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Ocelot *Leopardus pardalis* in Belize: the impact of trap spacing and distance moved on density estimates

Adam Dillon and Marcella J. Kelly

Abstract We used remote cameras to obtain information on an elusive species and to examine the effects of different camera trapping methodologies on abundance estimates. We determined activity pattern, trail use, trap success, and density of ocelot *Leopardus pardalis* in seven camera-trap surveys across two habitat types in western Belize: tropical broad-leaf rainforest and tropical pine forest. Ocelots in the rainforest were active mostly at night, in particular immediately after sunset, and they travelled on low-use roads (especially in the wet season) and high-use roads (especially in the dry season) more than established and newly cut trails. Trap success was relatively high in the rainforest (2.11–6.20 captures per 100 trap nights) and low in the pine forest (0.13–0.15 captures per 100 trap nights). Camera trapping combined with mark-recapture statistics gave densities of 25.82–25.88 per 100 km^2 in the broad-leaf versus 2.31–3.80 per 100 km^2 in the pine forest. Density estimates increased when animals repeatedly captured at the same camera (zero-distance moved animals) were included in the buffer size analysis. Density estimates were significantly negatively correlated with distance between cameras. We provide information on ocelot population status from an unstudied portion of its range and advise that camera trap methodologies be standardized to permit comparisons across sites.

Keywords Activity patterns, Belize, camera traps, density, *Leopardus pardalis*, movement, ocelot.

Introduction

Historically, ocelots *Leopardus pardalis* occurred in large numbers and ranged from the southern United States to northern Argentina but hunting pressure and habitat loss caused population declines (Murray & Gardner, 1997). Ocelots were earlier categorized as Vulnerable on the IUCN Red List (IUCN, 2006) but as a result of a reduction in hunting pressure and bans on the international fur trade in the 1980s they have been categorized as a species of Least Concern since 1996 (IUCN, 2006). However, there remains little data on ocelot populations in many areas of their range and habitat loss continues to threaten their persistence (Sunquist & Sunquist, 2002).

Abundance estimates are important for species' conservation, allowing the examination of temporal trends and determination of the potential number of individuals a reserve can support. However, obtaining information on population status of ocelots is difficult because they are solitary, elusive and often live in densely vegetated, remote habitats. Track surveys, scat analysis, and radio telemetry have provided insights regarding ocelot diet and behaviour but have had limited success in measuring population status (Emmons, 1987; Ludlow & Sunquist, 1987; Konecny, 1989; Sunquist *et al.*, 1989; Crawshaw, 1995). Camera trapping techniques have been used to estimate the density of tigers (Karanth, 1995; Karanth & Nichols, 1998; Karanth *et al.*, 2004), jaguars (Kelly, 2003; Maffei *et al.*, 2004; Silver *et al.*, 2004; Soisalo & Cavalcanti, 2006) and, more recently, ocelots (Trolle & Kery, 2003; Maffei *et al.*, 2005; Di Bitetti *et al.*, 2006; Haines *et al.*, 2006). Although camera trapping has become a valuable tool for monitoring elusive felids there is currently debate concerning proper camera trapping protocol. For example, camera trapping studies use varying camera spacing (e.g. 1–5 km apart) yet it has been shown that, within a short trapping period (≤15 days), increased trap distance leads to an underestimate of density (Wegge *et al.*, 2004). In addition, some studies include animals captured repeatedly at a single camera station (zero-distance moved) in the density estimation process (Kelly, 2003; Silver *et al.*, 2004) whereas others do not (Trolle & Kery, 2003; Silver *et al.*, 2004; Maffei *et al.*, 2005; Di Bitetti *et al.*, 2006).

The goals of this study were: (1) to obtain information on ocelot trap success, activity patterns, trail use, and density for two habitats in western Belize, (2) to provide the first density estimate of ocelots in Central America

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and extrapolate these numbers across the reserves surveyed, and (3) to examine the impacts of camera spacing and zero-distance moved animals on density estimation, thus aiding the standardization of camera trapping protocol across studies and species. Providing baseline data on ocelot numbers will aid ocelot conservation, and standardizing camera trapping methodology has wide ranging applications for other threatened species.

