



**UNIVERSIDAD AUTONOMA DE QUERETARO
FACULTAD DE CIENCIAS NATURALES**

**Densidades y coexistencia de felinos con
lluvias oscilantes: un estudio en Belice.**

Tesis

Que como parte de los requisitos para obtener

el grado de

Maestría en

Ciencias Biológicas

Presenta

Querétaro 2019



Universidad Autónoma de Querétaro
Facultad de Ciencias Naturales
Maestría en Ciencias Biológicas

Density and coexistence of felids and fluctuating rainfall: a case study in Belize

Tesis

Que como parte de los requisitos para obtener el Grado de
Maestría en Ciencias Biológicas

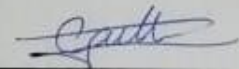
Presenta:

Emma Eloina Sanchez

Dirigido por:

Dr. Carlos Alberto López González

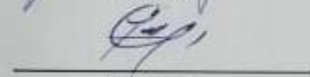
Dr. Carlos Alberto López González
Presidente


Firma

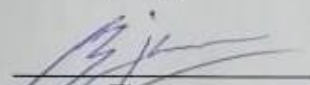
Dr. Robert Wallace Jones
Secretario


Firma

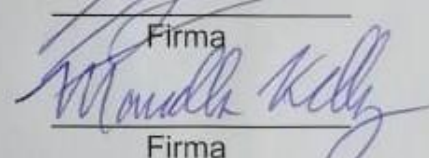
Dr. Israel Gustavo Carrillo Angeles
Vocal

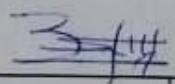

Firma

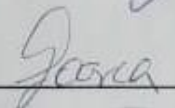
Dr. Bart Johannes Harmsen
Suplente


Firma

Dr. Marcella J. Kelly
Suplente


Firma


Dra. C.S. Juana Elizabeth Elton
Punte
Director de la Facultad


Dra. Ma. Guadalupe Flavia
Loarca Piña
Director de Investigación y Posgrado

RESUMEN

Monitoreo de poblaciones para implementar el manejo adaptativo para conservación de vida silvestre, a menudo solo usa prospecciones cortos de 2-3 meses por año. Este estudio utiliza una prospección de 12 meses consecutivos con trampas cámara para la captura de felinos, específicamente jaguar, ocelote y puma en Cockscomb Basin, Belice, para estimar densidades e interacciones espacio-temporal como respuesta a las temporadas estacional. Primero, se utilizó estimadores de población en el marco de captura y recaptura espacialmente explícitos (SECR) para estimar densidades de jaguares y ocelotes por temporada de lluvias en un periodo de un año y evaluar su relación a estas. Segundo, se evaluó cambios en actividad, patrones de sobre-posición e interacción entre pares de especies de felinos a través de las temporadas en el año y su relación a las lluvias. Los datos se dividieron en cuatro periodos para ocelote y jaguar (Promedio (\pm SD) = 90.1 and 91.5 \pm 1). Se identificaron 36 y 31 individuos en 642 y 225 capturas para jaguares y ocelotes, respectivamente. La densidad promedio de jaguares fue 5.5 /100 km² y para ocelotes fue 8.2/ 100km². Los tres modelos de alto rango para jaguares (AIC \leq 2) sustentaron variación en el parámetro de movimiento, sigma (σ), con sexo, pero el parámetro de detección (g0) fue ambiguo, el cual sustento variación constante y modelos de variación en sexo y temporalidad. Los dos modelos competidores de ocelotes fueron igualmente sustentados por variación en σ por sexo, mientras que también sustentaron variación por sexo y un constante en g0. El promedio general de jaguar fue más alto en el segundo periodo (7.09 ind/ 100km², 0.95 IC: 3.32-10.86) mientras que para ocelote el más alto fue en el cuarto periodo (11.16 ind/ 100km², 0.95 IC: 6.25-16.08). Las tres especies tenían actividad nocturno-crepuscular y porcentajes consistentemente altos de superposición durante todo el año, independientemente de la lluvia (66%-91%). La interacción espacial-temporal y estacionalidad entre pares de felinos se evaluó utilizando 2-way ANOVA para determinar frecuencia de eventos por trampa utilizado por pares de felinos entre un intervalo de 48 horas. La frecuencia de pares de felinos observados por trampa no tuvo relación con la estacionalidad y en consecuencia no se incluyó en los análisis siguientes, pero si hubo diferencias entre pares ($p > 0.05$, $df = 1$, $F = 0.08$). La prueba de Tukey determinó que los ocelotes y pumas tienen menos probabilidad de compartir trampas en un lapso de 48 horas. Por último, utilizando diferencias de tiempo entre capturas consecutivas entre pares de felinos, se determinó que periodos entre capturas entre la misma especie son más cortos que entre las distintas especies (T-test: valor-p < 0.05). Ocelote y puma tienen periodos más largos entre capturas que entre jaguares y ambas especies pero no es significativo (T-test: valor-p > 0.05). La comparación de pares de sexo entre la misma especie fue significativa entre F-M y M-M (Kruskal-Wallis: valor-p < 0.05 ; Mann-Whitney U: FM-MM valor-p < 0.05). Diferencias entre capturas de los sexos M-M y F-M entre distintas especies fueron significativas, las capturas entre M-M fueron en menor tiempo. Se ha puesto mucha atención a la protección de los jaguares en Belice; sin embargo el estado de las cuatro especies restantes de felinos es relativamente desconocido, especialmente fuera de las áreas protegidas. Este es el primer estudio que examina la ecología e interacción de tres especies de felinos usando estas variables en un bosque tropical.

