**Estimating population density and survival of ocelots (*Leopardus pardalis*) in six study sites over multiple years in Belize, Central America**

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# Estimating population density and survival of ocelots (*Leopardus pardalis*) in six study sites over multiple years in Belize, Central America

Christopher B. Satter

Abstract (Academic)

The elusive and nocturnal nature of the ocelot *Leopardus pardalis* poses difficulty in gaining basic information on demographic parameters needed to better inform conservation. My study used camera trapping data from long-term monitoring of ocelot populations on six different protected areas in Belize over a time span ranging from 1 to 12 years, with 1,700 ocelot detections in 65,157 total trap nights. I used classical and spatially explicit methods, including multi-session robust design, to estimate and compare ocelot density and survival across sites and time. Full likelihood single session models estimated densities ranging from 6.4 - 22.5 individuals/100km$^2$ in the broadleaf forested sites. Robust design models estimated densities from 8.8 - 22.8 individuals/100 km$^2$ and ocelots had high annual survival (71-79%) in 2 broadleaf sites. Contrary to predictions, robust design models had higher precision than full likelihood models less than half the time. Spatially explicit models estimated density ranging between 7.2 – 22.0 individuals/100 km$^2$ in broadleaf sites, and much lower estimates at 0.9 individuals/100 km$^2$ in the pine forest site. Accounting for sex in spatially explicit methods, which directly incorporate locations of captures into the model, increased precision in density estimates by reducing individual heterogeneity in capture probability. The spatial models also demonstrated that males moved larger distances than females and had slightly higher detection rates. Ocelot populations remained relatively stable over time at the long term sites. My study produced methodologically rigorous abundance/density estimates for ocelots in Belize and the first ever ocelot survival estimates.

# Estimating population density and survival of ocelots (Leopardus pardalis) in six study sites over multiple years in Belize, Central America

Christopher B. Satter

Abstract (Public)

The cryptic and nocturnal nature of the ocelot *Leopardus pardalis* creates difficulty in gaining basic insight into their ecology and behavior. To effectively conserve and manage ocelot populations we need sound estimates of population size and survival rates from long-term studies covering a gradient of habitat types. For this reason, I used camera-trapping methodology in combination with robust analytical methods to estimate population size and survival rates of the ocelot across six different protected areas in Belize. Habitats included pine and broadleaf forest, marsh, and savanna grasslands, and included multi-use production (timber-managed) forests. Using remote game cameras, I photo-captured a total of 257 male and 266 female unique individual ocelots in over 1,700 detections across my study sites over a time span ranging from 1 to 12 years. In addition, from six or more years of data, I was able to estimate an annual survival rate for ocelots, ranging from 71 to 79% in two of the broadleaf sites. Population densities ranged from a low of ~ 0.9 individuals/100 $km^2$ in the pine forest site to 6.4 - 22.8 ocelots/100 $km^2$ in the broadleaf sites. I also found that males moved larger distances on the landscape than females and males are slightly more detectable. Ocelot populations remained relatively stable over time and these results will inform the long-term conservation of the species both in Belize and in other parts of their geographical range, by providing the first survival estimates from wild ocelots outside of the United States.

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## I.    Introduction

The medium-sized wild cat known as the ocelot (*Leopardus pardalis*) has a current geographic range from southern Texas to northern Argentina, including the islands of Trinidad and Margarita (Sunquist and Sunquist, 2002) (Fig.1). Ocelots share the *Leopardus* lineage with seven other felids, and this is the only lineage in subfamily Felinae with 36 chromosomes rather than 38 (Hunter and Barrett, 2011). Currently, there are at least four recognized genetically distinct populations ranging from southern Texas to northern Argentina, but, historically ocelots ranged from Arizona to Arkansas and Louisiana in the southern US (Hunter and Barrett, 2011). Fossil records reveal that ocelots also inhabited Florida (Sunquist and Sunquist, 2002). Currently the only breeding populations in the US inhabit Laguna Atascosa National Wildlife Refuge in Southern Texas. Ocelots are currently listed as Appendix I on the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), which prohibits all international trade of skins and live animals. Despite this, ocelots, as well as other sympatric felids, are still being hunted for their fur (Sunquist and Sunquist, 2002). For example, the United States refused 3,772 shipments of wildlife imports from Mexico between years 2000-2004 and the estimated value of a single jaguar (*Panthera onca*) skin is between $1,300-$20,000 U.S (Wyler and Sheikh, 2008). Currently, no information on wild cat imports or pelt values is available, but the fur trade is thought to be in decline in the US due to change in policymaker and public opinions regarding fur use. International trade of animal fur was banned in the 1980s, however, before that, poaching and habitat loss were the main drivers causing ocelot population decline, and currently habitat loss and fragmentation remain a large threat (Sunquist and Sunquist, 2002).

The world's tropical forests are under heavy anthropogenic pressure with an estimated 5.8 million hectares of humid tropical forest lost between 1990 and 1997 (Achard et al. 2002;

Geist and Lambin, 2002). Agricultural expansion is the leading cause of deforestation (Achard et al. 2002; Geist and Lambin, 2002). Newer studies using Earth observation satellite data estimated an overall global forest loss of 2.3 million square kilometers and global forest gain of 0.8 square kilometers between 2000 and 2012 (Hansen et al., 2013). In Belize, the switch from forestry as the main economic driver to agriculture and large-scale aquaculture has increased deforestation rates (Young, 2008). During 1990-2000, the deforestation rate in Belize (2.3% per year) was nearly double that of the rest of Central America (1.2% per year) (Young, 2008; Di Fiore, 2002; Wynam and Stein, 2010). However, recent reports show that the mainland of Belize still has about 63% forest cover (Foster et al. 2014; Cherrington et al. 2010; Meerman, 2011). Currently, it is estimated that 43% of the mainland is uninhabited by humans and comprises of national, private, and/or candidate protected areas (Foster et al. 2014), but it is estimated that only 17% of the mainland is protected against wildlife extraction (Foster et al. 2014). Belize has a population density of 14 people per $km^2$, making it one of the least populated countries in Central America (Belize Statistics Office, 2010). However, Belize has a human population growth rate of 2.3% per year in rural areas, the highest in Central America (Foster et al., 2014; United Nations, 2013).

The elusive nature of the ocelot, along with its preference for closed, dense tropical and subtropical forests and/or dense scrubland (Harveson et al. 2004), creates difficulty in studying and understanding its ecology (Brown 1989; Shindle 1995; Emmons and Feer 1997; Murray and Gardner 1997; López-González, Brown and Gallo Reynoso 2003; Di Bitetti, Paviolo and De Angelo 2006). Twenty years ago, Karanth (1995) and Karanth and Nichols (1998) pioneered the technique of using remotely-triggered infrared cameras combined with capture-recapture analysis for studying elusive, wide-ranging tigers (*Panthera tigris*) in India. Since then this

technique has become widely used as a reliable, non-invasive method for estimating abundance and population density, especially for large cats with distinctive individual markings (Kelly et al., 2013). For example, the technique has been widely used on tiger populations (Karanth and Nichols, 1998; Wang and Macdonald, 2009; Sunarto et al., 2013), jaguar populations in Central and South America (Silver et al., 2004; Silveira et al., 2009; Maffei et al., 2011), leopard (*Panthera pardus)* populations (Borah et al., 2014; Wang and Macdonald, 2009; Thapa et al., 2014) and other large cats. Camera trapping methodology, however, has only rarely been applied to smaller felid species, such as ocelots (Dillon and Kelly, 2007) and geoffroy's cats (*Leopardus geoffroyi*) (Cuellar et al., 2006) along with several African and Asiatic species (Can et al., 2011; Srivathsa et al., 2015). Typically, the larger and more charismatic big cats are better studied, leaving small felids generally understudied (Maffei et al., 2005). Fewer than 10 publications exist for each of 14 small cat species with threatened status (Brodie, 2009). Despite smaller felids sharing a globally threatened status with the larger felids, research efforts are strongly skewed towards larger species (Brodie, 2009).

Previously, reported densities for ocelots in the broadleaf forests of Belize ranged from 11.24 to 25.88 ocelots per 100 $km^2$ and 38.1 individuals per 100 $km^2$ (Dillon and Kelly, 2008; Davis, 2008). Densities in the pine forests of Belize ranged from 2.3 to 3.8 individuals per 100 $km^2$ and 2.1 individuals per 100 $km^2$ (Dillon and Kelly, 2007; Davis, 2008). Outside of Belize, ocelots had the highest densities in Peru and Venezuela estimated at 40 to 80 adult individuals per 100 $km^2$, and 75.2 to 94.7 ocelots per 100 $km^2$ in the Peruvian Amazon near the Ecuador border (Ludlow and Sunquist, 1987; Emmons, 1988; Kolowski and Alonso, 2010). The lowest ocelot densities outside of Belize were in the Mexican State of Sonora at 5.7 individuals per 100

km$^2$ (Carillo and Lopez Gonzalez, 2002). See Table 2.1 for a comprehensive overview of ocelot densities throughout their geographic range.

Survival and mortality rates are unknown throughout majority of ocelot's geographic range. One study in southern Texas estimated an annual survival rate of 87% for resident ocelots and 57% for transient ocelots (Haines et al., 2005). Human disturbance caused 45% of ocelot mortality, usually in the form of vehicle collisions, and 35% were related to natural mortality, such as disease or animal attacks (Haines et al., 2005). Ocelots have low reproductive rates and relatively long interbirth intervals in comparison to other cat species of similar size (Sunquist and Sunquist, 2002. Relatively long gestation periods, with typically only 1-2 kittens per litter, makes ocelots potentially vulnerable to habitat loss and fragmentation (Hunter and Barrett, 2011, Sunquist and Sunquist, 2002). Information is needed on population status and trends throughout their range in order to determine in which areas ocelot populations are increasing or in decline.

In this study, I used camera-trapping methodology and capture-recapture analyses on data collected from a long-term, remote camera study to estimate population abundance, density, and survival of the ocelot, which occurs sympatrically with jaguars and three other felids across varied habitat types in Belize, Central America (Fig 1.2). Ocelots make excellent candidates for non-invasive camera-trapping methods implementing capture-recapture analyses due to their distinctive coat patterns (Fig. 1.2). I used both classical and spatially explicit capture-recapture methods to obtain ocelot density estimates from a long-term, multi-site, camera-trapping study targeting jaguars, pumas, and ocelots. My research fills an important knowledge gap considering that the last population estimates for ocelots in Belize were published in 2008 and 2009 (Dillon and Kelly, 2008; Davis, 2009) and used only older, classical methods that are known to include problematic assumptions. In addition, my thesis research is the first study to estimate ocelot

survival rates using robust design methodology, thereby producing the first survival rates for ocelots outside of the United States. This critical demographic information is useful for management of the species in a country with increasing anthropogenic pressures and deforestation rates. My thesis work consisted of three primary objects: 1) Estimate population density for ocelots in 4 field sites in Belize, Central America by using classical capture-recapture estimators for ocelots. 2) Estimate survival rates in two sites with 6 or more years of data using open robust design capture-recapture models, 3) Estimate population density for ocelots in 6 field sites in Belize, Central America by utilizing session specific and multi-session spatially explicit capture-recapture estimators for ocelots.

Figure 2.1. Ocelot range map across the Americas (adapted from The IUCN Red List of Threatened Species).
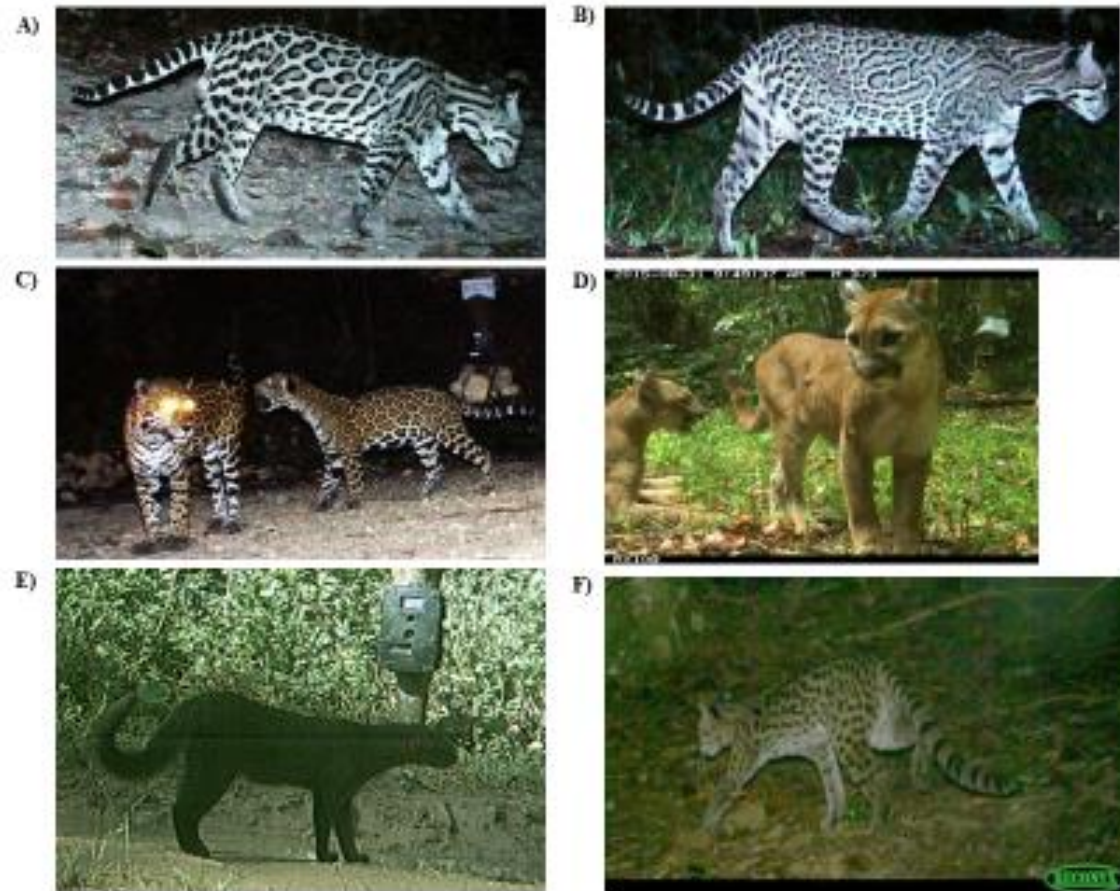
**Figure 1.2.** Ocelots (note distinctly different coat patterns that allow individual identification) and four species of sympatric felids found in Belize, Central America: A) Ocelot male (*Leopardus pardalis*), B) Ocelot female (lactating), C) Jaguar (*Panthera onca*), D) Puma (*Puma concolor*), E) Margay (*Leopardus wiedii*) and F) Jaguarundi (*Puma yagouaroundi*).

**II.** **Estimate population density for ocelots in 4 field sites in Belize, Central America by utilizing classical capture-recapture estimators for ocelots (*Leopardus pardalis*), and survival rates using closed robust design capture-recapture models in two sites with 6 or more years of data.**

**Abstract**

The ocelot (*Leopardus pardalis*) is a medium-sized Neotropical felid ranging from southern Texas to northern Argentina, including the islands of Trinidad and Margarita. In Belize, Central America, ocelots occur across a wide range of habitat types, such as primary and secondary broadleaf forest, marsh forest, pine forest, and savanna grasslands. However, we lack knowledge of basic demographic parameters because it is challenging to conduct surveys for this cryptic and nocturnal species. Yet, estimating abundance, density, and survival for ocelots across different habitats is critical to enable us to better inform wildlife conservation and management. I used camera-trapping methodology to estimate ocelot density on four study sites using full likelihood single session closed capture-recapture models and full likelihood multi-session robust design, open capture-recapture models on two sites containing six or more years of data across Belize. I compared models using Akaike's Information Criterion corrected for small sample sizes (AICc, Burnham and Anderson, 2002). I used R-package RMark to estimate animal abundance, implementing the ½ MMDM approach to estimate density. Using closed capture-recapture models, I found ocelot density varied from 6.4 - 22.5 individuals/100km$^2$ across four sites, and 8.8 to 22.8/100 km$^2$ on two sites using robust design capture-recapture models. Although estimates were generally similar between the techniques, robust design models produced lower precision than closed full likelihood models in 4 of the 6 years in Hill Bank but increased

precision in 4 of the 7 years in La Milpa, including one year with equal precision for both approaches. Annual survival rates from robust design analysis were between 71 to 79% in the two long-term sites. I found no evidence of ocelot survival differing between the 2 sites as both had overlapping confidence intervals. Additionally, I found no evidence that densities varied by year for either modeling approach as confidence intervals overlapped for all years/sites. Thus, ocelot populations appear to be stable over time rather than decreasing or increasing. Our results provide valuable information on ocelot status and trends across variable habitat types in Belize. This study is especially important due to increased anthropogenic disturbance in areas adjacent to protected areas.

**Key words:** abundance, Belize, camera-trapping, capture-recapture, density, *Leopardus pardalis* MMDM, robust design, small carnivores, survival

**Introduction**

The ocelot (*Leopardus pardalis*), categorized as least concern on the IUCN Red List, is Latin America's third largest cat, and has a geographic range from southern Texas to northern Argentina, including the islands of Trinidad and Margarita (Sunquist and Sunquist, 2002). The ocelot is known to inhabit a wide variety of habitat types (López González, Brown and Gallo-Reynoso, 2003) from thornscub to lowland rainforest (Hunter and Barrett, 2011), usually below elevations of 1,200 m (Nowell and Jackson, 1996). Ocelot populations are thought to be in decline due to habitat loss across their range (Sunquist and Sunquist, 2002). Studies have shown that ocelots can live in areas with natural ecosystems but generally do not do as well in human altered landscapes (Sunquist and Sunquist, 2002).

The ocelot is primarily nocturnal, elusive, and cryptic in nature. In Belize, Central America, ocelots are sympatric with other felids: jaguars (*Panthera onca*), pumas (*Puma concolor*), margays (*Leopardus wiedii*), and jaguarundis (*Puma yagouaroundi*). The secretive nocturnal lifestyle of the ocelot and its preference for dense cover, intact tropical forest, and secondary forest makes estimating population sizes difficult (Harveson et al., 2004; Horne et al., 2009; López González et al., 2000). Remotely-triggered infrared cameras combined with capture-recapture analysis for studying elusive, wide-ranging species with distinctive coat patterns was first pioneered for tigers (*Panthera tigris*) in India (Karanth, 1995; Karanth and Nichols, 1998). Since then camera-trapping studies have targeted some of the smaller felid species, such as ocelots (Dillon and Kelly, 2007), geoffroy's cats (*Leopardus geoffroyi*) (Cuellar et al., 2006), and several African and Asiatic species (Can et al., 2011; Srivathsa et al., 2015), although to a much lesser extent than their larger cousins (Maffei et al., 2005). Despite being excellent climbers, radio telemetry studies have found that ocelots hunt on the ground and therefore could be a good candidate species for camera trapping studies (Sunquist and Sunquist, 2002; Moreno et al., 2006). Additionally, in Belize, Davis et al. (2011) found evidence to support a positive association between ocelot trap success and road width and length. Other camera trapping studies in Belize also have shown that logging roads are preferred by ocelots likely because they are easier to travel and are used more by prey (Dillon and Kelly, 2007). In camera-trapping studies, cameras are usually placed along roads and trails that are well traveled by the target species in order to increase encounter probability (Royle et al., 2013). Thus, ocelots are likely excellent candidates for capture-recapture studies because they readily use road systems and can be identified by their unique coat markings (Trolle and Kery, 2003, 2005).

Previously reported densities for ocelots in the broadleaf forests of Belize ranged from 11.24 to 38.10 individuals per 100 km$^2$ (Dillon and Kelly, 2008; Davis, 2009). Densities in the pine forests of Belize were much lower and ranged from 2.11 to 3.80 individuals per 100 km$^2$ (Dillon and Kelly, 2007; Davis, 2009). Outside of Belize, ocelots had the highest densities in the Peruvian Amazon near the Ecuador border at 75.2 to 94.7 ocelots per 100 km$^2$ and 40 to 80 adult individuals per 100 km$^2$ in Peru and Venezuela (Kolowski and Alonso, 2010; Ludlow and Sunquist, 1987; Emmons, 1988). The lowest ocelot densities outside of Belize were in the Mexican State of Sonora at 5.7 individuals per 100 km$^2$ (Carillo and Lopez Gonzalez, 2002). See Table 2.1 for a comprehensive overview of ocelot densities throughout their geographic range.

The majority of studies measuring survival rates for ocelots have occurred in southern Texas on a small remnant population. For example, in southern Texas, Haines et al. (2005), using Mayfield (1961, 1975) methodology, estimated annual survival to be 0.87 for resident ocelots and 0.57 for transients. To our knowledge there have not been any survival estimates produced for ocelots outside the US and none using robust design capture-recapture models. Estimating density and survival using robust design models is useful for long-term data sets because such models explicitly account for population closure, utilizing closed-population models during the secondary sampling periods. However, between primary periods the population can be open. In addition, unlike Jolly-Seber models, they allow for temporary emigration to occur between primary periods, and thus can produce estimates of annual survival (Bailey et al., 2004). Using a method to estimate survival that does not account explicitly for these assumptions is more likely to result in biased estimates of population parameters (Bailey et al., 2004). For example, the assumptions of robust design models are: the population is assumed closed (no migration) across all secondary sampling occasions within primary sampling sessions, temporary emigration is

assumed to be random, Markovian, or a temporary response to first capture, and all individuals in the population have equal survival probability, regardless of availability for capture (Pollock, 1982).

In this study, I use motion-sensitive cameras and closed single session full likelihood capture-recapture methods at four study sites in Belize to determine how estimated density of ocelots vary over time. I also use open full likelihood robust design models to estimate survival over time in two sites in Belize. In addition, I predicted that precision of our estimates would improve using a robust design framework because data are pooled across years. Therefore, I compared the precision of our density estimates produced by open versus closed capture-recapture models. Density and survival are key demographic parameters that increase understanding of basic ocelot ecology and provide vital information essential to long-term ocelot conservation.

**Materials and methods**

*Study area*

The Belize mainland is approximately 63% forested (Foster et al., 2014; Cherrington et al., 2010; Meerman, 2011), and 43% of the mainland is uninhabited by humans. This includes national, private, or candidate protected areas, but it is estimated that only 17% of the mainland is protected against wildlife extraction (Foster et al. 2014; Cherrington et al., 2010; Meerman, 2011). Due to natural events 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 (P. Cho, pers. comm.), however, other forest types exist and are represented in our 6 study sites as described below (Figure 1).

1.      **Fireburn Rerserve** is located in northeastern Belize, approximately 5 – 15 km NE of the Caribbean coastline (Miller, 2006). The reserve is primarily tropical moist lowland forest, with an average rainfall of 152. 4 cm (Miller, 2006) and elevation of 1 m. The study site is surrounded by conservation areas including the Shipstern Wildlife Reserve to the north and Freshwater Creek Forest Reserve to the Southeast, as well as a large Mennonite community named Little Belize, to the west, where intensive agriculture occurs (Miller, 2006). Fireburn Reserve has low canopy cover, extensive saltwater swamp, and has been recovering from Hurricane Dean since 2008, resulting in a thick understory of downed trees and tangled secondary growth (Kelly – personal comm).