Study site

This research was conducted in the vicinity of Las Cuevas Research Station within the Chiquibul Forest Reserve and National Park and the Mountain Pine Ridge Forest Reserve of western Belize (Belize Forestry Department Ref. No. CD/60/3/03; Fig. 1). These reserves, along with areas of northern Guatemala and southern Mexico, comprise La Selva Maya (the Mayan Forest), the largest intact tropical rainforest in Central America (CEPF, 2005). Rainfall averages 1,500 mm per year with a rainy season from June to January (Johnson & Chaffey, 1973). We conducted surveys in two dominant and adjacent habitats; tropical broad-leaf rainforest (629 km^2) and tropical pine forest (379 km^2). The broad-leaf rainforest is a dense secondary forest, with areas of primary and gallery forest, which is subjected to frequent hurricanes (Beletsky, 1999). Dominant canopy trees include the cohune palm *Orbigyna cohune*, ironwood *Dialium guinense*, quamwood *Schizolobium parahybum*, sapodilla *Manilkara zapota*, nargusta *Terminalia amonzonia* and cieba *Ceiba pentandra*, growing on limestone substrate (Beletsky, 1999). The tropical pine forest is dominated by Caribbean pine *Pinus caribaea*, mountain pine *Pinus oocarpa* and palmetto palm *Acoelorrhaphe wrightii*, growing on a granite substrate (Beletsky, 1999). This forest was largely decimated by the southern pine beetle *Dendroctonus frontalis* from 1999 to 2003, creating a more open canopy with a dense understory (Billings *et al.*, 2004) but is rapidly recovering from the bark beetle infestation (J. Meerman, pers. obs.).

Methods

We conducted seven camera surveys, between January 2002 and June 2004, using a combination of CamTrakker (CamTrakker, Georgia, USA), DeerCam (models 100 and 200, DeerCam, Park Falls, USA), and TrailMaster (models 1550 and 550, Goodson & Associates, Lenexa, USA) cameras. Five grids were established in the rainforest and two in the pine forest (Table 1). Each station consisted of a pair of opposing cameras, at a height of 25–40 cm, to photograph both flanks of the animal. We programmed cameras to run continuously, with a 30 second delay between pictures. No bait or lure was

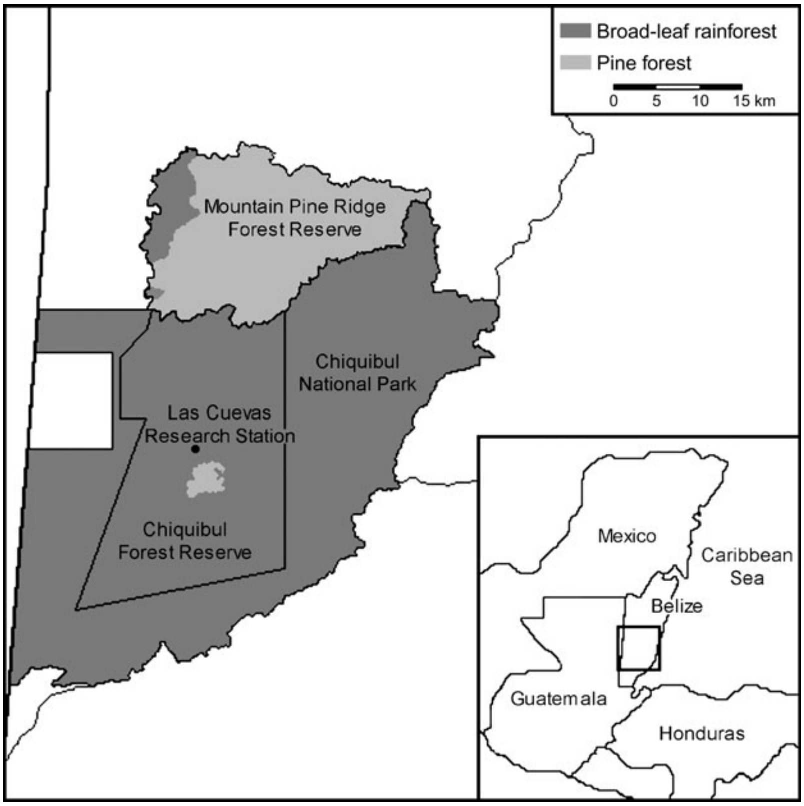

Fig. 1 Location of Chiquibul Forest Reserve and National Park and the Mountain Pine Ridge Forest Reserve in western Belize, indicating forest types. The box in the inset indicates the location of the main figure in Belize.

