The Journal of Wildlife Management 83(2):283–294; 2019; DOI: 10.1002/jwmg.21598

Research Article

Long-Term Monitoring of Ocelot Densities in Belize

CHRISTOPHER B. SATTER,[1] *Department of Fish and Wildlife Conservation, Virginia Tech, 310 W Campus Drive, Cheatham Hall, Blacksburg, VA 24061, USA*

BEN C. AUGUSTINE, *Atkinson Center for a Sustainable Future and Department of Natural Resources, Cornell University, G02 Fernow Hall, Ithaca, NY 14850, USA*

BART J. HARMSEN, *Panthera, 8 W 40th Street, 18th Floor, New York, NY 10018, USA*

REBECCA J. FOSTER, *Panthera, 8 W 40th Street, 18th Floor, New York, NY 10018, USA*

EMMA E. SANCHEZ, *Panthera, 8 W 40th Street, 18th Floor, New York, NY 10018, USA*

CLAUDIA WULTSCH, *Sackler Institute for Comparative Genomics, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA*

MIRANDA L. DAVIS, *Ecology and Evolutionary Biology, University of Connecticut, 75 N. Eagleville Road, Unit 3043, Storrs, CT 06269, USA*

MARCELLA J. KELLY, *Department of Fish and Wildlife Conservation, Virginia Tech, 310 W Campus Drive, Cheatham Hall, Blacksburg, VA 24061, USA*

ABSTRACT Ocelots (*Leopardus pardalis*) are listed as least concern on the International Union for Conservation of Nature (IUCN) Red list of Threatened Species, yet we lack knowledge on basic demographic parameters across much of the ocelot's geographic range, including population density. We used camera-trapping methodology and spatially explicit capture-recapture (SECR) models with sex-specific detection function parameters to estimate ocelot densities across 7 field sites over 1 to 12 years (from data collected during 2002–2015) in Belize, Central America. Ocelot densities in the broadleaf rainforest sites ranged between 7.2 and 22.7 ocelots/100 km^2, whereas density in the pine (*Pinus* spp.) forest site was 0.9 ocelots/100 km^2. Applying an inverse-variance weighted average over all years for each broadleaf site increased precision and resulted in average density ranging from 8.5 to 13.0 ocelots/100 km^2. Males often had larger movement parameter estimates and higher detection probabilities at their activity centers than females. In most years, the sex ratio was not significantly different from 50:50, but the pooled sex ratio estimated using an inverse weighted average over all years indicated a female bias in 1 site, and a male bias in another. We did not detect any population trends as density estimates remained relatively constant over time; however, the power to detect such trends was generally low. Our SECR density estimates were lower but more precise than previous estimates and indicated population stability for ocelots in Belize. © 2018 The Authors. *Journal of Wildlife Management* published by Wiley Periodicals, Inc. on behalf of The Wildlife Society.

KEY WORDS Belize, camera-trapping, density, multi-session models, ocelots, sex-specific models, spatially explicit capture-recapture.

The medium-sized ocelot (*Leopardus pardalis*) has a wide geographic distribution across the Americas, ranging from southern Texas, USA, to northern Argentina (Sunquist and Sunquist 2002). Currently, the ocelot is listed on Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), which prohibits all international trade of skins and live animals. This protection via CITES stemmed from heavy hunting of ocelots during the 1960s and 1970s for their fur (Murray and Gardner 1997, Salvador and Espinosa 2015), a practice that continues today in parts of Central and South America, and Trinidad and Tobago. Currently, ocelots are mainly threatened by habitat degradation and loss (Hunter and Barrett 2011). In Belize and in other Neotropical countries, large-scale agriculture, infrastructure developments, and increased human populations have been the leading causes of deforestation (Young 2008, Nogueira and Nogueira-Filho, 2011, Aide et al. 2013). Low reproductive rates, long inter-birth intervals, and small litter sizes make ocelots potentially vulnerable to population declines and habitat loss (Hunter and Barrett 2011). In Belize, ocelots occur sympatrically with 4 other felid species and play a vital role as a mesopredators in ecosystem trophic dynamics (de Oliveira et al. 2010). To better understand the ecology of ocelots throughout their geographic range and improve

Received: 3 January 2018; Accepted: 2 October 2018

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

[1]*E-mail: chrissatter@vt.edu*

long-term management and conservation of a species occurring across human-altered landscapes, it is important to determine population demographic parameters, especially abundance and density (Lebreton et al. 1992, Reed et al. 2002, Royle et al. 2013).

Currently, there are 2 general approaches to estimating population density from capture-recapture data: classical and spatial capture-recapture models. Classical non-spatial capture-recapture methods estimate density by applying an *ad hoc* buffer surrounding the cameras or the trapping array to derive the total area encompassing the population of interest and dividing the estimated abundance by this estimated effective survey area. Commonly this buffer is defined by a radius equal to half of the mean maximum distance moved among traps for all individuals (Silver et al. 2004, Paviolo et al. 2009). However, these classical non-spatial, capture-recapture techniques are problematic because they often lead to an overestimate of density (Soisalo and Cavalcanti, 2006, Silveira et al. 2010, O'Brien 2011, Sollmann et al. 2012, Meek et al. 2014). Spatial capture-recapture models were developed in part to resolve this problem of converting abundance to density. For this reason, we applied spatially explicit capture-recapture methods (SECR) that incorporate the spatial location of individual ocelot captures into the density estimation process (Efford et al. 2009). Spatial information is important for estimating the location of each ocelot's activity center in conjunction with an estimated detection function, which can jointly be used to estimate population density directly (the number of activity centers over the study area), thus overcome many of the limitations of classical capture-recapture methods (Sollmann et al. 2011, Royle et al. 2013).

Standard SECR software (e.g., the secr R package; Efford 2018) provides a flexible analysis framework for including individual covariates, such as sex, as predictors for the detection function parameters (*g0*), the baseline detection probability (at the activity center), and for the spatial scale parameter (σ), which determines the range over which detection probability declines as the distance between an activity center and detector increases. Several ocelot studies have reported that social system dynamics between male and female ocelots typically follow that of other felids, with male territories overlapping $\geq$1 females (Murray and Gardner 1997, Sunquist and Sunquist 2002, Di Bitetti et al. 2006, Dillon and Kelly 2008) and male ocelots potentially using roads or trails where cameras are placed more intensively than females (Royle et al. 2013). These differences in space use between sexes are likely to effect *g0* and σ in a camera trapping context and should be considered explicitly within the models to avoid negatively biased estimates that occur in the presence of un-modeled individual heterogeneity in detection function parameters (Sandell, 1989, Sollmann et al. 2011).

Camera-trapping methods in conjunction with spatial capture-recapture models are one of the most effective methods for obtaining demographic data on rare and elusive species such as ocelots (Royle et al. 2013, da Rocha et al. 2016). We lack knowledge on basic demographic parameters for ocelots because it is challenging to conduct surveys for this cryptic, nocturnal species, yet abundance and density are strong indicators of overall health of natural populations within the species' range (Silveira et al. 2010, da Rocha et al. 2016). In Belize, Central America, studies estimating density of ocelots have not been published since 2007 and 2008 (Dillon and Kelly 2007, 2008; Davis 2008), and those studies used classical, non-spatial density estimation methods, which likely led to overestimates. Further, large-scale camera-trapping surveys monitoring ocelots over multiple years and sites are absent throughout their range; however, long-term, multi-site studies hold potential to substantially improve population parameter estimates, especially those of density. For example, in sparse camera trap data sets (i.e., low numbers of detections, spatial recaptures, camera stations, or unique individuals identified), increased precision in parameter estimates can be achieved by pooling information across multiple surveys through time at the same site. Large-scale spatiotemporal camera-trapping datasets also provide essential information in understanding species landscape distribution, beyond that provided by contemporary population estimates (Foster and Harmsen 2012). We highlight the importance of long-term studies for monitoring wildlife populations though time to uncover population trends (da Rocha et al. 2016) and provide new insights into the ecology and population status of ocelots in Belize.

Our objectives were to estimate ocelot density and sex-specific detection and movement parameters of ocelots in 7 separate study sites in Belize. We expected to find differences in population densities between those sites dominated by broadleaf forests and a site containing primarily native tropical pine forest because of differences in habitat preference and canopy cover (Harveson et al. 2004, Di Bitetti et al. 2006). Past research has demonstrated male ocelots have larger home ranges than females and their home ranges encompass $\geq$1 female ocelot (Di Bitetti et al. 2006, Dillon and Kelly 2008). Traversing these larger home ranges should lead to greater exposure to the trapping grid and we therefore predicted that male ocelots would have higher detectability at their activity centers than females.