(Palabras clave: Belice, densidad, felinos, interacción, actividad, SECR)

SUMMARY

Population monitoring to develop adaptive management plan for wildlife conservation often only uses snapshot surveys conducted over 2-3 months per year. This study uses a 12 month consecutive camera trap survey of felids, namely the jaguar, ocelot, and puma in Cockscomb Basin, Belize, to estimate densities and spatial-temporal activity in response to fluctuating rainfall. First, we used closed population density estimators in spatially explicit capture recapture (SECR) framework to estimate the densities of jaguars and ocelots across the seasons within a year and we assessed the relationship to rainfall. Second, changes in activity and pattern of overlap and interaction between sympatric felids across seasons within a year and in relation to rainfall were assessed. Data were divided into four periods with mean of 90.1 and 91.5 days, for ocelots and jaguars, respectively. There were 36 and 31 individuals in 642 and 225 captures for jaguars and ocelots, respectively. Average jaguar density was 5.5 ind/100 km² while mean ocelot density was 8.2 ind/100 km². Jaguar top three models (AIC_c ≤ 2) all supported a variation in the movement parameter, sigma (σ), with sex, while detection parameter (g_0) was ambiguous, supporting variation as constant and models with variation, on sex and season. The two competing ocelot models equally supported variation on σ by sex, while there was support for sex and the constant model for g_0 . Jaguar overall density was highest in the second period (7.09, 95% CI: 3.32 – 10.86 ind/ 100km²) while ocelot overall density was in the fourth period (11.16, 95% CI: 6.25 – 16.08 ind/ 100 km²). All three species were nocturnal-crepuscular in activity with consistently high percentages of overlap throughout the year regardless of rainfall (66%-91%). Spatial-temporal interaction and seasonality was evaluated between felid pairs using 2-way ANOVA to examine the frequency of events per trap used by felid pairs within a 48-hour intervals. The frequency of observed felid pairs per trap was unrelated to rainfall therefore not included in further analysis, there were differences between pairs (p-value > 0.05, df = 1, F = 0.08). The Tukey test of mean differences we found that ocelots and pumas were less likely to share traps than ocelots and jaguars within the 48-hour interval. Last, using time differences between consecutive captures of felid pairs, captures was shorter in same species pairs than different species of felids but not significant (T-test: p-value > 0.05). Ocelot and pumas had longer periods between captures while periods of captures between them and jaguars were shorter (T-test: p-value > 0.05). Sex pairs' comparison within same species suggested significant difference between F-M and M-M consecutive captures (Kruskal-Wallis: p-values <0.05; Mann-Whitney U: FM-MM p-value <0.05). Captures of MM and F-M sex pairs within different species pairs were significant with M-M having shorter mean periods between captures. Much attention has been given to protection of jaguars in Belize however, the status of remaining four felid species is relatively unknown, especially outside of reserves. This is the first study to examine the ecology and interaction of three target species of felids using these variables in a tropical forest.

(Keywords: Belize, density, felids, interaction, activity, SECR)

Dedication

To my son, Darren. The greatest motivation I could ask for.
And, to my parents and family for their everlasting support.

