Journal of Zoology

ZSL LIVING CONSERVATION

Journal of Zoology. Print ISSN 0952-8369

# Ocelot home range, overlap and density: comparing radio telemetry with camera trapping

A. Dillon* & M. J. Kelly

Department of Fisheries and Wildlife, Virginia Tech, Blacksburg, VA, USA

**Keywords**
ocelot; Belize; camera traps; density; home range; MMDM.

**Correspondence**
Adam Dillon, Department of Fisheries and Wildlife, Virginia Tech, 147 Cheatham Hall, Blacksburg, VA 24061-0321, USA.
Tel: +847 712 4582
Email: adillon@vt.edu

*Current address: Adam Dillon, 2022 Dexter Ave N Apt B, Seattle, WA 98109, USA.

Editor: Nigel Bennett

Received 29 October 2007; revised 25 March 2008; accepted 27 March 2008

doi:10.1111/j.1469-7998.2008.00452.x

## Abstract

Because ocelots *Leopardus pardalis* and other solitary carnivores are elusive and hard to study, little is known about their density and population status. In the past few years, camera trapping and mark–recapture statistics have been used to estimate the density of a number of felids. Although camera trapping is now providing baseline data for managers and conservationists alike, recent doubts have been raised concerning the accuracy of the standard camera trapping procedure. We used radio telemetry to gain new information on ocelot home-range size and spatial organization in Central America, and compared the radius of our average ocelot home range with the standard camera trapping buffer. We compared the resulting density estimates to assess the current camera trapping methodology's ability to estimate animal density. Five adult ocelots (two male and three female) were tracked to determine an average ocelot home range of 26.09 $km^2$ (95% fixed kernel) and 18.91 $km^2$ (100% minimum convex polygon), with males demonstrating larger ranges than females. All ocelots had larger home ranges in the dry season. Male–male home-range overlap averaged 9% while female–female overlap averaged 21%. Males shared 56% of their range with a primary female and 16% with a second and third female, while females shared 58% of their home range with a primary male and 3% with a secondary male. Density estimates based on the average home-range radius (11.24–12.45 ocelots per 100 $km^2$) were less than those determined from standard camera trapping methods (25.88 ocelots per 100 $km^2$), but similar to those determined using twice the camera trapping buffer to estimate density (12.61 ocelots per 100 $km^2$). Our results suggest that a standard camera trapping protocol may overestimate ocelot density. Accurate representation of animal densities and standardization of density estimation techniques are paramount for comparative analyses across sites and are vital for felid conservation.

## Introduction

Historically, ocelots *Leopardus pardalis* ranged in large numbers from the southern United States to northern Argentina (Murray & Gardner, 1997). Owing to hunting pressure and habitat loss throughout the 1980s and mid-1990s, ocelots were considered to be Vulnerable on the IUCN Red List (IUCN, 2006). Although bans on the international fur trade have decreased the ocelot's status to a species of Least Concern (IUCN, 2006), habitat loss continues to threaten persistence and population data are scarce (Sunquist & Sunquist, 2002). Gaining information on status is difficult because, like many felids, ocelots are solitary and elusive by nature. Recently, remote camera trapping has been used to study a variety of felids (e.g. tigers *Panthera tigris* Karanth & Nichols, 1998; Karanth *et al*., 2006; jaguars *Panthera onca* Kelly, 2003; Maffei, Cuellar & Noss, 2004; Silver *et al*., 2004; pumas *Puma concolor* Kelly *et al*., 2008; ocelots *L. pardalis* Maffei *et al*., 2005; DiBitetti, Paviolo & DeAngelo, 2006; Dillon & Kelly, 2007; bobcats *Lynx rufus* Heilbrun *et al*., 2006; Kelly & Holub, 2008; Geoffroy's cat *Oncifelas geoffroyi* Cuellar *et al*., 2006).

The standard method to estimate animal density via camera traps is to estimate population size through capture–recapture statistics and divide the abundance estimate by the effective trap area of the camera survey. The effective trap area is determined by placing a buffer, equal to 1/2 the mean maximum distance moved (1/2 MMDM) of all 'recaptured' animals, around the entire camera trapping grid (Karanth, 1995), or around each camera station (Silver *et al*., 2004). Because most camera studies lack data on the target animal's home range, the 1/2 MMDM buffer is used as a proxy for home-range radius (Wilson & Anderson, 1985; Karanth & Nichols, 2002).

Although camera trapping is quickly becoming an accepted technique for estimating felid abundance and density, recent studies have shown that reduced spacing between cameras (Dillon & Kelly, 2007), small survey area (Maffei & Noss, 2008) and lack of information on true home-range size (Soisalo & Cavalcanti, 2006) can underestimate the effective survey area, resulting in overestimates of density. Overestimation of density could lead to underestimates of the risk faced by threatened and endangered felid species and could hence slow the implementation of conservation strategies.

This study used camera trapping surveys and radio telemetry tracking of ocelots simultaneously. We obtained information on ocelot ranging behavior, allowing us to determine whether 1/2 MMDM was an appropriate surrogate for home-range radius. Our goals were: (1) to use radio telemetry to provide much-needed information on ocelot movement, home-range size and territory overlap; (2) to estimate buffer values from camera trapping and radio telemetry and compare their resulting density estimates; (3) to provide guidelines for future camera trapping surveys.