Table 1 Habitat type, camera spacing, number of cameras, season, dates, number of trapping occasions and number of trap nights for each of the seven camera trapping grids.

Camera grid[1]	Habitat	Mean camera spacing (m) ± SD	No. of camera stations	Season	Dates	Trapping occasions[2]	No. of trap nights
ORF1	Rainforest	2,922 ± 280	7	Dry	13/1/02–16/2/02	12	238
ORF2	Rainforest	510 ± 38	16	Wet	3/7/02–15/8/02	15	688
ORF3	Rainforest	2,691 ± 639	17	Dry	5/1/03–4/4/03	30	1,513
ORF4	Rainforest	2,896 ± 520	14	Wet	16/6/03–16/7/03	10	420
ORF5	Rainforest	1,342 ± 280	15	Wet	21/8/03–20/9/03	10	450
OPF1	Pine forest	2,911 ± 535	19	Dry	11/1/04–4/4/04	28	1,577
OPF2	Pine forest	1,039 ± 301	13	Wet	26/4/04–27/6/04	31	806

[1] ORF, ocelot rainforest; OPF, ocelot pine forest

[2] A trapping occasion consisted of a 3-day time period

used to attract animals and surveys were conducted for 30–90 days. We checked cameras every 10–14 days to change batteries and film and ensure proper functioning. Non-functioning cameras were replaced immediately. Although rare, double malfunctions did occur and those stations were omitted from analyses. Rarely did cameras run out of film or batteries between our frequent checks but for those that did, we subtracted those trap nights from the total.

Of the seven camera surveys three were set up specifically to estimate ocelot density, with distance between stations based on the smallest ocelot home range of 2 km^2 (Emmons, 1988). Camera stations were placed along roads, existing trails, and on newly cut trails at 0.5–1.5 km apart using a global positioning system (GPS) to determine location. Average camera spacing was determined by measuring the distance from a station to all adjacent stations and calculating the mean. The remaining four grids were initially set up to estimate jaguar density (ORF1, ORF3, ORF4 and OPF1) and were used to estimate ocelot density simultaneously (Table 1). To determine ocelot trap success for each survey the number of ocelot captures was divided by the available trap nights times 100.

We combined ocelot photographs from the five rainforest camera surveys to analyse ocelot rainforest activity patterns. We calculated the percentage of ocelots captured at each hour of the day as determined by the date and time stamp on each photograph and performed a χ^2 goodness of fit test to determine if ocelots were equally active during day and night. Camera stations were set up on one of the four following trail or road types; newly cut trails, established trails, low-use roads, and high-use roads. Newly cut trails were created with a machete through dense brush to place cameras at the required location. These trails were established no longer than 1 week prior to conducting the survey and, where possible, targeted game trails for camera placement. Established trails were narrow hiking trails or footpaths actively used by researchers on a regular basis (>1 per week). Low-use roads were old logging (dirt) roads that were much wider than footpaths and were travelled often by foot and occasionally (<1 per week) by 4-wheel drive or all-terrain vehicles. High-use roads were dirt roads that were travelled almost daily by 4-wheel drive vehicles and/or all-terrain vehicles. We used a χ^2 goodness of fit test to determine if ocelots used particular trail types more often than expected. In addition, we determined means and 95% confidence intervals for the proportion of ocelot pictures from each trail type and compared this with the proportion of stations available in each trail type to determine preference or avoidance. We divided the data into wet and dry seasons to determine whether trail preference changed by season.