2.      **The La Milpa site of The Rio Bravo Conservation Management Area (RBCMA)** is split into two field sites, La Milpa and Hill Bank, and has been owned and managed by a local, non-governmental organization (NGO) called Programme for Belize (PfB) since 1982. The RBCMA is 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 (PfB, 2008). Annual rainfall averages from 300 to 350 cm per year and elevation ranges from 40 to 160 m.  La Milpa field station, which lies in the northern Orange Walk District abuts the commercial Mennonite farmlands of Blue Creek, and contains the third largest archeological site in Belize (PfB, 2008). La Milpa is primarily broadleaf forest and has strict conservation regulations due to the tourism potential; as a result, logging within the interior of the reserve is prohibited. However, some logging occurs on the edge in the "secondary forest products zone" (Kelly and Rowe, 2014). Additionally, the area currently has high levels of archeological research with associated digging.

3.      **The Hill Bank site of RBCMA** is a rich mosaic of habitats primarily composed of lowland broadleaf forest, freshwater swamp, and pine savanna. The site was logged intensively for over 300 years until the logging camps were abandoned in 1982, due to depleted timber stocks (Kelly and Rowe, 2014). In 1995, the site was established as a conservation field station with a focus on maintaining biodiversity, income, rehabilitation of forest quality, and other environmental goods and services through sustainable timber management (Kelly and Rowe, 2014). Guidelines following the sustainable forest management plan initiated by the Forest Department of Belize were set into place in 1997 (pfB, 2008; Bird, 1998). Timber harvest is done on a 40 year rotation, and is also in accordance with rules of the Forest Stewardship Council (FSC) and by the Rainforest Alliance (PfB, 2008).

4.      **Gallon Jug Estates**, located in northwestern Belize, is privately owned and undergoes sustainable logging (40 year rotation) along with coffee, cacao, and cattle production. The 520 km$^2$ estate is bordered by the Rio Bravo Conservation Management Area (RBCMA) to the north and east, and the Maya Biosphere Reserve in Guatemala to the west (Miller, 2005). Gallon Jug is composed primarily of lowland broadleaf moist evergreen seasonal forests with an average rainfall of 162.5 cm per year (Miller, 2005), and has an altitude of 40 to 160 m.

*Camera trap survey*

Ocelots make excellent candidates for capture-recapture analysis because they can be individually identified in remote camera photographs by their spot patterns. In this long term data set, two remotely triggered, infrared game cameras were placed on opposite sides of trails (new and old), roads, and logging roads to photograph the flanks of both sides of a passing animal. A total of 20 to 50 camera stations was established depending on site and year, and cameras were spaced on average 2 to 3 km apart to ensure that I surveyed a large enough area to

maximize the number of felid photographs and capture as many individually distinct felids as possible (Silver et al., 2004). Camera stations were placed so that each individual felid has a non-zero probability of being captured (Silver et al., 2004). To do this, locations for each camera station were originally based on the smallest known home range estimates for jaguars at 2 to 3 km intervals (Silver et al. 2004), however, some surveys included cameras set at 1.5 km apart, specifically for ocelots (Di Bitetti et al., 2006, Haines et al., 2006; Emmons, 1988). Camera stations were checked every 10 - 14 days in order to change film, SD cards, batteries, and conduct overall maintenance of cameras and remove encroaching vegetation. The total sampling period was no longer than 3 months to meet the assumption of geographic and demographic closure (no births, deaths, or migration).

*Modeling framework – Classical approach*

I created capture histories for each individual ocelot for 6 years in Hill Bank, 7 years in La Milpa, 3 years in Gallon Jug, and 1 year in Fireburn. The capture history matrix was constructed with the rows representing the capture history of each identified individual and columns representing captures on each occasion by denoting a "0" if the individual ocelot was not photographed (captured) or a "1" if it was photographed. Camera trapping data often contain a large number of 0 capture events on a daily basis that make computation problematic, therefore I collapsed capture occasions to various sampling blocks depending on year and site to represent a single capture occasion. The classical closed-capture-recapture methods estimate the capture probability of an individual's first encounter ($p_i$), recapture probability ($c_i$), and the number of animals in the population ($N$) (White and Burnham, 1999). The number of captured and recaptured individuals is commonly analyzed in a capture-recapture (C-R) framework using software programs such as CAPTURE and MARK. Pollock, (1974) and Otis et al. (1978)

accounted for three factors influencing capture probability: time ($M_t$ -capture probabilities vary

from sample to sample), behavior ($M_b$ - a trap response of animals to the first capture) and

heterogeneity ($M_h$ - each individual has a unique capture probability), and combinations of these

components. I used program CAPTURE to test population closure and Package RMark (Laake,

2013) to estimate population size using five closed capture-recapture, full likelihood

parameterization models as defined in Table 2.3. (Pollock, 1974; Otis et al., 1978; White and

Burnham, 1999). I calculated the maximum distance moved among camera stations for all

individuals in each year, then took the average to calculate the mean maximum distance moved

(MMDM). However, for one year (2010) in our Hill Bank site I calculated the ½ overall mean

maximum distance moved (½ OMMDM) from the pooled maximum distances across all six

trapping grids ranging from 2010 to 2015, following Dillon and Kelly (2007). This was done

because of an insufficient number of individuals with spatial-recaptures (Individuals captured at

two more camera stations), which are vital for calculating the ½ MMDM and the variance in

density (Wilson and Anderson, 1985). I applied the ad hoc method of buffering the camera traps

with the (½ MMDM) around each camera station and dissolving internal buffers in Arc GIS

version 10.0 (Environmental Systems Research Institute, Inc.  2012) to determine the effective

sampling area. I divided abundance estimated in RMark by the effective sampling area (A), to

derive an estimate of population density, defined by $\widehat{D} = \widehat{N}/A$. I used Akaike's Information

Criterion corrected for small sample sizes as our model selection criterion (AICc, Burnham and

Anderson, 2002) and considered models within 2 delta-AICc to be competing, however I only

used abundance estimates from the highest ranking model to generate density estimates.

 *Modeling framework – Robust Design*

In addition to full likelihood parameterization closed capture models in RMark, I also estimated abundance, density, and annual survival in Hill Bank over a 6 year period and La Milpa over a 7 year period. To do this, I applied extended classical capture-recapture to robust design full likelihood capture-recapture models to estimate the following parameters: S − annual survival, gamma-prime ($\gamma'$) − the probability of being outside of the study area and thus, unavailable for capture during the primary session ($i$) given that the animal was not available for capture during the previous primary session ($i - 1$) and survives to the trapping session ($i$), gamma-double-prime ($\gamma''$) − the probability of being outside of the study area and unavailable for capture during the primary session ($i$) given that the animal was available for capture during the previous primary session ($i - 1$) and survives to trapping session ($i$), and capture and recapture probabilities (p & c) (Cooch and White, 2006). Pollock's (1984) classic robust design differs from standard Cormack-Jolly-Seber models (CJS) in that multiple (>1) occasion can be used in the secondary sampling periods within each primary sampling period (Cooch and White, 2006). The secondary sampling intervals are close enough in time (in this case, a period of < 3 months) that the population is considered closed (i.e., no births, deaths, or migration) and secondary periods are separated by primary sampling intervals between which the population can be open (in our case, usually one year), thus immigration, emigration, births and deaths are more likely to occur (Bailey et al., 2004). In robust design, capture and recapture probabilities are estimated from each secondary sampling period along with population size for each primary period using closed-population capture-recapture models (Otis et al., 1978; White et al., 1982; Bailey et al., 2004). Annual survival rates are estimated from data pooled together within each primary period and both primary and secondary period information are used to estimate

emigration rates (Kendall and Nichols, 1995; Kendall et al., 1997; Kendall, 1999; Bailey et al., 2004).

I applied random movement' and no movement' multi-session models and ran every possible combination of the parameters outlined above for a total of 8 candidate models for both sites, as defined in Table 2.3. I held the survival parameter constant across all sites and years (a.k.a. sessions) but allowed all other parameters to vary by year or remain constant over all years. The no movement model (null model) sets $\gamma'' = \gamma' = 0$, thus not allowing for temporary emigration or immigration into the population. Therefore, the gamma parameter is not estimated. It is assumed that individuals that are 'observable' remain so through the duration of sampling occasions and individuals that are not 'observable' also remain that way through all sampling occasions (Cooch and White, 2006). It is recommended to always include the no movement model in the candidate model set unless you have strong contradictory evidence otherwise (Cooch and White, 2006). I tested the null, (i.e. no movement) model against the random movement model ($\gamma'' = \gamma'$), which sets emigration to be random, therefore the probability of emigrating during an interval is the same as the probability of staying away (i.e., the probability of not immigrating), therefore it only estimates one gamma parameter (Cooch and White, 2006). All models were evaluated using the Akaike's Information Criterion (Akaike, 1973) corrected for small sample sizes (AICc) in R-package RMark (AICc, Burnham and Anderson, 2002; Laake, 2013). For both sites I considered top models competing if they were within 2 delta AIC. The robust design estimates parameters $\gamma'$, $\gamma''$, p, and c, which are essential to achieving unbiased estimates of survival rates. I consider these 'nuisance parameters' given that only the survival rate was of direct interest to me and carried the most ecological relevance in our study system (Rosenblatt et al. 2016). I compared abundance and density estimates from our full

likelihood parametrization models in RMark to those produced by Robust Design in RMark by comparing precision between the two estimates.

**Results**

Across all 4 sites and years, I collected a total sample effort consisting of: 29,137 trap nights with 1,347 ocelot detections, 179 male ocelots, 223 female ocelots, and 14 individuals of unknown sex (Table 2.2). However, the same individuals may have been caught during multiple years for each site. The largest distance moved within all sites and years was 11.1 km for males and 6.0 km for females, with the exception of one female ocelot in Gallon Jug with a maximum distance moved of 20 km.

*Hill Bank*

For Hill Bank, I recorded a total of 267 ocelot detections in 10,287 trap nights over 6 years of camera-trapping surveys and the number of unique individuals captured during each sampling year varied from 11 to 22 (Table 2.2). Across all years the highest ranking models were either the linear time trend, behavior or null model (Table 2.3). In 2 of the 6 years the behavior model was the top model, however the behavior model was within 2 delta AIC of the top model in all 6 years but had convergence issues in 3 of the 6 years. For all years, abundance across all 5 candidate models for each year produced very similar abundance estimates with overlapping CI's, with the exception being when a model experienced convergence failure (Table 2.3).

The farthest distance traveled in Hill Bank across all years for males was 10.1 km and 6.0 km for females. The largest ½ MMDM was 2.5 km in 2014 and the smallest was 1.4 km in 2010 (Table 2.4). In 2010, I only had one individual ocelot with spatial recaptures at 3 different camera stations. Because spatial-recaptures are vital for calculating the ½ MMDM and the

variance in density I was unable to estimate an average distance moved across all individuals and therefore calculated the ½ overall mean maximum distance moved (½ OMMDM) from the pooled maximum distances across all six trapping grids ranging from 2010 to 2015 following Dillon and Kelly (2007). The ½ OMMDM was 2.1 km and was used to estimate the effective sampling area for 2010 (Table 2.4). Density estimates for each year based on analysis from RMark varied from 6.8 to 14.6 individual ocelots per 100 $km^2$ and the effective sampling area ranged from 156.4 to 162.10 $km^2$ (Table 2.4; Fig 2.2).

My top robust design model was a 'random movement model' which held parameters constant across all 6 years (Table 2.5). Density estimates produced by the top model ranged from 8.8 to 12.3 and produced lower precision than closed capture-recapture models in 4 of the 6 years in Hill Bank and had increased precision than closed capture-recapture models in 2 of the 6 years in which confidence intervals were generated (Table 2.6; Fig. 2.3). The robust design models produced larger density point estimates in 5 of 6 years but CIs overlap between methods (Table 2.7; Fig 2.3). The top model estimated an annual survival rate of ~ 79% (Table 2.6; Fig 2.7). My second top model was a 'no movement model' also holding parameters constant across all years and estimated an annual survival rate of ~78%. (Table 2.7).

*La Milpa – results*

For La Milpa, I recorded a total of 445 ocelot detections in 11,122 trap nights over 7 years of camera-trapping surveys and the number of unique individuals captured during each sampling year varied from 14 to 37 (Table 2.2). Across all years the highest ranking models were either a time, linear time trend, behavior, or null model. In 2010, I used the abundance estimates from the second top model (linear time) to generate density because the top model (behavior) failed to converge. Other than 2010, I had no convergence issues with top or competing models

and across all years the abundance estimates for all 5 candidate models for each year produced

very similar abundance estimates with overlapping CI's (Table 2.3).

The farthest distance traveled across all years for males was 11.1 km and 6.0 km for

females. The largest ½ MMDM was 2.4 km in 2010 and the smallest was 1.7 in 2014 (Table

2.4). Density estimates for each year based on analysis from RMark varied from 8.1 to 22.5

individuals per 100 km$^2$ and the effective sampling area varied from 149.1 to 200.7 km$^2$ (Table

2.5; Fig 2.4).

The top ranking model in robust design was a 'random movement model', which held

survival constant across all 7 years but allowed (p and c) to vary by year (session). However, I

did not consider this model as our top model because the interaction effect in the model

contained 7 additional parameters but did not increase the delta AIC by at least two units (AICc,

Burnham and Anderson, 2002; Arnold, 2010) (Table 2.5). I considered our second ranking

model as our top model, which was also a 'random movement model' holding the survival

parameter constant across sessions, but allowing capture probability (p) to vary by sessions

(Table 2.5). Density estimates produced by the top model ranged from 8.1 to 22.8 and produced

increased precision over closed classical capture-recapture models in 4 of 7 years including one

year with equal precision for both approaches, and with the greatest improvement in precision in

2013 (Table 2.6, Fig. 2.3). Robust design models produced higher density point estimates in only

2 of 7 years but produced equal point estimates to closed capture-recapture models in two years.

All estimates had overlapping CIs (Table 2.6; Fig. 2.5). The top model estimated an annual

survival rate of ~71%. (Table 2.7; Fig 2.5).

*Gallon Jug – results*

For Gallon Jug, I recorded a total of 603 ocelot detections in 6,328 trap night over 3 years of camera-trapping surveys and the number of unique individuals captured during each sampling year varied from 41 to 51 (Table 2.2). The farthest distance traveled across all years for males was 9.6 km and 20.0 km for females. Across all years the top models were either a time + behavior or behavior model (Table 2.3). In 2013, the top model was a time + behavior model, however three lower ranking models had convergence issues. There was only one competing model (null model) across all three years which occurred in 2014. In all years all 5 candidate models for each year produced very similar abundance estimates with overlapping CI's, with the exception being when a low ranking model experienced convergence failure (Table 2.5).

The largest ½ MMDM was 2.6 km in 2015 and the smallest was 2.0 km in 2014 (Table 2.4). Density estimates for each year based on analysis from RMark varied from 15.0 to 18.2 individuals per 100 $km^2$ and the effective sampling area varied from 267.5 to 361.7 $km^2$ (Table 2.4; Fig 2.2).

*Fireburn – results*

For Fireburn, I recorded a total of 32 ocelot detections in 1,400 trap nights over 1 year of a camera-trapping survey and the number of unique individuals captured during the 2009 sampling year was 14 (Table 2.2). The farthest distance traveled across all years for males was 7.6 km and 2.6 km for females. In 2009, the top model was the null model but competed with behavior and a linear time model. The null and linear time trend models both produced very similar abundance estimates but were about 2.6 units lower than the behavior model, however all estimates contained overlapping CI's (Table 2.7). The ½ MMDM was estimated to be 2.3 km, and density was estimated at 7.0 individuals per 100 $km^2$ with an effective sampling area of 221.3 $km^2$ (Table 2.4; Fig 2.2).

*Ocelot Densities across sites and years*

I found no evidence of ocelot densities differing within or among sites based on overlapping confidence intervals (Table 2.4; Fig 2.2). Although relatively stable, point estimates in some years fluctuated slightly, but this was likely due to sampling or environmental stochasticity (Table 2.4; Fig 2.2). Additionally, I found no evidence that densities varied by year for either the closed capture-recapture or robust design approach as confidence intervals overlapped for all years/sites (Table 2.6; Fig 2.3). I did not find evidence of the population increasing or decreasing over time, rather populations appear to be stable.

**Discussion**

Traditionally, camera-trapping studies in Belize targeting felids have focused mainly on jaguars and pumas (*Puma concolor*) (Harmsen et al. 2010; Kelly et al. 2008; Rabinowitz and Nottingham, 1986). More recently, in Belize, camera-trapping studies have focused on photographic capture-recapture analysis of smaller felids, but jaguars and pumas have still been the primary aim of these studies (Harmsen et al. 2011; Kelly et al. 2008; Silver et al. 2004; Kelly, 2003). Although non-invasive genetic studies including small wild cats of Belize have been increasing (Wultsch et al. 2014; Mesa-Cruz et al. 2014), capture-recapture studies on the smaller felids in Belize are still largely absent. The last published study on ocelots was more than 5 years ago (Davis et al. 2011) and ocelot studies focusing on estimating population size occurred more than 7 years ago (Dillon and Kelly, 2008). My study represents one of the first to estimate ocelot density over a large-scale, multi-year, and multi-site landscape covering a wide variety of habitat types across Northern Belize.

Gallon Jug had the highest number of ocelot detections with an average of 200 detections each year during the 3 years surveyed. This is impressive considering that this site, which has timber extraction, borders the completely protected La Milpa site where I averaged 64 ocelot detections per year over a 7 year period. Across all sites and years the number of individuals with spatial-recaptures ranged from 1 to 24, with the highest occurring in Gallon Jug and the lowest in the Hill Bank 2010 survey. One of the limitations of using the classical approach to estimate density is that a minimum of at least two individuals must be spatially-recaptured to generate confidence intervals for density estimates (Wilson and Anderson, 1985). However, the relatively high number of spatial-recaptures across sites and years suggest that an average trap spacing of at least 2 km is appropriate for targeting ocelots. Average trap spacing was fairly consistent across all sites and years in this study, varying from 1.0 to 2.4 (km). Thus, I believe this study obtained sufficient spatial recaptures across all sites and years (with one exception - Hill Bank 2010) to reliably estimate abundance and density for ocelots.

I found ocelot densities to be the highest on average, across years, in La Milpa and Gallon Jug with both sites averaging ~ 16 individuals/100 km$^2$ in each year, although densities across all sites exhibited overlapping CI's. Both La Milpa and Gallon Jug, w hich are adjacent to each other, also contained the largest effective sampling areas. I found that the majority of the density estimates increased with decreasing effective sampling area, which may be a result of too few spatial-recaptures in some years, thus resulting in potentially inflated density estimates. Other studies have shown that the classical ½ MMDM approach can overestimate density (Dillon and Kelly 2007; Gerber et al., 2012; Soisalo and Cavalcanti, 2006; Silveira et al., 2009). Precision was worse in sites and years where the effective sampling area was lower, which has been documented in other studies implementing classical capture recapture methods (Tobler and

Powell, 2012). However, it should be noted that smaller effective sampling areas did not always equate to higher density estimates.

My density estimate in La Milpa for 2008 was estimated to be 22.5 individuals/100 km$^2$ (95% CI = 17.7 – 27.4), much lower than that produced by Davis (2009), who estimated 38.8 individuals/100 km$^2$ (95% CI = 25.70 - 51.9) in the same year, with the same data. Both estimates were generated from camera grids containing 40 camera stations and produced similar abundance estimates. I estimated abundance to be 40.5 ocelots compared to 39.0 estimated by Davis (2009). It seems the difference in density estimates from our two studies arises from the estimated ½ MMDM. I generated a ½ MMDM = 1.7 km, resulting in an effective sampling size of 179.5 km$^2$, compared to Davis (2009) who estimated a ½ MMDM = 1.5 and a smaller effective sample area of 100.5 km$^2$. The difference in the ½ MMDM between our surveys may be due to Davis (2009) having a high number of one-sided individuals and using only left sided individuals in her analysis, whereas I may have benefited from having a data set expanding through multiple years, and thus been able to individually identify an additional ocelot with higher certainty due to having both sides of the ocelot captured. However, this highlights a limitation of the classical approach in that two different density estimates can be generated from the same abundance estimate, since the buffering method is highly sensitive to the mean maximum movement estimates. Unlike spatial capture-recapture methods (see Chapter 3) the parameter N (population size) is functionally unrelated to the sample area, leaving the investigator to estimate an ad hoc buffer in order to generate density estimates (Royle et al. 2013). Another limitation of classical capture-recapture analysis is that models incorporating individual covariates, like sex, cannot be specified if covariate values are missing (Cooch and

White, 2006). Therefore, I was unable to model sex as an individual covariate (as in Chapter 3), which may aid in accounting for individual heterogeneity (Royle et al. 2013).

I expected density estimates produced by robust design methodology to have better precision over closed full likelihood models due to robust design models accounting for capture probabilities in both primary and secondary samples and pooling information in over multiple years. In Hill Bank robust design models were less precise than closed capture-recapture models in 4 of the 6 years in Hill Bank but more precise in 4 of the 7 years in La Milpa, including one year with equal precision for both approaches. La Milpa likely gained precision from robust design models because it was a larger data set and less sparse than Hill Bank. In general, more complex models require larger sample sizes to produce high precision in the estimates.

It is possible that in years with fewer spatial-recaptures and smaller spatial movements of ocelots could be caused by environmental factors such as rainfall. Dillon and Kelly (2008) found adult ocelot home ranges to be larger in the dry season. Oliveira et al. (2010) found a correlation between rainfall and ocelot density, although it was not correlated with home range size. I recommend potentially using some type of site level covariate measuring environmental variables in future analysis. In addition, if male and female ocelots have different home-range sizes and/or encounter rates, models that do not account for sex may lead to a negative bias in density estimates (Tobler and Powell, 2012). I attempted to use sex as an individual covariate but due to missing values for most years and RMark's inability to accommodate missing individual covariate observations, I was not able to do so. This led me to only account for sex using spatially explicit modeling techniques discussed in Chapter 3.

Annual survival for ocelots in Hill Bank was 0.79%, which was slightly higher than in La Milpa where annual survival was estimated at 0.71%. However, it does not seem that survival of

ocelots differs strongly between sites considering that both sites have overlapping confidence intervals. Temporary emigration was higher in La Milpa (0.23) than Hill Bank (0.04), although both sites had estimates with relatively low precision, potentially due to small sample sizes in some years (Rosenblatt et al. 2016). For both years/sites I found no evidence that densities for either approach varied by year as all sites had overlapping confidence intervals. This is interesting on another front because La Milpa is completely protected while Hill Bank is selectively logged. This is good news for ocelot conservation in Belize as the cats appear to be stable over time and do not appear to be decreasing or increasing across the sites that do or do not experience timber extraction.

Our study provides useful insight into past and current ocelot density across four sites in Belize. Camera-trapping methodology implementing capture-recapture methods provides a robust tool for monitoring wildlife populations. In addition, I produced the first estimates of survival for ocelots in Belize from long-term data by implementing methodological analysis in robust design. Further, by collecting data over multiple sites and years we are able to better track wildlife populations and observe trends through time. This is a more powerful approach then a onetime snapshot of demographic parameters that may not reveal environmental and sampling stochasticity.