STUDY AREA

The Belize mainland is approximately 63% forested (Cherrington et al. 2010), and 43% of the mainland is uninhabited by humans (Foster et al. 2016). This includes national, private, or candidate protected areas, but only 17% of the mainland is protected against wildlife extraction (Cherrington et al. 2010, Foster et al. 2016). Because of natural disasters, such as frequent hurricanes, along with anthropogenic disturbances, the most common forest type in Belize is secondary moist broadleaf forest with interspersed patches of primary forest. However, the landscape encompasses a wide range of land cover types, including tropical rainforest, secondary forest with patches of old growth, pine savanna, seasonally inundated lowland forests, wetlands, pine, mangrove, and littoral forests (Fig. 1).

Our 7 study sites hosted a rich variety of flora and fauna. Some of the most common species characteristic of Belize include broadleaf-dominated sites with mahogany (*Swietenia macrophylla*), Spanish cedar (*Cedrela mexicana*), sapodilla

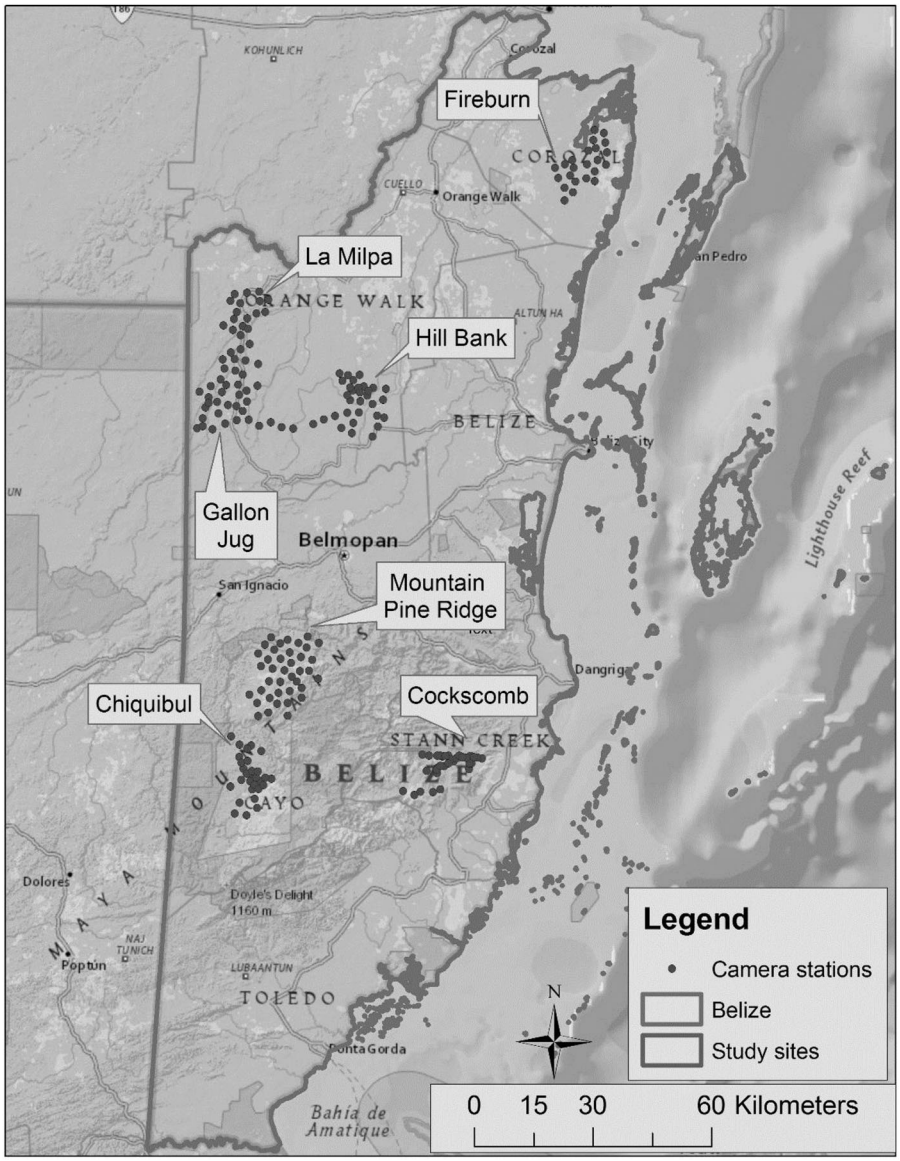

Figure 1. Locations for ocelot camera-trap surveys for 7 sites in Belize, Central America, 2002–2016. Shapefiles were adapted from the Biodiversity and Environmental Resource Data System of Belize (BERDS; Meerman and Clabaugh 2017).

(*Manilkara zapota*), ramon (*Brosimum alicastrum*), and cohune palm (*Attalea cohune*). The pine ridge-savanna-dominated sites included Caribbean pine (*Pinus caribaea*), Mexican yellow pine (*Pinus oocarpa*), calabash (*Cresentia cujete*), oak (*Quercus* spp.), and palmetto palm (*Acoelorrhaphe wrightii*). Coastal and mangrove sites included red mangrove (*Rhizophora mangle*), black mangrove (*Avicennia germinans*), white mangrove (*Laguncularia racemosa*), and buttonwood (*Conocarpus erectus*). Dominant fauna included all 5 species of wild felid: jaguar (*Panthera onca*), puma (*Puma concolor*), ocelot (*Leopardus pardalis*), jaguarundi (*Puma yagouaroundi*), and margay (*Leopardus wiedii*). A wide diversity of mammal species share the landscape including white-lipped peccary (*Tayassu pecari*), collared peccary (*Pecari tajacu*), Baird's tapir (*Tapirus bairdii*), white-tailed deer (*Odocoileus virginianus*), red brocket deer (*Mazama americana*), paca (*Agouti paca*), and Central American agouti (*Dasyprocta punctate*).

Study Sites

We grouped sites into the following categories: lowland broadleaf rainforest (Fireburn Reserve, Hill Bank, and Gallon Jug Estate), upland broadleaf rainforest (La Milpa, Cockscomb Basin Wildlife Sanctuary, and Chiquibul Forest Reserve and National Park), and native upland tropical pine forest (The Mountain Pine Ridge Forest Reserve).

The Fireburn Reserve in northeastern Belize was primarily tropical moist lowland forest, with an average annual rainfall of 152.4 cm (Miller 2006) and elevation of 1 m. The reserve was approximately 7.4 km^2, had low canopy cover and extensive saltwater swamp. We conducted the camera-trapping survey for this site from March to July 2009.

The Rio Bravo Conservation and Management Area in northeastern Belize was split into 2 field sites, La Milpa and Hill Bank, and has been owned and managed by a local,

non-governmental organization (i.e., Programme for Belize) since 1982. The Rio Bravo Conservation and Management Area was the largest private reserve and second largest protected area in Belize, encompassing approximately 1,053 km^2 of land, and 4% of the total land cover in Belize (Programme for Belize 2008). Annual rainfall averaged from 300 cm to 350 cm and elevation ranged from 40 m to160 m. La Milpa was primarily upland broadleaf forest and had strict conservation regulations because of the tourism potential; as a result, logging within the interior of the reserve was prohibited. However, some logging occurred on the edge in the secondary forest products zone (Kelly and Rowe 2014). We conducted 7, 2–3-month camera-trapping surveys in each year in 2008 and 2010–2015. Hill Bank was a rich mosaic of land cover types primarily composed of lowland broadleaf forest, freshwater swamp, and pine savanna. At the time of study, timber harvest was conducted on a 40-year rotation, and was in accordance with rules of the Forest Stewardship Council and by the Rainforest Alliance (Programme for Belize 2008). For this site, we conducted 6, 2–3-month camera-trapping surveys in each year from 2010 to 2015.

The Gallon Jug Estate located in northwestern Belize was privately owned and underwent selective logging (40-yr rotation) along with coffee, cacao, and cattle production. Gallon Jug Estates was originally 538 km^2 until a portion of it was recently purchased by The Forestland Group, which reduced the area to 113 km^2. The area was comprised primarily of lowland broadleaf moist evergreen seasonal forests with an average annual rainfall of 162.5 cm (Miller 2006), and an elevation of 40 m to 160 m. For this site, we conducted 4, 2–3-month camera-trapping surveys in each year from 2013 to 2016.

The Cockscomb Basin Wildlife Sanctuary consisted of 425 km^2 of evergreen and semi-evergreen upland broadleaf tropical moist rainforest on the eastern slope of the Maya Mountain Massif in central eastern Belize (Silver et al. 2004, Harmsen et al. 2010). Elevation ranged from 50 m to 1,120 m and annual rainfall averaged around 270 cm. For this site, we conducted 12, 2–3-month camera-trapping surveys, 2 in 2003 and 1 in each year from 2004 to 2008 and 2011 to 2015.