Each photographed ocelot was identified by its unique spot patterns (Trolle & Kery, 2003). We collapsed each 3-day trapping period into a single trapping occasion and created a capture history for each ocelot within a survey. We used programme *CAPTURE* (Otis *et al.*, 1978; White *et al.*, 1982; Rexstad & Burnham, 1991) to estimate abundance for each survey. There were not enough ocelot captures in the pine forest to use *CAPTURE*, and therefore we substituted the probability of capture from the rainforest and divided the number of captures by this probability to estimate abundance (J. Nichols, pers. comm.). Because the probability of capture in the rainforest appears to be higher than that of the pine forest, our results probably represent a conservative estimate of ocelot density for the latter.

We determined the effective trap area of each grid by calculating a buffer value equivalent to ½ the mean maximum distance moved (½MMDM) among all ocelots photographed more than once (Karanth & Nichols, 1998). Buffers were placed around each station, dissolved, and combined to determine the effective area sampled. Although there is debate about the appropriate buffer value for camera surveys (Trolle & Kery, 2005; Soisalo &

Cavalcanti, 2006) this method has been determined to be robust in simulation studies (Wilson & Anderson, 1985) and is commonly used (Karanth & Nichols, 1998; Trolle & Kery, 2003; Maffei *et al.*, 2004; Silver *et al.*, 2004; Di Bitetti *et al.*, 2006). Ocelots captured repeatedly at a single camera station have a maximum distance moved of zero. We calculated densities both including and excluding these zero-distance animals to determine the impact on density estimates. We also pooled the maximum distances of ocelots across all five grids to determine a single buffer value for the entire rainforest habitat. This ½ overall mean maximum distance moved (½OMMDM) was determined both excluding and including zero-distance moved ocelots. Because of insufficient ocelot captures in the pine forest we used the ½OMMDM buffer values from the rainforest to determine the effective trapping area of each pine forest survey. This assumes similar ocelot movement patterns across habitats, an assumption that cannot be tested by this study.

To determine density we divided the population estimate from *CAPTURE* by the effective trap area, calculated in four separate ways for the broad-leaf rainforest and two for the pine forest, as described above. The standard error for each density estimate followed Nichols & Karanth (2002). There were not enough captures to determine a standard error for the pine forest density estimates. We used Spearman rank correlations to determine if distance between cameras affected density estimates across the five rainforest surveys.

Results

Across surveys, camera spacing was 510–2,922 m, total number of trap nights was 5,692, and 36 individual ocelots were captured 159 times (Tables 1 & 2). Trap success was 2.11–6.20 and 0.13–0.15 captures per 100 trap nights in the rainforest and pine forest, respectively (Table 2).

After eliminating photographs with time stamp malfunctions, we used 145 ocelot captures to construct the activity budget for the rainforest. Ocelots were not active equally night and day (all animals, $\chi^2 = 59.6$, $P < 0.001$; males, $\chi^2 = 41.4$, $P < 0.001$; females, $\chi^2 = 16.3$, $P < 0.001$) but demonstrated nocturnal behaviour with the majority of activity between 19.00 and 4.00, peaking after sunset at 19.00 and again at 1.00 (Fig. 2). When separated by sex, males and females showed similar activity patterns, with females appearing more variable, probably because of the small sample size. Ocelots did not use trails as expected by their relative distribution ($\chi^2 = 42.9$, $P < 0.001$). Across all grids and seasons, ocelots were photographed on new and established trails less than they were available and on low- and high-use roads more than they were available (Fig. 3a). When separated by season, ocelots avoided new trails and preferred low-use roads in the wet season, and avoided new and established trails and preferred high-use roads in the dry season (Fig. 3b).

CAPTURE was unable to reject the closure assumption for any camera survey. With only one exception, model M_h (jackknife estimator) had the highest model selection value (or second highest relative to the null model) and for consistency was used to estimate the ocelot population size for each survey. This model assumes each ocelot has a unique capture probability, which is logical because of ocelot territoriality and unequal home range sizes between sexes. Population estimates were 6–26 and 1–3 in the rainforest and pine forest, respectively (Table 2).

Table 2 Number of ocelot captures, recaptures, individuals, males, females and unknown individuals for each camera trapping grid (Table 1), with number of photo-captures per 100 camera-trap nights (i.e. camera-trap success), estimated population size (± SE) and estimated probability of capturing an ocelot. Estimated population size for the two camera grids in pine forest was determined using the probability of ocelot capture in the rainforest habitat.