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Table 2.1. Ocelot density estimates across various habitat types and estimation methods. MMDM = Mean maximum distance moved, SCR = Spatial capture-recapture. Studies organized in chronological order.

| Location | Habitat | Density/100 km$^2$ | Buffering method | Reference |
|---|---|---|---|---|
| Mexico | Thornscrub | 5.7 | ½ MMDM | Carillo and Lopez Gonzalez, 2002 |
| Brazil | Pantanal | 56.4 | ½ MMDM | Trolle and Kéry, 2003 |
| Argentina | Broadleaf/Pine | 7.7 | MMDM | Di Betetti et al. 2006 |
| Argentina | Brodleaf/Pine | 13.4 | ½ MMDM | Di Betetti et al. 2006 |
| Argentina | Brodleaf(Iguazú) | 12.8 | MMDM | Di Betetti et al. 2006 |
| Texas | Scrub (Yturria Ranch) | 30.0 | ½ MMDM | Haines et al. 2006 |
| Argentina | Brodleaf(Iguazú) | 19.9 | ½ MMDM | Di Betetti et al. 2006 |
| Belize | Broadleaf | 25.9 | ½ MMDM | Dillon and Kelly, 2008 |
| Belize | Broadleaf | 12.6 | MMDM | Dillon and Kelly, 2008 |
| Belize | Pine Forest | 2.1 | ½ MMDM | Davis, 2009 |
| Belize | Broadleaf | 38.8 | ½ MMDM | Davis, 2009 |
| Brazil | Atlantic Forest | 4.0 | ½ MMDM | Goulart et al. 2009 |
| Panama | tropical wet forest | 62.7 | ½ MMDM | Moreno et al. 2009 |
| Peru | Lowland tropical rainforest | 75.2 - 94.7 | ½ MMDM | Kolowski and Alonso, 2010 |
| Columbia | Colombian llanos | 11.1 | ½ MMDM | Diaz-Pulido and Payan, 2011 |
| Costa Rica | Tropical wet forest | 5.59 - 11.61 | Telemetry | González-Maya et al. 2011 |
| Bolivia | Chaco-Amazon Forest | 1.6 - 51.7 | SCR | Noss et al. 2012 |
| Mexico | Tropical deciduous Forest | 3 - 18 | SCR | Martínez-Hernández et al. 2014 |
| Ecuador | Evergreen terra firme tropical forest | 31.3 -34.8; 84.5 | MMDM; ½ MMDM | Salvador and Espinosa, 2015 |
| Brazil | Amazon Forest | 24.84 - 28.9 | SCR | da Rocha et al. 2016 |

Table 2.2. Ocelot and camera summary statistics for surveys conducted in each year and site in Belize, Central America (2008 - 2015). Trap nights represent total number of days across all camera stations with at least 1 camera functional. Site names are defined as: HB = Hill Bank, LM = La Milpa, GJ = Gallon Jug, FB = Fireburn, NA = not able to determine sexual identity.

| Site | Year | Average trap spacing (km) | Camera stations | Individuals captured | Total detections | #Individuals with spatial-recaptures | Survey length (days) | Trap nights |
|------|------|------|------|------|------|------|------|------|
| HB | 2010 | 2.3 | 19 | 11 (7 ♂, 4 ♀) | 23 | 1 | 75 | 1022 |
|    | 2011 | 2.4 | 20 | 16 (5 ♂, 10 ♀, 1 NA) | 48 | 6 | 82 | 1539 |
|    | 2012 | 1.9 | 20 | 19 (6 ♂, 13 ♀) | 54 | 8 | 82 | 1455 |
|    | 2013 | 2.0 | 26 | 12 (8 ♂, 4 ♀) | 23 | 2 | 70 | 1605 |
|    | 2014 | 2.0 | 26 | 22 (11 ♂, 11 ♀) | 75 | 8 | 98 | 2195 |
|    | 2015 | 2.1 | 31 | 16 (5 ♂, 11 ♀) | 44 | 6 | 82 | 2471 |
| LM | 2008 | 1.0 | 40 | 37 (20 ♂, 15 ♀, 2 NA) | 98 | 15 | 91 | 2543 |
|    | 2010 | 2.2 | 19 | 14 (6 ♂, 8 ♀) | 30 | 4 | 82 | 815 |
|    | 2011 | 2.2 | 20 | 25 (12 ♂, 11 ♀, 2 NA) | 58 | 4 | 90 | 1239 |
|    | 2012 | 2.2 | 21 | 25 (11 ♂, 13 ♀, 1 NA) | 50 | 9 | 72 | 1354 |
|    | 2013 | 2.3 | 22 | 25 (11 ♂, 14 ♀) | 70 | 10 | 80 | 1666 |
|    | 2014 | 2.3 | 23 | 21 (10 ♂, 10 ♀, 1 NA) | 54 | 10 | 82 | 1656 |
|    | 2015 | 2.3 | 30 | 26 (10 ♂, 13 ♀, 3 NA) | 85 | 9 | 86 | 1849 |
| GJ | 2013 | 2.2 | 30 | 41 (16 ♂, 25 ♀) | 209 | 20 | 85 | 2083 |
|    | 2014 | 2.3 | 35 | 41 (17 ♂, 22 ♀, 2 NA) | 174 | 19 | 85 | 2107 |
|    | 2015 | 2.4 | 33 | 51 (20 ♂, 31 ♀) | 220 | 24 | 92 | 2138 |
| FB | 2009 | 2.3 | 33 | 14 (4 ♂, 8 ♀, 2 NA) | 32 | 6 | 127 | 1400 |

Table 2.3. The top five full likelihood closed capture-recapture models used to estimate ocelot abundance in Belize, Central America (2008 - 2015), produced in RMark for each survey year in Hill Bank (HB), La Milpa (LM), Gallon Jug (GJ) and Fireburn (FB). Models were ranked by Akaike's Information Criterion corrected for small sample sizes (AICc). The delta AIC (ΔAICc) is the difference in AICc from the top model. Model parameterization defined as follows: Capture probability (p), recapture probability (c), time varying (time), linear trend over time (Time), number of individuals never caught ($f_0$), constant (~1). Model definitions: Null model = p(~1)c()f0(~1), Behavior model = p(~1)c(~1)f0(~1), linear time model = p(~Time)c()f0(~1), time model = p(~time)c()f0(~1), time behavioral model = p(~time + c)c()f0(~1), Fail = convergence failure. Table extends from pages 40 - 43.

| Site | Year | Model | Parameters | AICc | ΔAICc | AIC weight | Deviance | Abundance (95% CI) |
|------|------|-------|-----------|------|-------|-----------|----------|--------------------|
| HB | 2010 | p(~Time)c()f0(~1) | 3 | 74.149 | 0.000 | 0.488 | 55.758 | 13.0 (11.0 - 24.0) |
| | | p(~1)c(~1)f0(~1) | 3 | 75.082 | 0.933 | 0.306 | 56.691 | Fail |
| | | p(~1)c()f0(~1) | 2 | 75.877 | 1.728 | 0.206 | 59.580 | 14.0 (12.0- 26.0) |
| | | p(~time)c()f0(~1) | 13 | 91.225 | 17.076 | 0.000 | 49.936 | 13.0 (11.0 - 25.0) |
| | | p(~time + c)c()f0(~1) | 14 | 93.647 | 19.498 | 0.000 | 49.853 | 17.0 (11.0 - 133.0) |
| | 2011 | p(~1)c(~1)f0(~1) | 3 | 196.327 | 0.000 | 0.694 | 168.417 | 23.0 (17.0 − 73.0) |
| | | p(~1)c()f0(~1) | 2 | 198.793 | 2.466 | 0.202 | 172.922 | 16.0 (16.0 - 23.0) |
| | | p(~time)c()f0(~1) | 3 | 200.831 | 4.504 | 0.073 | 172.922 | 16.0 (16.0 - 23.0) |
| | | p(~time + c)c()f0(~1) | 22 | 202.633 | 6.306 | 0.030 | 133.392 | Fail |
| | | p(~Time)c()f0(~1) | 21 | 209.786 | 13.459 | 0.001 | 142.852 | 16.0 (16.0 - 23.0) |
| | 2012 | p(~1)c()f0(~1) | 2 | 220.766 | 0.000 | 0.536 | 186.297 | 20.0 (19.0 − 27.0) |
| | | p(~Time)c()f0(~1) | 3 | 222.24 | 1.475 | 0.257 | 185.740 | 20.0 (19.0 − 27.0) |
| | | p(~1)c(~1)f0(~1) | 3 | 222.692 | 1.927 | 0.205 | 186.192 | 20.0 (19.0 − 33.0) |
| | | p(~time)c()f0(~1) | 21 | 232.141 | 232.141 | 0.002 | 157.124 | 20.0 (19.0 − 27.0) |
| | | p(~time + c)c()f0(~1) | 22 | 234.385 | 234.385 | 0.001 | 157.114 | 20.0 (19.0 − 36.0) |
| | 2013 | p(~Time)c()f0(~1) | 3 | 79.309 | 0.000 | 0.528 | 61.817 | 15.0 (12.0 -27.0) |
| | | p(~1)c(~1)f0(~1) | 3 | 79.78 | 0.471 | 0.417 | 62.288 | Fail |
| | | p(~1)c()f0(~1) | 2 | 83.878 | 4.570 | 0.054 | 68.460 | 16.0 (13.0 -30.0) |
| | | p(~time)c()f0(~1) | 15 | 93.092 | 13.783 | 0.001 | 48.588 | 15.0 (13.0 - 28.0) |
| | | p(~time + c)c()f0(~1) | 16 | 94.26 | 14.951 | 0.000 | 47.312 | Fail |
| HB | 2014 | p(~1)c(~1)f0(~1) | 3 | 330.346 | 0.000 | 0.516 | 290.782 | 24.0 (22.0 − 39.0) |
| | | p(~1)c()f0(~1) | 2 | 331.358 | 1.012 | 0.311 | 293.817 | 22.0 (22.0 - 28.0) |

| Site | Year | Model | Parameters | AICc | ΔAICc | AIC weight | Deviance | Abundance (95% CI) |
|------|------|-------|-----------|------|-------|-----------|----------|---------------------|
| | | p(~Time)c()f0(~1) | 3 | 333.058 | 2.712 | 0.133 | 293.494 | 22.0 (22.0 - 28.0) |
| | | p(~time + c)c()f0(~1) | 26 | 335.493 | 5.147 | 0.039 | 247.172 | Fail |
| | | p(~time)c()f0(~1) | 25 | 342.87 | 12.524 | 0.001 | 256.762 | Fail |
| | 2015 | p(~1)c()f0(~1) | 2 | 187.296 | 0.000 | 0.466 | 155.879 | 17.0 (16.0 − 24.0) |
| | | p(~1)c(~1)f0(~1) | 3 | 187.978 | 0.682 | 0.331 | 154.523 | Fail |
| | | p(~Time)c()f0(~1) | 3 | 188.963 | 1.667 | 0.202 | 155.508 | 17.0 (16.0 - 24.0) |
| | | p(~time)c()f0(~1) | 21 | 201.535 | 14.239 | 0.000 | 129.055 | 17.0 (16.0 − 28.0) |
| | | p(~time + c)c()f0(~1) | 22 | 202.154 | 14.858 | 0.000 | 127.368 | Fail |
| LM | 2008 | p(~time)c()f0(~1) | 31 | 396.061 | 0.000 | 0.647 | 277.537 | 41.0 (38.0 - 49.0) |
| | | p(~time + c)c()f0(~1) | 32 | 397.272 | 1.212 | 0.353 | 276.628 | 47.0 (39.0 - 102.0) |
| | | p(~1)c()f0(~1) | 2 | 416.035 | 19.974 | 0.298 | 357.340 | 50.0 (38.0 - 50.0) |
| | | p(~Time)c()f0(~1) | 3 | 416.972 | 20.911 | 0.000 | 356.267 | 41.0 (38.0 - 50.0) |
| | | p(~1)c(~1)f0(~1) | 3 | 417.478 | 21.417 | 0.000 | 356.772 | 44.0 (38.0 − 68.0) |
| | 2010 | p(~1)c(~1)f0(~1) | 3 | 172.187 | 0.000 | 0.900 | 145.406 | Fail |
| | | p(~Time)c()f0(~1) | 3 | 176.751 | 4.564 | 0.092 | 149.970 | 16.0 (14.0 - 26.0) |
| | | p(~1)c()f0(~1) | 2 | 181.653 | 9.466 | 0.008 | 156.893 | 16.0 (14.0 − 26.0) |
| | | p(~time + c)c()f0(~1) | 43 | 208.462 | 36.275 | 0.000 | 94.583 | Fail |
| | | p(~time)c()f0(~1) | 42 | 212.255 | 40.068 | 0.000 | 100.714 | 16.0 (14.0 − 25.0) |
| | 2011 | p(~Time)c()f0(~1) | 3 | 159.336 | 0.000 | 0.909 | 119.425 | 30.0 (27.0 - 42.0) |
| | | p(~time)c()f0(~1) | 16 | 164.673 | 5.337 | 0.063 | 97.308 | 29.0 (26.0 − 39.0) |
| | | p(~time + c)c()f0(~1) | 17 | 166.358 | 7.021 | 0.027 | 96.797 | 37.0 (26.0 − 157.0) |
| | | p(~1)c(~1)f0(~1) | 3 | 173.575 | 14.239 | 0.001 | 133.664 | Fail |
| | | p(~1)c()f0(~1) | 2 | 178.207 | 18.870 | 0.000 | 140.328 | 29.0 (26.0 - 40.0) |
| | 2012 | p(~1)c()f0(~1) | 2 | 131.376 | 0.000 | 0.486 | 108.399 | 32.0 (27.0 − 47.0) |
| LM | | p(~Time)c()f0(~1) | 3 | 133.076 | 1.700 | 0.208 | 108.058 | 32.0 (28.0 - 47.0) |
| | | p(~1)c(~1)f0(~1) | 3 | 133.176 | 1.800 | 0.198 | 108.158 | 36.0 (27.0 − 95.0) |
| | | p(~time)c()f0(~1) | 13 | 135.636 | 4.260 | 0.058 | 89.426 | 31.0 (27.0 - 45.0) |
| | | p(~time + c)c()f0(~1) | 14 | 135.872 | 4.496 | 0.051 | 87.462 | Fail |
| | 2013 | p(~1)c(~1)f0(~1) | 3 | 240.164 | 0.000 | 0.590 | 191.940 | 33.0 (26.0 − 71.0) |

| Site | Year | Model | Parameters | AICc | ΔAICc | AIC weight | Deviance | Abundance (95% CI) |
|------|------|-------|------------|------|-------|------------|----------|--------------------|
| | | p(~1)c()f0(~1) | 2 | 242.054 | 1.890 | 0.229 | 195.860 | 26.0 (25.0 – 34.0) |
| | | p(~Time)c()f0(~1) | 3 | 242.533 | 2.369 | 0.805 | 194.308 | 26.0 (25.0 - 33.0) |
| | | p(~time + c)c()f0(~1) | 18 | 263.641 | 23.477 | 0.000 | 183.682 | 39.0 (26.0 - 186.0) |
| | | p(~time)c()f0(~1) | 17 | 264.059 | 23.895 | 0.000 | 186.293 | 26.0 (25.0 - 33.0) |
| | 2014 | p(~1)c()f0(~1) | 2 | 190.957 | 0.000 | 0.567 | 159.176 | 23.0 (21.0 – 31.0) |
| | | p(~Time)c()f0(~1) | 3 | 192.79 | 1.833 | 0.227 | 158.973 | 23.0 (21.0 – 40.0) |
| | | p(~1)c(~1)f0(~1) | 3 | 192.971 | 2.014 | 0.207 | 159.154 | 23.0 (21.0 - 38.0) |
| | | p(~time)c()f0(~1) | 17 | 212.759 | 21.802 | 0.000 | 149.089 | 23.0 (21.0 – 31.0) |
| | | p(~time + c)c()f0(~1) | 18 | 214.496 | 23.539 | 0.000 | 148.593 | 26.0 (22.0 – 75.0) |
| | 2015 | p(~1)c()f0(~1) | 2 | 231.142 | 0.000 | 0.549 | 199.078 | 27.0 (26.0 - 34.0) |
| | | p(~Time)c()f0(~1) | 3 | 232.711 | 1.569 | 0.250 | 198.614 | 27.0 (26.0 – 35.0) |
| | | p(~1)c(~1)f0(~1) | 3 | 233.173 | 2.031 | 0.199 | 199.076 | 27.0 (26.0 - 38.0) |
| | | p(~time)c()f0(~1) | 15 | 243.305 | 12.163 | 0.001 | 183.895 | 27.0 (26.0 - 34.0) |
| | | p(~time + c)c()f0(~1) | 16 | 245.219 | 14.077 | 0.000 | 183.620 | 29.0 (26.0 – 55.0) |
| GJ | 2013 | p(~time + c)c()f0(~1) | 14 | 372.772 | 0.000 | 0.951 | 275.765 | 49.0 (42.0 - 95.0) |
| | | p(~time)c()f0(~1) | 13 | 380.225 | 7.453 | 0.023 | 285.337 | Fail |
| | | p(~1)c(~1)f0(~1) | 3 | 380.353 | 7.581 | 0.021 | 306.177 | 43.0 (41.0 – 53.0) |
| | | p(~1)c()f0(~1) | 2 | 384.317 | 11.544 | 0.003 | 312.165 | Fail |
| | | p(~Time)c()f0(~1) | 3 | 384.95 | 12.178 | 0.002 | 310.774 | Fail |
| | 2014 | p(~1)c(~1)f0(~1) | 3 | 359.679 | 0.000 | 0.000 | 288.524 | 42.0 (40.0 – 52.0) |
| | | p(~1)c()f0(~1) | 2 | 361.069 | 1.390 | 0.296 | 291.939 | 40.0 (40.0 - 46.0) |
| GJ | | p(~Time)c()f0(~1) | 3 | 363.058 | 3.379 | 0.110 | 291.903 | 40.0 (40.0 - 46.0) |
| | | p(~time + c)c()f0(~1) | 14 | 376.775 | 17.097 | 0.000 | 282.767 | 44.0 (41.0 - 67.0) |
| | | p(~time)c()f0(~1) | 13 | 378.612 | 18.933 | 0.000 | 286.726 | 40.0 (40.0 - 46.0) |
| | 2015 | p(~time + c)c()f0(~1) | 17 | 390.398 | 0.000 | 0.746 | 283.625 | 58.0 (52.0 – 91.0) |
| | | p(~time)c()f0(~1) | 16 | 392.55 | 2.153 | 0.254 | 287.870 | 52.0 (51.0 - 58.0) |
| | | p(~Time)c()f0(~1) | 3 | 446.816 | 56.419 | 0.000 | 368.831 | 53.0 (51.0 - 59.0) |
| | | p(~1)c()f0(~1) | 2 | 480.141 | 89.744 | 0.000 | 404.172 | 52.0 (51.0 – 59.0) |
| | | p(~1)c(~1)f0(~1) | 3 | 480.954 | 90.557 | 0.000 | 402.970 | 51.0 (51.0 – 59.0) |

| Site | Year | Model | Parameters | AICc | ΔAICc | AIC weight | Deviance | Abundance (95% CI) |
|------|------|-------|------------|------|-------|------------|----------|--------------------|
| FB | 2009 | p(~1)c()f0(~1) | 2 | 124.884 | 0.000 | 0.537 | 102.860 | 16.0 (14.0 - 24.0) |
| | | p(~1)c(~1)f0(~1) | 3 | 126.365 | 1.481 | 0.256 | 102.283 | 18.0 (15.0 − 51.0) |
| | | p(~Time)c()f0(~1) | 3 | 126.817 | 1.932 | 0.204 | 102.734 | 16.0 (14.0 - 24.0) |
| | | p(~time + c)c()f0(~1) | 17 | 137.443 | 12.559 | 0.001 | 82.290 | Fail |
| | | p(~time)c()f0(~1) | 16 | 137.83 | 12.945 | 0.001 | 85.045 | 15.0 (14.0 - 23.0) |

Table 2.4. Abundance and density estimates for ocelots in Belize, Central America (2008 - 2015) from the top full likelihood capture-recapture models in Table 2.2 for each year and site along with their respective effective sample areas determined by placing circular buffers around camera stations equal to the ½ mean maximum distance moved (½ MMDM) by ocelots among cameras.  In Hill Bank (2010) I used the ½ overall mean maximum distance moved (1/2 OMMDM) from the pooled maximum distances across all six trapping grids ranging from 2010 to 2015 to accommodate the lack of spatial-recaptures. I divided abundance estimated in RMark by the effective sampling area (A), to derive an estimate of population density, defined by $\hat{D} = \hat{N}/A$. Site names are: HB = Hill Bank, LM = La Milpa, GJ = Gallon Jug, FB = Fireburn.

| Site | Year | Abundance (95% CI) | Buffer: ½ MMDM (km) | Effective sample area (km$^2$) | Density/100 km$^2$ (95% C.I) |
|------|------|--------------------|---------------------|-------------------------------|------------------------------|
| HB | 2010 | 13.0 (11.0 - 24.0) | 2.2 | 190.4 | 7.3 (4.5 - 10.1) |
| | 2011 | 23.0 (17.0 – 73.0) | 1.8 | 156.4 | 14.6 (1.8 - 27.4) |
| | 2012 | 20.0 (19.0 - 27.0) | 2.2 | 195.2 | 10.2 (7.6 - 12.7) |
| | 2013 | 15.0 (13.0 - 27.0) | 2.4 | 228.7 | 6.4 (2.7 - 10.2) |
| | 2014 | 24.0 (22.0 – 39.0) | 2.5 | 237.6 | 10.2 (7.0 - 13.4) |
| | 2015 | 17.0 (16.0 – 24.0) | 1.4 | 162.1 | 10.3 (8.3 - 12.3) |
| LM | 2008 | 41.0 (38.0 - 49.0) | 1.7 | 179.5 | 22.5 (17.7 - 27.4) |
| | 2010 | 16.0 (14.0 - 26.0) | 2.4 | 200.7 | 8.1 (4.6 - 11.6) |
| | 2011 | 30.0 (27.0 - 42.0) | 2.1 | 182.9 | 16.6 (12.4 -20.8) |
| | 2012 | 32.0 (27.0 – 47.0) | 2.3 | 200.6 | 16.0 (11.2 - 20.8) |
| | 2013 | 33.0 (26.0 – 71.0) | 1.9 | 165.3 | 19.9 (9.2 - 30.5) |
| | 2014 | 23.0 (21.0 – 31.0) | 1.7 | 149.1 | 15.3 (12.3 - 18.3) |
| | 2015 | 27.0 (26.0 - 34.0) | 1.9 | 188.8 | 14.4 (11.4 - 17.5) |
| GJ | 2013 | 49.0 (42.0 - 95.0) | 2.1 | 267.5 | 18.2 (10.7 - 25.6) |
| | 2014 | 42.0 (40.0 – 52.0) | 2.0 | 293.0 | 14.2 (12.3 - 16.2) |
| | 2015 | 58.0 (52.0 - 90.0) | 2.6 | 361.7 | 16.0 (10.9 - 21.1) |
| FB | 2009 | 16.0 (14.0 - 24.0) | 2.3 | 221.3 | 7.0 (4.7 - 9.3) |