## Study site

The study was conducted out of the Las Cuevas Research Station (16°43′53″N, 88°59′11″W), which is located within the Chiquibul Forest Reserve and National Park (CFRNP, 1670 $km^2$) of western Belize. These reserves, combined with areas of northern Guatemala and southern Mexico, comprise La Selva Maya, the largest intact tropical rainforest in Central America (CEPF, 2005). This region is subjected to frequent hurricanes and is dominated by secondary broadleaf forest, with areas of primary and gallery forest. The average annual rainfall is 150–200 cm, with a rainy season from June to December (Beletsky, 1999).

## Methods

### Camera trapping

We used a combination of CamTrakker (CamTrakker, GA, USA), DeerCam (models 100 and 200, DeerCam, Park Falls, WI, USA) and TrailMaster (models 1550 and 550, Goodson & Associates, Lenexa, KS, USA) cameras to conduct five surveys, utilizing seven to 17 camera stations at a variable systematic spacing of 510–2922 m for 238–1513 available trap nights (Dillon & Kelly, 2007). All surveys were conducted in the CFRNP between January 2002 and June 2004. Because previous results indicated that increased camera spacing increased the 1/2 MMDM and decreased estimated ocelot density (Dillon & Kelly, 2007), we used only the ocelot-specific camera grid of 15 stations at $\sim$1500 m ($1342 \pm 280$ m) spacing for comparative analysis in this paper. The smallest estimated ocelot home range was 2 $km^2$ (Emmons 1988) and hence our 1500 m spacing should leave no holes in the grid and each ocelot should have a probability of being captured. We used program CAPTURE (Otis *et al*., 1978; White *et al*., 1982; Rexstad & Burnham, 1991) to estimate ocelot abundance ($\hat{N}$), and we used the 1/2 MMDM of all ocelots photographed at more than one camera station to estimate the effective survey area (Karanth & Nichols, 1998).

### Radio telemetry

Tomahawk box traps (Tomahawk Trap Co. Model 109.5, Tomahawk, WI, USA) were baited with a live chicken and a combination of lures (marak lures: bobcat, coyote, gray fox, raccoon) from August 2003 to June 2004 (Animal Care & Use Committee #03-055-F&W and #04-115-F&W). Ocelots were immobilized with a mixture of telazol (25 mg), xylazine (15 mg) and butorphanol (1 mg). Additional doses of ketamine (20 mg) were administered as needed. Anesthetized animals were weighed, measured, photographed for identification and fitted with ATS M2140 (Advanced Telemetry Systems, Isanti, MN, USA) radio collars, at which point they were reversed using Yohimbine. Ocelot trapping was conducted at the end of the study in order to remove radio collars.

Error testing was performed on collars of known location to determine the average bearing error and standard deviation ($5.98^\circ \pm 4.92$) across the study site (White & Garrott, 1990; Millspaugh & Marzluff, 2001). From August 2003 to August 2004, all collared ocelots were located using an ATS R4000 receiver and a Yagi 3-element directional antenna. Simultaneous triangulation/biangulation locations were taken one to two times daily and at least 4 h apart to avoid autocorrelation (White & Garrott, 1990). The standard deviation of the bearing error was entered into program LOAS (Location Of A Signal – Ecological Software Solutions, http://www.ecostats.com) to estimate each ocelot location and error ellipse. If the error ellipse was larger than an arbitrarily determined 0.2 $km^2$, which seemed reasonable given the ocelots' ranging behavior, the estimated location was recorded but omitted from the analysis.

### Home range

Ocelot locations were separated into three intervals: 2003 wet season (August–December), 2004 dry season (January–April) and 2004 wet season (May–August). The Home Range Extension (Rodgers & Carr, 1998) in ArcView 3.2 was used to determine a 95% fixed kernel (FK) and a 100% minimum convex polygon (MCP) home range for each ocelot during each season. Kernel home ranges were determined using an arbitrary 95% contour, as is commonly used in kernel analysis (Worton, 1989). MCP home ranges were determined using 100% of the locations for each ocelot, excluding outliers resulting from large error ellipses. All kernel ranges were determined using unit variance standardization, least squares cross validation and a raster resolution of 70 (Seaman & Powell, 1996; Rodgers & Carr, 1998). We used Student's *t*-tests to determine whether male and female home-range sizes differed significantly and a paired *t*-test to determine whether home-range size differed between seasons (Sokal & Rohlf, 1995). We used a significance level of $\alpha = 0.10$ because our sample sizes were low for most comparisons.

### Minimum home-range overlap

Because MCP home ranges are two dimensional, they were used to determine the home-range overlap between ocelots.

For each target ocelot with $>20$ locations per seasons, the per cent every other ocelot overlapped its territory was determined per season. We averaged per cent overlap across seasons to determine average male–male and female–female per cent overlap. We determined the per cent a single female, two females and three females overlapped a single male and then averaged across seasons to determine overall male–female overlap. Because females were unequally overlapped by males, we determined a primary male (1°), secondary male (2°) and a combined male overlap and then averaged them across seasons to determine overall female–male overlap.