The Mountain Pine Ridge Forest Reserve was primarily native upland tropical pine species forest (species noted above) along with smaller areas of shrub and broadleaf forest, especially along the riparian corridors (Davis et al. 2011). The Mountain Pine Ridge Forest Reserve was 434 km^2 with areas that underwent naturally occurring annual forest fires (Kellman and Meave 1997, Davis et al. 2011). Elevation ranged from 120 m to 1,016 m and annual rainfall averaged 150 cm. The Mountain Pine Ridge Forest Reserve and Chiquibul Forest Reserve and National Park were separated by the Macal River, which created a sharp transition between pine forest and broadleaf forest (Davis et al. 2011). For this site, we conducted 14, 2–3-month surveys, 3 in 2004 and 1 in each year from 2005 to 2015.

The Chiquibul Forest Reserve and National Park was located in western Belize and was comprised of upland deciduous semi-evergreen, deciduous seasonal forest, and occasional Caribbean pine in the northern sector (Wright et al. 1959, Silver et al. 2004). Chiquibul Forest Reserve and National Park was approximately 1,744 km^2. Annual average rainfall was 150 cm to 200 cm (Beletsky 1999, Dillon and Kelly 2008) and elevation was approximately 500 m. Commercially important tree species such as mahogany, Spanish cedar, and Caribbean pine were selectively logged on a >40-year rotational basis within the Forest Reserve (Silver et al. 2004). For this site, we conducted 9, 2–3-month surveys, 3 in 2002, 3 in 2003, 2 in 2007, and 1 in 2008.

METHODS

Camera Trap Survey

Depending on site and year, we established 20–50 paired camera-trap stations (Table 1). Cameras were originally white flash, film cameras (DeerCam, Park Falls, WI, USA; CamTrakker, Augusta, GA, USA; and TrailMaster, Lenexa, KS, USA), but we began replacing them in 2010 with digital infrared Reconyx, digital white flash Reconyx (Holmen, WI, USA), digital white flash Moultrie (Birmingham, AL, USA), digital white flash HCO Scoutguard (International Falls, MN, USA), and Pantheracams, (New York, NY, USA). In all sites, except Cockscomb Basin Wildlife Sanctuary, we used 2 different brands per site (faster *vs.* slower trigger speeds) to avoid introducing camera bias. In Cockscomb Basin Wildlife Sanctuary, we used CamTrakker and DeerCams until 2008 and Panthercams from 2011 onward. We set cameras low to capture small and large cats, at a height of 30–50 cm, on available trees or handmade stakes to take 1–3 photos/event, with either a 15-, 30-, or 60-second delay between events, depending on allowable camera functions.

Ocelots have individually distinct coat patterns and like other felids commonly use roads and trails (Dillon and Kelly 2007); therefore, we placed cameras on opposite sides of trails, roads, and logging roads to photograph both flanks of a passing animal. To increase baseline encounter probability and ensure that each individual felid had a non-zero probability of being captured, we originally chose locations for each camera station based on the smallest home range estimates for ocelots, pumas, and jaguars at 1.5-km to 3-km intervals, depending on survey objectives (Emmons 1988, Silver et al. 2004, Di Bitetti et al. 2006, Haines et al. 2006*a*, *b*). To meet the assumption of demographic closure (no births, deaths, or migration), we kept the sampling periods to $\leq$3 months.

The ocelot's individually distinct coat patterns allowed 4 trained observers to identify ocelots to the individual level. First, a team of 2 observers assigned all ocelots across all sites and years an identity, then an independent team of 2 observers double checked and confirmed identities. Although most individuals had both flanks photographed simultaneously, there were some individuals where only a single flank was photographed during the study. Therefore, in those years and sites, we created the capture history by

Table 1. Ocelot summary statistics for camera-trapping surveys conducted in each year and site in Belize, Central America (2002–2016). Trap nights represent total number of days across all functional camera stations (≥1 camera functional/station).

Site[a]	Year	Average trap spacing (km)	Number of camera stations	Individuals captured[b]	Total detections	Individuals with spatial recaptures	Occasions	Trap nights
FB	2009	2.3	33	14 (4 M, 8 F, 2 UN)	32	6	127	1,400
LM	2008	1.0	40	37 (20 M, 15 F, 2 UN)	98	15	91	2,543
	2010	2.2	19	14 (6 M, 8 F)	30	4	82	815
	2011	2.2	20	25 (12 M, 11 F, 2 UN)	58	4	90	1,239
	2012	2.2	21	25 (11 M, 13 F, 1 UN)	50	9	72	1,354
	2013	2.3	22	25 (11 M, 14 F)	70	10	80	1,666
	2014	2.3	23	21 (10 M, 10 F, 1 UN)	54	10	82	1,656
	2015	2.3	30	26 (10 M, 13 F, 3 UN)	85	9	86	1,849
HB	2010	2.3	19	11 (7 M, 4 F)	23	1	75	1,022
	2011	2.4	20	16 (5 M, 10 F, 1 UN)	48	6	82	1,539
	2012	1.9	20	20 (7 M, 13 F)	54	8	82	1,455
	2013	2.0	26	12 (8 M, 4 F)	23	2	70	1,605
	2014	2.0	26	22 (11 M, 11 F)	75	8	98	2,195
	2015	2.1	31	16 (5 M, 11 F)	44	6	82	2,471
GJ	2013	2.2	30	41 (16 M, 25 F)	209	20	85	2,083
	2014	2.3	35	41 (17 M, 22 F, 2 UN)	174	19	85	2,107
	2015	2.4	33	51 (20 M, 31 F)	220	24	92	2,138
	2016	2.3	36	51 (15 M, 35 F, 1 UN)	210	19	86	2,379
CC	Feb–Apr 2003	1.9	19	14 (7 M, 6 F, 1 UN)	27	4	65	1,158
	Sep–Dec 2003	1.8	12	12 (6 M, 6 F)	45	5	91	913
	Feb–May 2004	2.0	19	21 (10 M, 10 F, 1 UN)	45	5	82	1,452
	Mar–Jun 2005	2.0	19	21 (11 M, 8 F, 2 UN)	47	5	90	1,647
	Mar–May 2006	2.0	19	18 (11 M, 5 F, 2 UN)	47	3	79	1,378
	Apr–Jul 2007	2.0	19	19 (8 M, 9 F, 2 UN)	39	8	90	1,579
	Apr–Jul 2008	1.3	34	24 (10 M, 14 F)	85	12	102	1,761
	Apr–Jul 2011	2.0	19	17 (9 M, 8 F)	46	4	90	1,588
	Apr–Jun 2012	2.0	19	20 (12 M, 6 F, 1 UN)	48	7	90	1,691
	Apr–Jun 2013	2.0	19	17 (10 M, 7 F)	65	12	115	2,166
	Jan–Jul 2014	1.8	20	25 (14 M, 8 F, 3 UN)	88	11	94	1,633
	Apr–Jun 2015	1.0	37	18 (9 M, 9 F)	80	9	91	1,684
MPR	Jan– Apr 2004	2.4	19	1 (1 M, 0 F)	1	0	85	1,534
	Apr– Jun 2004	0.8	16	1 (1 M, 0 F)	1	0	63	855
	Aug–Oct 2004	2.3	20	6 (4 M, 2 UN)	6	0	61	1,028
	Jun–Sep 2005	2.5	23	6 (5 M, 1 F)	19	5	92	1,979
	Jun–Sep 2006	2.6	25	6 (6 M, 0 F)	21	4	83	1,833
	Jun–Aug 2007	1.5	47	4 (4 M, 0 F)	16	3	73	2,894
	Nov 2008–Feb 2009	2.6	26	4 (4 M, 0 F)	6	0	97	1,327
	Oct 2009–Feb 2010	2.5	30	3 (2 M, 1 F)	8	3	116	2,211
	Oct 2010–Jan 2011	2.5	33	3 (1 M, 1 F, 1 UN)	3	0	85	2,166
	Oct–Dec 2011	2.5	35	1 (1 M, 0 F)	1	0	64	2,043
	Nov 2012–Jan 2013	3.6	40	1 (1 M, 0 F)	3	0	66	2,194
	Aug–Nov 2013	2.5	40	2 (2 M, 0 F)	5	1	64	2,214
	Oct 2014–Jan 2015	2.6	40	6 (4 M, 1 F, 1 UN)	13	3	85	3,022
	Jan–Apr 2015	2.6	40	2 (2 M, 0 F)	8	0	76	2,859
CF	Jan–Mar 2002	2.7	18	5 (3 M, 2 F)	10	2	67	559
	Mar–Jun 2002	2.0	9	7 (3 M, 4 F)	40	3	89	652
	Jul–Oct 2002	0.5	17	6 (2 M, 4 F)	25	4	106	731
	Jan–Apr 2003	1.6	19	17 (8 M, 9 F)	77	8	99	1,976
	Jun–Jul 2003	1.4	25	12 (9 M, 4 F)	17	6	37	773
	Aug–Sep 2003	0.8	17	8 (4 M, 4 F)	21	4	36	470
	Nov 2006–Jan 2007	2.7	15	10 (5 M, 5 F)	13	1	63	783
	Oct–Dec 2007	2.6	19	5 (1 M, 4 F)	7	0	34	378
	Jun–Aug 2008	1.8	29	9 (5 M, 4 F)	15	4	59	626