Camera grid[1]	Captures	Recaptures	Individuals	Males	Females	Unknown	Captures per 100 trap nights	Estimated population size ± SE[2]	Probability of capture
Broad-leaf rainforest									
ORF1	10	6	4	2	2	0	2.11	6 ± 1.97	0.1875
ORF2	23	18	5	1	4	0	5.71	6 ± 1.49	0.2667
ORF3	82	63	19	9	10	0	5.60	21 ± 3.27	0.1281
ORF4	20	6	14	8	5	1	4.37	26 ± 7.02	0.1120
ORF5	21	12	9	4	5	0	6.20	10 ± 2.74	0.1665
Pine forest									
OPF1	2	0	2	0	1	1	0.13	3	
OPF2	1	0	1	1	0	0	0.15	1	
Total	159	105	54	25	27	2			

[1] ORF, ocelot rainforest; OPF, ocelot pine forest

[2] Calculated using the Otis jackknife heterogeneity estimator (M_h) from programme *CAPTURE*

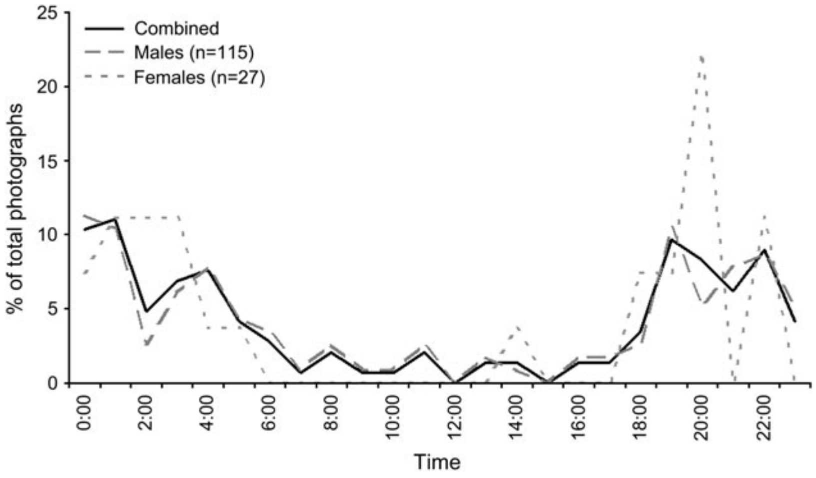

Fig. 2 Camera trapping activity budget for males, females, and all ocelots combined in the rainforest site.

Across surveys ocelot movement between cameras was 0.93–2.43 km when zero-distance moved animals were excluded and 0.93–1.95 km when included (in the unique ½MMDM analysis). Three surveys (ORF1, ORF2 and ORF5) contained no zero-distance moved ocelots and the effective trap area remained the same. But for two grids (ORF3 and ORF4) the ½MMDM decreased when zero-distance moved ocelots were included, resulting in a smaller buffer and effective trap area. Across all rainforest grids the ½OMMDM value was 1.56 km excluding zero-distance moved ocelots and 1.24 km including them. As expected, the resulting effective trap area decreased when the zero-distance moved ocelots were included but to a lesser extent than when using the unique ½MMDM method.