### Daily distance moved

Consecutive radio telemetry locations between 12 and 36 h apart were used to determine the daily distance moved for each ocelot. We averaged the linear distance between each pair of consecutive readings across all locations to estimate an average daily distance moved per individual. We used Student's *t*-tests to determine whether there were differences between the sexes.

### Buffer values

We followed standard methodology, determining the maximum distance moved of each ocelot photographed at more than one camera station, and averaged those distances across all cats (Karanth & Nichols, 1998). We estimated two camera trapping buffers: the standard 1/2 MMDM (Karanth, 1995; Karanth & Nichols, 1998) and a more conservative full MMDM buffer (Soisalo & Cavalcanti, 2006). These buffers were placed around each camera station to estimate the effective survey area (Silver *et al*., 2004).

Because the standard camera trapping protocol uses a 1/2 MMDM buffer as a proxy for the radius of a home range (Karanth, 1995; Karanth & Nichols, 1998), we used our radio telemetry data to determine the 1/2 MMDM across a home range and the average home-range radius. Our camera survey was conducted in the wet season; therefore, we used only our radio telemetry data from either wet season to determine our buffer values. We averaged home-range size (95% FK and 100% MCP) across all ocelots and then assumed a circular home range to determine each radius, respectively. These buffers were placed around each camera station to estimate the effective survey area.

### Density: camera trapping and radio telemetry

To estimate ocelot density, we divided the population estimate ($\hat{N}$) derived from program CAPTURE by five separate values of the effective survey area, each derived from a separate buffer value: (1) camera trapping 1/2 MMDM; (2) camera trapping full MMDM; (3) radio telemetry 1/2 MMDM across a home range; (4) radius of an average wet season 95% FK radio telemetry home range; (5) the radius of an average wet season 100% MCP radio telemetry home range. The standard error for each density estimate followed Nichols & Karanth (2002).

## Results

### Camera trapping

We obtained 22 ocelot captures of nine individuals (four male and five female) and 13 recaptures over 412 trap nights, resulting in a trap success of 5.34 ocelots per 100 trap nights. Estimated ocelot population size was $10 \pm 2.74$ using the M(h) model and capture probability was 0.1665 with no violation of closure ($z = 0.55$, $P = 0.71$). Five ocelots were used to determine a 1/2 MMDM of 1.24 km, resulting in an effective survey area of 38.64 $km^2$.

### Radio telemetry

Throughout the study, we had 13 ocelot live captures of seven individuals (three males and four females, with six recaptures) over 1040 trap nights, resulting in a trap success of 1.25 ocelots per 100 trap nights. Although seven ocelots were captured, one female was captured at the end of the study and therefore not collared. An old adult male was collared and tracked for a month before dying. Because this male had no established territory, he was omitted from the analysis, resulting in five radio-collared ocelots (two male, three female). A total of 686 locations were taken throughout the year, 11 of which were omitted due to large error ellipses. Within individual seasons, ocelots were located between 34 and 109 times ($\bar{X} = 57.4 \pm 20.0$).

### Home range

Average home range for all ocelots was $26.09 \pm 7.33$ $km^2$ (95% FK) and $18.91 \pm 4.60$ $km^2$ (100% MCP) (Table 1; Fig. 1). Average 95% FK home ranges were significantly larger for males than females ($\bar{X}$'s = 33.21, 21.33 $km^2$; $t = 3.34$; $P = 0.044$) but their 100% MCP home ranges were not significantly different ($\bar{X}$'s = 19.73, 18.37 $km^2$; $t = 0.28$; $P = 0.796$). The wet season home ranges were significantly larger than the dry season ranges (95% FK: $\bar{X}$'s = 24.74, 31.32 $km^2$, $t = 3.28$, $P = 0.082$; 100% MCP: $\bar{X}$'s = 18.47, 19.56 $km^2$, $t = 3.71$, $P = 0.066$) for the three ocelots (one male and two female) tracked across all seasons.

### Minimum home-range overlap

Although five ocelots (two males and three females) were collared and tracked for this study, there were likely other individuals in the study area that were not captured; therefore, the home-range overlap reported here represents a minimum per cent overlap. The per cent of a male's home range overlapped by the second male was 2.55–14.79% ($\bar{X} = 9\%$) (Fig. 2). The per cent of a female's home range that was overlapped by another female was 3.90–25.96% (1°♀$\bar{X} = 16\%$, 2°♀$\bar{X} = 4\%$) and by both other females was 0.03–3.84% ($\bar{X} = 1\%$). The per cent of a male's home range that was overlapped by a single female was 46.10–62.89% ($\bar{X} = 56\%$), by any two females was 4.27–24.05% ($\bar{X} = 15\%$) and by all three females was 0.02–2.80% ($\bar{X} = 1\%$). The