[a] Site names: FB, Fireburn Forest Reserve; LM, La Milpa; HB, Hill Bank; GJ, Gallon Jug; CC, Cockscomb; MPR, Mountain Pine Ridge Forest Reserve; CF, Chiquibul Forest Reserve and National Park.
[b] M, Male; F, Female; UN, unknown.

appending captures of individuals photographed on only 1 flank to captures of individuals simultaneously photographed on both flanks ≥1 time. We selected the right or left flank based on whichever side maximized the number of individuals captured (i.e., more right-sided only flanks captured would be appended to double-flank captures to increase sample size). The procedures employed in this study were approved by the Forest Department of Belize, Ministry of Natural Resources and Environment, with the following permit numbers for each year: 2002, CD/60/3/02 (35); 2003, CD/60/3/03(25); 2005, CD/60/3/05(20); 2006, CD/60/3/06(21); 2007, CD/60/3/07(50); 2008, CD/60/3/08(09); 2009, CD/60/3/09(08); 2010, CD/60/3/10(23); 2011, CD/60/3/11(10); 2012, CD/60/3/12(36); 2013, CD/60/3/13(32); 2014, CD/30/3/14(36); 2015, CD/60/3/15 (34).

SECR Models

We created capture histories and camera operation histories for each site and year. We defined the sampling occasion as a 1-day period and the camera operation history documented the spatial coordinates of each camera station along with a record of which camera stations had operational cameras deployed on each occasion. Sex information was associated

with each ocelot in the capture history when available and recorded as unknown for individuals whose sex could not be determined. We ran conditional likelihood SECR models using R package secr, assuming half-normal detection functions and proximity detectors, reflecting an independent Bernoulli encounter model (Efford 2011). We accommodated the unknown sexes using the hcov command, which specifies a partially observed finite mixture for individual sex. The maximum likelihood-based SECR models are fit using a discrete approximation of the state space, or area that the population occupies. We defined the state space by buffering the trapping array by 3 times the estimated σ (Efford et al. 2004) and discretized the state space at 250-m intervals (i.e., we set hypothetical home range centers at 250-m intervals).

We fit all possible combinations of pre-defined variables (trap-specific behavioral response to capture on *g0*, and sex effects on σ or *g0*), resulting in 8 candidate models (Table S1, available online in Supporting Information). However, in 1 of 6 years in our Hill Bank site, and in 1 of 11 years in our Cockscomb site, we fit <8 candidate models because of sparse data (Table S1). We modeled detection function as *g0*~1 (intercept-only model), indicating a fixed constant baseline encounter rate across individuals, occasions, and detectors; *g0*~bk indicating a trap-specific behavioral response (e.g., encounter probability is modified for an individual depending on previous capture in that trap); and *g0*~sex, indicating that the encounter probability varied by individual sex. We modeled the spatial scale parameter as σ~1, indicating σ was fixed as constant across all individuals and σ~sex, indicating σ was sex-specific. We modeled the density component as D~1, indicating density was fixed as constant across trapping sessions. In 5 of the 7 sites, we also estimated density for each year independently; however, because data were very sparse (low detections and low numbers of individuals) in 2 of the sites (Chiquibul Forest Reserve and National Park and Mountain Pine Ridge Forest Reserve), we ran multi-session models (Royle et al. 2013). By sharing parameters (i.e., *g0* and σ) across years, multi-session models allow information about detection to be pooled over multiple years, increasing sample sizes per estimated parameter and thus improving precision and potentially reducing bias in density estimates (Boulanger et al. 2002, MacKenzie et al. 2005, White 2005, da Rocha et al. 2016). In the multi-session models, density was either fixed as constant (D~1) or allowed to vary across trapping sessions (D~session). We fixed all other parameters as constant across all trapping sessions. We used Akaike's Information Criterion corrected for small sample sizes (AIC_c) as our model selection criterion (Anderson and Burnham, 2002). Throughout all years and in each site, we considered competing models to be ≤ 2 ΔAIC_c and averaged only the density estimates for competing models. We considered sex-specific parameters (i.e., *g0* and σ) to be significantly different when the confidence intervals did not contain zero. Finally, assuming density and sex ratio did not vary across years at each site, we calculated a single density and sex ratio estimate for each site using an inverse-variance weighted average of the yearly estimates (Borenstein et al. 2010). This method produced a single, more precise average estimate for each site, excluding sites for which we fit non-sex-effect multi-session models. This allowed for information about density and sex ratio to be pooled across years, given that the density parameter in these sex-specific conditional likelihood models cannot be held fixed in a multisession model because it is a derived parameter.

RESULTS

Across all 7 sites and years we had a sample size of: 85,273 trap nights and 2,555 ocelot detections resulting in a trap success rate of 3.00 detections/100 trap nights over all sites combined. We photographed 384 adult ocelots: 174 males, 182 females, and 28 of unknown sex. The number of ocelot detections at each site across years ranged from 32 to 813. The number of unique ocelots captured at each site in any given sampling year varied from 1 to 51, with spatial recaptures (i.e., captured at >1 camera station) ranging from 0 to 24. Years with lower numbers of spatial recaptures produced density estimates with slightly lower precision (Table 1).

In the Fireburn Reserve, the top model held *g0* constant and allowed σ to vary by sex and yielded a density estimate of 9.3 ocelots/100 km^2 (95% CI = 4.5–19.1; Figs. 2 and 3). Sex ratio expressed as the probability of being a female was approximately 0.6 and the confidence interval overlapped 0.5 (Fig. 4). The top model produced a *g0* estimated for both sexes at 0.022 (0.011–0.044), with no competing models (Table S2). The sex-specific estimate of σ for males was approximately 2.9 times larger than females. Males had an estimated σ of 2.6 km (95% CI = 1.0–6.9), and female estimated σ was 0.9 km (95% CI = 0.6–1.4; Table S3). The male σ estimate was significantly different than the female σ (Table S3).

In La Milpa, the yearly density estimates varied from 8.5–22.1 ocelots/100 km^2 (Fig. 2), with an inverse-variance weighted average over the years of 11.5 (95% CI = 9.0–14.0) ocelots/100 km^2 (Fig. 3). Sex ratio was approximately 0.5 in 4 of 7 survey years and approximately 0.6 in 3 of 7 years, but all confidence intervals overlapped the 0.5. The inverse-variance weighted average of the sex ratio estimated over all years was 0.5 (95% CI = 0.4–0.6; Fig. 4). The *g0* parameter estimates for both sexes ranged from 0.004 to 0.025 (Table S2). Top models with a sex effect on *g0* occurred in 3 out of 7 years (2010, 2011, and 2015) with males approximately 6.7, 1.9, and 1.7 times (respectively) more likely to be detected at their activity centers than females (Table S2). But, the male *g0* estimates were significantly different from female *g0* in only 1 of those 3 years (2010; Table S2). In some years, baseline encounter rates increased with a trap-specific behavioral effect (*g0*~bk), or a trap-specific behavioral effect in addition to a sex effect (*g0*~sex + bk; Table S3). The σ parameter estimates ranged from 1.4 km to 2.7 km for years in which top models contained a single σ for both sexes (Table S3). But, sex-specific σ effects were important in 4 of 6 years, with males having 1.3 to 1.8 times larger σ estimates than females. Male σ estimates ranged from 1.8 km to 2.9 km, and female σ estimates ranged from 1.4 km to 2.3 km (Table S3). Male σ

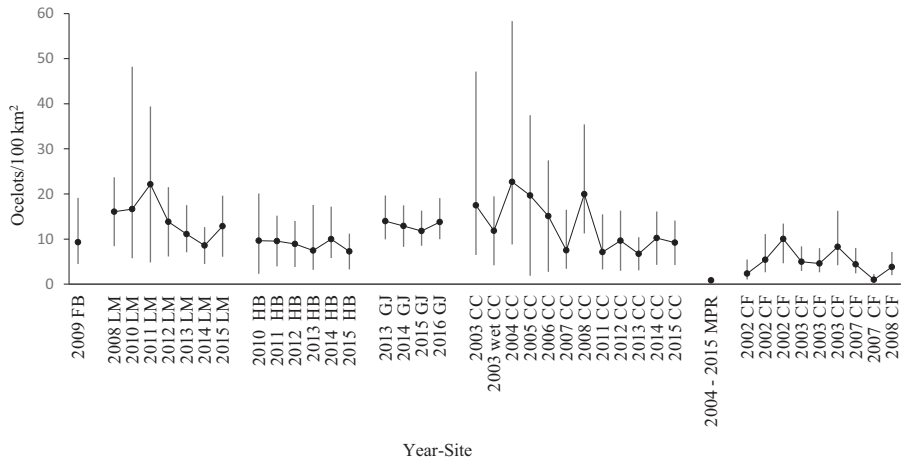

Figure 2. Density estimates and 95% confidence intervals for ocelots in Belize, Central America, 2002–2016, for each year estimated using spatially explicit capture-recapture models, incorporating maximum likelihood based models with a half-normal detection function. CF = Chiquibul Forest Reserve and National Park, FB = Fireburn Reserve, LM = La Milpa, HB = Hill Bank, GJ = Gallon Jug, MPR = Mountain Pine Ridge Forest Reserve (MPR), CC = Cockscomb Basin Wildlife Sanctuary, wet CC = rainy season in Cockscomb Basin Wildlife Sanctuary.

estimates were significantly different from females in 2 of the 4 years that modeled σ as sex-specific (Table S3).