ACKNOWLEDGEMENTS

First of all, I would like to acknowledge CONACyT for providing me opportunity to study in Mexico by providing me a scholarship. It has been an unforgettable experience. I thank Panthera Corporation for funding this project carried out in 2013-2014. I want to thank Belize Audubon Society (BAS), co-managers of Cockscomb Basin Wildlife Sanctuary, for their support to carry for the first time a survey of this nature at the reserve. Also, I thank the BAS-CBWS Park Manager, Nicascio Coc, and the wardens, Mario, Brigilio, Federico, and Fedrito who assisted us with field trips within the reserve. Especially, during the rainy season when travelling through muddy trails and crossing flooded rivers became challenging. Without their skills and manpower we would not have been able to complete these field adventures with dexterousness. I learnt a lot of “bush skills” from you guys.

I want to also express my gratitude to my committee. You all have made that this thesis project better with comments and feedback. I thank both Bart and Becci for providing permission to use Cockscomb data to do this thesis on behalf of Panthera Belize. I thank you both for giving me the opportunity to work in the 2013-2014 project and the four years in which I learnt a lot. Many thanks! It was four years well spent! I hope there are more opportunities to collaborate. I thank Carlos, Thesis Director, for his guidance and friendship these two-plus years. And for allowing to work and experience what it is like to be part of his wild but necessary projects! I hope we keep in touch. Also, to Marcella for providing the opportunity to make a short visit to her lab at Virginia Tech. Though it was a short visit, I accomplished a lot and brought back memories and experiences to share. I hope we continue working together in the future as Belize is a lab in the tropics for us.

I also thank the students from the Laboratorio de Zoología, The Dark side. It has been fun learning from you all, your thesis projects, your experiences, and part of the Mexican culture. My repertoire of words, understanding of Spanish language, correct Spanish conversation has improved due to my daily interaction with you all.

Last but not least, I want to thank my parents and family for their support. Throughout my education they have always been there next to me and providing with what they can. I am forever grateful with my parents for taking care of my son while I was away. My son would not have been in better care and loving home than with them. To the rest of my family, for encouraging me to make this step in my career. Knowing that I have their support has been more than enough. And to everyone that has contributed in completing this thesis and degree. There is need for space to have all your names listed. Again, many thanks!

Table of Contents

RESUMEN	ii
SUMMARY	iv
LIST OF FIGURES	8
INTRODUCTION.....	11
METHODS	17
Study area	17
Camera Trapping.....	19
Data Processing	20
DENSITY ANALYSIS	20
Spatially Explicit Capture Recapture.....	20
Model Selection	23
COEXISTENCE: SPATIAL-TEMPORAL INTERACTION.....	25
Activity Pattern and Rainfall	25
Spatial and Temporal coexistence	26
RESULTS.....	29
DENSITIES OF SYMPATRIC FELIDS JAGUAR (<i>PANTHERA ONCA</i>) AND OCELOT (<i>LEOPARDUS PARDALIS</i>) USING SECR	29
Jaguar Density Estimation and Seasonality	31
Jaguar Detection Probability and Spatial Parameter	33
Ocelot Detection Probability and Spatial Parameter	40
Male only Models: Detection, Spatial Parameter and Season	42
ACTIVITY PATTERN AND COEXISTENCE OF THREE SYMPATRIC FELIDS	44
Felid Pairs Overlap	47
Spatial-temporal Interaction: Felid pairs and Season.....	50
DISCUSSION.....	59
Density and Detection of Sympatric Felids	59
Temporal Activity Pattern.....	65
Spatial-Temporal Interaction.....	66
MANAGEMENT IMPLICATIONS	70
APPENDIX I	72
APPENDIX II	73
Appendix III	74
BIBLIOGRAPHY.....	76

LIST OF TABLES

Table 1. A summary of detection across four consecutive seasons for jaguars and ocelots in Cockscomb Basin Wildlife Sanctuary (CBWS), Belize. (1: Mar-Jun, 2013; 2: Jun-Sep, 2013; 3: Sep-Dec, 2013; 4: Dec, 2013-Mar, 2014).

Table 2. Mean densities (individuals/100 km²) estimated from competing models for jaguars in CBWS, Belize.

Table 3. Mean sex specific density (individuals/100 km²) estimates of jaguar with confidence intervals and standard errors estimated from the top competing models.