Table 2.5. Robust design multi-session full likelihood capture-recapture models to estimate ocelot abundance and survival in Belize, Central America (2008, 2010 - 2015) over 6 years in Hill Bank (HB) and 7 years La Milpa (LM). Models were ranked by Akaike's Information Criterion corrected for small sample sizes (AICc). Parameter definitions: Gamma', the probability that an individual stays away from the study area in *i*, given that it was a temporary migrant in *i*-1; Gamma´´, the probability that an animal in the study area in period *i*-1 moves out of the study area in *i*; detection probability (p); redetection probability (c); years (sessions); fixed (constant) survival in all years (S (~1)), number of individuals never caught (f$_0$); and not estimated (). All possible combinations of the parameters were run for a total of 8 candidate models listed below for both sites. Parameterization specified random movement' (migration into and out of the study area is random) and therefore the model only estimates one gamma parameter (Gamma~1 ´´. Random), and no movement', which does not allow for temporary migration into the population, therefore, the gamma parameter is not estimated (Gamma ´´ (~1)). Survival was fixed (constant) across all sessions and all other parameters varied by session (~session) or were fixed (~1) across sessions. The top ranking model in LM contained 7 additional parameters and did not increase the delta AIC by at least two units, therefore I only presented results from the second top model only.

| Site | Model | Parameters | AICc | dAICc | AIC weight | Deviance |
|------|-------|------------|------|-------|------------|----------|
| HB | S(~1)Gamma"(~1. random)Gamma'()p(~1)c(~1)f0(~session) | 10 | 1229.304 | 0.000 | 0.501 | 1277.147 |
|  | S(~1)Gamma"(~1)Gamma'()p(~1)c(~1)f0(~session) | 10 | 1229.421 | 0.118 | 0.472 | 1277.265 |
|  | S(~1)Gamma"(~1.random)Gamma'()p(~1)c()f0(~session) | 9 | 1235.482 | 6.178 | 0.023 | 1285.498 |
|  | S(~1)Gamma"(~1)Gamma'()p(~-1 + session * c)c()f0(~session) | 20 | 1241.170 | 11.866 | 0.001 | 1266.229 |
|  | S(~1)Gamma"(~1)Gamma'()p(~-1 + session * c)c()f0(~session) | 14 | 1241.351 | 12.047 | 0.001 | 1280.316 |
|  | S(~1)Gamma"(~1)Gamma'()p(~-1 + session * c)c()f0(~session) | 20 | 1241.706 | 12.402 | 0.001 | 1266.765 |
|  | S(~1)Gamma"(~1)Gamma'()p(~1)c()f0(~session) | 9 | 1242.977 | 13.674 | 0.001 | 1292.994 |
|  | S(~1)Gamma"(~1)Gamma'()p(~-1 + session)c()f0(~session) | 13 | 1243.633 | 14.330 | 0.000 | 1284.847 |
| LM | S(~1)Gamma"(~1.random)Gamma'()p(~-1 + session * c)c()f0(~session) | 23 | 1878.188 | 0.000 | 0.564 | 1891.079 |
|  | S(~1)Gamma"(~1.random)Gamma'()p(~-1 + session)c()f0(~session) | 16 | 1878.708 | 0.520 | 0.435 | 1907.144 |
|  | S(~1)Gamma"(~1)Gamma'()p(~-1 + session)c()f0(~session) | 15 | 1890.708 | 12.520 | 0.001 | 1921.318 |
|  | S(~1)Gamma"(~1)Gamma'()p(~-1 + session * c)c()f0(~session) | 22 | 1892.928 | 14.740 | 0.000 | 1908.076 |
|  | S(~1)Gamma"(~1)Gamma'()p(~1)c()f0(~session) | 10 | 1933.904 | 55.716 | 0.000 | 1975.211 |
|  | S(~1)Gamma"(~1.random)Gamma'()p(~1)c(~1)f0(~session) | 11 | 1934.677 | 56.489 | 0.000 | 1973.867 |
|  | S(~1)Gamma"(~1)Gamma'()p(~1)c(~1)f0(~session) | 11 | 1961.800 | 83.612 | 0.000 | 2000.990 |
|  | S(~1)Gamma"(~1)Gamma'()p(~1)c()f0(~session) | 9 | 1963.054 | 84.866 | 0.000 | 2006.467 |

Table 2.6. Abundance and density estimates for ocelots in Belize, Central America (2008, 2010 - 2015) in Hill Bank and La Milpa sites comparing RMark closed capture-recapture (CC), full likelihood parameterization models to open population robust design (RD) models. In Hill Bank (2010) I used the ½ overall mean maximum distance moved (½ OMMDM) from the pooled maximum distances across all six trapping grids ranging from 2010 to 2015 to accommodate the lack of spatial-recaptures. MMDM = Mean maximum distance moved.

| Site | Year-model | Abundance (95% CI) | Buffer: ½MMDM (km) | Effective sample Area (km$^2$) | Density/100 km$^2$ (95% C.I) |
|------|------------|--------------------|--------------------|-------------------------------|------------------------------|
| HB   | 2010-CC    | 13.0 (11.0 - 24.0) | 2.2 | 190.4 | 7.3 (4.5 - 10.1) |
|      | 2010-RD    | 16.8 (13.0 - 30.0) |     |       | 8.8 (4.7 – 12.9) |
|      | 2011-CC    | 23.0 (17.0 - 73.0) | 1.8 | 156.4 | 14.6 (1.8 - 27.4) |
|      | 2011-RD    | 19.0 (17.0 - 30.0) |     |       | 12.3 (8.6 -15.9) |
|      | 2012-CC    | 20.0 (19.0 - 27.0) | 2.2 | 195.2 | 10.2 (7.6 - 12.7) |
|      | 2012-RD    | 23.0 (20.0 - 34.0) |     |       | 11.7 (7.7 - 15.7) |
|      | 2013-CC    | 15.0 (13.0 - 27.0) | 2.4 | 228.7 | 6.4 (2.7 - 10.2) |
|      | 2013-RD    | 17.0 (13.0 - 29.0) |     |       | 7.4 (3.0 - 11.7) |
|      | 2014-CC    | 24.0 (22.0 - 39.0) | 2.5 | 237.6 | 10.2 (7.0 - 13.4) |
|      | 2014-RD    | 25.0 (23.0 - 36.0) |     |       | 10.5 (7.5 - 13.5) |
|      | 2015-CC    | 17.0 (16.0 - 24.0) | 1.4 | 162.1 | 10.3 (8.3 - 12.3) |
|      | 2015-RD    | 19.0 (17.0 - 30.0) |     |       | 11.8 (8.2 - 15.4) |
| LM   | 2008-CC    | 41.0 (38.0 - 49.0) | 1.7 | 179.5 | 22.5 (17.7 - 27.4) |
|      | 2008-RD    | 50.0 (38.0 - 50.0) |     |       | 22.8 (17.8 - 27.8) |
|      | 2010-CC    | 16.0 (14.0 - 26.0) | 2.4 | 200.7 | 8.1 (4.6 - 11.6) |
|      | 2010-RD    | 18.0 (50.0 - 30.0) |     |       | 8.9 (4.7 - 13.1) |
|      | 2011-CC    | 30.0 (27.0 - 42.0) | 2.1 | 182.9 | 16.6 (12.4 -20.8) |
|      | 2011-RD    | 29.0 (26.0 - 40.0) |     |       | 16.0 (12.3 - 19.7) |
|      | 2012-CC    | 32.0 (27.0 – 47.0) | 2.3 | 200.6 | 16.0 (11.2 - 20.8) |
|      | 2012-RD    | 40.0 (27.0 - 43.0) |     |       | 15.4 (11.2 - 19.6) |
|      | 2013-CC    | 33.0 (26.0 – 71.0) | 1.9 | 165.3 | 19.9 (9.2 - 30.5) |
|      | 2013-RD    | 26.0 (25.0 - 33.0) |     |       | 15.9 (13.2 - 18.5) |
|      | 2014-CC    | 23.0 (21.0 – 31.0) | 1.7 | 149.1 | 15.3 (12.3 - 18.3) |
|      | 2014-RD    | 23.0 (21.0 – 31.0) |     |       | 15.3 (12.4 - 16.3) |
|      | 2015-CC    | 27.0 (26.0 - 34.0) | 1.9 | 188.8 | 14.4 (11.4 - 17.5) |
|      | 2015-RD    | 27.0 (26.0 - 34.0) |     |       | 14.4 (11.4 - 17.5) |

Table 2.7. Robust Design estimates for ocelots in Belize, Central America (2008, 2010 - 2015) from top models in Hill Bank (HB) and the top model in La Milpa (LM). Models were considered competing models with 2 delta AIC or less. Parameters below are defined as probability of annual survival (S), Random emigration (*y)* = the probability of emigrating during an interval is the same as the probability of not immigrating during an interval ($\gamma'' = \gamma'$), detection probability (p), and redetection probability (c), and Session = survey years.

|  | Parameter | Estimate | SE | 95% CI |
|---|---|---|---|---|
| HB top model | S - survival | 0.79 | 0.05 | (0.67 - 0.87) |
|  | *y* - random | 0.04 | 0.12 | (0.00 - 0.93) |
|  | p - session 1 | 0.08 | 0.02 | (0.05 - 0.12) |
|  | c - session 1 | 0.14 | 0.01 | (0.12 - 0.16) |
| HB 2nd top model | S - survival | 0.78 | 0.05 | (0.67 - 0.87) |
|  | p - session 1 | 0.08 | 0.01 | (0.06 - 0.10) |
|  | c - session 1 | 0.14 | 0.01 | (0.12 - 0.16) |
| LM top model | S - survival | 0.71 | 0.04 | (0.63 - 0.78) |
|  | *y* - random | 0.23 | 0.07 | (0.12 - 0.39) |
|  | p - session 1 | 0.07 | 0.01 | (0.06 - 0.09) |
|  | p - session 2 | 0.03 | 0.01 | (0.02 - 0.06) |
|  | p - session 3 | 0.12 | 0.02 | (0.08 - 0.16) |
|  | p - session 4 | 0.12 | 0.02 | (0.09 - 0.17) |
|  | p - session 5 | 0.16 | 0.02 | (0.12 - 0.20) |
|  | p - session 6 | 0.13 | 0.02 | (0.10 - 0.18) |
|  | p - session 7 | 0.18 | 0.02 | (0.14 - 0.23) |
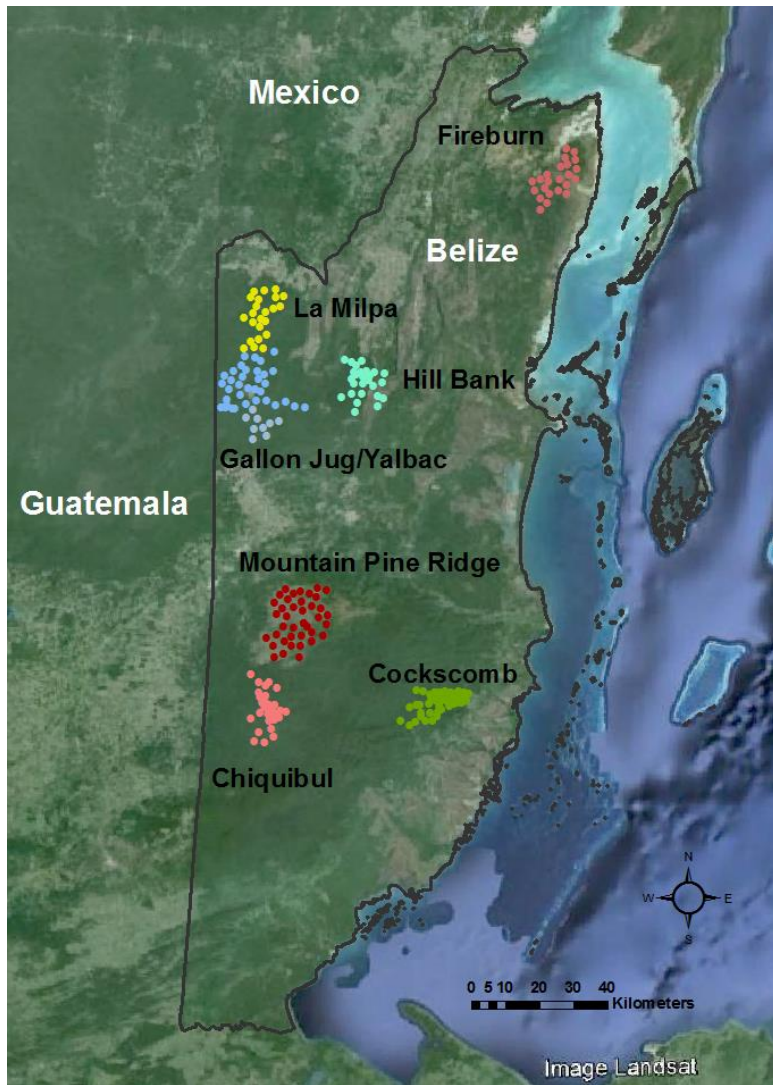
Figure 2.1. Locations for camera-trap surveys across sites in Belize, Central America (2002 - 2015). The 4 sites presented in this analysis are shown with 3 other sites currently part of a long-term camera trapping study.
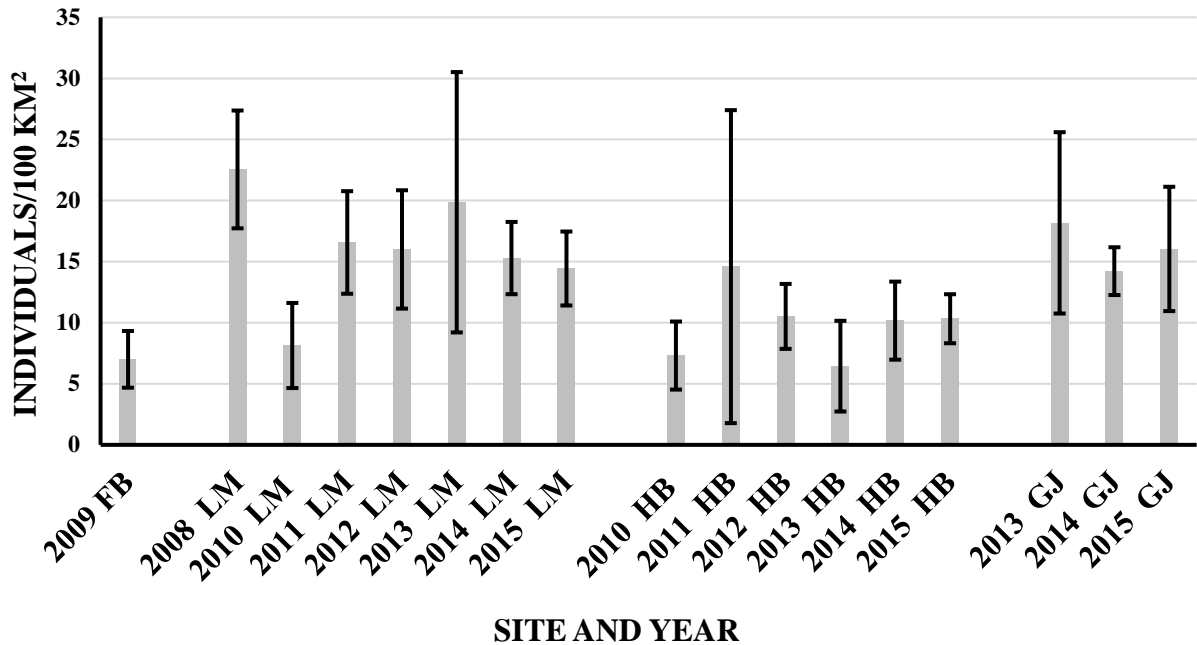
Figure 2.2. Density estimates and 95% confidence intervals for ocelots in La Milpa (LM), Hill Bank (HB), Gallon Jug (GJ), and Fireburn (FB) across multiple years (2008 - 2015). Density was estimated by dividing abundance estimated in RMark using closed capture-recapture full likelihood models by the effective sampling area (A), to derive an estimate of population density, defined by $\hat{D} = \hat{N}/A$. In Hill Bank (2010) the ½ overall mean maximum distance moved (1/2 OMMDM) from the pooled maximum distances across all years was used to estimate the effective sampling area.

Figure 2.3. Density estimates and 95% confidence intervals for ocelots in Belize, Central America (2008, 2010 - 2015) in A) Hill Bank and B) La Milpa comparing RMark closed capture-recapture (CC) full likelihood parameterization models to open population robust design (RD) models. Density was estimated by dividing abundance estimated in RMark and Robust Design by the effective sampling area (A), to derive an estimate of population density, defined $\widehat{D} = \widehat{N}/A$. In Hill Bank (2010) the ½ overall mean maximum distance moved (½OMMDM) from the pooled maximum distances across all years was used to estimate the effective sampling area to accommodate a low number of spatial-recaptures.

Figure 2.4. Robust Design survival estimates for ocelots in Belize, Central America (2008, 2010 - 2015) in Hill Bank (sustainably logged) over 6 years and La Milpa (protected) over 7 years.

**III.     Comparing session-specific and multi-session spatially explicit capture-recapture density estimators for ocelots (*Leopardus pardalis*).**

**Abstract**

The ocelot (*Leopardus pardalis*) has a wide geographic distribution across the Americas ranging from southern Texas to northern Argentina, including the islands of Trinidad and Margarita. Although ocelots are listed as "least concern" on the IUCN red list of endangered species, determining population status is still important because they are subject to illegal hunting for both recreation and fur trade, they are often killed in retaliation for poultry killing, habitat degradation is prevalent throughout their current range, and they have very low reproductive rates with relatively long gestation periods. Population abund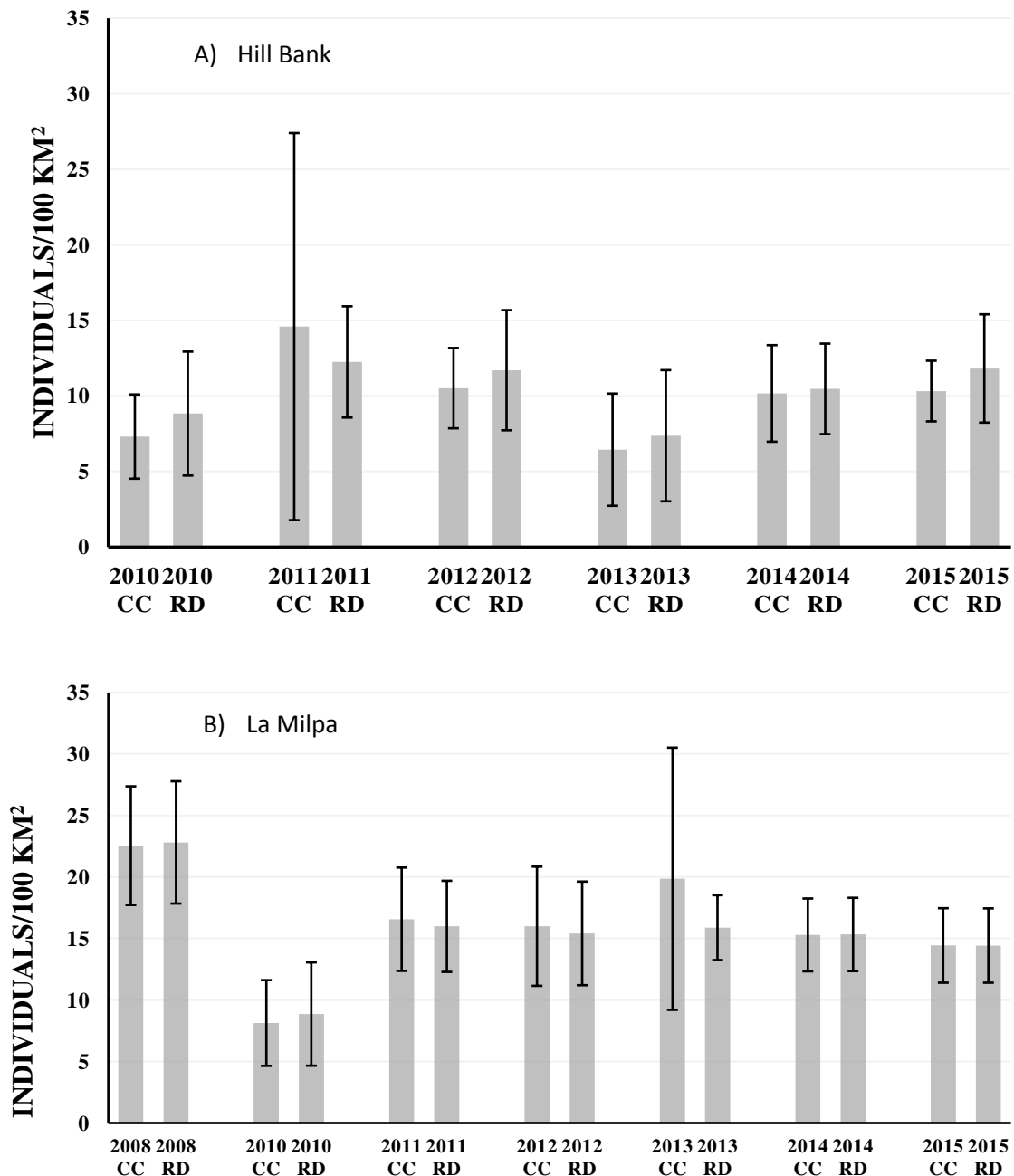ance and density are strong indicators of overall health of a species within its range. Within Belize, Central America, studies estimating abundance and density of ocelots have not been published since 2008. Several classical density estimation (i.e. non-spatial capture-recapture) studies have been conducted for ocelots, however, density estimates applying newer spatial capture-recapture methods are lacking.  In this study, I used camera-trapping methodology within a spatially explicit framework incorporating a sex-specific covariate, to estimate density for ocelots across six field sites in Belize. In Belize, ocelots occur over a wide range of habitat types, such as primary and secondary broadleaf forest, marsh forest, pine forest, and savanna grasslands. However, we lack knowledge of basic demographic parameters because it is challenging to conduct surveys for this cryptic and nocturnal species. Past research in Belize showed similar results to ours in that ocelot densities are higher in broadleaf rainforest habitat compared to pine forest habitat.  Density in my broadleaf rainforest sites ranged between 7.2 and 22 individuals per 100 km$^2$, and was 0.9 individuals per 100 km$^2$ on the pine forest site.  The spatial models demonstrated that males

moved larger distances and had slightly higher detection rates than females. However, in most years the sex ratio, expressed as the probability of being female was $\geq 50\%$. I also compared ocelot densities produced by both spatial and non-spatial approaches. In most of the surveys spatial capture-recapture models produced lower density point estimates, but precision varied widely across years and sites. However, in some years non-spatial models produced lower density estimates than spatial models, which may be explained by the individual covariate (sex) not being accounted for in classical models, which likely lead to negatively biased estimates. Spatial capture-recapture methods proved advantageous over non-spatial capture-recapture models because of their ability to better accommodate sparse data, account for missing covariates, and estimate density directly, thus alleviating the need to apply an *ad hoc* buffering approach. This study produced some of the first long-term, multi-site, and multi-year spatial capture-recapture density estimates for the ocelot in Belize and is the first study to account for sex-specific detection and movement parameters of ocelots using spatial capture-recapture models.

**Key words:** abundance, Belize, camera-trapping, density*, Leopardus pardalis*, multi-session models, sex-specific models, spatial capture-recapture, small carnivores

**Introduction**

Currently, the small spotted felid known as 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. The 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). Ocelots are still hunted for their fur, but their main threat comes from habitat degradation (Hunter and Barrett, 2011). In Belize, large-scale agriculture has been the leading cause of deforestation (Young, 2008). In addition, ocelots have very low reproductive rates, long interbirth intervals and typically have litter sizes of 1-2, with relatively long gestation periods, which makes ocelots potentially vulnerable to habitat loss and fragmentation (Hunter and Barrett, 2011). In Belize, ocelots occur sympatrically with four other felid species and are thought to play a vital role in ecosystem trophic dynamics, as ocelots are generalist and highly adaptable (Oliveira et al. 2010).