In Hill Bank, the yearly density estimates varied from 7.2–10.0 ocelots/100 km^2 (Fig. 2), with an inverse-variance weighted average over the years of 8.5 (95% CI = 6.3–10.8) ocelots/100 km^2 (Fig. 3). Sex ratio was 0.5 in 1 of 6 years, was ≤0.4 in 2 of 6 years, and ≥0.6 in 3 of 6 years, but all confidence intervals overlapped 0.5. The inverse-variance weighted average of the sex ratio estimated over all years was 0.6 (95% CI = 0.5–0.6; Fig. 4). The *g0* parameter estimates for both sexes ranged from 0.005 to 0.054 (Table S2). Only 1 year (2011) had top models with a sex effect on *g0* and showed males to be 3.0 and 3.3 times more likely to be detected at their activity centers than females during that survey year. Male *g0* estimates were significantly different from female estimates in 2011 (Table S2). In some years *g0* rates increased with a trap-specific behavioral effect (*g0*∼bk), or a trap-specific behavioral effect in addition to a sex effect (*g0*∼sex + bk; Table S2). The σ parameter estimates ranged from 1.5 to 3.1 for males and 0.9 to 1.7 for females depending on survey year (Table S3). Single σ estimates for both sexes combined ranged from 1.0 km to 2.2 km (Table S3). Sex-specific σ estimates were important in 4 of 6 years and males had approximately 1.5 to 1.9 times larger σ than females in all 4 years. Male σ estimates were significantly different from females in 2 of the 4 years that modeled σ as sex-specific (Table S3).

In Gallon Jug, the yearly density estimates varied from 12.9 to 14.0 ocelots/100 km^2 (Fig. 2), with an inverse-variance weighted average over the years of 13.0 (95% CI = 10.8–15.2) ocelots/100 km^2 (Fig. 3). Sex ratio was approximately 0.6 in all 4 years, but all confidence intervals overlapped 0.5.

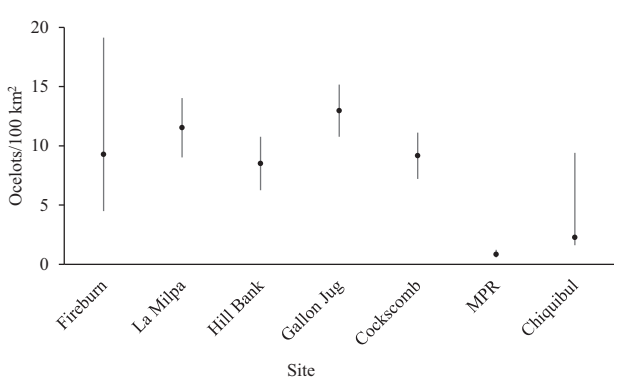

Figure 3. Density estimates and 95% confidence intervals for ocelots estimated using an inverse-variance weighted average of the yearly estimates across sites in Belize, Central America, 2002–2016. The exceptions are density estimates produced for Fireburn Reserve and National Park (FB) and Mountain Pine Ridge Forest Reserve (MPR) because FB contained only 1 year of data and MPR produced a fixed density estimate in a multi-session framework.

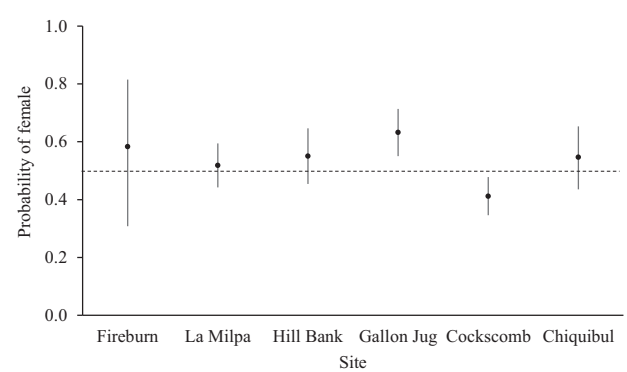

Figure 4. Sex ratio estimates and 95% confidence intervals for ocelots in Belize, Central America, 2002–2016, expressed as the probability of being a female, and estimated using an inverse-variance weighted average of the yearly estimates across sites. The exceptions are density estimates produced for Fireburn Reserve (FB) and Chiquibul Forest Reserve and National Park (CFRNP) because FB contained only 1 year of data and CFRNP was a multi-session model estimating a constant sex ratio parameter across years. In Mountain Pine Ridge Forest Reserve, we did not model sex covariates because of the sparseness of the data set. Horizontal dotted line indicates 0.5 sex ratio.

The inverse-variance weighted average of the sex ratio estimated over all years was 0.6 (95% CI = 0.6–0.7; Fig. 4). The *g0* parameter estimates for both sexes ranged from 0.010 to 0.016 (Table S2). In 2015 and 2016, the top model estimated a sex effect on *g0*, showing males to be approximately 1.5 and 1.8 times more likely to be detected at their activity centers than females during those survey years. Male *g0* estimates were significantly different from female *g0* estimates in both years that contained a sex-specific *g0* (Table S2). In some years, baseline encounter rates increased with a trap-specific behavioral effect (*g0*∼bk), or a trap-specific behavioral effect in addition to a sex effect (*g0*∼sex + bk; Table S2). Survey years in which top models calculated a single σ for both sexes ranged from 1.9 km to 3.1 km (Table S3). The σ parameter estimates ranged from approximately 1.3 to 1.4 times larger for males than females in 2 of 4 years when top models contained a sex effect on σ. Male σ estimates were significantly different from females in both years that modeled σ as sex-specific (Table S3).

In Cockscomb, the yearly density estimates varied from 6.7 to 22.7 ocelots/100 km^2 (Fig. 2) with an inverse-variance weighted average over the years of 9.2 (95% CI = 7.2–11.1) ocelots/100 km^2 (Fig. 3). Sex ratio was approximately 0.5 in 7 of 12 surveys, and all confidence intervals overlapped 0.5. The inverse-variance weighted average of the sex ratio estimated over all years was 0.4 (95% CI = 0.3–0.5; Fig. 4). The *g0* parameter estimates for both sexes ranged from 0.001 to 0.072 (Table S2). In 6 of 12 surveys, the top models supported a sex effect on *g0*, with males ranging from approximately 1.9 to 7.4 times more likely to be detected than females at their activity centers. Male *g0* estimates were significantly different than female *g0* estimates in 5 of 6 years (Table S2). In some years, baseline encounter rates increased with a trap-specific behavioral effect (*g0*∼bk), or a trap-specific behavioral effect in addition to a sex effect (*g0*∼sex + bk; Table S2). In survey years in which top models calculated a single estimate, σ for both sexes ranged from 0.9 km to 5.3 km (Table S3). The σ ranged from approximately 1.9 to 2.4 times larger for males than for females in 5 of 12 surveys. Male σ estimates were significantly different from females in all 5 surveys that modeled σ as sex-specific (Table S3).

In the Mountain Pine Ridge Forest Reserve, we did not include sex covariates because of the sparseness of the data (low detections of very few individuals). Therefore, all parameter estimates are not sex-specific and are reported from the top multi-session model, which held density constant across all years (Fig. 2). The estimated density was very low at 0.9 (95% CI = 0.6–1.2) ocelots/100 km^2. The estimated *g0* for the top model was also low at 0.005 (95% CI = 0.004–0.008; Table S2). The trap-specific behavioral effect on the encounter rate (*g0*∼bk) yielded an estimate of 0.013 (95% CI = 0.005–0.033; Table S2), and σ was estimated to be 3.4 km (95% CI = 2.8–4.2; Table S3).