Table 4. Back transformed estimates of parameters (g_0 and σ) for jaguar's competing models. Male (M) and female (F) estimates of parameters are provided when the model supported sex differences ($\sigma =$ meters). Design of fitted models are available in Appendix 1.

Table 5. Mean densities (individuals/100 km²) estimated from competing models for ocelots in CBWS, Belize.

Table 6. Mean sex specific density (individuals/100 km²) estimates of ocelots with confidence intervals and standard errors estimated from the top competing models.

Table 7: Back transformed estimates of parameters (g_0 and σ) for ocelot competing models. Male (M) and female (F) estimates are provided when the model supported sex differences of parameters ($\sigma =$ meters). Design of fitted models are available in Appendix 1.

Table 8. First and second ranked models. Back-transformed parameters, g_0 and for jaguar and ocelot. S indicates when the parameter values correspond to high (H) and low (L) seasonal rainfall.

Table 9: Summary of independent captures of sympatric felids used to evaluate activity pattern.

Table 10. Percent overlap (95% CI) for each felid species pair between wet and dry season in CBWS, Belize.

Table 11: Frequency of events in which pairs were recorded on the same trap within 48-hrs interval in CBWS, Belize.

Table 12. Number of time differences in which consecutive pairs of different species were observed.

Table 13. Tukey Pairwise test of mean differences for sex pairs between captures of different species in CBWS, Belize.

LIST OF FIGURES

Figure 1. Forest types in Cockscomb Basin Wildlife Sanctuary and surrounding areas.

Figure 2: Elevation map for Cockscomb Basin Wildlife Sanctuary.

Figure 3: Cockscomb Basin Wildlife Sanctuary, Belize, including major rivers, trails and camera trap stations.

Figure 4. Barplot of the four seasonal periods showing the fluctuating rainfall (cm) recorded during the year of the survey.

Figure 5: Mean overall and sex specific densities (individuals/100km²) for jaguars with standard errors estimated from the candidate model average using MLE for each seasonal period.

Figure 6. Jaguar sex specific detection probability as a function of distance estimated with first competing model, Fit 1 ($g_0 \sim 1$ $\sigma \sim \text{sex}$).

Figure 7. Jaguar sex specific detection probability as a function of distance as estimated with second competing model, Fit 2 ($g_0 \sim \text{sex}$ $\sigma \sim \text{sex}$).

Figure 8. Jaguar sex specific detection probability as a function of distance estimated from the third competing model, Fit 3 ($g_0 \sim \text{season}$ $\sigma \sim \text{sex}$).

Figure 9. Mean overall and sex specific densities (individuals/ 100km²) for ocelots with standard errors estimated from the candidate model average using MLE for each session.

Figure 10. Ocelot sex specific detection probability as a function of distance estimated with the first ranked model, Fit 1 ($g_0 \sim \text{sex}$ $\sigma \sim \text{sex}$).

Figure 11: Ocelot detection probability as a function of distance from activity centre estimated with the second ranked model ($g_0 \sim 1 \text{ sigma} \sim \text{sex}$).

Figure 12. Boxplot comparing density estimates (O = Overall, F = Female, M = Male) for both jaguar and ocelots overall estimates and sex specific. These are mean estimates using competing model for each session.

Figure 13: Female jaguar activity pattern in CBWS compared between high and low seasons.

Figure 14: Female ocelot activity pattern in CBWS compared between high and low seasons.

Figure 15: Female puma activity pattern in CBWS compared for high and low seasons.

Figure 16: Activity pattern of pumas of unknown sex in CBWS compared between high and low seasons.

Figure 17: Activity of jaguars and ocelots across the survey presented into seasonal periods for dry (A and B) and wet (C and D) seasons.

Figure 18. Jaguar and puma activity patterns across the survey presented seasonal periods of dry (A and B) and wet (C and D) season rainfall.

Figure 19: Ocelot and puma activity patterns across the survey presented into seasonal periods of dry (A and B) and wet (C and D) season.

Figure 20: Interaction effects plot of mean frequency of events of pairs and seasonal (H= High, L=Low) rainfall. Pairs: JO (Jag-Oce); JP (Jag-Pum); PO (Pum-Oce).

Figure 21. Tukey test results used to comparing pairs, which was the most significant variable of the interaction model. Significance is indicated for p-value <0.05.

Figure 22. Mean time differences and (95%) CI between consecutive captures per trap throughout the year.