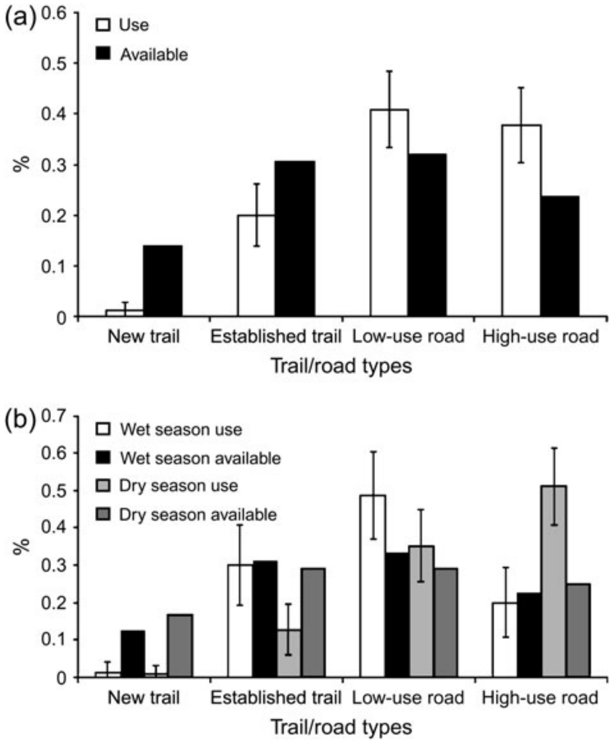

Fig. 3 Percentage use of trail and road types (with 95% confidence intervals) by ocelots for all camera trap grids combined in the rainforest compared to (a) overall availability and (b) availability by season.

Ocelot density estimates for the rainforest were 10.79–53.72 ocelots per 100 km^2 using unique ½MMDM values (Fig. 4). For two grids inclusion of zero-distance moved ocelots increased density estimates and their standard errors. This difference was substantial for one survey (ORF3), where density doubled from 19.3 to 38.5 ocelots per 100 km^2 (Fig. 4). When pooling distances moved (i.e. ½OMMDM) across all rainforest surveys, density was 11.74–29.78 or 17.84–38.96 ocelots per 100 km^2 when zero-distance moved ocelots were excluded or included, respectively (Fig. 4). As expected, buffer sizes decreased and density estimates and standard errors increased when including zero-distance moved ocelots. In the pine forest ocelot density estimates were 2.31–3.01 or 3.38–3.80 ocelots per 100 km^2 when zero-distance moved ocelots were excluded or included in the ½OMMDM analysis, respectively (Fig. 4). There were negative relationships between density estimates and camera spacing that were significant in three out of four cases (Fig. 5).

Discussion

The extent to which ocelots exhibit nocturnal behaviour is variable from site to site (Ludlow & Sunquist, 1987; Emmons, 1988; Konecny, 1989; Sunquist *et al.*, 1989; Crawshaw, 1995; Di Bitetti *et al.*, 2006) but the results from this study demonstrated that, although active at any time, ocelots are nocturnal in the rainforest habitat

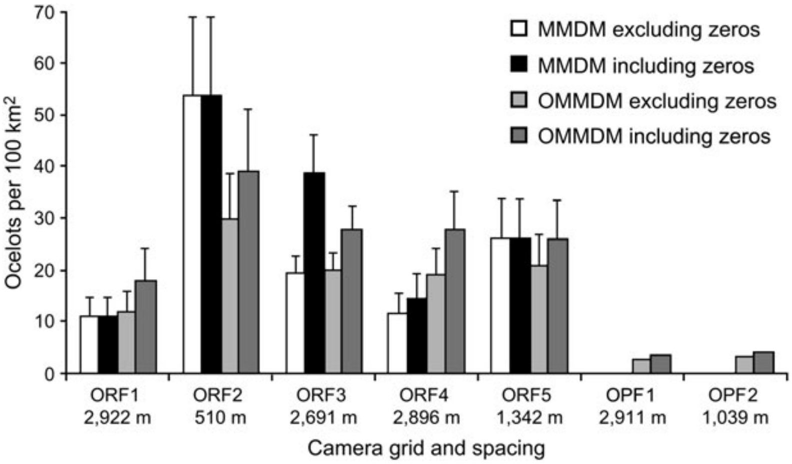

Fig. 4 Estimates of ocelot density per 100 km^2 (with SE bars) for each rainforest camera grid (ORF1-5) using both ½MMDM and ½OMMDM values and excluding and including zero-distance moved ocelots (see text for details), and for the two pine forest camera grids (OPF1-2) using the rainforest ½OMMDM values and excluding and including zero-distance moved ocelots.

surveyed. More data are needed to assess ocelot activity in the pine forest habitat.