In the Chiquibul, we ran a multi-session model holding all parameters constant across sessions except for density, which was allowed to vary across trapping sessions and thus estimate density separately for each survey. The yearly densities varied from 1.0–10.0 ocelots/100 km^2 (Fig. 2) with an inverse-variance weighted average over the years of 2.3 (95% CI = 1.6–9.4) ocelots/100 km^2 (Fig. 3). Sex ratio was approximately 0.5 and the confidence intervals overlapped 0.5 (Fig. 4). The *g0* parameter estimate for both sexes was 0.276 (Table S2). Sex-specific σ estimates were approximately 2.2 times larger for males than females. Estimated σ was 2.5 km for males and 1.2 km for females (Table S3). The male σ estimate was significantly different from females over all sessions (Table S3).

Using SECR methods, we found little evidence that ocelot densities varied at each site over time or among sites considering overlapping confidence intervals, except for the Mountain Pine Ridge Forest Reserve (pine forest), which had lower densities than the broadleaf sites. The sex ratio within and among all sites for most years contained overlapping confidence intervals, meaning that although the estimates tended towards slightly more females, the sex ratio was not significantly different from 50:50. However, we did find evidence of departure from 50:50 sex ratio with a female bias in Gallon Jug Estate and a male bias in Cockscomb Basin Wildlife Sanctuary when applying the inverse-variance weighted averages over all years. The majority of *g0* and σ estimates for all site-years were significantly higher for males than females.

DISCUSSION

For at least a century, capture-recapture models have been a primary tool for estimating abundance and density (Royle et al. 2013). Spatial capture-recapture models were only recently developed to further supplement and resolve several limitations of classical capture-recapture models by incorporating the spatial organization of the trapping grid relative to the individuals' trapping locations (Sun et al. 2014). Most previous studies on ocelots have used traditional capture-recapture methods applying the mean maximum distance moved approaches, but few studies have applied spatial-capture recapture methods (Martínez-Hernández et al. 2015, da Rocha et al. 2016). This is the first ocelot study to derive population density estimates from large-scale and long-term camera-trapping surveys that ranged over multiple sites and years, and one of only a few to use the SECR approach. In addition, this is the first study to account for sex-specific detection and movement parameters of ocelots using SECR models. Although the use of sex-specific detection function parameters precludes holding density fixed in a multi-session model (in the secr package, not generally), we applied fixed-effect inverse-variance weighted averages across years, within each site, to obtain a single, more precise average density estimate. In addition to year-specific models, we applied multi-session models allowing parameters to vary across years or remain constant (including density because sex-specific parameters were not considered in these sparse data sets) across sessions to improve precision and obtain reliable estimates from data that might otherwise be too sparse to model separately for each survey (Sollmann et al. 2011, Royle et al. 2013, da Rocha et al. 2016).

Our single-year density estimates ranged from 7.2 to 14.0 ocelots/100 km^2, with inverse-variance weighted

averages ranging from 8.5 to 13.0 ocelots/100 km^2 in the lowland broadleaf rainforest sites (Fireburn Reserve, Hill Bank, Gallon Jug Estate), which were interspersed with marshes, swamps, mangroves, and savannas. Excluding our Chiquibul site, which experienced high camera theft and produced sparse data, yearly density estimates in the upland broadleaf rainforest sites (La Milpa, Cockscomb Basin Wildlife Sanctuary), ranged from 7.2 to 22.7 ocelots/100 km^2, with inverse weighted averages ranging from 9.2 to 11.5 ocelots/100 km^2. The native upland tropical pine forests of Mountain Pine Ridge Forest Reserve, however, had the lowest density of all at 0.9 ocelots/100 km^2. In the Mountain Pine Ridge Forest Reserve, camera trapping grids contained the largest number of well-spaced camera stations; however, we obtained too few ocelot captures, especially of females, to use a sex covariate, potentially producing a negatively biased estimate (Royle et al. 2013). This bias would be minimal if most individuals at this site were male, as indicated by the extreme male bias in captures. Despite very low occurrences of ocelots in the Mountain Pine Ridge Forest Reserve, we were still able to estimate ocelot density by pooling information across years in a multi-session model framework. In addition, density estimates for ocelots occurring in pine-forests across their range are lacking. However, previous studies have reported that ocelots have overall lower detectability in pine forested sites, and preferred habitat with dense canopy cover (>95%) and avoided open areas with <75% canopy cover (Harveson et al. 2004, Di Bitetti et al. 2006, Horne et al. 2009).

The density estimates in some years in the Chiquibul site should be treated with caution because of the sparseness of data. For example, some of the surveys included pilot studies with few camera stations, low detections, and few unique individuals identified. Additionally, in some years the area suffered from camera theft resulting in shortened surveys and lower numbers of encounter occasions. In 1 survey where <1 spatial recapture (<2 recaptures of the same individual at different traps) occurred, potentially biased density estimates may have resulted (Sollmann et al. 2012). However, several sampling years contained sufficient data to produce unbiased estimates.

Most previously reported densities for ocelots were estimated using classical capture-recapture methods making direct comparisons to our SECR study complicated. For example, Dillon and Kelly (2007, 2008) estimated higher ocelot densities than this study in the Chiquibul forest at 11.24–25.88 ocelots/100 km^2. Similarly, in La Milpa, Davis (2008) estimated higher than this study at 38.1 ocelots/100 km^2, and in the Mountain Pine Ridge Forest Reserve, both Dillon and Kelly (2008) and Davis (2008) estimated higher densities than this study at 2.11–3.80 ocelots/100 km^2. Classical capture-recapture methods in some cases have been reported to overestimate density in other studies (Soisalo and Cavalcanti 2006, Dillon and Kelly 2007, Silveira et al. 2010, Gerber et al. 2012) and it is likely these previous estimates in the same areas were also overestimates given small grid sizes and small sample sizes, resulting in inadequately estimated animal movement parameters.

Outside of Belize, classical capture-recapture methods have estimated the highest ocelot densities in the Peruvian Amazon near the Ecuador border at 75.2–94.7 ocelots/100 km^2, and 40–80 ocelots/100 km^2 in Peru and Venezuela (Ludlow and Sunquist 1987, Emmons 1988, Kolowski and Alonso 2010). The lowest ocelot densities were in the Mexican State of Sonora at 5.7 ocelots/100 km^2 (Carrillo and López-González, 2002). All these classical capture-recapture studies perhaps should be closely re-examined in light of the SECR advancements to determine if they are potential overestimates given what we know of the pitfalls of classical capture-recapture approaches. Three other studies used spatial capture-recapture methods to estimate ocelot density occurring in Sierra-Tanchipa Biosphere Reserve, Mexico; Amanã Reserve, Brazil; and the Sierra Madre Occidental, northwestern Mexico. Habitats were comprised of a mosaic of vegetation types including, but not limited to, tropical deciduous forest, thornscrub, oak, woodlands, and tropical rainforest, and resulted in ocelot densities ranging from 0.51 to 25 ocelots/100 km^2 (Martínez-Hernández et al. 2015, da Rocha et al. 2016, Gómez-Ramírez et al. 2017), closer to the ranges we observed.

Average trap spacing across our sites ranged from 1.0 to 2.4 km and produced a high number of ocelot detections and spatial recaptures. Thus, this camera spacing appears appropriate for ocelots. However, other studies attempting similar estimates for cats with differing body sizes, should pay careful attention to camera spacing relative to movement parameters of the target species (Satter et al. 2013, Satter 2017). Our cameras were spaced closer together than twice the estimated value of σ and produced sufficient numbers of spatial recaptures. Ocelot detections in Fireburn Reserve were the lowest at 32 (for 1 year) and the highest in Gallon Jug at 813 (for 4 years). The high ocelot detection rate in Gallon Jug over only a 4-year period was impressive considering that this site, which has timber extraction, borders the completely protected La Milpa site where we obtained 445 ocelot detections over a 7-year period. Small coffee, cacao, livestock areas and small human settlements within the Gallon Jug Estate boundaries facilitate a degree of disturbance; therefore, we suspect that this may partially explain high ocelot detections. Like other small- and medium-sized felids, ocelots are generalists and likely prey heavily on small rodents (Grassman et al. 2005, de Oliveira et al. 2010, Bashir et al. 2013) and may benefit from agricultural production areas, which offer a rich food supply to rodents and other small-mammal populations (Schmid-Holmes and Drickamer 2001).

We chose to use sex as an individual covariate for 2 reasons. First, we used sex to account for individual heterogeneity in *g0* by accounting for differences in activity rates and landscape features such as roads and trails where the majority of cameras were placed (Sollmann et al. 2011, Royle et al. 2013). Secondly, we used sex-specific σ to account for individual heterogeneity in detection that would result if females had smaller home ranges in general than males, which has been shown to be the case for ocelots across their range (Gardner et al. 2010, Sollmann et al. 2011, Royle et al.