Figure 23. Comparison of Different and Same pairs of species' time difference between consecutive capture per trap across the year.

Figure 24. Time difference per trap between unlike pairs of species.

Figure 25. Time differences between sex pairs within consecutive captures between same pairs.

Figure 26. Time difference between consecutive captures per trap for same species pairs across the year.

Figure 27. Comparison of time differences between consecutive captures per trap for each pair of felid species.

Figure 28. Overall time difference between sex pairs of consecutive captures of different species of felids, per trap in CBWS, Belize.

INTRODUCTION

Population management and conservation of cryptic species require reliable estimates of population size paired with spatial information to make informed decisions and implement effective management plans (Carbone et al., 2001; Rabinowitz and Zeller, 2010; McCarthy et al., 2015). It is challenging to sample species of that exhibit elusive behaviour, wide ranging movements and occur at low density in tropical forests (Sollmann et al., 2011).

Camera trapping and density estimates

Camera trapping studies have popularity due to their effectiveness in tackling these challenges through their non-invasive ability to capture an assortment of individuals of the target population along with other non-target species that pass in front of the camera (Foster, 2008). Camera trap survey method is one of the most common tools employed for density estimation across the globe, especially in felid species in different habitats such as jaguars (Gutiérrez-González et al., 2012; Boron et al., 2016; Coronel-Arellano et al., 2017; Harmsen et al., 2017), pumas (Kelly et al., 2008; Negrões et al., 2010), tigers (Karanth, 1995), clouded leopards (Sollmann et al., 2014), ocelots (Trolle and Kéry, 2003a; de la Torre et al., 2016; Satter et al., 2019), and bobcats (Heilbrun et al., 2003). Consequently, it is an important tool to study elusive species including but not limited to density estimation and carnivore assemblage coexistence.

Improvements in camera trapping design methods, especially for felids density estimation, have occurred from field-work since Karanth (1995) to enhanced application of data analysis on camera trap data. Studies of large felids have recognized the benefits of considering individual location, movement and sex variables used in SECR to estimate population size (Sollmann et al., 2011; Noss et al., 2012; Tobler et al., 2013; Jůnek et al., 2015; Boron et al., 2016). Tobler and Powell (2013) simulations of jaguar data identified important biases related to such as size of study area, length of surveys, sex covariates compared

between conventional Capture-Recapture (CR) and Spatially Explicit Capture-Recapture (SECR) methods.

Female jaguars have been suggested to actively avoid camera traps thus reducing female trap success rates (Srbek-Araujo, 2018) which in turn affect detection probabilities and density. Camera trap success rates across a continuous time gradient may be also affected by food availability, for example in pumas (Benson et al., 2006) or restricted by rearing of cubs (Srbek-Araujo, 2018). Wilsterman et al. (2018) argues that the subtle changes in rainfall characteristic of tropical environment can stimulate hormones relating to courtship and mating where, female behaviour is characterized by actively advertising their mating availability. Thus for jaguars, this could imply travelling on trails to send their message for males. Continuous camera trapping over longer periods could possibly detect fluctuations in female detection probability and overall fluctuations in density of the population, if any, which in turn can be reflected on population density and population structure (Jędrzejewski et al., 2017). Continuous assessments of these species are important to continue monitoring local populations, therefore this study provides a single site population assessment and coexistence where these species live in sympatry with SECR.

Seasonality in the tropical environment is often differentiated between wet and dry conditions relating to rainfall fluctuations (Wilsterman et al., 2018). Neotropical rainforests are characteristically warm and wet year-round (Waide, 2008), however, there is marked seasonality in resources and resultant life history adaptations (Rand and Rand 1985, van Schaik et al. 1993, Braker and Greene 1994). As a result, many species of prey feed on a variety of mast seeding or fruit production, typical in many terrestrial ecosystems including tropical forest (Ostfeld and Keesing, 2000). Consumers of masting events are drawn to the area and increase in density and consequently attract predators leading to variability in consumer and resource ratios (Ostfeld and Keesing, 2000).

Continuous long-term camera trap surveys through seasonal rainfall are rare for large and medium sized felid species (Gutiérrez-González et al., 2015; Gómez-Ramírez et al., 2017) due to their elusive wide ranging nature that increases costs for surveys and at the same time increase female probability

captures to better estimate density of the population (Jędrzejewski et al., 2017). A recent IUCN assessment of jaguar status suggested methodological bias resulted in overly optimistic densities about their status throughout their range (Quigley et al., 2017). Thus, it is necessary to standardize and improve current methodology across species in order to evaluate current wild populations, especially for felids.