Ocelots avoided new and established trails and selected low- and high-use roads. This highlights the importance of using existing road systems for camera trapping, or of establishing a permanent trail system, such that ocelots come to use these paths, as has been noted in other studies (Maffei *et al.*, 2004). Ocelots perhaps preferred high-use roads during the dry season because these roads are easier to traverse during the season when prey and water become more scarce and they must travel further to meet their energy requirements (Ludlow & Sunquist, 1987).

With nearly 3 km between traps, a few ocelots displaying long distance movements or dispersal are captured at multiple stations, inflating the MMDM and potentially underestimating density. This study highlights the strong impact of buffer size on density estimates and suggests that when camera spacing is large relative to the radius of the animal's home range, zero-distance animals should be included in the analysis to avoid inflated buffer values. Excluding these animals should not be the norm but rather, camera spacing should be taken into account in the decision about whether or not to include them. However, in a recent study, GPS-collared jaguars demonstrated that camera

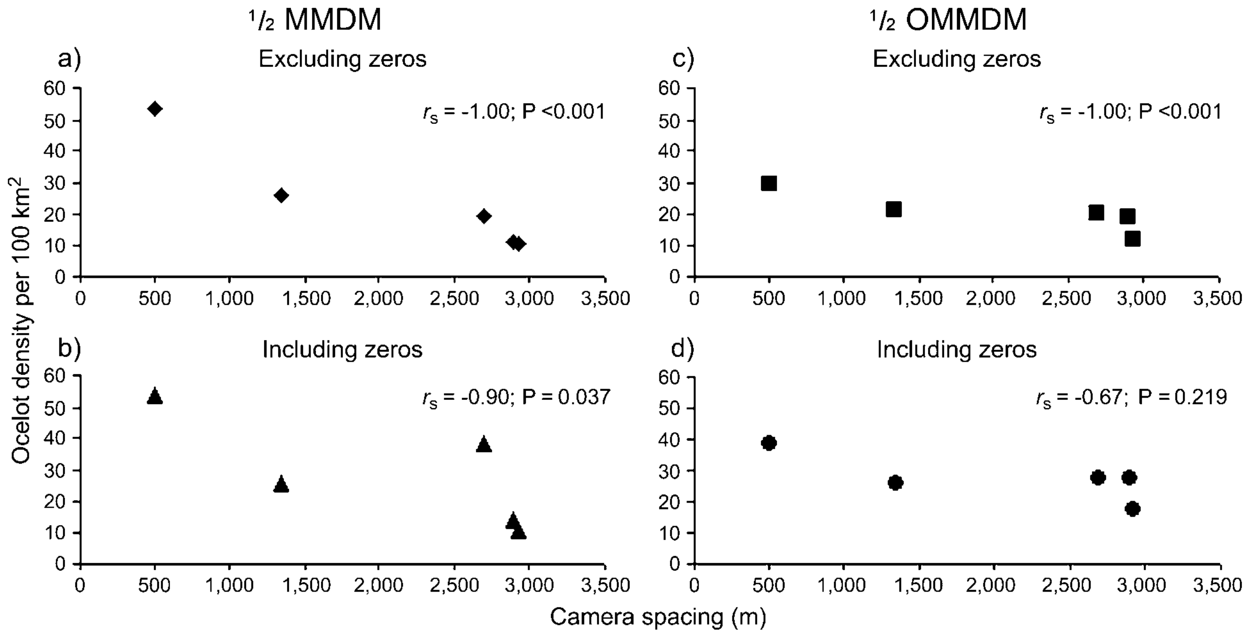

Fig. 5 Estimates of ocelot density in the rainforest determined using both ½MMDM and ½OMMDM values and excluding and including zero-distance moved individuals (see text for details) versus average camera spacing, with correlation coefficients.

traps underestimated distances moved (Sosiolo & Cavalcanti, 2006). We cannot assess whether our cameras may have underestimated ocelot distances until home range data are available for analysis.

With close camera spacing the true maximum distance moved by an animal may be impossible to detect because there is a trade-off between close camera spacing and the need to cover a sufficient area. Our 510 m grid covered a small effective survey area of 11–20 km^2 that is probably not large enough to include many complete ocelot home ranges yet is large enough to include many home range edges or transient animals, leading to an overestimate of density. Of the distances we used we believe that our 1.34 km camera spacing was most appropriate as all animals were captured at multiple stations and the area surveyed was probably large enough to encompass many home ranges. While there is no ideal size for the area to be surveyed, our results indicate that 40–50 km^2 is adequate to obtain precise density estimates for rainforest habitat at our site.