2013) and specifically in Belize (Dillon and Kelly 2008), resulting in females being exposed to fewer traps than males (Sollmann et al. 2011). Not accounting for individual heterogeneity in detection parameters typically results in a negatively biased density estimate because individuals with higher detection probabilities are detected more frequently and dominate the detection parameter estimates (Sollmann et al. 2011, Abadi et al. 2013, Royle et al. 2013, Tobler and Powell 2013). Further, sex-specific detection parameters are key to correctly estimating the population sex ratio. A study conducted in Argentina reported that ocelots had a 2:1 ratio of females to males within the study population (Di Bitetti et al. 2006). Our study generally determined that approximately 50% of the population was female, but because those females moved less and sometimes had lower detectability at their activity centers, we could have incorrectly concluded the population was male-biased without accounting for sex-specific detection parameters. In addition, some years within sites contained top models showing support for a trap-specific behavioral response to capture on $g0$. Although, it is possible that ocelots did exhibit some type of behavioral response to capture, this would be surprising given that camera traps were not baited. However, it is likely that these models were absorbing some individual heterogeneity in capture probability.

Dillon and Kelly (2008) demonstrated a high degree of overlap between male and female ocelots in Belize and observed that up to 50–90% of a male's typical home range encompassed >1 female. Other studies reported that ocelots follow similar social system patterns with males having larger territories that overlap several females (Murray and Gardner 1997, Sunquist and Sunquist 2002, Di Bitetti et al. 2006, Dillon and Kelly 2008). Our results provide some evidence for males being more detectable than females. For example, for most of the years within each site, incorporating sex as an individual covariate on $g0$ was significant. Additionally, in sites and years incorporating sex as an individual covariate on $g0$, males were estimated to be approximately 1.5 to 7.4 times more likely to be detected at their activity centers than females. Our results corroborate the notion of males having larger home ranges than females because most of our surveys contained significant σ estimates. In Hill Bank, La Milpa, Gallon Jug, Cockscomb, and the Chiquibul, most of the surveys estimated male σ to be ~1.3–2.2 times larger than females. We surveyed Fireburn for only 1 year and the estimated σ for males was approximately 2.9 times larger than females. Thus, in general, male ocelots have wider movements and therefore are more likely to have higher exposure to the trapping grid and higher detectability.

We emphasize the importance of long-term studies such as this, which take advantage of data collected from a study designed to target multiple carnivore species. In addition to improving the population density estimates over single surveys, long-term surveys allow for the estimation of survival, recruitment, dispersal, and population growth rate. Therefore, estimating these parameters using open population SCR models (Gardner et al. 2010, Chandler and Clark 2014) is the subject of future work. Except for the Mountain Pine Ridge Forest Reserve site, which appears to have naturally low ocelot densities, we found no evidence that densities varied within or among the other predominantly broadleaf sites. In Belize, ocelot populations appear stable across time and space, with the caveat that our estimates were not precise enough to rule out gradual population decline. However, the application of open-population, spatial capture-recapture models should allow for population trends to be estimated more precisely and potential declines to be detected with more statistical power.

MANAGEMENT IMPLICATIONS

With careful attention to trap spacing and grid extent, SECR methods can be used on medium-sized felids within a camera grid targeting species of different body sizes. We urge other studies to adopt an SECR approach especially considering the possibility of overestimating density using previous density estimation approaches.

ACKNOWLEDGMENTS

We thank the Belize Forest Department, Program for Belize, Gallon Jug Estate, Yalbac Ranch and Cattle Company, Las Cuevas Research Station, Friends for Conservation and Development, Wildtracks, Belize Audubon Society, and Bull Run Farm (G. W. and M. Y. Headley) for permission to conduct this research. We thank local personnel such as N. "Chapal" Bol, and M. Aguilar for their local knowledge and expertise, and numerous volunteers and assistants (especially A. Dillon and T. Mc Namara) over the years who conducted field and lab work, from multiple universities, especially the University of Belize and Virginia Tech. We thank the National Science Foundation, the Philadelphia Zoo, Virginia Tech, Wildlife Conservation Society, and Panthera for funding over the years.

LITERATURE CITED

Abadi, F, A. Botha, and R. Altwegg. 2013. Revisiting the effect of capture heterogeneity on survival estimates in capture-mark-recapture studies: does it matter? PLoS ONE 8:e62636.

Aide, T. M., M. L. Clark, H. R. Grau, D. López-Carr, M. A. Levy, D. Redo, M. Bonilla-Moheno, G. Riner, M. J. Andrade-Núñez, and M. Muñiz. 2013. Deforestation and reforestation of Latin America and the Caribbean (2001–2010). Biotropica 45:262–271.

Anderson, D. R., and K. P. Burnham. 2002. Avoiding pitfalls when using information-theoretic methods. Journal of Wildlife Management 66: 912–918.

Bashir, T., T. Bhattacharya, K. Poudyal, S. Sathyakumar and Q. Qureshi. 2013. Integrating aspects of ecology and predictive modelling: implications for the conservation of the leopard cat (*Prionailurus bengalensis*) in the Eastern Himalaya. Acta Theriologica 59:35–47.

Beletsky, L. 1999. Belize and northern Guatemala. Academic Press, London, United Kingdom.

Borenstein, M., L. V. Hedges, J. Higgins, and H. R. Rothstein. 2010. A basic introduction to fixed-effect and random-effects models for meta-analysis. Research Synthesis Methods 1:97–111.

Boulanger J., G. C. White, B. N. McLellan, J. Woods, M. Proctor, and S. Himmer. 2002. A meta-analysis of grizzly bear DNA mark-recapture projects in British Columbia, Canada. Ursus 13:137–152.

Carrillo, S., and C. A. López-González. 2002. Distribution, ecology and conservation of jaguars in Sonora, Mexico. Final Report presented to National Fish and Wildlife Foundation, Washington, D.C., USA.

Chandler, R. B., and J. D. Clark. 2014. Spatially explicit integrated population models. Methods in Ecology and Evolution 5:1351–1360.

Cherrington, E. A., Edgar E, P. Cho, B. F. Howell, B. E. Hernandez, E. R. Anderson, A. I. Flores, B. C. Garcia, E. Sempris, and D. E. Irwin. 2010. Forest cover and deforestation in Belize: 1980–2010. SERVIR Media Resources, Washington, D.C., USA.

Davis, M. L. 2008. Densities, habitat-use, and mesopredator release of the ocelot in Belize. Thesis, Virginia Tech, Blacksburg, USA.

Davis, M. L., M. J. Kelly, and D. F. Stauffer. 2011. Carnivore co-existence and habitat use in the Mountain Pine Ridge Forest Reserve, Belize. Animal Conservation 14:56–65.

da Rocha, D. G., R. Sollmann, E. E. Ramalho, R. Ilha, and C. K. Tan. 2016. Ocelot (*Leopardus pardalis*) density in central Amazonia. PLoS ONE 11: e0154624.

de Oliveira, T. G., M. A. Tortato, L. Silveira, C. B. Kasper, F. D. Mazim, M. Lucherini, A. T. Jácomo, J. B. G. Soares, R. V. Marques, and M. Sunquist. 2010. Ocelot ecology and its effect on the small-felid guild in the lowland Neotropics. Biology and Conservation of Wild Felids 559–580.

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

Dillon, A., and M. J. Kelly. 2008. Ocelot home range, overlap and density: comparing radio telemetry with camera trapping. Journal of Zoology 275:391–398.

Di Bitetti, M. S., A. Paviolo, and C. D. De Angelo. 2006. Density, habitat use and activity patterns of ocelots (*Leopardus pardalis*) in the Atlantic Forest of Misiones, Argentina. Journal of Zoology 270:153–163.

Efford, M. 2018. secr 3.1-spatially explicit capture-recapture models. <ftp://ess.r-project.org/R-CRAN/web/packages/secr/vignettes/secr-overview.pdf>. Accessed 10 Sep 2018

Efford, M. G., D. L. Borchers, and A. E. Byrom. 2009. Density estimation by spatially explicit capture-recapture: likelihood-based methods. Pages 255–269 *in* D. L. Thomson, E. G. Cooch, and M. J. Conroy, editors. Modeling demographic processes in marked populations. Springer, Boston, Massachusetts, USA.

Efford, M. G. 2011. SECR-spatially explicit capture-recapture in R. University of Otago, Dunedin, New Zealand.

Efford, M. G., D. K. Dawson, and C. S. Robbins. 2004. DENSITY: software for analyzing capture-recapture data from passive detector arrays. Animal Biodiversity and Conservation 27:217–228.

Emmons, L. 1988. A field study of ocelots (*Felis pardalis*) in Peru. Revue D Ecologie-La Terre Et La Vie 43.

Foster, R. J., and B. J. Harmsen. 2012. A critique of density estimation from camera-trap data. Journal of Wildlife Management 76:224–236.

Foster, R. J., B. J. Harmsen, D. W. Macdonald, J. Collins, Y. Urbina, R. Garcia, and C. P. Doncaster. 2016. Wild meat: a shared resource amongst people and predators. Oryx 50:63–75.