To better understand the ecology of ocelots and to improve long-term management and conservation of the species it is crucial to determine population demographic parameters such as abundance and density (Royle et al. 2013). Traditional, or classical non-spatial capture-recapture methods estimate abundance typically by using a variety of models that account for effects of time, behavior, and individual heterogeneity (see Chapter 2). But density, rather than abundance, is needed to compare across sites that survey areas of different sizes. Classical methods estimate population density by applying an *ad hoc* buffer strip surrounding the camera grid to derive the total area contributing to the population of interest, and dividing the abundance by this survey area. One of the most common methods is to add a circular buffer around each camera trap with a radius equal to ½ of the Mean Maximum Distance Moved (½ MMDM) among traps for all individuals and dissolve the internal, overlapping buffers to calculate area sampled (Silver et al. 2004; Paviolo et al. 2008). Classical non-spatial capture-recapture techniques are known to be problematic for several reasons. First, there are multiple ways to calculate a buffer strip when using the *ad hoc* approach and these can vary from study to study with little standardization, and differences in buffering approaches can cause density estimates to vary for the same abundance

estimates (O'Brien, 2011). Second, the problem with the approach of implementing an *ad hoc* buffering method of using ½ MMDM to calculate the effective trapping area, is that it may cause population density to be overestimated (Gerber et al. 2012). Other studies have shown that often the ½ MMDM is often too small to accurately capture true maximum animal movement distances especially when compared to telemetry data on actual home range movements, thus the survey area is too small and density is overestimated (Gerber et al. 2012; Soisalo and Cavalcanti 2006; Silveira et al. 2009). Overestimating density is highly problematic for threatened and endangered species as we might assume a larger population than actually exists. Accordingly, some researchers suggest using the full MMDM is a better approximation of home range radius, but there is no theoretical reason to do so (Parmenter et al. 2013).

The third problem with classical density estimation techniques is that they are highly sensitive to camera trap spacing and extent of the survey grid, which is related to the sampling design being properly scaled to the target species (Meek et al. 2014). For example, Dillon and Kelly (2007) showed that as camera spacing increased, ocelot density estimates declined, likely due to the larger movements recorded by ocelots, leading to a larger buffer surrounding the trapping array. Ocelot density may be underestimated using camera trapping grids where trap spacing was designed for larger carnivores, such as jaguars, that have larger home ranges. Trap spacing may have a strong influence on rates of detection and recaptures, and therefore density estimates. For example, trap spacing where trapping grids have "holes" or traps spaced too far apart relative to the movement of individuals can lead to individuals not being detected (violating the assumption of a positive capture probability) and lower or zero recapture rates across different traps, which is necessary for estimating movement parameters (Sollmann et al. 2012).

Accordingly, long distance movements from traps too far apart for the target species will likely overestimate MMDM, resulting in underestimating density.

Spatial capture-recapture models were developed because of these problems associated with traditional techniques. For this reason, I applied spatially explicit capture-recapture methods (SECR) that incorporate the spatial location of individual ocelot captures. This information is important for estimating each individual's activity center, which can then be used to directly estimate population density (as the number of activity centers over the state space) and thus overcome many of the limitations with classical capture-recapture methods (Sollman et al. 2011, Royle et al. 2013).

Unlike classical capture-recapture methods, SECR models allow for individual covariates such as sex to be used and can accommodate missing observations (Efford, 2012). Several studies on ocelots have shown that social system dynamics between male and female ocelots typically follow that of other felids with male territories overlapping one or more females (Murray and Gardner, 1997; Sunquist and Sunquist, 2002; Di Bitetti et al. 2006; Dillon and Kelly, 2008). The difference in space use and movement between sexes is likely to impact the baseline encounter probability in a camera trapping context and should be taken into account (Sollman et al. 2011, Royle et al. 2013).

Camera-trapping methods in conjunction with spatial capture-recapture models have been proven to be one of the most effective methods for obtaining demographic data on rare and elusive species such as ocelots (da Rocha, 2016; Royle et al. 2013). In this study, I estimated ocelot density from a long term multi-site and multi-year camera trapping data set using sex-specific spatial capture-recapture models. Additionally, I compare these results to those of the classical approach (Chapter 2). I highlight the importance of long-term studies for monitoring

wildlife populations over time in order to uncover trends (da Rocha, 2016), and provide new insight into ocelot ecology and population status in Belize.

**Materials and methods**

*Study area*

This study estimated density for 6 sites in Belize, across multiple years (See Chapter Two for details regarding the other four sites). The six study sites encompass a wide range of habitat types including tropical rainforest, old growth forest, secondary forest, savanna habitat, seasonally inundated lowland forests, wetlands or swamps called bajos, pine savanna, and pine forests.

1. **Chiquibul Forest Reserve and National Park (CFRNP)** is located in western Belize and comprises deciduous semi-evergreen, deciduous seasonal forest and occasional pine (*Pinus carribea*) in the northern sector (Silver et al. 2004; Wright et al. 1959). The Chiquibul Forest Reserve and National Park is roughly 1,744 km$^2$. The rainy season is from June to December and annual rainfall is 150 – 200 cm (Dillon and Kelly 2008; Beletsky, 1999). Elevation is approximately 500 m.  Commercially important tree species such as mahogany (*Swietenia macrophylla*), cedar (*Cedrela odorata*) and pine (*Pinus carribea*) are selectively logged on a > 40 year rotational basis within the Forest Reserve (Silver et al. 2004).

2. **The Mountain Pine Ridge Forest Reserve (MPR)** is primarily native tropical pine (*Pinus carribea*) forest along with smaller areas of shrub and broadleaf forest, especially along the riparian corridors (Davis et al. 2011). The MPR is contiguous to CFRNP to the north and is located within the Cayo District of central eastern Belize. It is 434 km$^2$ with areas that undergo

naturally occurring annual forest fires (Davis et al. 2010; Kellman and Meave, 1997). Elevation

ranges from 120 to 1,016 m and annual rainfall averages from 155 to 211 cm with a wet season

between June and December. The MPR and CFRNP are separated by the Macal River, which

creates a sharp transition between pine forest and broadleaf forest (Davis et al. 2011).

*Camera trap survey*

Depending on site and year, I established 20 to 50 camera stations, with each station integrating

2 remotely triggered, infrared game cameras. Ocelots, like other felids, have been shown to

commonly use roads and trails (Dillon and Kelly, 2007), therefore I placed cameras on opposite

sides of trails, roads, and logging roads to photograph the flanks of both sides of a passing

animal. To increase encounter probability and ensure that each individual felid has a non-zero

probability of being captured, I originally chose locations for each camera station based on the

smallest home range estimates for jaguars at 2 to 3 km intervals (Silver et al. 2004), however,

some surveys included cameras set at 1.5 km apart, specifically for ocelots (Di Bitetti et al.,

2006, Haines et al., 2006; Emmons, 1988). I evaluated whether this spacing (1.5 to 3 km) was

appropriate for ocelots by estimating the movement parameter, sigma ($\sigma$), from the SECR

models as it has been suggested that cameras should be spaced within a distance of at least twice

the estimated value of $\sigma$ (Sollmann et al. 2012, Sun et al. 2014).   To meet the assumption of

demographic closure (no births, deaths, or migration), I kept the sampling periods no longer than

3 months.

*Modeling framework*

Spatial capture-recapture models directly account for the locations of animal captures

along with individual movements relative to the camera stations (Royle et al. 2013). This allows

the models to estimate an activity center as unobserved random variables for each individual and

treat encounter probability as a decreasing function of distance between the estimated activity

center and the camera trap locations where each individual was photo-captured (Royle et al.

2013). I created two types of data files: trap deployment file containing x-y coordinates of the

trap locations denoting a "1" if the camera station was operational or "0" if non-operational and

a capture data file containing sampling session, animal identity, trap location, sample occasion,

and sex of individuals. I ran spatial capture-recapture models in R package secr incorporating

maximum likelihood based models with a half-normal detection function (Efford, 2012). I chose

detector type "proximity" which is analogous to the Bernoulli encounter model and allows

individuals to be captured at most once in each trap during each sampling occasion (Royle et al.

2013). I used each day as a sampling occasion. I designated our state-space buffer (i.e. the buffer

surrounding the trapping grid) to be large enough to include all potential home-range centers of

ocelots exposed to the trapping grid. To accomplish this I set my buffer to be at least 3σ (Efford

et al. 2004), which allows slightly more than 95% of discrete state-space points to be within

2.447 (standard deviation) units of each individual ocelot's home range center (Royle et al.

2013). I superimposed a grid mesh of 250 meters over the state-space to ensure that grid

resolution was at a fine enough scale to pick up on sex differences in our parameter estimates. I

used Akaike's Information Criterion corrected for small sample sizes as our model selection

criterion (AICc, Burnham and Anderson, 2002).

Two important parameters in SECR models are the baseline encounter probability

parameter (g0), defined as detection probability at the home range center, and the spatial scale

parameter sigma (σ), defined as the spatial scale over which detection declines from the home

range center. I fit all possible combinations of pre-defined variables, resulting in 8 candidate

models (listed in Table 3.1). However, years or sites with sparse data may have had fewer than 8

models. First, I held density constant across all years in each site (D~1) or allowed it to vary by

year (D~session). Second, for g0, I fit the following parameter effects: g0~1, (intercept-only

model) indicates that the baseline encounter rate is held constant across animals, occasions and

detectors, g0~bk, indicates a trap-specific behavioral response (e.g. encounter probability is

modified for an individual depending on previous capture in that trap) and g0~sex, indicates that

the encounter probability varies by the individual covariate (sex). Third, I either held the spatial

scale parameter sigma constant across all years in each site (sigma~1) or allowed for a sex effect

on sigma (sigma~sex). In four of my six sites, I estimated density for each year independently.

However, because data were very sparse in two of the sites (CFRNP and MPR), I ran multi-

session models. By sharing parameters (i.e. g0 and σ ) across years and surveys, multi-session

models allow information to be pooled over multiple years, increasing sample sizes, and

resulting in improved precision and lower bias in density estimates (da Rocha et al. 2016).

I chose to use the individual covariate "sex" for two primary reasons: first, I applied sex

to account for individual heterogeneity in encounter probability (g0) by accounting for

movement differences in males versus females (e.g. if females are more sedentary, they might be

detected less often) and depending on sex, individuals may or may not use certain landscape

features as often, such as roads, where the majority of my detectors were placed (Sollmann et al.

2011; Royle et al. 2013). Secondly, I applied sex to the spatial scale parameter (σ) to account for

individual heterogeneity in the event that females have smaller home ranges in general than

males, which Dillon and Kelly (2008) has been shown to be the case for ocelots (Gardner et al.,

2010; Sollmann et al. 2011; Royle et al. 2013).  By incorporating an individual covariate it

allowed me to reduce negative bias in my density estimates (Tobler and Powell, 2012; Sollman

et al. 2011; Royle et al. 2013). It should be noted that R-package secr also allows for missing

observations of the covariate values (Efford, 2009). Throughout all years and in each site, I

considered competing models to be within 2 delta AIC, and averaged only the density estimates

for competing models.

I compared the density estimates of SECR models to those estimated using the classical

capture-recapture approach (Chapter 2) to determine if confidence intervals overlapped, and if

not, the estimates were considered different from each other.

**Results**

Across all 6 sites and years I had a total sample size of: 64,244 trap nights, 1,683 ocelot

detections, 258 male ocelots, 268 female ocelots, and 18 individuals of unknown sex. However,

the same individuals may have been caught during multiple years for each site.

*Hill Bank – results*

On Hill Bank I recorded a total of 267 ocelot detections over 6 years of camera-trapping surveys

(Table 3.2). The number of unique individuals captured during each sampling year varied from

11 to 22 (Table 3.2). The number of individuals with spatial-recaptures varied from 1 to 8

depending on year (Table 3.2). In 2010, one individual was photo captured at 3 different camera

stations but was the only individual spatially recaptured during that survey period (Table 3.2).

Years with lower numbers of spatial-recaptures produced density estimates with slightly lower

precision (Table 3.2; Fig 3.1). Density varied from 7.2 - 10.0 individuals/100 km$^2$ (Table 3.3; Fig

3.1). Sex ratio, expressed as the probability of being a female, was 50% in 2014 and was ≤ 40%

in two of six survey years and ≥ 60% in three of six years (Fig 3.2), and all CIs overlapped the

50:50 ratio. Baseline encounter rate (g0) ranged from 0.005 to 0.054 (Table 3.4). Only one year

(2011) had a top model with a sex effect on the baseline g0 and showed males to be ~ 3.3 times more likely to be detected than females during that survey year (Table 3.4).  In some years g0 rates increased with a trap specific behavioral effect (g0~bk), or a trap specific behavioral effect plus sex effect (g0~sex + bk) (Table 3.4; 3.5). The spatial scale parameter ($\sigma$) ranged from 1.5 to 3.1 for males and 0.9 to 1.7 for females depending on survey year (Table 3.6, Fig 3.3). Movement parameter ($\sigma$) estimates calculating an average ($\sigma$) for sex ranged from 1.0 to 2.2 km (Table 3.6; Fig 3.3). Sex specific $\sigma$ estimates were important in four of six years and males had ~ 1.5 to 1.9 times larger $\sigma$ than females in all four years (Table 3.5; Fig 3.6).

*La Milpa – results*

On La Milpa I recorded a total of 445 ocelot detections over 7 years of camera-trapping surveys (Table 3.2). The number of unique individuals captured during each sampling year varied from 14 to 37 (Table 3.2). The number of individuals with spatial-recaptures varied from 4 to 15 depending on year (Table 3.2). Years with lower numbers of spatial-recaptures produced density estimates with slightly less precision (Table 3.2; Fig 3.1). Density varied from 8.5 - 22.1 individuals/100 km$^2$ (Table 3.3; Fig 3.1). Sex ratio, expressed as the probability of being a female was ~ 50% in four of seven survey years and ~ 60% in three of seven years (Fig 3.2), and all CIs overlapped the 50:50 ratio. Average baseline encounter rates (g0) estimated for both sexes ranged from 0.004 to 0.025 (Table 3.4). The top model included a sex effect on the baseline encounter rate g0 in 3 out of 7 years (2010, 2011 and 2015) (Table 3.5). In 2010, 2011, and 2012 males were ~ 6.7, 1.9, and 1.7 times (respectively) more likely to be detected than females (Table 3.4). In some years baseline encounter rates increased with a trap specific behavioral effect (g0~bk), or a trap specific behavioral effect plus sex effect (g0~sex + bk) (Table 3.4). The spatial scale parameter ($\sigma$) ranged from 1.4 to 2.7 km for years in which top

models produced an average σ for sex (Table 3.6). Sex specific σ effects were important in four

of six years and males had 1.3 to 1.8 times larger σ estimates than females in all four years.

(Table 3.5, 3.6). Male specific σ ranged from 1.8 to 2.9 km, and female specific σ estimates

ranged from 1.4 to 2.3 km (Table 3.6).

*Gallon jug – results*

On Gallon Jug I recorded a total of 603 ocelot detections over 3 years of camera-trapping

surveys (Table 3.2). The number of unique individuals captured during each sampling year

varied from 41 to 51 (Table 3.2). The number of individuals with spatial-recaptures varied from

19 to 24 depending on year (Table 3.2). Density varied from 14.6 - 18.2 individuals/100 km$^2$

(Table 3.3). Sex ratio, expressed as the probability of being a female was ~ 60% in all three

years, and all CIs overlapped the 50:50 ratio (Fig 3.2). Average baseline encounter rate (g0)

estimated for both sexes ranged from 0.010 to 0.016 (Table 3.4). In 2015, the top model

estimated a sex effect on g0, showing males to be ~ 1.5 times more likely to be detected than

females during that survey year (Table 3.4). In some years baseline encounter rates increased

with a trap specific behavioral effect (g0~bk), or a trap-specific behavioral effect plus sex effect

(g0~sex + bk) (Table 3.4). Survey years in which top models calculated an average (σ) for sex

ranged from 1.9 to 3.1 km (Table 3.5, 3.6). The spatial scale parameter (σ) ranged from ~ 1.3 to

1.4 times larger for males than females in 2 of 3 years which top models contained a sex effect

on sigma (Table 3.5, 3.6).

*Fireburn – results*

On Fireburn I recorded a total of 32 ocelot detections in 2009 (Table 3.2). The number of unique

individuals captured during the sampling period was 14, and a total of 6 individuals was

spatially-recaptured (Table 3.2). The top model yielded a density of 9.3 individuals/100 km$^2$ (95% CI: 4.5 – 19.1) (Table 3.3). Sex ratio, expressed as the probability of being a female was ~ 60%, and the CI overlapped the 50:50 ratio (Fig 3.2). The top model produced an average baseline encounter rate (g0) estimated for both sexes at 0.022 (0.011 – 0.044), with no competing models (Table 3.4, 3.5). The sex specific estimate of the spatial scale parameter ($\sigma$) for males was ~ 2.9 times larger than females (Table 3.6; Fig 3.3). Males had an estimated $\sigma$ of 2.6 km (95% CI: 1.0 – 6.9), and 0.9 km (95% CI: 0.6 – 1.4) for females (Table 3.6; Fig 3.3).

*Secr – multi-session models*

*Chiquibul – results*

In Chiquibul I recorded a total of 225 ocelot detections in 9 camera-trapping surveys (Table 3.2). The number of unique individuals captured during each sampling year varied from 5 to 16 (Table 3.2). Individuals with spatial-recaptures varied from 0 to 8 depending on year, and years with lower numbers of spatial-recaptures produced density estimates with slightly lower precision (Table 3.4; Fig 3.1). I ran a multi-session model holding all parameters constant across surveys with the exception of density which was allowed to vary across years and thus estimate density separately for each survey (Table 3.5). Densities ranged from 1 - 10 individuals/100 km$^2$ (Table 3.3; Fig 3.1). Sex ratio, expressed as the probability of being a female was ~ 50%, and the CI overlapped the 50:50 ratio (Fig 3.2). The average baseline encounter rate (g0) estimated for both sexes was 0.276 (Table 3.4). Sex specific ($\sigma$) estimates were ~ 2.1 times larger for males than females (Table 3.6; Fig 3.3). Males had an estimated $\sigma$ of 2.5 km, and females 1.2 km (Table 3.6; Fig 3.3).

*Mountain Pine Ridge – results*

In the MPR I recorded a total of 111 ocelot detections in 14 surveys over a 12 years period (Table 3.2). The number of unique individuals captured during each sampling year varied from 1 to 6 (Table 3.2). The number of individuals with spatial-recaptures varied from 0 to 5 depending on year (Table 3.2). No sex covariates were used in MPR due to the sparseness of the data set. Therefore, all parameter estimates are not sex specific and are reported from the top multi-session model which held density constant across all years (Table 3.5). Density was very low at 0.9 (95% CI: 0.6 – 1.2) individuals/100 km$^2$. The estimated baseline encounter rate (g0) for the top model was 0.005 (0.004 – 0.008) (Table 3.4). The trap-specific behavioral effect on the encounter rate (g0~bk) yielded an estimate of 0.013 (0.005 – 0.033) (Table 3.4), and σ was estimated to be 3.4 km (Table 3.6).

*Ocelot Parameter estimates across sites/years and classical vs spatially explicit methods.*
Using SECR methods, I found no evidence of ocelot densities varying within or among sites considering overlapping CIs (Fig 3.1). The probability of being female within and among all sites contained overlapping CIs meaning that while tending towards slightly more females, the sex ratio is not appreciably different from 50:50. Male and female sigma's within all years for each site contained overlapping CIs, with the exception of Chiquibul whereby males and female CIs were non-overlapping (Fig 3.3). However, due to the sparseness of the data set in Chiquibul the results are conservative and should be treated with caution. Density estimates produced by spatially explicit methods had overlapping CIs with the closed capture-recapture (CC) and robust design (RD) models in all years except in La Milpa 2014, when SECR models produced a lower density with CIs that were just barely non-overlapping compared to CC and RD (Fig 3.4, 3.5).

**Discussion**

For at least a century capture-recapture (CR) 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 solve several limitations of classical CR models by incorporating the spatial organization of the trapping grid relative to the individuals' trapping locations (Sun et al. 2014). The majority of the studies on ocelots have used traditional capture-recapture methods applying the mean maximum distance moved (MMDM) approach, while only a handful of studies have applied spatial-capture recapture methods (da Rocha et al. 2016; Martínez-Hernández et al. 2014).

This is the first ocelot study to derive population density estimates from large-scale camera-trapping surveys that ranged over multiple sites and years. In addition, this is the first study to account for sex-specific detection and movement parameters of ocelots using spatial capture-recapture models. The most recent ocelot studies in Belize were conducted by Dillon and Kelly (2007, 2008) and Davis (2009), and they applied classical capture-recapture techniques, making this study the very first to apply spatial-capture recapture density methods for ocelots in Belize. In addition to year-specific models I applied multi-session models allowing parameters to vary across years (i.e. density) or remain constant across sessions in order to improve precision and obtain reliable estimates from data that might otherwise be too sparse to model separately for each survey (da Rocha, 2016; Royle et al. 2013; Sollmann et al. 2011).

Female ocelots in Belize have been shown to have smaller home ranges than males (Dillon and Kelly, 2008), resulting in females potentially being exposed to fewer traps (Sollmann et al. 2011). Therefore, if the sex of an individual is not accounted for explicitly in the model, then unaccounted heterogeneity in encounter probability (g0) and the movement parameter

sigma (σ) may lead to biased estimates (Royle et al. 2013). Not accounting for Individual heterogeneity typically results in a negatively biased estimate because individuals with higher detection probabilities are detected more frequently often dominating the detection estimate and leading to a negative bias of density (Abadi et al. 2013; Tobler and Powell, 2012; Sollman et al. 2011; Royle et al. 2013). A study conducted in Argentina found that ocelots had a 2:1 ratio of females to males within the study population (Di Bitetti et al 2006). Although this study generally found ≥ 50% females in the population there was high variability and CIs overlapping 50:50 sex ratio. Nevertheless, with a high proportion of females in the population, it is important to account for sex differences in the models. .

Dillon and Kelly (2008) demonstrated a high degree of overlap between male and female ocelots in Belize and found that up to 50 – 90% of a male's typical home-range encompassed more than one female. Other studies have found 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). The results from my analysis may show some support for males being slightly more detectable than females, in some, but not all survey years. However, our results do corroborate the notion of males having larger home-ranges than females since majority of our surveys showed some support for males having larger movement parameter estimates (σ) than females. In Hill Bank, La Milpa, and Gallon Jug, the majority of the surveys estimated male σ's to be ~ 1.3 to 1.9 times larger than females. Fireburn was surveyed for only one year and the estimated σ for males was ~ 2.9 times larger than females, whereas in the Chiquibul across nine survey sessions male σ's were ~2.1 times larger than females. Thus, male ocelots appear to generally have wider movements, and therefore may be more likely to have higher exposure to the trapping grid and higher detectability.