**Table 1** Average 95% fixed kernel (FK) and 100% minimum convex polygon (MCP) home ranges ($km^2$) across all seasons for each ocelot *Leopardus pardalis* (number of seasons), males, females and all ocelots combined

| Average home range across all seasons | | | | | | | |
|---|---|---|---|---|---|---|---|
| 95% FK | | | | 100% MCP | | | |
| Male | | Female | | Male | | Female | |
| O7 | 29.87 (1) | O6 | 25.23 (3) | O7 | 14.89 (1) | O6 | 1.66 (3) |
| O26 | 36.55 (3) | O32 | 19.00 (3) | O26 | 24.56 (3) | O32 | 15.28 (3) |
| | | O35 | 19.77 (1) | | | O35 | 23.18 (1) |
| Average male | 33.21 ± 4.72 | Average female | 21.33 ± 3.40 | Average male | 19.73 ± 6.84 | Average female | 18.37 ± 4.22 |
| Average ocelot 26.09 ± 7.33 | | | | Average ocelot 18.91 ± 4.60 | | | |

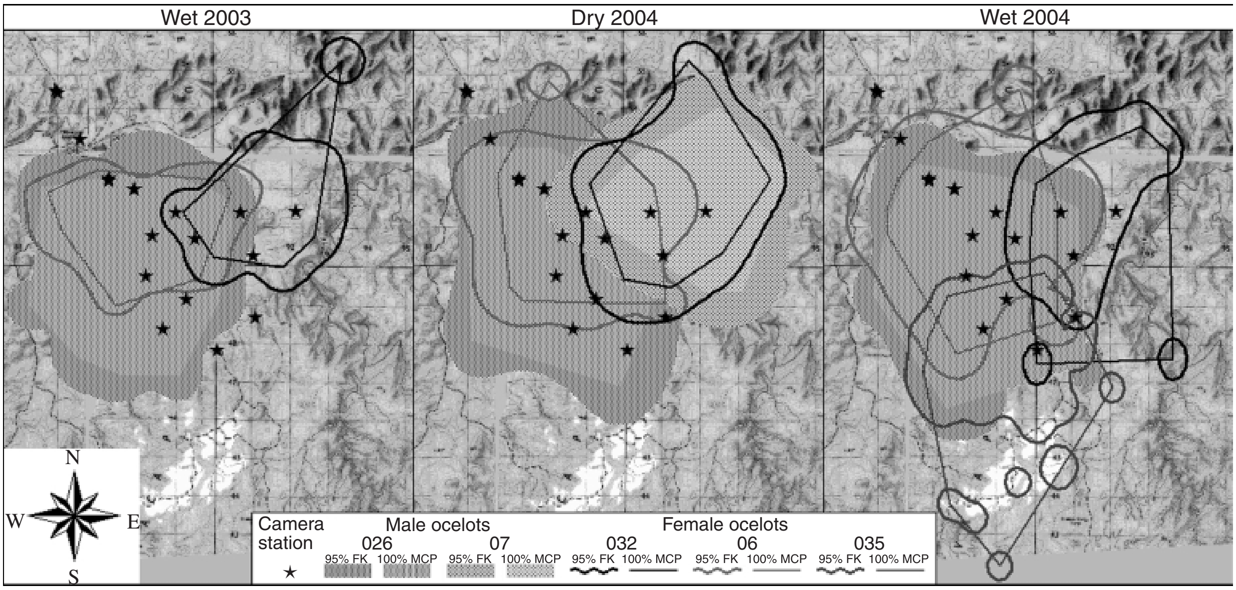


**Figure 1** Location of each camera station and the 95% fixed kernel (FK) and 100% minimum convex polygon (MCP) home range for each ocelot *Leopardus pardalis* during each season.

per cent of a female's home range that was overlapped by a single male was 1.26–92.94% ($1^{\circ}$♂$\bar{X} = 58\%$, $2^{\circ}$♂$\bar{X} = 3\%$) and by both males was 2.73–12.53% ($\bar{X} = 5\%$). Because all single-season home ranges were used to determine average home-range overlap, some ocelots were included more than once in this analysis.

## Daily distance moved

The average daily distance moved for all ocelots was 1.90 ± 0.25 km. Daily distance moved was significantly higher for males than for females ($\bar{X}$'s = 2.14, 1.74, $t = 3.33$, $P = 0.045$).

## Buffer values

The camera trapping 1/2 MMDM and full MMDM buffer values were 1.24 and 2.47 km, respectively (Table 2). The maximum distances moved for radio telemetry ocelots ranged from 6.70 to 7.67 km with a 1/2 MMDM of 3.53 km. Radii of the average ocelot wet season home range were 2.73 km (95% FK) and 2.50 km (100% MCP). The effective trap area ranged from 38.64 to 120.67 $km^2$ (Table 2).

## Density: camera trapping and radio telemetry

The estimated ocelot densities determined via 1/2 MMDM and full MMDM camera trapping buffers were 25.88 and 12.61 ocelots per 100 $km^2$, respectively (Table 2). The estimated ocelot density determined via radio telemetry ranged from 8.29 to 12.45 ocelots per 100 $km^2$ (Table 2). Although the radio telemetry density estimates were lower than the camera trapping density estimates, those derived from the radius of an average ocelot home range were similar to those derived from a full MMDM camera trapping buffer.