Gardner, B., J. A. Royle, M. T. Wegan, R. E. Rainbolt, and P. D. Curtis. 2010. Estimating black bear density using DNA data from hair snares. Journal of Wildlife Management 74:318–325.

Gerber, B. D., S. M. Karpanty, and M. J. Kelly. 2012. Evaluating the potential biases in carnivore capture-recapture studies associated with the use of lure and varying density estimation techniques using photographic-sampling data of the Malagasy civet. Population Ecology 54:43–54.

Gómez-Ramírez, M. Á., C. E. Gutiérrez-González, and C. A. López-González. 2017. Ocelots thrive in a non-typical habitat of northwestern Mexico. Endangered Species Research 32:471–478.

Grassman, L. I., M. E. Tewes, N. J. Silvy, and K. Kreetiyutanont. 2005. Spatial organization and diet of the leopard cat (*Prionailurus bengalensis*) in north-central Thailand. Journal of Zoology 266:45–54.

Haines, A. M., L. I. Grassman Jr, M. E. Tewes, and J. E. Janečka. 2006*a*. First ocelot (*Leopardus pardalis*) monitored with GPS telemetry. European Journal of Wildlife Research 52:216–218.

Haines, A. M., J. E. Janecka, M. E. Tewes, L. I. Grassman Jr, and P. Morton. 2006*b*. The importance of private lands for ocelot *Leopardus pardalis* conservation in the United States. Oryx 40:90–94.

Harmsen, B. J., R. J. Foster, S. Silver, L. E. Ostro, and C. P. Doncaster. 2010. Differential use of trails by forest mammals and the implications for camera-trap studies: a case study from Belize. Biotropica 42.1:126–133.

Harveson, P. M., M. E. Tewes, G. L. Anderson, and L. L. Laack. 2004. Habitat use by ocelots in south Texas: implications for restoration. Wildlife Society Bulletin 32:948–954.

Horne, J. S., A. M. Haines, M. E. Tewes, and L. L. Laack. 2009. Habitat partitioning by sympatric ocelots and bobcats: implications for recovery of ocelots in southern Texas. Southwestern Naturalist 54:119–126.

Hunter, L., and P. Barrett. 2011. Carnivores of the world. Princeton University Press, Princeton, New Jersey, USA.

Kellman, M., and J. Meave. 1997. Fire in the tropical gallery forests of Belize. Journal of Biogeography 24:23–34.

Kelly, M. J., and C. Rowe. 2014. Analysis of 5-years of data from Rio Bravo Conservation and Management Area (RBCMA) and one year of data from Gallon Jug/Yalbac Ranch, on trap rates and occupancy for predators and prey, including jaguar density estimates in unlogged versus sustainably logged areas. Progress Report for the Forest Department of Belize and Rio Bravo Conservation and Management Area, Programme for Belize. Virginia Tech, Blacksburg, USA.

Kolowski, J. M., and A. Alonso. 2010. Density and activity patterns of ocelots (*Leopardus pardalis*) in northern Peru and the impact of oil exploration activities. Biological Conservation 143:917–925.

Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67–118.

Ludlow, M. E., and M. E. Sunquist. 1987. Ecology and behavior of ocelots in Venezuela. National Geographic Research 3:447–461.

MacKenzie, D. I., J. D. Nichols, N. Sutton, and K. Kawanishi. 2005. Improving inferences in population studies of rare species that are detected imperfectly. Ecology 86:1101–1113.

Martínez-Hernández, A., O. C. Rosas-Rosas, F. Clemente-Sánchez, L. A. Tarango-Arámbula, J. Palacio-Nunez, L. C. Bender, and J .G. Herrera-Haro. 2015. Density of threatened ocelot *Leopardus pardalis* in the Sierra Abra-Tanchipa Biosphere Reserve, San Luis Potosí, Mexico. Oryx 49:619–625.

Meek, P. D., G. Ballard, A. Claridge, R. Kays, K. Moseby, T. O'Brien, A. O'Connell, J. Sanderson, D. E. Swann, M. Tobler, and S. Townsend. 2014. Recommended guiding principles for reporting on camera trapping research. Biodiversity and Conservation 23:2321–2343.

Meerman, J., and J. Clabaugh. 2017. Biodiversity and Environmental Resource Data System of Belize. <http://www.biodiversity.bz>. Accessed 18 Sep 2017.

Miller, C. M. 2006. Jaguar density in Fireburn, Belize. University of Belize, Belize City, Belize.

Murray, J. L., and G. L. Gardner. 1997. *Leopardus pardalis*. Mammalian Species Archive 548:1–10.

Nogueira, S. S., and S. L. Nogueira-Filho. 2011. Wildlife farming: an alternative to unsustainable hunting and deforestation in Neotropical forests? Biodiversity and Conservation 20:1385–1397.

O'Brien, T. G. 2011. Abundance, density and relative abundance: a conceptual framework. Pages 71–96 *in* A. F. O'Connell, J. D. Nichols, and K. U. Karanth, editors. Camera traps in animal ecology. Springer, Tokyo, Japan.

Paviolo, A., Y. E. Di Blanco, C. D. De Angelo, and M. S. Di Bitetti. 2009. Protection affects the abundance and activity patterns of pumas in the Atlantic Forest. Journal of Mammalogy 90:926–934.

Programme for Belize. 2008. Forestry—timber extraction. Programme for Belize, Belize City, Belize. <http://www.pfbelize.org>. Accessed 27 Feb 2009.

Reed, J. M., L. S. Mills, J. B. Dunning, E. S. Menges, K. S. McKelvey, R. Frye, S. R. Beissinger, M. C. Anstett, and P. Miller. 2002. Emerging issues in population viability analysis. Conservation Biology 16:7–19.

Royle, J. A., R. B. Chandler, R. Sollmann, and B. Gardner. 2013. Spatial capture-recapture. Academic Press, Cambridge, Massachusetts, USA.

Salvador, J., and S. Espinosa. 2015. Density and activity patterns of ocelot populations in Yasuní National Park, Ecuador. Mammalia 80:395–403.

Sandell, M. 1989. The mating tactics and spacing patterns of solitary carnivores. Pages 164–182 *in* J. L. Gittleman, editor. Carnivore behavior, ecology and evolution. Cornell University Press, Ithaca, New York, USA.

Satter, C. B. 2017. Estimating population density and survival of ocelots in six study sites over multiple years in Belize, Central America. Thesis, Virginia Tech, Blacksburg, USA.

Satter, C. B., F. A. Widodo, B. C. Augustine, C. Rowe, M. J. Kelly, and S. Sunarto. 2013. Estimating leopard cat (*Prionailurus bengalensis sumatranus*) population density in Sumatra, Indonesia. Wild Felid Monitor 9:22–23.

Schmid-Holmes, S., and L. C. Drickamer. 2001. Impact of forest patch characteristics on small mammal communities: a multivariate approach. Biological Conservation 99:293–305.

Silveira, L., A. T. Jácomo, S. Astete, R. Sollmann, N. M. Tôrres, M. M. Furtado, and J. Marinho-Filho. 2010. Density of the Near Threatened jaguar *Panthera onca* in the caatinga of north-eastern Brazil. Oryx 44:104–109.

Silver, S. C., L. E. Ostro, L. K. Marsh, L. Maffei, A. J. Noss, M. J. Kelly, R. B. Wallace, H. Gómez, and G. Ayala. 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., and S. M. Cavalcanti. 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. Biological Conservation 129:487–496.

Sollmann, R., M. M. Furtado, B. Gardner, H. Hofer, A. T. Jácomo, N. M. Tôrres, and L. Silveira. 2011. Improving density estimates for elusive carnivores: accounting for sex- specific detection and movements using spatial capture-recapture models for jaguars in central Brazil. Biological Conservation 144:1017–1024.

Sollmann, R., B. Gardner, and J. L. Belant. 2012. How does spatial study design influence density estimates from spatial capture-recapture models? PLoS ONE 7:e34575.

Sun, C. C., A. K. Fuller, and J. A. Royle. 2014. Trap configuration and spacing influences parameter estimates in spatial capture-recapture models. PLoS ONE 9:e88025.

Sunquist, M., and F. Sunquist. 2002. Wild cats of the world. University of Chicago Press, Chicago, Illinois, USA.

Tobler, M. W., and G. V. Powell. 2013. Estimating jaguar densities with camera traps: problems with current designs and recommendations for future studies. Biological Conservation 159:109–118.

White G. C. 2005. Correcting wildlife counts using detection probabilities. Wildlife Research 32:211–216.

Wright, A. C. S., R. H. Arbuckle, and V. E. Vial. 1959. Land in British Honduras. Volume Colonial Research Publication No. 24, London, England.

Young, C. A. 2008. Belize's ecosystems: threats and challenges to conservation in Belize. Tropical Conservation Science 1:18–33.

Associate Editor: Kevin McKelvey.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.