. 2016; Martínez-Hernández et al. 2015). Our results would suggest a healthy ocelot population in this region, as expected for wet forest ecosystems with consistent prey availability and relatively contiguous habitat (Pérez-Irriego and Santos-Moreno 2014; Gomes da Rocha et al. 2016, Vargas Soto et al. 2021). These estimates should be revisited periodically to detect trends in population growth, ideally using a consistent sampling scheme to ensure reliability and comparability.

Higher ocelot densities than those discussed above have only been reported using CR methods, with estimates as high as 95 individuals/100 km² in Peru. These values should, however, be taken with some caution, as CR values depend on the estimated sampling area but provide little guidance on how to estimate this area. There is, for example, considerable debate regarding how to calculate the mean maximum distance moved, MMDM (Kolowski and Alonso 2010), and whether to use the MMDM or 1/2 MMDM (Bustamante 2008; Noss et al. 2012) as a buffer distance in sampling area estimates. This uncertainty has led some researchers to report both values (Kolowski and Alonso 2010) and while this helps to compare across studies, it does little to resolve the debate. Relying on CR methods alone can thus prevent reliable comparisons across time and space. Spatial Capture–Recapture models avoid this pitfall by estimating density directly (Efford et al. 2009), making it a more robust method. SCR is the current standard in the field, despite some limitations (Harmsen et al. 2020). In our case, the CR method using the full MMDM estimated a similar density as SCR, in line with previous comparative studies (Noss et al. 2012). However, while both methods provided consistent results, neither can avoid the limiting requirement of having to identify individuals.

We tested two methods for unmarked species, both of which yielded similar density estimates, as has been reported in previous studies (Loonam et al. 2021). In both cases we used the ideal gas model (Hutchinson and Waser 2007) as an underlying assumption of movement, and the same estimates for speed and detection area size, so this result was expected. The confidence interval was consistently narrower for TTE, although this could be due to an underestimation of the variance by the delta method (Moeller et al. 2018) rather than to a more precise estimation compared with the REM. Both methods have similar requirements, such as the need for an independent estimate of sampling or detection area and of the mean speed at which the study species is moving. The TTE approach, however, has some apparent advantages over REM. For example, photos can be processed faster with the TTE, since researchers only need to find the first detection for each occasion (Moeller et al. 2018). This may not be a significant improvement for species that occur at low densities like ocelots, but it could prove advantageous for more common species. The methods for unmarked species estimated significantly different densities than SCR and had varying estimates between survey years. There was also no consistent directional relationship between SCR and TTE/REM estimates, as TTE and REM provided a lower density estimate than SCR for one year, and higher ones for the other two years. In some cases, the confidence intervals of the REM and TTE included the SCR estimate, but the uncertainty in these cases was so large as to make the estimate practically non-informative. As the ocelot population is unlikely to be changing as abruptly as suggested by the REM/TTE methods, it is more likely that the above-mentioned issues are due to differences in the design of the camera grid between years (Loonam et al. 2021).

Our results suggest the optimal sampling designs for SCR and CR, which require maximizing the potential number of encounters with different individuals (Dupont et al. 2021), are incompatible with the design necessary for the REM and TTE methods, which are based on assumptions of random camera trap distribution. Ideally, comparative studies should use separate grids for each method; stations for methods like REM and TTE would be placed at random, while stations for CR methods can target high use locations. In our case, stations deployed in 2018 and 2019 favored on-trail placements to maximize detections of predators like jaguars, pumas, and ocelots (Di Bitetti et al. 2014). As a result, the mean detection frequency and time to first encounter are likely inflated for these surveys. Similar issues have been solved in other studies by using only data that conform to the assumptions of the model. Cusack et al. (2015), for example, used only nighttime data when estimating lion density to avoid the inflated detection frequency at shade trees during the day. In our case, it was the placement of cameras on- versus off-trail that resulted in higher-than-expected detection frequencies, and considering only cameras off trails resulted in estimates that were closer to the expected density (based on SCR), and more consistent between survey years. Stratified sampling designs that distribute stations proportionally to the different habitats available could help improve REM/TTE estimates—in future studies or for reanalysis of existing data sets—but require that researchers identify the factors that may bias detection frequency for their study species and place camera stations accordingly.

In addition to the requirements regarding study design, current methods for unmarked species require estimating some parameters independently, such as the species' mean speed, and the dimensions of the camera's detection zone. Each of these parameters could bring additional error to the calculations if not properly estimated. Alternatives like the Space-To-Event or Instantaneous Sampling methods eliminate the need for these estimations, but they are only applicable for relatively common species that are detected frequently (Moeller et al. 2018). In the case of the TTE method, the way to estimate some parameters (e.g., the distance across the sampling area) also seems ad hoc (e.g., Loonam et al., 2021). As we have shown, however, tools developed for REM to estimate movement rate and detection zone parameters (Rowcliffe et al. 2011, 2016) provide a more consistent methodology that can be similarly applied within the TTE framework.

Current density estimation methods for camera-trap studies based on capture–recapture are only applicable to the fraction of species that have distinctive individual features. On the Osa Peninsula, for example, only three species have recognizable markings, out of nearly 30 that are regularly detected with camera-traps, and they are all within the same family (Felidae). For the majority of species it is not possible to distinguish individuals from photographs, and alternative methods to estimate their density are necessary. Such methods will be particularly important for studies of competitive and trophic interactions among species, as well as in the implementation and assessment of conservation strategies. Errors in these estimations could be particularly costly if endangered or at-risk species are being studied. Current options like the REM and TTE can produce results similar to SCR and CR estimates, but particular care needs to be given to study design and data analysis, to avoid detection biases. In particular, random placement of cameras is critical to fulfill the assumptions of the model. Further studies in different landscapes and with other communities should be performed to identify potential sources of bias for different species. Currently, comparisons across studies should be made with care, as different methods can produce significantly different results. We expect clearer requirements about each analysis method will be further developed in the coming years, allowing for more informed and accurate comparisons, and a better understanding of interaction among species.

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Declarations

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