# Discussion

This study provides new information on ocelot home-range size, overlap and density in Central America. Ocelot home-

 

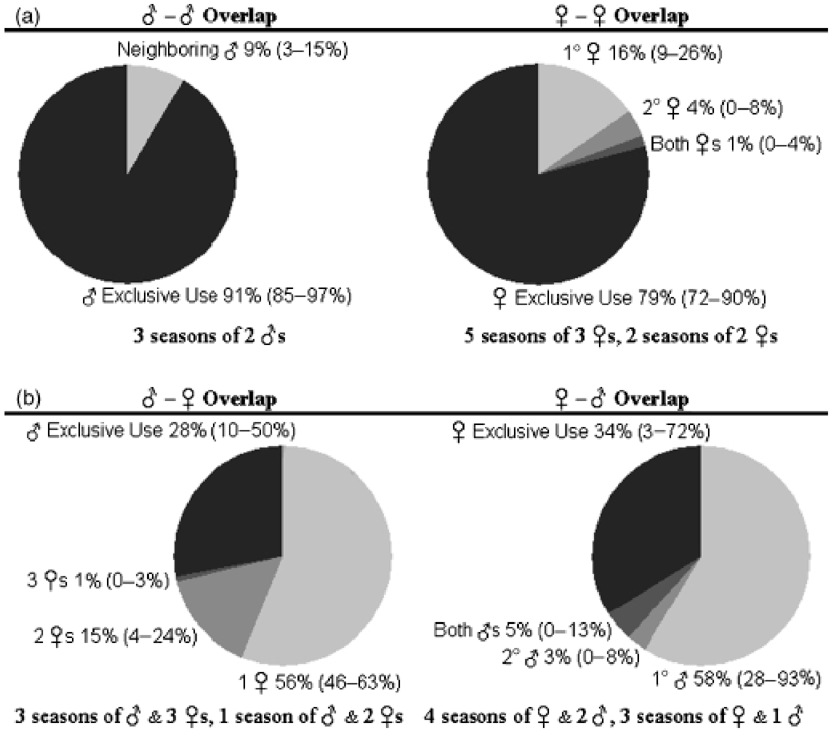


**Figure 2** Per cent of male and female ocelot's *Leopardus pardalis* 100% MCP home range that was used exclusively and overlapped by neighboring (a) same-sex and (b) opposite-sex ocelots, with respective sample sizes. MCP, minimum convex polygon.

range size was much larger in the broadleaf forest of western Belize then in most other areas of their range (Table 3). As suspected, male ocelots demonstrated larger home ranges and daily distances than females, and all ocelots demonstrated larger home ranges during the dry season, when food is thought to be more scarce. Ocelots demonstrated a high degree of same-sex and opposite-sex home-range overlap. Male ocelots are known to overlap more than one female's range (Murray & Gardner, 1997) and our results supported this, with 50–90% of a male's territory being overlapped by up to three females. Interestingly, up to 13% of a female's territory was overlapped by two males, suggesting the potential for females to exert mate choice. In areas where home ranges are smaller (i.e. Bolivia, Maffei & Noss, 2008), ocelots may exhibit more exclusive range use because they can more efficiently patrol and mark their territories, behavior that is likely more difficult across large ranges. This insight points to flexibility in ocelot movement patterns and social structure across sites, which may impact camera trapping density estimation at each location.

The effective survey area, and more specifically the buffer value, likely introduces the largest source of variation in density estimation. The standard camera trapping 1/2 MMDM produced buffers that were less than half the size of all radio telemetry buffers. Because the theoretical basis for the camera trapping 1/2 MMDM buffer is to approximate the radius of the animal's home range, our results call into question the reliability of this proxy and point to the potential for the standard camera trapping methodology to overestimate density (Soisalo & Cavalcanti, 2006).

**Table 2** Estimated population size ($\hat{N}$) from CAPTURE M(h) model, camera trapping and radio telemetry buffer values and their respective effective survey areas, densities and standard errors

| Buffer source | $\hat{N}$ | Buffer value (km) | Effective area (km$^2$) | Density per 100 km$^2$ | Standard error per 100 km$^2$ |
|---|---|---|---|---|---|
| Camera trapping (five ocelots) | | | | | |
| 1/2 MMDM | 10 | 1.24 | 38.64 | 25.88 | 7.92 |
| Full MMDM | 10 | 2.47 | 79.33 | 12.61 | 3.66 |
| Radio telemetry (four ocelots) | | | | | |
| 1/2 MMDM | 10 | 3.53 | 120.67 | 8.29 | 2.29 |
| 95% Fixed kernel radius | 10 | 2.73 | 88.97 | 11.24 | 3.22 |
| 100% MCP radius | 10 | 2.50 | 80.31 | 12.45 | 3.50 |

MMDM, mean maximum distance moved; MCP, minimum convex polygon.