Our results report densities ranging from 7.2 - 14 ocelots/100km$^2$ in the lowland riparian broadleaf forest sites that are interspersed with marsh, swamp, mangrove and savannah habitats. In the upland broadleaf forest sites our density estimates ranged from 9 - 22 ocelots/100km$^2$. The lowest estimates come from the native tropical pine forests of MPR, estimating 0.9 ocelots/100km$^2$, and the broadleaf forest site of Chiquibul Forest, with 1 - 10 ocelots/100km$^2$. I should highlight that the estimates from the MPR and Chiquibul sites should be treated as conservative due to the sparseness of data. MPR data was too sparse to use a sex covariate and as a result likely produced a negatively biased estimate (Royle et al. 2013). However, despite very low occurrences of ocelots in the MPR I was still able to estimate ocelot density by pooling information across years in a multi-session models framework. In the Chiquibul site a large portion of the surveys included pilot studies with very few camera stations, detections, occasions and unique number of individuals identified. Additionally, the area suffered from camera theft and thus shortened surveys in many instances. Too few camera stations in some surveys may have led to assumption violations. Additionally, in surveys where too few spatial recaptures (fewer than two recaptures of the same individual at different traps) occurred, potentially biased density estimates could result (Sollmann et al. 2012).

Average trap spacing across sites ranged from 1 to 2.4 km, which produced a high number of ocelot detections and spatial-recaptures. Ocelot detections in Fireburn were the lowest, estimated at 32, and the highest in Gallon Jug at 603. The high ocelot detections in Gallon Jug over only a 3 year period was impressive considering that this site, which has timber extraction, borders the completely protected La Milpa site where I totaled 445 ocelot detections over a 7 year period.

Ocelots are elusive by nature, inhabit dense tropical forest, and are nocturnal and difficult to study (Harveson et al. 2004; Di Bitetti et al. 2006). As a result, data sets for such wild cats are limited. Yet long term data sets are vital to determining trends over time. It is commonly known that larger felids usually living at low densities are vulnerable to large-scale habitat loss (Sollman et al. 2011), but little is known about the long-term resilience of smaller cat species like ocelots. This is why I emphasize the importance of long-term studies such as this, which takes advantage of data collected from a study originally designed for jaguars. For all years/sites, I found no evidence that densities varied within or among sites; all years/sites had overlapping confidence intervals. However, the exception was MPR where ocelot densities were very low, with a CIs that did not overlap the other sites. Thus ocelot populations in Belize appear stable over time and do not appear to be decreasing or increasing across the sites with long term data. I have shown spatially-explicit models to be a robust methodical tool for estimating ocelot density even when surveys were primarily designed for jaguars. However, other studies attempting similar estimates for small cats should pay careful attention to camera spacing relative to movement parameters of the target small cat species. Our cameras were spaced within at least twice the estimated value of sigma, thus producing optimal numbers of spatial-recaptures. Belize, like many other countries, is under threat from deforestation, growing human populations, and infrastructure development. Therefore, research and conservation efforts devoted to estimating wildlife populations are key to effective management and long-term population sustainability.

IV. Conclusion - *Comparison of classical to spatially explicit methods and their implications for ocelots*

Ocelot density estimates from non-spatial capture-recapture models are often reported to be higher than spatial capture-recapture models when the estimates between the two methods are compared (da Rocha et al. 2016). Inflated density estimates often occur because of the ad hoc buffering method of using ½ mean maximum distance moved (½ MMDM) to calculate the effective trapping area (Gerber et al. 2012). Several studies have shown that the ½ MMDM is often too small when compared to telemetry data on actual home range, therefore the survey area is too small and density is overestimated (Soisalo and Cavalcanti 2006; Silveira et al. 2009). Overestimating density is highly problematic for threatened and endangered species as we would wrongly assume a larger population than actually exists. Some researchers suggest using the full MMDM is a better approximation of home range radius, but there is no theoretical reason to do so.

Spatial capture-recapture models were developed because of many of the problems associated with traditional techniques. Spatial capture-recapture models overcome many of the limitations of the traditional methods because they are designed to directly estimate density. Therefore, spatial models are advantageous over non-spatial models because they account for heterogeneous detection probabilities among individuals by incorporating spatial–scale parameters built directly into the model; which accrue from spatial organization of individuals' relative to the sampling locations (Sun et al. 2014). Spatial models relax the assumption of strict geographic closure because they allow for temporary movements around the state-space, including outside of the trapping grid, and account for variable exposure to traps. The buffer width in classical capture-recapture models constrains the estimates of the mean maximum distance moved because movement is not captured outside of the camera trap grid, which has a direct impact on density (Sollman et al. 2011). In spatial capture-recapture the larger state-space

buffer surrounding the grid allows animal movements beyond the trapping grid to be estimated

without truncation (Sollman et al. 2011). Therefore, by accounting for the spatial organization of

traps and locations of animal captures, the models can estimate the individual-specific detection

probabilities, as well as the most likely location of activity centers of individuals even when they

might be outside the trapping grid (Sun et al. 2014).

I compared the densities from the non-spatial models in closed capture-recapture (CC) to

the spatially explicit models (SECR) in four sites: Hill Bank, La Milpa, Gallon Jug, and

Fireburn. In addition, I also compared CC methods to robust design (RD) and SECR methods in

Hill Bank and La Milpa. In the Fireburn site, the non-spatial CC model produced a lower density

estimate compared to the spatial estimate, with slightly better precision, although both

approaches had overlapping confidence intervals. In the Gallon Jug site, non-spatial models

produced larger estimates than spatial models, with similar precision and overlapping confidence

intervals in all three sampling years. In the Hill Bank site, I found that the non-spatial density

estimates were lower in two of six years, with slightly better precision than spatial models, and

overlapping CIs for all three methods. However, in one of those years (2010) in calculating the

classical estimates I had to use the ½ overall mean maximum distance moved (½ OMMDM)

across all six sites to calculate CIs. This was done to accommodate an insufficient number of

spatial-recaptures, whereas in SECR models I was still able to produce a density estimate

directly from the model, with reasonable precision. In the La Milpa site, non-spatial densities

were lower in two of the seven years with increased precision, but all three approaches contained

overlapping CIs.  In summary, for the majority of the sampling years across sites, spatial capture-

recapture models produced lower density point estimates but the CIs overlapped with other

methods. Thus I did not find significantly lower estimates from SECR models as has been found

in other studies, most likely because our camera spacing was appropriate and our grids large relative to ocelot ranging behavior.

I suspect that when non-spatial models produced lower density estimates, it may have resulted from individual covariates not being used, which likely lead to negatively biased estimates (Tobler and Powell, 2012; Sollman et al. 2011; Royle et al. 2013). Unlike R-package 'secr', R-package 'RMark' does not allow for missing covariates values (Cooch and White, 2006), which is why I was only able to apply the sex covariate to the spatial models.  However, applying individual covariates to models results in a tradeoff because accounting for individual heterogeneity may cause decreased precision but less bias in the parameter estimates. The sparser the data the larger potential for imprecision in parameter estimates (da Rocha et al. 2016). To properly compare all parameter estimates from the two approaches I would have ideally used sex as a covariate in both spatial and non-spatial models and compared the sex-specific probabilities of both approaches. For example, I could compare capture probabilities among males and females to see if both applications would estimate males having higher detection probabilities than females, as I observed using spatial models. However, it should be noted that not accounting for the trapping location in non-spatial models discards information about differences between the sexes (Sollman et al. 2011).

In a classical capture-recapture framework investigators often collapse capture occasions to various sampling blocks to overcome computational problems from having too many zero capture events. However, this approach may reduce information in sparse data sets, potentially causing behavioral models to not converge, and produce poor precision in estimating a potential behavioral response to capture or individual heterogeneity in capture probability.  For example if an individual is initially captured on day 1 and day 5 and the capture events are combined into a

single occasion then information on recapture probability for day 5 is lost. In spatial capture-recapture models, the capture occasions are not collapsed and potential recapture information is retained, thus estimating heterogeneity or behavior with better precision in sparse data sets. In both non-spatial and spatial capture-recapture methods, obtaining individuals that have been spatially recaptured is very important in obtaining unbiased estimates of density. In the 2010 survey conducted in the Hill Bank site, I obtained only one individual with spatial recaptures. One of the limitations of using the classical approach to estimate density is that a minimum of at least two individuals must be spatially-recaptured in order to generate confidence intervals for density estimates (Wilson and Anderson, 1985). Thus, using the non-spatial approach I was unable to generate confidence intervals for our density estimates, while spatial capture-recapture models were still able to produce an estimate with reasonable precision.

Applying spatial capture-recapture methods is advantageous over non-spatial capture-recapture because of their ability to incorporate additional information (e.g. individual capture locations) into the models. Spatial models can also better accommodate sparse data, account for missing covariates and has density directly built into the models, relieving investigators from applying ad hoc buffering approaches. Because spatial capture-recapture models include spatial processes they can be used to tackle questions directly related to animal population and landscape ecology (Royle et al., 2013). Royle et al. (2013) recommended only applying spatial capture-recapture models to density estimation and considers traditional closed population models to be mostly obsolete, other than as a conceptual device (Royale et al. 2013). However, traditional capture-recapture models may still be useful in situations where the effective sample area is known, such as on an island or fenced off area. In general, SECR techniques are

replacing CC techniques, but few studies have the large scale, long-term data to assess and compare such methods.

Future work will entail estimating density in the Cockscomb Basin site using muti-session models to analyze 13 years of camera-trapping data. I would also like to resurvey the Chiquibul site to obtain a more recent estimate of population density, given that camera theft in the area has reduced. Finally, I plan to estimate survival and site fidelity across all sites containing long-term data using spatial open population models, as opposed to the non-spatial open population models used in this study. This study represents a successful large-scale application of density and survival estimation techniques and offers new insight into the little-known demography of the elusive small felid, the ocelot.

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Table 3.1. Predictor variables and individual covariates used in detection models using R-package secr for spatial capture-recapture analysis conducted across 6 sites over multiple years in Belize, Central America (2002 - 2015).

| Parameter | Description |
|---|---|
| g0 ~ 1 | Encounter probability is constant across animals, occasions and detectors |
| g0 ~ bk | Encounter probability is modified for an individual depending on previous capture in that trap |
| g0 ~ sex | Encounter probability varies by sex |
| sigma ~ 1 | Spatial scale parameter is constant across animals, occasions and detectors |
| sigma ~ sex | Spatial scale parameter varies by sex |
| pmix ~ h2 | 2-class finite mixture for heterogeneity in sex ratio |

Table 3.2. Ocelot summary statistics for surveys conducted in each year and site in Belize, Central America (2002 - 2015). Trap nights represent total number of days across all camera stations with at least 1 camera functional. Site names are defined as: HB = Hill Bank, LM = La Milpa, GJ = Gallon Jug, FB = Fireburn, CF = Chiquibul Forest, MPR = Mountain Pine Ridge. NA = not able to determine sexual identity.

| Site | Year | Average trap Spacing (km) | Camera stations | Individuals captured | Total detections | Individuals with spatial-recaptures | Occasions | Trap nights |
|---|---|---|---|---|---|---|---|---|
| HB | 2010 | 2.3 | 19 | 11 (7 ♂, 4 ♀) | 23 | 1 | 75 | 1022 |
| | 2011 | 2.4 | 20 | 16 (5 ♂, 10 ♀, 1 NA) | 48 | 6 | 82 | 1539 |
| | 2012 | 1.9 | 20 | 20 (7 ♂, 13 ♀) | 54 | 8 | 82 | 1455 |
| | 2013 | 2.0 | 26 | 12 (8 ♂, 4 ♀) | 23 | 2 | 70 | 1605 |
| | 2014 | 2.0 | 26 | 22 (11 ♂, 11 ♀) | 75 | 8 | 98 | 2195 |
| | 2015 | 2.1 | 31 | 16 (5 ♂, 11 ♀) | 44 | 6 | 82 | 2471 |
| LM | 2008 | 1.0 | 40 | 37 (20 ♂, 15 ♀, 2 NA) | 98 | 15 | 91 | 2543 |
| | 2010 | 2.2 | 19 | 14 (6 ♂, 8 ♀) | 30 | 4 | 82 | 815 |
| | 2011 | 2.2 | 20 | 25 (12 ♂, 11 ♀, 2 NA) | 58 | 4 | 90 | 1239 |
| | 2012 | 2.2 | 21 | 25 (11 ♂, 13 ♀, 1 NA) | 50 | 9 | 72 | 1354 |
| | 2013 | 2.3 | 22 | 25 (11 ♂, 14 ♀) | 70 | 10 | 80 | 1666 |
| | 2014 | 2.3 | 23 | 21 (10 ♂, 10 ♀, 1 NA) | 54 | 10 | 82 | 1656 |
| | 2015 | 2.3 | 30 | 26 (10 ♂, 13 ♀, 3 NA) | 85 | 9 | 86 | 1849 |
| GJ | 2013 | 2.2 | 30 | 41 (16 ♂, 25 ♀) | 209 | 20 | 85 | 2083 |
| | 2014 | 2.3 | 35 | 41 (17 ♂, 22 ♀, 2 NA) | 174 | 19 | 85 | 2107 |
| | 2015 | 2.4 | 33 | 51 (20 ♂, 31 ♀) | 220 | 24 | 92 | 2138 |
| FB | 2009 | 2.3 | 33 | 14 (4 ♂, 8 ♀, 2 NA) | 32 | 6 | 127 | 1400 |
| CF | Jan 02 - Mar 02 | 2.7 | 18 | 5 (3 ♂, 2 ♀) | 10 | 2 | 67 | 559 |
| | Mar 02 -Jun 02 | 2.0 | 9 | 7 (3 ♂, 4 ♀) | 40 | 3 | 89 | 652 |
| | Jul 02 - Oct 02 | 0.5 | 17 | 6 (2 ♂, 4 ♀) | 25 | 4 | 106 | 731 |
| | Jan 03 - Apr 03 | 1.6 | 19 | 17 (8 ♂, 9 ♀) | 77 | 8 | 99 | 1976 |
| | Jun 03 - Jul 03 | 1.4 | 25 | 12 (9 ♂, 4 ♀) | 17 | 6 | 37 | 773 |
| | Aug 03 - Sep 03 | 0.8 | 17 | 8 (4 ♂, 4 ♀) | 21 | 4 | 36 | 470 |
| | Nov 06 - Jan 07 | 2.7 | 15 | 10 (5 ♂, 5 ♀) | 13 | 1 | 63 | 783 |

| Site | Year | Average trap Spacing (km) | Camera stations | Individuals captured | Total detections | Individuals with spatial-recaptures | Occasions | Trap nights |
|---|---|---|---|---|---|---|---|---|
| CF | Oct 07 - Dec 07 | 2.6 | 19 | 5 (1 ♂, 4 ♀) | 7 | 0 | 34 | 378 |
| | Jun 08 - Aug 08 | 1.8 | 29 | 9 (5 ♂, 4 ♀) | 15 | 4 | 59 | 626 |
| MPR | Jan 04 - Apr 04 | 2.4 | 19 | 1 (1 ♂, 0 ♀) | 1 | 0 | 85 | 1534 |
| | Apr 04 - Jun 04 | 0.8 | 16 | 1 (1 ♂, 0 ♀) | 1 | 0 | 63 | 855 |
| | Aug 04 - Oct 04 | 2.3 | 20 | 6 (4 ♂, 2 NA) | 6 | 0 | 61 | 1028 |
| | Jun 05 - Sep 05 | 2.5 | 23 | 6 (5 ♂, 1 ♀) | 19 | 5 | 92 | 1979 |
| | Jun 06 - Sep 06 | 2.6 | 25 | 6 (6 ♂, 0 ♀) | 21 | 4 | 83 | 1833 |
| | Jun 07 - Aug 07 | 1.5 | 47 | 4 (4 ♂, 0 ♀) | 16 | 3 | 73 | 2894 |
| | Nov 08 - Feb 09 | 2.6 | 26 | 4 (4 ♂, 0 ♀) | 6 | 0 | 97 | 1327 |
| | Oct 09 - Feb 10 | 2.5 | 30 | 3 (2 ♂, 0 ♀) | 8 | 3 | 116 | 2211 |
| | Oct 10 - Jan 11 | 2.5 | 33 | 3 (1 ♂, 1 ♀, 1 NA) | 3 | 0 | 85 | 2166 |
| | Oct 11 - Dec 11 | 2.5 | 35 | 1 (1 ♂, 0 ♀) | 1 | 0 | 64 | 2043 |
| | Nov 12 - Jan 10 | 3.6 | 40 | 1 (1 ♂, 0 ♀) | 3 | 0 | 66 | 2194 |
| | Aug 13 - Nov 13 | 2.5 | 40 | 2 (2 ♂, 0 ♀) | 5 | 1 | 64 | 2214 |
| | Oct 14 - Jan 15 | 2.6 | 40 | 6 (4 ♂, 1 ♀, 1 NA) | 13 | 3 | 85 | 3022 |
| | Jan 15 - Apr 15 | 2.6 | 40 | 2 (2 ♂, 0 ♀) | 8 | 0 | 76 | 2859 |

*Table 3.2. Continued

Table 3.3. Density estimates and 95% confidence intervals in Belize, Central America (2002 - 2015) for each year estimated using spatial capture-recapture models in R package secr, incorporating maximum likelihood based models with a half-normal detection function. Also reported is year of the survey, state-space buffer and area of the state-space (mask area) across sites in Belize. HB = Hill Bank, LM = La Milpa, GJ = Gallon Jug, FB = Fireburn, CF = Chiquibul Forest, MPR = Mountain Pine Ridge.

| Site | Year | State-space buffer (km) | Mask area km$^2$ | Density/100 km$^2$ (95% C.I) |
|------|------|------|------|------|
| HB | 2010 | 6.0 | 476.0 | 9.6 (2.3 to 20.1) |
| | 2011 | 6.0 | 475.1 | 9.6 (3.9 - 15.2) |
| | 2012 | 6.0 | 476.3 | 8.9 (3.8 - 14.0) |
| | 2013 | 6.6 | 576.6 | 7.4 (3.2 - 17.6) |
| | 2014 | 6.6 | 574.6 | 10.0 (5.8 - 17.2) |
| | 2015 | 6.6 | 671.1 | 7.2 (3.3 - 11.2) |
| LM | 2008 | 8.1 | 678.5 | 16.0 (8.4 - 23.7) |
| | 2010 | 8.1 | 670.1 | 16.6 (5.7 - 48.2) |
| | 2011 | 8.1 | 675.0 | 22.1 (4.8 - 39.4) |
| | 2012 | 8.1 | 675.3 | 13.8 (6.2 - 21.5) |
| | 2013 | 8.1 | 725.6 | 11.1 (7.1 - 17.5) |
| | 2014 | 8.1 | 725.7 | 8.5 (4.5 - 12.6) |
| | 2015 | 8.1 | 725.5 | 12.8 (6.1 - 19.6) |
| GJ | 2013 | 8.1 | 817.0 | 14.0 (10.0 - 20.0) |
| | 2014 | 8.1 | 996.3 | 12.9 (8.3 - 17.5) |
| | 2015 | 8.1 | 992.4 | 11.8 (8.5 - 16.3) |
| FB | 2009 | 8.1 | 701.4 | 9.3 (4.5 - 19.1) |
| CF | Jan 02 - Mar 02 | 8.1 | 847.7 | 2.4 (1.0 - 5.5) |
| | Mar 02 -Jun 02 | 8.1 | 847.7 | 5.4 (2.6 - 11.1) |
| | Jul 02 - Oct 02 | 8.1 | 847.7 | 10.0 (4.6 - 21.7) |
| | Jan 03 - Apr 03 | 8.1 | 847.7 | 4.9 (2.9 - 8.4) |
| | Jun 03 - Jul 03 | 8.1 | 847.7 | 4.6 (2.6 - 8.0) |
| | Aug 03 - Sep 03 | 8.1 | 847.7 | 8.3 (4.2 - 16.2) |
| | Nov 06 - Jan 07 | 8.1 | 847.7 | 4.4 (2.4 - 8.0) |
| | Oct 07 - Dec 07 | 8.1 | 847.7 | 1.0 (0.4 - 2.3) |
| | Jun 08 - Aug 08 | 8.1 | 847.7 | 3.8 (2.0 - 7.2) |
| MPR | Jan 04 - Apr 15 | 8.1 | 1208.8 | 0.9 (0.6 - 1.2) |

Table 3.4. Summaries of encounter probability (g0) estimates and 95% CI in Belize, Central America (2002 - 2015) from competing models (delta AICc of two or less) for each year across sites. Dash marks (-) indicate that effect was not supported in top models. Sessions = number of individual surveys. HB = Hill Bank, LM = La Milpa, GJ = Gallon Jug, FB = Fireburn, CF = Chiquibul Forest, MPR = Mountain Pine Ridge. In CF I conducted 9 surveys (sessions) total in years 2002. 2003, 2007, and 2008 with some years containing multiple sessions.

| Site | Year | g0 (95% CI) ♂,♀ | g0 (95% CI) ♀ | g0 (95% CI) ♂ | g0 + bk (95% CI) ♂,♀ | g0 + bk (95% CI) ♀ | g0 + bk (95% CI) ♂ |
|---|---|---|---|---|---|---|---|
| HB | 2010 | 0.047 (0.022 - 0.099) | - | - | - | - | - |
|  | 2010 | 0.012 (0.002 - 0.078) | - | - | 0.060 (0.001 - 0.733) | - | - |
|  | 2011 | - | 0.020 (0.009 - 0.045) | 0.066 (0.032 - 0.131) | - | - | - |
|  | 2011 | 0.042 (0.024 - 1.889) | - | - | - | - | - |
|  | 2011 | - | 0.010 (0.004 - 0.031) | 0.030 (0.010 - 0.088) | - | 0.023 (0.003 - 0.152) | 0.064 (0.004 - 0.551) |
|  | 2012 | 0.010 (0.005 – 0.023) | - | - | 0.039 (0.008 - 0.174) | - | - |
|  | 2012 | 0.013 (0.006 - 0.028) | - | - | 0.040 (0.006 - 0.179) | - | - |
|  | 2013 | 0.005 (0.001 - 0.018) | - | - | 0.032 (0.002 - 0.339) | - | - |
|  | 2014 | 0.008 (0.004 - 0.014) | - | - | 0.030 (0.009 - 0.093) | - | - |
|  | 2015 | 0.049 (0.029 - 0.081) | - | - | - | - | - |
|  | 2015 | 0.054 (0.296 - 0.095) | - | - | - | - | - |
| LM | 2008 | 0.004 (0.002 - 0.007) | - | - | 0.033 (0.010 - 0.102) | - | - |
|  | 2008 | 0.004 (0.002 -0.007) | - | - | 0.033 (0.010 - 0.102) | - | - |
|  | 2010 | - | 0.006 (0.001 - 0.026) | 0.040 (0.015 - 0.102) | - | - | - |
|  | 2011 | 0.006 (0.0016 - 0.0020) | - | - | 0.053 (0.005 - 0.402) | | |
|  | 2011 | - | 0.0042 (0.0011 - 0.0015) | 0.008 (0.001 - 0.062) | - | 0.038 (0.003 -0.329) | 0.067(0.003 - 0.674) |
|  | 2012 | 0.015 (0.0087 - 0.0259) | - | - | - | - | - |
|  | 2012 | 0.010 (0.004 -0.023) | - | - | 0.019 (0.003 - 0.104) | - | - |
|  | 2013 | 0.016 (0.007 - 0.036) | - | - | 0.045 (0.009 - 0.198) | - | - |
|  | 2014 | 0.025 (0.015 - 0.039) | - | - | - | - | - |
|  | 2014 | 0.015 (0.007 - 0.034) | - | - | 0.029 (0.005 - 0.137) | - | - |
|  | 2014 | 0.0246 (0.0154 - 0.0393) | - | - | - | - | - |
|  | 2015 | 0.011 (0.005 - 0.024) | - | - | 0.05 (0.01 - 0.19) | - | - |
|  | 2015 | 0.009 (0.004 - 0.020) | - | - | 0.05 (0.01 - 0.19) | - | - |

| Site | Year | g0 (95% CI) ♂,♀ | g0 (95% CI) ♀ | g0 (95% CI) ♂ | g0 + bk (95% CI) ♂,♀ | g0 + bk (95% CI) ♀ | g0 + bk (95% CI) ♂ |
|---|---|---|---|---|---|---|---|
| LM | 2015 | - | 0.007 (0.003 - 0.016) | 0.012 (0.003 - 0.051) | - | 0.03 ( 0.007 - 0.151) | 0.06 (0.006 - 0.368) |
| GJ | 2013 | 0.016 (0.010 - 0.027) | - | - | 0.078 (0.030 - 0.190) | - | - |
| | 2014 | 0.012 (0.007 - 0.021) | - | - | 0.063 (0.021 - 0.175) | - | - |
| | 2014 | 0.010 (0.006 - 0.018) | - | - | 0.063 (0.021 - 0.174) | - | - |
| | 2015 | - | 0.006 (0.004 - 0.009) | 0.009 (0.004 - 0.020) | - | 0.05 ( 0.02 - 0.11) | 0.08 (0.024 - 0.230) |
| FB | 2009 | 0.022 (0.011 - 0.044) | - | - | - | - | - |
| CF | 9-sessions | 0.276 (0.181 - 0.398) | - | - | - | - | - |
| MPR | Jan 04 – Apr 15 | 0.005 (0.004 - 0.008) | - | - | - | - | - |

*Table 3.4. Continued.