When grid specific ½MMDM values were used to estimate ocelot density a greater than five-fold difference separated the largest and smallest estimate. Because the rainforest camera surveys were conducted in the same area and within 22 months, the variation in density is more likely because of camera spacing and inclusion of zero-distance animals rather than actual changes in ocelot density. Pooling animal distances moved across all surveys and including zero-distance animals ameliorates this effect somewhat as this density estimate (½OMMDM, 25.82 ocelots per 100 km^2) was most similar to our ocelot specific 1.34 km camera survey (ORF5, 25.88 ocelots per 100 km^2).

Whereas it would be economical and efficient to estimate several animal densities (e.g. jaguars and ocelots) simultaneously during a single camera survey, our results call into question the efficacy of such a technique. There is an inverse relationship between camera spacing and density estimates. Because of the variation in home range size among different animals and across habitats, camera trapping specifications should be tailored specifically to the species and habitat being studied. As a guideline for ocelots, we suggest a pilot study be conducted with camera stations spaced at approximately 1.5 km. If multiple animals are photographed at only one station, then cameras are probably too far apart and should be placed closer together.

Although ocelots occur in a wide range of habitats, our results show they occur in much higher numbers in the rainforest than the pine forest, pointing to the importance of rainforest habitat for ocelots in Belize. La Selva Maya is a biodiversity hotspot and a high priority area for conservation (CEPF, 2005) yet no information has previously been published on ocelot abundance there. Given that this area is experiencing some of the fastest habitat loss on earth (CEPF, 2005) the lack of information on ocelot population status hampers our ability to provide for their conservation. This study provides baseline data for comparison with future abundance estimates in the rainforest. Ongoing research in the pine forest will determine whether ocelot numbers increase as the pine forest regenerates from the bark beetle infestation.

This study has provided the first estimates of ocelot density for Central America and provided recommendations for standardizing camera trapping protocol across sites and surveys that will facilitate comparisons. Our estimates of ocelot density in the rainforest were low compared to several other sites within the ocelot's range but were similar to estimates in the thorn scrub forest of Texas (Haines *et al.*, 2006), the subtropical forests of Brazil (Crawshaw, 1995) and the Atlantic forests of Argentina (Di Bitetti *et al.*, 2006; Table 3). Given the 628.5 km^2 of rainforest and 378.8 km^2 of pine forest in the Chiquibul Forest Reserve and National Park and the Mountain Pine Ridge Forest Reserve, respectively, an estimated population of 170–187 ocelots resides within the forested areas of these two reserves combined, representing an important area within La Selva Maya for ocelot conservation and monitoring. Long-term monitoring will

Table 3 Estimated ocelot density (per 100 km^2) in various habitats, with corresponding method and reference.

Location	Habitat	Method	Density	Reference
Argentina	Atlantic forest	Remote camera	12.9–19.1	Di Bitetti *et al.*, 2006
Belize	Tropical rainforest	Remote camera	25.8–25.9	This study
Belize	Tropical pine forest	Remote camera	2.3–3.8	This study
Bolivia	Dry forests	Remote camera	24.0–66.0	Maffei *et al.*, 2005
Brazil	Subtropical forest	Radio telemetry	13.7	Crawshaw, 1995
Brazil	Pantanal	Remote camera	62.0	Trolle & Kery, 2003
Peru	Tropical rainforest	Radio telemetry	80.0	Emmons, 1987
Texas	Thorn scrub forest	Remote camera	30.0	Haines *et al.*, 2006
Venezuela	Llanos	Radio telemetry	40.0	Ludlow & Sunquist, 1987

continue in both protected areas with nested grids of camera traps inside the larger jaguar/puma camera trapping grids. In addition, analysis of data on a micro- and macro-habitat scale across both reserves is currently underway and will elucidate factors that influence ocelot trap success and densities at these sites, giving us further insight into ocelot ecology across habitats.

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