**Table 3** Average ocelot *Leopardus pardalis* home range ($km^2$) in various habitats with the corresponding method and sample size (*n*)

| Location | Habitat | Method | Male (*n*) | Female (*n*) |
|---|---|---|---|---|
| Brazil[a] | Subtropical forest | MCP | 43.25 (11) | 16.03 (10) |
| Belize[b] | Tropical rainforest | MCP | 19.73 (2) | 18.37 (3) |
| | | Fixed kernel | 33.21 (2) | 21.33 (3) |
| Belize[c] | Subclimax rainforest | MCP | 31.25 (1) | 14.68 (1) |
| Texas[d] | Thorn scrub | Harmonic–Contour | 17.67 | 11.04 |
| Venezuela[e] | Llanos | Minimum area | 10.40 (2) | 3.35 (6) |
| Venezuela[f] | Llanos | MCP | 9.70 (1) | 2.54 (2) |
| Texas[g] | Thorn scrub | MCP | 6.25 (3) | 2.87 (3) |
| Bolivia[h] | Tropical dry forest | MCP | 3.94 (2) | 2.99 (4) |
| Texas[i] | Thorn scrub | Minimum area | 2.50 | 2.10 |
| Peru[j] | Tropical rainforest | MCP | – | 1.98 (1) |

[a]Crawshaw (1995).
[b]This study.
[c]Konecny (1989).
[d]Tewes (1986).
[e]Ludlow & Sunquist (1987).
[f]Sunquist, Sunquist & Daneke (1989).
[g]Laack (1991).
[h]Maffei & Noss (2008).
[i]Navarro (1985).
[j]Emmons (1988).
MCP, minimum convex polygon.

Our study demonstrated that the standard camera trapping 1/2 MMDM buffer substantially underestimated the radius of an average home range, whereas the full camera trapping MMDM buffer was much similar to the average home-range radius. Use of the full MMDM camera trapping buffer, as suggested by Parmenter *et al*. (2003), Trolle & Kery (2005) and Soisalo & Cavalcanti (2006), produced estimates of density that were very similar to those estimates based on our home-range radii.

In contrast to the results above, Maffei & Noss (2008) found that the camera trapping 1/2 MMDM accurately reflected ocelot home range in Bolivia, and found that the undersized total survey area was leading to lower buffer values and overestimates of density. If the total grid size was too small to capture animals' true maximum distances moved, buffers would underestimate true maximum distance. To prevent this, Maffei & Noss (2008) suggested that each camera grid cover a minimum of three to four average home ranges. With an average home range of 18.91–26.09 $km^2$, our total survey area would have to be 56.73–104.36 $km^2$. Our maximum survey area was 227.10 $km^2$ across all five camera surveys conducted in this region (Dillon & Kelly, 2007). This was well above the suggested minimum size, and yet the 1/2 MMDM never increased higher than 1.47–1.64 km, which only comprised 53–66% of the home-range radius buffer. While Maffei & Noss (2008) reveal an important insight into how a small grid size can affect buffer value and density estimation, the results of this study suggest that the standard camera trapping 1/2 MMDM buffer is overestimating density by underestimating the radius of a true home range rather than covering too small a survey area. Perhaps the wider ranging the individual, the more difficult it is to accurately capture the animal's movement across a large home range with few camera traps. Therefore, the size of an animal may be less important than its ranging behavior, which is consistent with Williams, Nichols & Conroy's (2002) suggestion that 1/2 MMDM approaches are most useful when animal home ranges are small relative to the sample grid area.

Because different individuals of the same species have different home-range sizes and movement patterns, camera trapping may need to be tailored to the local population. It is particularly important to obtain information on home-range size in order to determine the appropriate camera spacing, buffer size and total grid size. Appropriate camera spacing should be based on the target animal's home-range size and is a compromise between the need to fully saturate the survey area and the need to cover a large area. A nested grid approach (Maffei & Noss, 2008) may aid in determining the appropriate camera spacing for a target species. Although a minimum of one camera per home range is acceptable, having up to four cameras per station, as suggested by White *et al*. (1982), is recommended for wider ranging species to increase capture success. If a large per cent of animals are being captured at only one camera station, maximum distances are not accurately being recorded and the stations may be too far apart. Finally, when estimating animal density, animals with wide-ranging behavior appear to be more accurately represented by using a full camera trapping MMDM to determine the effective area sampled. Standardized camera trapping methodology will allow more realistic comparative studies.

Given the results of our current study, we conclude that our previous ocelot densities via camera trapping alone may have been too high. Extrapolating densities determined from a more realistic home-range radii (11.24–12.45 ocelots per 100 km$^2$) resulted in 188–208 ocelots in the entire CFRNP (1670 km$^2$) rather than ~432 when extrapolating densities derived from 1/2 MMDM. Although the La Selva Maya is a biodiversity hotspot and the largest intact forest in Central America, it is undergoing rapid habitat loss. This threat may contribute to the challenges faced by the low-density population of ocelots in the region, potentially inhibiting their survival.

Our study has provided a useful insight into ocelot home-range size, overlap and ranging behavior in Central America. Information on ranging behavior has dramatically impacted our estimates of home-range radius and subsequent ocelot density. Given the substantial increase in the number of studies using remote cameras for density estimation, particularly for felids, standardization of techniques is imperative for comparative analyses, both across sites and within sites across years. Camera spacing, total survey area and degree of concordance between home-range radius and 1/2 MMDM from cameras have emerged as three important topics for continued methodological research. Until we advance methodology, either through simulation studies or by conducting camera trapping on a population of a known size, our density estimates for many species via remote camera traps may be no better than educated guesses or may simply reflect only indices of abundance.