Table 3.5.  The top maximum likelihood models used to estimate ocelot density in Belize, Central America (2002 - 2015), produced in R package secr for each survey year in Hill Bank (HB), La Milpa (LM), Gallon Jug (GJ) and Fireburn (FB), Chiquibul Forest (CF) and Mountain Pine Ridge (MPR). Models were ranked by Akaike's Information Criterion corrected for small sample sizes (AICc). The delta AIC (dAICc) is the difference in AICc from the top model. Model parameterization defined as follows: Encounter probability (g0), encounter probability is modified for an individual depending on previous capture in that trap (g0~bk), encounter probability varies by sex (g0~sex), Spatial scale parameter is constant across animals, occasions and detectors (sigma~1), Spatial scale parameter varies by sex (sigma~sex), Spatial scale parameter varies by sex with a linear trend fixed across sessions (sigma~Sex), 2-class finite mixture for heterogeneity in sex ratio (pmix ~ h2). Table extends from pages 86 - 91.

| Site | Year | Model | # Par | LogLik | AICc | dAICc | AICcwt |
|------|------|-------|-------|--------|------|-------|--------|
| HB | 2010 | D~1, g0~1, sigma~1, pmix~h2 | 3 | -126.999 | 263.426 | 0.000 | 0.663 |
|    |      | D~1, g0~bk, sigma~1, pmix~h2 | 4 | -125.058 | 264.782 | 1.356 | 0.337 |
|    | 2011 | D~1, g0~sex, sigma~1, pmix~h2 | 4 | -270.020 | 551.676 | 0.000 | 0.346 |
|    |      | D~1, g0~1, sigma~sex, pmix~h2 | 4 | -270.441 | 552.517 | 0.841 | 0.227 |
|    |      | D~1, g0~bk + sex, sigma~1 , pmix~h2 | 5 | -268.591 | 553.183 | 1.507 | 0.163 |
|    |      | D~1, g0~bk, sigma~sex, pmix~h2 | 5 | -269.054 | 554.107 | 2.431 | 0.103 |
|    |      | D~1, g0~sex, sigma~sex, pmix~h2 | 5 | -269.595 | 555.189 | 3.513 | 0.060 |
|    |      | D~1, g0~bk, sigma~1, pmix~h2 | 4 | -271.890 | 555.416 | 3.740 | 0.053 |
|    |      | D~1, g0~1, sigma~1, pmix~h2 | 3 | -274.229 | 556.458 | 4.782 | 0.032 |
|    |      | D~1, g0~bk + sex, sigma~sex, pmix~h2 | 6 | -268.187 | 557.708 | 6.032 | 0.017 |
|    | 2012 | D~1, g0~bk, sigma~1, pmix~h2 | 4 | -305.629 | 622.115 | 0.000 | 0.429 |
|    |      | D~1, g0~bk, sigma~sex, pmix~h2 | 5 | -304.020 | 622.655 | 0.540 | 0.327 |
|    |      | D~1, g0~bk + sex, sigma~1 , pmix~h2 | 5 | -305.024 | 624.664 | 2.549 | 0.120 |
|    |      | D~1, g0~1, sigma~sex, pmix~h2 | 4 | -307.599 | 626.055 | 3.940 | 0.060 |
|    |      | D~1, g0~bk + sex, sigma~sex, pmix~h2 | 6 | -303.984 | 626.968 | 4.853 | 0.038 |
|    |      | D~1, g0~1, sigma~1, pmix~h2 | 3 | -310.795 | 629.190 | 7.075 | 0.013 |
|    |      | D~1, g0~sex, sigma~sex, pmix~h2 | 5 | -307.565 | 629.745 | 7.630 | 0.009 |
|    |      | D~1, g0~sex, sigma~1, pmix~h2 | 4 | -310.210 | 631.278 | 9.163 | 0.004 |
|    | 2013 | D~1, g0~bk, sigma~1, pmix~h2 | 4 | -143.617 | 300.949 | 0.000 | 0.544 |

| Site | Year | Model | # Par | LogLik | AICc | dAICc | AICcwt |
|------|------|-------|-------|--------|------|-------|--------|
| HB | | D~1, g0~1, sigma~1, pmix~h2 | 3 | -147.299 | 303.598 | 2.649 | 0.145 |
| | | D~1, g0~1, sigma~sex, pmix~h2 | 4 | -144.978 | 303.671 | 2.722 | 0.140 |
| | | D~1, g0~bk, sigma~sex, pmix~h2 | 5 | -142.446 | 304.893 | 3.944 | 0.076 |
| | | D~1, g0~sex, sigma~1, pmix~h2 | 4 | -146.042 | 305.798 | 4.849 | 0.048 |
| | | D~1, g0~bk + sex, sigma~1 , pmix~h2 | 5 | -143.034 | 306.069 | 5.120 | 0.042 |
| | | D~1, g0~sex, sigma~sex, pmix~h2 | 5 | -144.969 | 309.937 | 8.988 | 0.006 |
| | | D~1, g0~bk + sex, sigma~sex, pmix~h2 | 6 | -142.406 | 313.612 | 12.663 | 0.000 |
| | 2014 | D~1, g0~bk, sigma~sex, pmix~h2 | 5 | -444.512 | 902.773 | 0.000 | 0.690 |
| | | D~1, g0~bk, sigma~1, pmix~h2 | 4 | -447.809 | 905.972 | 3.200 | 0.139 |
| | | D~1, g0~bk + sex, sigma~sex, pmix~h2 | 6 | -444.476 | 906.551 | 3.778 | 0.104 |
| | | D~1, g0~bk + sex, sigma~1 , pmix~h2 | 5 | -446.861 | 907.473 | 4.700 | 0.066 |
| | | D~1, g0~1, sigma~sex, pmix~h2 | 4 | -453.510 | 917.373 | 14.600 | 0.000 |
| | | D~1, g0~sex, sigma~sex, pmix~h2 | 5 | -453.201 | 920.151 | 17.378 | 0.000 |
| | | D~1, g0~1, sigma~1, pmix~h2 | 3 | -459.576 | 926.485 | 23.712 | 0.000 |
| | | D~1, g0~sex, sigma~1, pmix~h2 | 4 | -458.841 | 928.034 | 25.261 | 0.000 |
| | 2015 | D~1, g0~1, sigma~1, pmix~h2 | 3 | -239.151 | 486.301 | 0.000 | 0.450 |
| | | D~1, g0~1, sigma~sex, pmix~h2 | 4 | -237.837 | 487.310 | 1.009 | 0.272 |
| | | D~1, g0~bk, sigma~1, pmix~h2 | 4 | -238.771 | 489.178 | 2.877 | 0.107 |
| | | D~1, g0~sex, sigma~1, pmix~h2 | 4 | -239.138 | 489.913 | 3.612 | 0.074 |
| | | D~1, g0~sex, sigma~sex, pmix~h2 | 5 | -237.392 | 490.785 | 4.484 | 0.048 |
| | | D~1, g0~bk, sigma~sex, pmix~h2 | 5 | -237.751 | 491.502 | 5.201 | 0.033 |
| | | D~1, g0~bk + sex, sigma~1, pmix~h2 | 5 | -238.743 | 493.485 | 7.184 | 0.012 |
| | | D~1, g0~bk + sex, sigma~sex, pmix~h2 | 6 | -237.226 | 495.785 | 9.484 | 0.004 |
| LM | 2008 | D~1, g0~bk, sigma~1, pmix~h2 | 4 | -587.968 | 1185.185 | 0.000 | 0.525 |
| | | D~1, g0~bk, sigma~sex, pmix~h2 | 5 | -587.441 | 1186.818 | 1.633 | 0.232 |
| | | D~1, g0~bk + sex, sigma~1 , pmix~h2 | 5 | -587.813 | 1187.561 | 2.376 | 0.160 |
| | | D~1, g0~bk + sex, sigma~sex, pmix~h2 | 6 | -587.028 | 1188.856 | 3.671 | 0.084 |
| | | D~1, g0~1, sigma~sex, pmix~h2 | 4 | -612.896 | 1235.042 | 49.857 | 0.000 |
| | | D~1, g0~1, sigma~1, pmix~h2 | 3 | -614.800 | 1236.327 | 51.142 | 0.000 |

| Site | Year | Model | # Par | LogLik | AICc | dAICc | AICcwt |
|------|------|-------|-------|--------|------|-------|--------|
| LM | | D~1, g0~sex, sigma~sex, pmix~h2 | 5 | -612.690 | 1237.315 | 52.130 | 0.000 |
| | | D~1, g0~sex, sigma~1, pmix~h2 | 4 | -614.799 | 1238.848 | 53.663 | 0.000 |
| | 2010 | D~1, g0~sex, sigma~1, pmix~h2 | 4 | -132.337 | 277.119 | 0.000 | 0.566 |
| | | D~1, g0~1, sigma~1, pmix~h2 | 3 | -135.555 | 279.511 | 2.392 | 0.171 |
| | | D~1, g0~1, sigma~sex, pmix~h2 | 4 | -134.011 | 280.466 | 3.347 | 0.106 |
| | | D~1, g0~bk + sex, sigma~1 , pmix~h2 | 5 | -132.150 | 281.800 | 4.681 | 0.055 |
| | | D~1, g0~sex, sigma~sex, pmix~h2 | 5 | -132.322 | 282.144 | 5.025 | 0.046 |
| | | D~1, g0~bk, sigma~1, pmix~h2 | 4 | -135.292 | 283.028 | 5.909 | 0.030 |
| | | D~1, g0~bk, sigma~sex, pmix~h2 | 5 | -132.864 | 283.227 | 6.108 | 0.027 |
| | | D~1, g0~bk + sex, sigma~sex, pmix~h2 | 6 | -132.046 | 288.092 | 10.973 | 0.000 |
| | 2011 | D~1, g0~bk, sigma~1, pmix~h2 | 4 | -303.084 | 616.167 | 0.000 | 0.493 |
| | | D~1, g0~bk + sex, sigma~1 , pmix~h2 | 5 | -302.004 | 617.166 | 0.999 | 0.299 |
| | | D~1, g0~bk, sigma~sex, pmix~h2 | 5 | -302.678 | 618.514 | 2.347 | 0.153 |
| | | D~1, g0~bk + sex, sigma~sex, pmix~h2 | 6 | -301.948 | 620.562 | 4.395 | 0.055 |
| | | D~1, g0~1, sigma~sex, pmix~h2 | 4 | -308.991 | 627.982 | 11.815 | 0.000 |
| | | D~1, g0~1, sigma~1, pmix~h2 | 3 | -310.442 | 628.026 | 11.859 | 0.000 |
| | | D~1, g0~sex, sigma~1, pmix~h2 | 4 | -309.673 | 629.345 | 13.178 | 0.000 |
| | | D~1, g0~sex, sigma~sex, pmix~h2 | 5 | -308.914 | 630.986 | 14.819 | 0.000 |
| | 2012 | D~1, g0~1, sigma~sex, pmix~h2 | 4 | -300.705 | 611.410 | 0.000 | 0.442 |
| | | D~1, g0~bk, sigma~sex, pmix~h2 | 5 | -299.765 | 612.688 | 1.278 | 0.233 |
| | | D~1, g0~sex, sigma~sex, pmix~h2 | 5 | -300.553 | 614.265 | 2.855 | 0.106 |
| | | D~1, g0~bk, sigma~1, pmix~h2 | 4 | -302.490 | 614.979 | 3.569 | 0.074 |
| | | D~1, g0~1, sigma~1, pmix~h2 | 3 | -304.404 | 615.950 | 4.540 | 0.046 |
| | | D~1, g0~bk + sex, sigma~sex, pmix~h2 | 6 | -299.728 | 616.123 | 4.713 | 0.042 |
| | | D~1, g0~bk + sex, sigma~1, pmix~h2 | 5 | -301.793 | 616.743 | 5.333 | 0.031 |
| | | D~1, g0~sex, sigma~1, pmix~h2 | 4 | -303.523 | 617.046 | 5.636 | 0.026 |
| | 2013 | D~1, g0~bk, sigma~1, pmix~h2 | 4 | -388.132 | 786.264 | 0.000 | 0.597 |
| | | D~1, g0~bk, sigma~sex, pmix~h2 | 5 | -388.101 | 789.359 | 3.095 | 0.127 |
| | | D~1, g0~bk + sex, sigma~1 , pmix~h2 | 5 | -388.128 | 789.413 | 3.149 | 0.124 |

| Site | Year | Model | # Par | LogLik | AICc | dAICc | AICcwt |
|------|------|-------|-------|--------|------|-------|--------|
| LM |  | D~1, g0~1, sigma~1, pmix~h2 | 3 | -391.520 | 790.183 | 3.919 | 0.084 |
|  |  | D~1, g0~bk + sex, sigma~sex, pmix~h2 | 6 | -388.099 | 792.865 | 6.601 | 0.022 |
|  |  | D~1, g0~1, sigma~sex, pmix~h2 | 4 | -391.487 | 792.974 | 6.710 | 0.021 |
|  |  | D~1, g0~sex, sigma~1, pmix~h2 | 4 | -391.519 | 793.037 | 6.773 | 0.020 |
|  |  | D~1, g0~sex, sigma~sex, pmix~h2 | 5 | -391.458 | 796.074 | 9.810 | 0.004 |
|  | 2014 | D~1, g0~1, sigma~1, pmix~h2 | 3 | -320.996 | 649.403 | 0.000 | 0.307 |
|  |  | D~1, g0~bk, sigma~1, pmix~h2 | 4 | -319.860 | 650.220 | 0.817 | 0.204 |
|  |  | D~1, g0~1, sigma~sex, pmix~h2 | 4 | -319.881 | 650.263 | 0.860 | 0.200 |
|  |  | D~1, g0~bk, sigma~sex, pmix~h2 | 5 | -318.911 | 651.823 | 2.420 | 0.092 |
|  |  | D~1, g0~sex, sigma~sex, pmix~h2 | 5 | -319.090 | 652.179 | 2.776 | 0.077 |
|  |  | D~1, g0~sex, sigma~1, pmix~h2 | 4 | -320.986 | 652.473 | 3.070 | 0.066 |
|  |  | D~1, g0~bk + sex, sigma~1 , pmix~h2 | 5 | -319.858 | 653.717 | 4.314 | 0.036 |
|  |  | D~1, g0~bk + sex, sigma~sex, pmix~h2 | 6 | -318.448 | 654.896 | 5.493 | 0.020 |
|  | 2015 | D~1, g0~bk, sigma~sex, pmix~h2 | 5 | -458.888 | 930.775 | 0.000 | 0.393 |
|  |  | D~1, g0~bk, sigma~1, pmix~h2 | 4 | -460.795 | 931.495 | 0.720 | 0.274 |
|  |  | D~1, g0~bk + sex, sigma~1 , pmix~h2 | 5 | -459.406 | 931.812 | 1.037 | 0.234 |
|  |  | D~1, g0~bk + sex, sigma~sex, pmix~h2 | 6 | -458.554 | 933.529 | 2.754 | 0.099 |
|  |  | D~1, g0~1, sigma~sex, pmix~h2 | 4 | -466.646 | 943.196 | 12.421 | 0.000 |
|  |  | D~1, g0~sex, sigma~sex, pmix~h2 | 5 | -466.594 | 946.188 | 15.413 | 0.000 |
|  |  | D~1, g0~sex, sigma~1, pmix~h2 | 4 | -468.833 | 947.572 | 16.797 | 0.000 |
|  |  | D~1, g0~1, sigma~1, pmix~h2 | 3 | -470.575 | 948.241 | 17.466 | 0.000 |
| GJ | 2013 | D~1, g0~bk, sigma~sex, pmix~h2 | 5 | -982.506 | 1976.727 | 0.000 | 0.757 |
|  |  | D~1, g0~BK + sex sigma~sex, pmix~h2 | 6 | -982.398 | 1979.267 | 2.540 | 0.213 |
|  |  | D~1, g0~bk + sex, sigma~1, pmix~h2 | 5 | -985.974 | 1983.662 | 6.935 | 0.024 |
|  |  | D~1, g0~bk sigma~1, pmix~h2 | 4 | -988.612 | 1986.336 | 9.609 | 0.006 |
|  |  | D~1, g0~1 sigma~sex, pmix~h2 | 4 | -1011.079 | 2031.268 | 54.541 | 0.000 |
|  |  | D~1, g0~sex sigma~sex, pmix~h2 | 5 | -1010.894 | 2033.502 | 56.775 | 0.000 |
|  |  | D~1, g0~sex sigma~1, pmix~h2 | 4 | -1019.283 | 2047.678 | 70.951 | 0.000 |
|  |  | D~1, g0~1 sigma~1, pmix~2 | 3 | -1023.223 | 2053.094 | 76.367 | 0.000 |

| Site | Year | Model | # Par | LogLik | AICc | dAICc | AICcwt |
|------|------|-------|-------|--------|------|-------|--------|
| GJ | 2014 | D~1, g0~bk, sigma~sex, pmix~h2 | 5 | -890.439 | 1792.642 | 0.000 | 0.501 |
| | | D~1, g0~bk, sigma~1, pmix~h2 | 4 | -892.611 | 1794.365 | 1.723 | 0.212 |
| | | D~1, g0~bk+ sex, sigma~1, pmix~h2 | 5 | -891.595 | 1794.955 | 2.313 | 0.158 |
| | | D~1, g0~bk + sex, sigma~sex, pmix~h2 | 6 | -890.400 | 1795.345 | 2.703 | 0.130 |
| | | D~1, g0~1, sigma~sex, pmix~h2 | 4 | -913.338 | 1835.818 | 43.176 | 0.000 |
| | | D~1, g0~sex, sigma~sex, pmix~h2 | 5 | -913.317 | 1838.399 | 45.757 | 0.000 |
| | | D~1, g0~sex, sigma~1, pmix~h2 | 4 | -916.959 | 1843.061 | 50.419 | 0.000 |
| | | D~1, g0~1, sigma~1, pmix~h2 | 3 | -919.224 | 1845.114 | 52.472 | 0.000 |
| | 2015 | D~1, g0~bk + sex, sigma~1, pmix~h2 | 5 | -1128.498 | 2268.329 | 0.000 | 0.641 |
| | | D~1, g0~bk + sex, sigma~sex, pmix~h2 | 6 | -1128.459 | 2270.828 | 2.499 | 0.184 |
| | | D~1, g0~bk, sigma~1, pmix~h2 | 4 | -1131.342 | 2271.553 | 3.224 | 0.128 |
| | | D~1, g0~bk, sigma~sex, pmix~h2 | 5 | -1131.087 | 2273.507 | 5.178 | 0.048 |
| | | D~1, g0~sex, sigma~1, pmix~h2 | 4 | -1186.710 | 2382.289 | 113.960 | 0.000 |
| | | D~1, g0~sex, sigma~sex, pmix~h2 | 5 | -1186.694 | 2384.721 | 116.392 | 0.000 |
| | | D~1, g0~1, sigma~sex, pmix~h2 | 4 | -1196.855 | 2402.580 | 134.251 | 0.000 |
| | | D~1, g0~1, sigma~1, pmix~h2 | 3 | -1202.093 | 2410.696 | 142.367 | 0.000 |
| FB | 2009 | D~1, g0~1, sigma~sex, pmix~h2 | 4 | -196.019 | 404.482 | 0.000 | 0.696 |
| | | D~1, g0~sex, sigma~sex, pmix~h2 | 5 | -195.460 | 408.420 | 3.938 | 0.097 |
| | | D~1, g0~bk, sigma~sex, pmix~h2 | 5 | -195.499 | 408.498 | 4.016 | 0.093 |
| | | D~1, g0~sex, sigma~1, pmix~h2 | 4 | -198.113 | 408.671 | 4.189 | 0.086 |
| | | D~1, g0~1, sigma~1, pmix~h2 | 3 | -202.244 | 412.888 | 8.406 | 0.010 |
| | | D~1, g0~bk + sex, sigma~sex, pmix~h2 | 6 | -194.496 | 412.992 | 8.510 | 0.010 |
| | | D~1, g0~bk + sex, sigma~1, pmix~h2 | 5 | -198.035 | 413.570 | 9.088 | 0.007 |
| | | D~1, g0~bk, sigma~1, pmix~h2 | 4 | -201.596 | 415.636 | 11.154 | 0.000 |
| CF | 9-sessions | D~1, g0~1, sigma~Sex, pmix~h2 | 4 | -1139.215 | 2286.978 | 0.000 | 1.000 |
| | | D~1, g0~1, sigma~1,pmix~h2 | 3 | -1162.552 | 2331.428 | 44.450 | 0.000 |
| | | D~1, g0~bk, sigma~Sex~h2 | 5 | -1263.576 | 2537.985 | 251.007 | 0.000 |
| | | D~1, g0~bk, sigma~1, pmix~h2 | 4 | -1269.521 | 2547.590 | 260.612 | 0.000 |
| MPR | 14-sessions | D~1, g0~bk sigma~1 | 4 | -785.353 | 1579.681 | 0.000 | 0.958 |

| Site | Year | Model | # Par | LogLik | AICc | dAICc | AICcwt |
|------|------|-------|-------|--------|------|-------|--------|
| MPR | | D~1, g0~1 sigma~1 | 3 | -789.685 | 1585.942 | 6.261 | 0.042 |
| | | D~session, g0~1 sigma~1 | 16 | -779.658 | 1610.074 | 30.393 | 0.000 |

Table 3.6. Summaries of scale parameter sigma (σ, km) estimates and 95% confidence intervals for ocelots in Belize, Central America (2002 - 2015) from competing models (delta AICc of two or less) for each year across sites. Dash marks (-) indicate that effect was not supported in top models. HB = Hill Bank, LM = La Milpa, GJ = Gallon Jug, FB = Fireburn, CF = Chiquibul Forest, MPR = Mountain Pine Ridge. In CF I conducted 9 surveys (sessions) total in years 2002, 2003, 2007, and 2008 with some years containing multiple sessions.

| Site | Year | σ km (95% CI) ♂,♀ | σ km (95% CI) ♂ | σ km (95% CI) ♀ |
|------|------|-------------------|-----------------|-----------------|
| HB | 2010 | 1.0 (0.7 - 1.3) | - | - |
| | 2010 | 1.2 (0.7 - 2.1) | - | - |
| | 2011 | 1.2 (1.0 - 1.5) | - | - |
| | 2011 | - | 1.5 (1.1 - 1.9) | 0.9 (0.7 - 1.2) |
| | 2011 | 1.4 (1.04 - 1.97) | - | - |
| | 2012 | 2.2 (1.6 - 3.1) | | |
| | 2012 | - | 2.6 ( 1.7 – 3.9) | 1.7 (1.2 – 2.4) |
| | 2013 | 2.2 (1.3 - 3.9) | - | - |
| | 2014 | - | 3.1 (2.2 - 4.3) | 1.6 (1.1 - 2.3) |
| | 2015 | 1.0 (0.8 - 1.3) | - | - |
| | 2015 | - | 1.4 (0.5 - 3.6) | 0.9 (0.7 - 1.2) |
| LM | 2008 | 2.7 (2.1 - 3.6) | - | - |
| | 2008 | - | 2.9 (2.1 -4.1) | 2.3 (1.5 - 3.3) |
| | 2010 | 1.4 (1.0 - 2.1) | - | - |
| | 2011 | 1.9 (1.2 - 2.9) | - | - |
| | 2011 | 1.8 (1.2 - 2.8) | - | - |
| | 2012 | - | 2.4 (1.2 - 5.0) | 1.4 (1.0 - 1.9) |
| | 2012 | - | 2.7 (1.1 - 6.4) | 1.5 (1.0 - 2.3) |
| | 2013 | 1.7 (1.3 - 2.2) | - | - |
| | 2014 | 1.6 (1.3 - 2.0) | - | - |
| | 2014 | 1.8 (1.4 - 2.4) | - | - |
| | 2014 | | 1.8 (1.0 - 3.3) | 1.4 (1.1 - 1.8) |
| | 2015 | | 2.1 (1.0 - 4.6) | 1.4 (1.0 - 2.1) |
| | 2015 | 2.0 (1.5 - 2.6) | - | - |
| | 2015 | 1.9 (1.5 - 2.5) | - | - |
| GJ | 2013 | - | 2.3 (1.6 - 3.5) | 1.6 (1.3 - 1.9) |
| | 2014 | - | 2.1 (1.7 - 2.6) | 1.6 (1.3 - 2.0) |
| | 2014 | 1.9 (1.6 - 2.3) | - | - |
| | 2015 | 3.1 (2.6 - 3.7) | - | - |

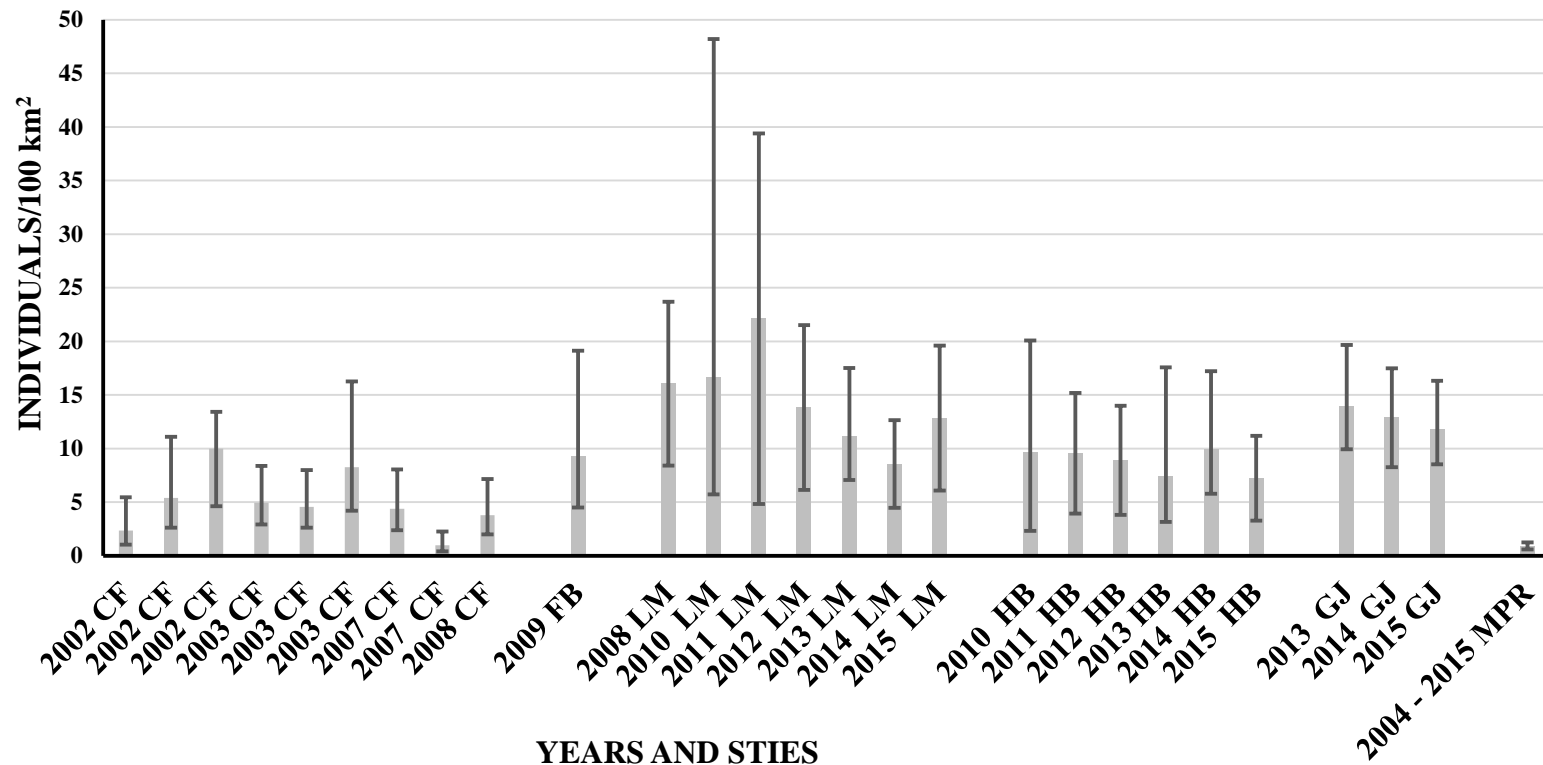| Site | Year | σ km (95% CI) ♂,♀ | σ km (95% CI) ♂ | σ km (95% CI) ♀ |
|------|------|-----------------|-----------------|-----------------|
| FB | 2009 | - | 2.6 (1.0 - 6.9) | 0.9 (0.6 - 1.4) |
| CF | 9-sessions 2002, 2003, 2007, 2008 | - | 2.5 (2.4 - 2.7) | 1.2 (1.1 - 1.2) |
| MPR | Jan 04 - Apr 15 | - | 2.5 (2.4 - 2.7) | 1.2 (1.1 - 1.2) |

*Table 3.6. Continued

Figure 3.1. Density estimates and 95% confidence intervals for ocelots in Belize, Central America (2002 - 2015) for each year estimated using spatial capture-recapture models in R package secr, incorporating maximum likelihood based models with a half-normal detection function. CF = Chiquibul Forest, FB = Fireburn, LM = La Milpa, HB = Hill Bank, GJ = Gallon Jug, MPR = Mountain Pine Ridge.
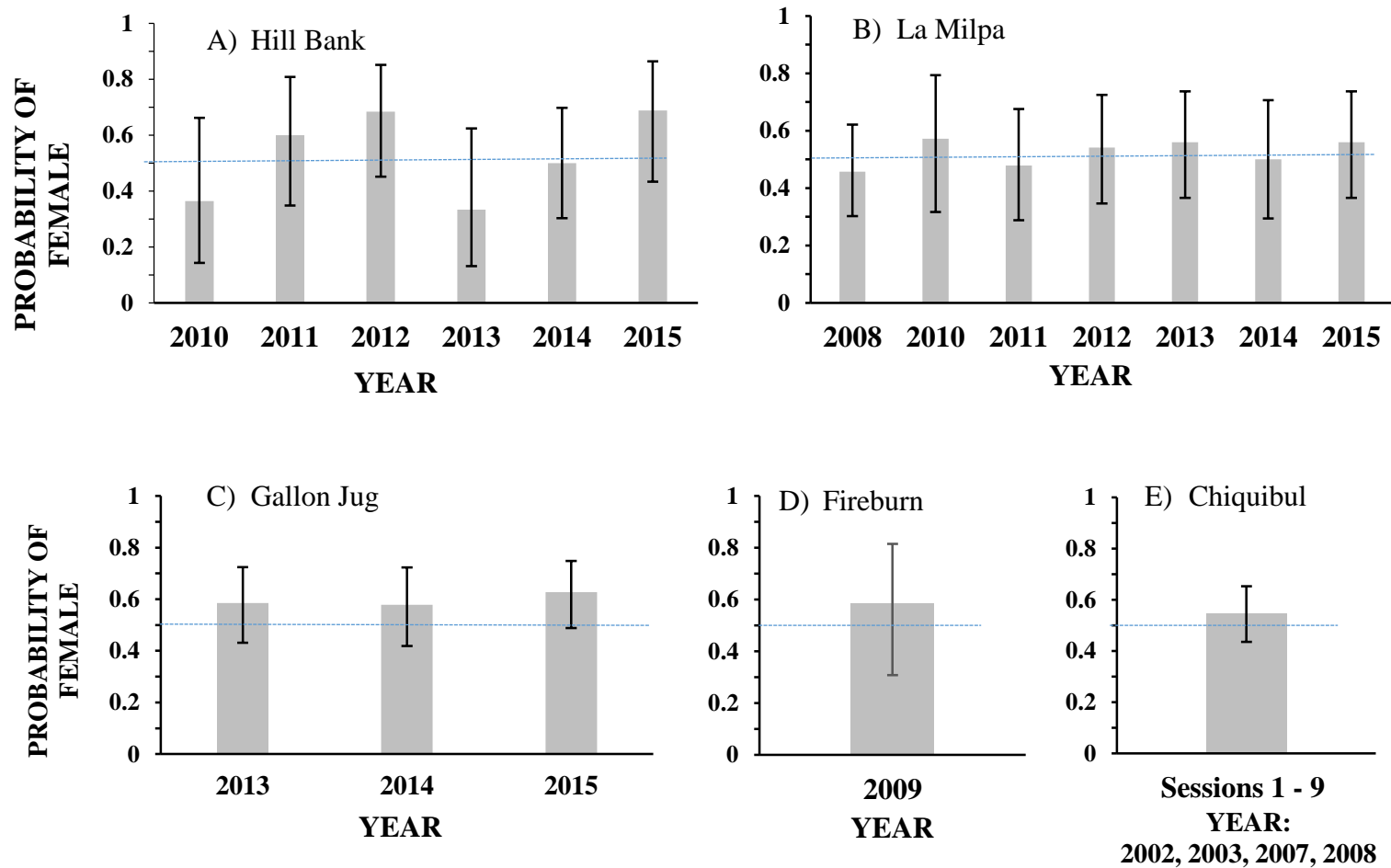
Figure 3.2. Sex ratio estimates and 95% confidence intervals for ocelots in Belize Central America (2002 - 2015), expressed as the probability of being a female, shown for each study site and year. Horizontal dotted line indicates 50:50 sex ratio.
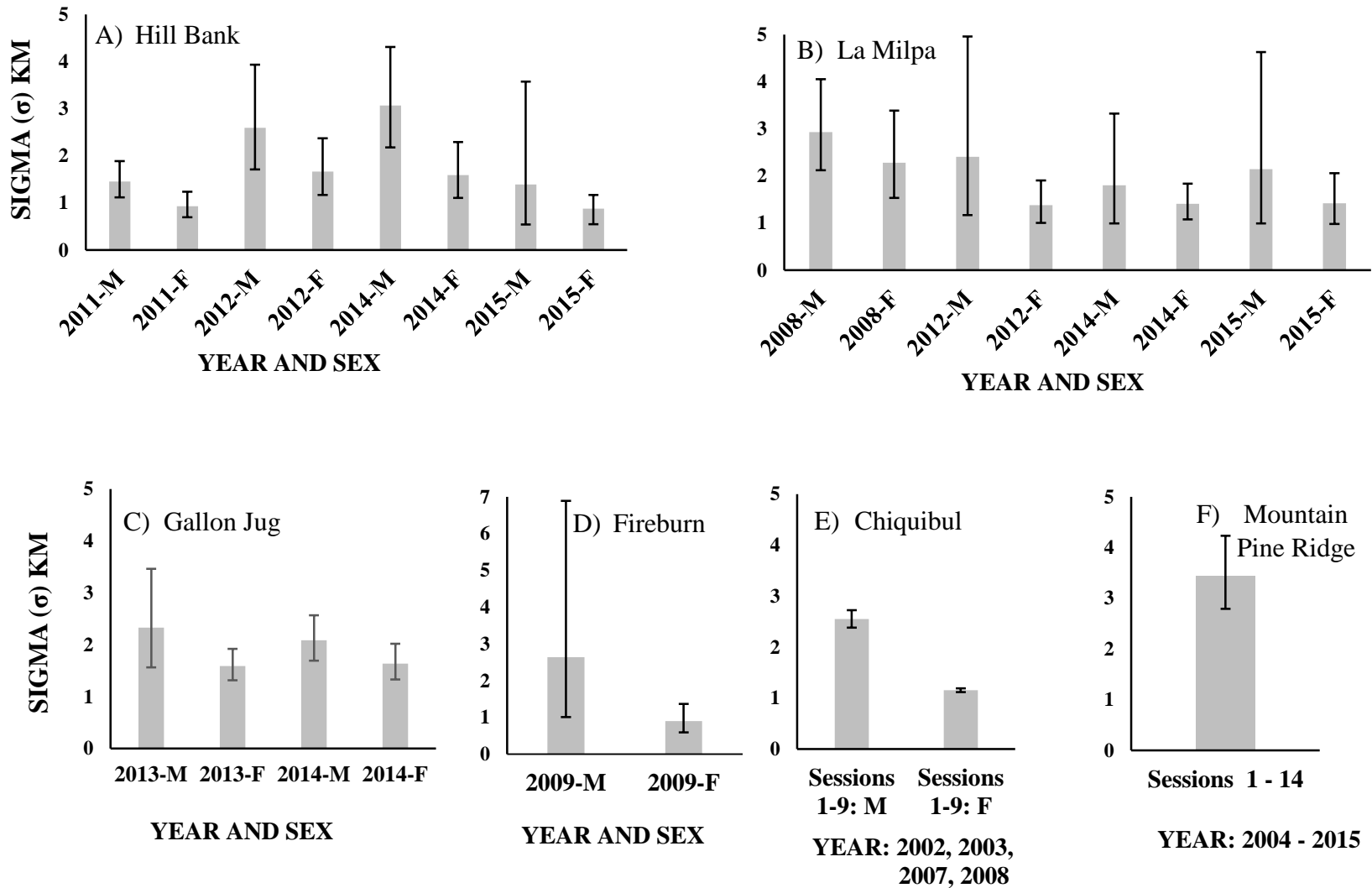
Figure 3.3. Estimates of the ocelot movement parameter sigma (σ), and 95% confidence intervals for all years across six sites in Belize Central America (2002 - 2015), in which R package secr top models contained a sex effect on the σ parameter. M = male, F = female.
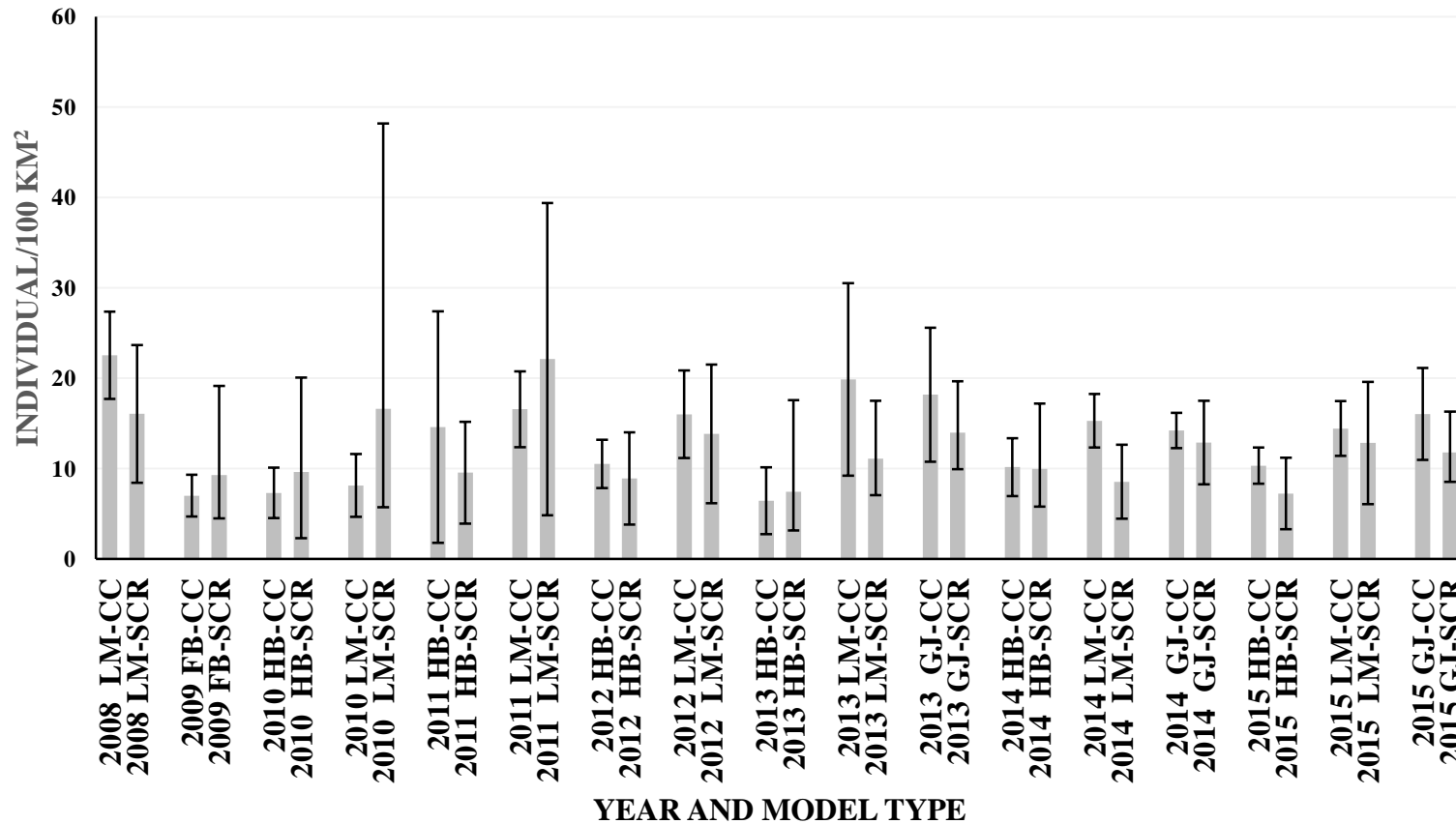
Figure 3.4. Density estimates and 95% confidence intervals for ocelots in Belize, Central America (2008 - 2015) in La Milpa (LM), Fireburn (FB), Hill Bank (HB) and Gallon Jug (GJ) comparing closed capture-recapture (CC) models to spatial capture-recapture models (SCR).
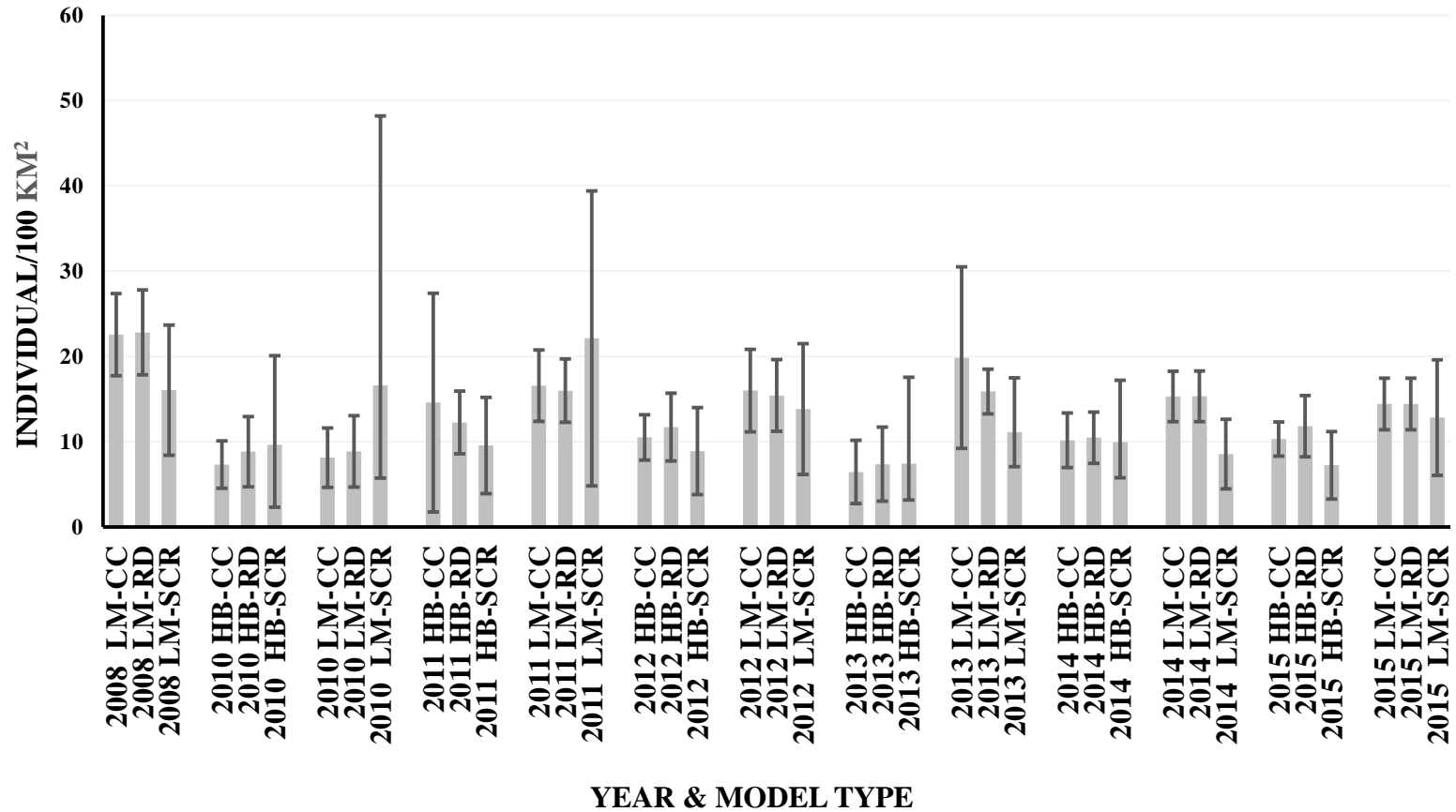
Figure 3.5. Density estimates and 95% confidence intervals for ocelots in Belize, Central America (2008, 2010 - 2015) in HB = Hill Bank and LM = La Milpa, comparing closed capture-recapture (CC) models, open population robust design (RD) models and spatial capture-recapture models (SCR).