## Acknowledgments

We thank the government of Belize, Department of Forestry, for permission to conduct this research and the entire Las Cuevas Research Station staff for their assistance, cooperation and logistical support. In particular, we thank Nicodemus Bol, Victor Quiroz, Isidro Bol, Celia Bol, Judy Bol, Norberto Coc, Enrique Saquil and Chris Minty. We are incredibly grateful to the many research technicians (Shaina Aguilar, Brandon Barr, Jodi Berg, Autumn Bonomi, Jennie Burns, Hilary Camblos, Alex Chidakel, Brooke George, Nik Gour, Ryan Hilgris, Zach Hurst, Megan Jones, Sarai Kanouse, Matt Kedziora, Miki Kern, Chris Law, Dennis Lorenz, Tom McNamara, Simon M-Bourgeois, Lucy Manning, Shonene Scott, Andrew Wastell, Jennifer White) who put in long hours in the field. We thank Virginia Tech, the Wildlife Conservation Society, the Philadelphia Zoo, Hidden Valley Inn and the Acorn Alcinda Foundation (Kennedy Tree Farm) for funding that made this research possible.

## References

Beletsky, L. (1999). *Belize and northern Guatemala*. London, UK: Academic Press, 20–33.

CEPF (2005). *Northern region of the Mesoamerica biodiversity hotspot*. Washington, DC, USA: Critical Ecosystem Partnership Fund.

Crawshaw, P.G. (1995). *Comparative ecology of ocelot (Felis pardalis) and jaguar (Panthera onca) in a protected subtropical forest in Brazil and Argentina*. PhD dissertation, University of Florida, Gainesville, FL, USA.

Cuellar, E., Maffei, L., Arispe, R. & Noss, A. (2006). Geoffroy's cats at the northern limit of their range: activity patterns and density estimates from camera trapping in Bolivian dry forests. *Stud. Neotrop. Fauna Environ.* **41**, 169–177.

DiBitetti, M.S, Paviolo, A. & DeAngelo, C. (2006). Density, habitat use and activity patterns of ocelots (*Leopardus pardalis*) in the Atlantic forest of Misiones, Argentina. *J. Zool. (Lond.)* **270**, 153–163.

Dillon, A. & Kelly, M.J. (2007). Ocelot *Leopardus pardalis* in Belize: the impact of trap spacing and distance moved on density estimates. *Oryx* **41**, 469–477.

Emmons, L.H. (1988). A field study of ocelots in Peru. *Revue Ecol. Terra Vie* **43**, 133–157.

Heilbrun, R.D, Silvy, N.J, Peterson, M.J. & Tewes, M.E. (2006). Estimating bobcat abundance using automatically triggered cameras. *Wildl. Soc. Bull.* **34**, 69–73.

IUCN (2006). *2006 IUCN red list of threatened species*. Gland, Switzerland: IUCN, http://www.redlist.org, accessed 28 August 2007.

Karanth, K.U. (1995). Estimating tiger (*Panthera tigris*) populations from camera-trap data using capture–recapture models. *Biol. Conserv.* **71**, 333–338.

Karanth, K.U. & Nichols, J.D. (1998). Estimation of tiger densities in India using photographic captures and recaptures. *Ecology* **79**, 2852–2862.

Karanth, K.U. & Nichols, J.D. (2002). *Monitoring tigers and their prey: a manual for researchers, managers and conservationists in tropical Asia*. Bangalore, Karnataka, India: Center for Wildlife Studies.

Karanth, K.U., Nichols, J.D., Kumar, N.S. & Hines, J.E. (2006). Assessing tiger population dynamics using photographic capture–recapture sampling. *Ecology* **87**, 2925–2937.

Kelly, J.M. & Holub, E.L. (2008). Camera trapping of carnivores: trap success among camera types and across species, and habitat selection by species on Salt Pond Mountain, Giles County, Virginia. *Northeast. Nat.* **15**. in press.

Kelly, M.J. (2003). Jaguar monitoring in the Chiquibul Forest, Belize. *Carib. Geogr.* **13**, 19–32.

Kelly, M.J, Noss, A.J., DiBitetti, M.S., Maffei, L., Arispe, R., Paviolo, A., De Angelo, C.D. & DiBlanco, Y.E. (2008). Estimating puma densities from camera trapping across three study sites: Bolivia, Argentina, Belize. *J. Mammal* **89**, 408–415.

Konecny, M.J. (1989). Movement pattern and food habits of four sympatric carnivore species in Belize, Central America. In *Advances in neotropical mammalogy*: 243–264. Redford, K.H. & Eisenberg, J.F. (Eds). Gainesville, FL: Sandhill Crane Press.

Laack, L.L. (1991). *Ecology of the ocelot (Felis pardalis) in South Texas*. MS thesis, Texas A&I University, Kingsville, TX, USA.

Ludlow, M.E. & Sunquist, M.E. (1987). Ecology and behavior of ocelots in Venezuela. *Natl. Geogr. Res.* **3**, 447–461.
Maffei, L., Cuellar, E. & Noss, A. (2004). One thousand jaguars (*Panthera onca*) in Bolivia's Chaco? Camera trapping in the Kaa-Iya National Park. *J. Zool. (Lond.)* **262**, 295–304.
Maffei, L., Noss, A.J., Cuellar, E. & Rumiz, D.I. (2005). Ocelot (*Felis pardalis*) population densities, activity, and ranging behaviour in the dry forests of eastern Bolivia: data from camera trapping. *J. Trop. Ecol.* **21**, 1–6.
Maffei, L.A. & Noss, A.J. (2008). How small is too small? Camera trap survey areas and density estimates for ocelots in the Bolivian Chaco. *Biotropica* **40**, 71–75.
Millspaugh, J.J. & Marzluff, J.M. (2001). *Radio tracking and animal populations*. San Diego, CA: Academic Press.
Murray, J.L. & Gardner, G.L. (1997). *Leopardus pardalis*. Mammalian Species No. 548:1–10.
Navarro, D. (1985) *Status and distribution of the ocelot (Felis pardalis) in south Texas*. MS thesis, Texas A&I University, Kingsville, TX, USA.
Nichols, J.D. & Karanth, K.U. (2002). Statistical concepts: estimating absolute densities of tigers using capture-recapture sampling. In *Field monitoring tigers and their prey: a manual for researchers, managers and conservationists in tropical Asia*: 121–137.Karanth, K.U. & Nichols, J.D. (Eds). Bangalore, India: Centre for Wildlife Studies.
Otis, D.L., Burnham, K.P., White, G.C. & Anderson, D.R. (1978). Statistical inference from capture data on closed animal populations. *Wildl. Monogr*. **62**, 1–135.
Parmenter, R.R., Yates, T.L., Anderson, D.R., Burnham, K.P., Dunnum, J.L., Franklin, A.B., Friggens, M.T., Lubow, B.C., Miller, M., Olson, G.S., Parmenter, C.A., Pollard, J., Rexstad, E., Shenk, T.M., Stanley, T.R. & White, G.C. (2003). Small-mammal density estimation: a field comparison of grid-based vs. web-based density estimators. *Ecol. Monogr*. **72**, 1–26.
Rexstad, E. & Burnham, K.P. (1991). *User's guide for interactive program CAPTURE: abundance estimation of closed animal populations*. Fort Collins, CO: Colorado State University.
Rodgers, A.R. & Carr, A.P. (1998). HRE: the home range extension for ArcView. Ontario, Ministry of Natural Resources, Centre of Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada.
Seaman, D.E. & Powell, R.A. (1996). An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* **77**, 2075–2085.
Silver, S.C., Ostro, L.E.T., Marsh, L.K., Maffei, L., Noss, A.J., Kelly, M.J., Wallace, R.B., Gomez, H. & Ayala, G. (2004). The use of camera traps for estimating jaguar *Panthera onca* abundance and density using capture/recapture analysis. *Oryx* **38**, 148–154.
Soisalo, M.K. & Cavalcanti, M.C. (2006). Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture–recapture sampling in combination with GPS radio-telemetry. *Biol. Conserv*. **129**, 487–496.
Sokal, R.R. & Rohlf, F.J. 1995. *Biometry, the principles and practice of statistics in biological research*, 3rd edn. New York: Freeman and Company.
Sunquist, M.E. & Sunquist, F. (2002). *Ocelot, in wild cats of the world*. Chicago, IL: University of Chicago Press, 120–129.
Sunquist, M.E., Sunquist, F. & Daneke, D.E. (1989). Ecological separation in a Venezuelan llanos carnivore community. In *Advances in neotropical mammalogy*: 197–232. Redford, K.H. & Eisenberg, J.F. (Eds). Gainesville, FL: Sandhill Crane Press.
Tewes, M.E. (1986) *Ecological and behavioral correlates of ocelot spatial patterns*. Dissertation, University of Idaho, Moscow, ID, USA.
Trolle, M. & Kery, M. (2005). Camera-trap study of ocelots and other secretive mammals in the northern Pantanal. *Mammalia* **69**, 3–4.
White, G.C., Anderson, D.R., Burnham, K.P. & Otis, D.L. (1982). Capture–recapture and removal methods for sampling closed populations. Los Alamos National Laboratory LA-8787-NERP, 165pp.
White, G.C. & Garrott, R.A. (1990). *Analysis of wildlife radio-tracking data*. San Diego, CA: Academic Press.
Williams, B.K., Nichols, J.D. & Conroy, M.J. (2002). *Analysis and management of animal populations*. Boston: Academic Press.
Wilson, K.R. & Anderson, D.R. (1985). Evaluation of a nested grid approach for estimating density. *J. Wildl. Mgmt*. **49**, 675–678.
Worton, B J. (1989). Kernel methods for estimating the utilization distribution in home range studies. *Ecology* **70**, 164–168.

 