Activity patterns and Coexistence

Populations are driven by both biotic and abiotic factors shaping their community structure and population dynamics (Trivellone et al., 2017). Wilsterman et al. (2018) explains that individual hormonal responses in tropical environments are linked to changes in rainfall, coexistence with predators and conspecifics, food availability and temperature rather than photoperiod cues in temperate climates. Predator and prey coexistence is a combination of maximizing predatory strategies of hunting while prey develop avoidance techniques (Eriksen et al., 2011; Harmsen et al., 2011b; de Matos Dias et al., 2018). However, predator versus predator coexistence creates an environment of competition where usually large species outcompete smaller ones both spatially and temporally (Emiliano Donadio and Buskirk, 2006; Ramesh et al., 2017) or attraction-repulsion are expressed as harassment or tolerance (Elbroch et al., 2017). Another potential source of variability (seasonal and daily) can be linked to hormones causing changes in behaviour (e.g reproduction) and though in the tropics changes are very small, fauna can express high sensitivity to these changes across the year (Wilsterman et al., 2018). In an ecosystem when high density of competing predators, there needs to be separation of resources, such as space use, habitat, and food.

Top predators, such as felids, are known for causing cascading effects on subordinate or smaller carnivore guild (Bischof et al., 2014). Durant (1998) argued coexistence can be facilitated through heterogeneity in environmental factors (habitat structure) or in the biological community (populations) and proposed that the weaker or less competitive of the assemblage would avoid competition by seeking refuges. Abundance of dingos (*Canis lupus dingo*) in

Australia had significant negative effects on domestic cat behaviour and abundance (Brook et al., 2012). Likewise, competition among multiple carnivores guild, cheetah and wild dogs persist through avoidance in temporal and spatial scales and employing a different hunting strategy and thus are displaced to areas of minimal resource availability (Durant, 1998; Vanak et al., 2013). Ocelots have negative effects on smaller felid species in areas where the larger predators, jaguars and pumas are rare or extirpated leading to changes in activity pattern, occurrence and increased density (Di Bitetti et al., 2010; Kasper et al., 2016).

Currently, studies further support this mechanism in other ecosystems where temporal, spatial, and foraging segregation among competitors facilitate co-existence. For example, spatial avoidance of wolf packs by cougars (Akenson et al., 2005), dietary partitioning on preferred prey between swift foxes and coyotes (Kitchen et al., 1999) and tigers, leopard, and dhole in India (Ramesh et al., 2012; Ramesh et al., 2017) temporal segregation by ocelot, pumas and humans (Massara et al., 2018), and temporal segregation of carnivore guild in Madagascar (Gerber et al., 2012). Dominance hierarchies lead subdominant species to less favourable conditions affecting food source and habitat, for example, pumas (Elbroch and Kusler, 2018) and cheetahs (Durant, 1998). Soto and Palomares (2015) suggested that fine scale habitat variables enables coexistence among five carnivores thriving in a homogeneous landscape.

This study used a one year (12 months) consecutive camera trapping with early and late, wet and dry periods. The tropical forests of Belize are considered a stronghold for jaguar survival with high density but with new improved analysis of capture-recapture densities need to be reassessed (Sanderson et al., 2002; Quigley et al., 2017). Cockscomb Basin Wildlife Sanctuary (CBWS), Belize, a tropical evergreen forest reserved established as the first jaguar reserve after Rabinowitz and Nothingham (1986) jaguar study. Authors such as Silver et al. (2004), Weckel et al., (2006), Foster et al., (2008), Davis (2009), Harmsen et al., (2011), Higgingbottom (2012), and Harmsen et al., (2017) have studied jaguars, ocelots, and pumas, co-occurring sympatric felid species, using camera trapping in this reserve, however, periods of surveys do not go beyond one season in compliance to close population assumptions to estimate density.

In Belize, Harmsen et al., (2017) and Satter et al., (2019) have concluded that stable large population of jaguars and ocelots through long-term monitoring using several years with multiple one season surveys. Continuous assessments of these species are important to continue monitoring local populations, therefore this study provides a seasonal single site population assessment and coexistence where these species live in sympatry with SECR. Cockscomb Basin Wildlife Sanctuary (CBWS) is well known for its high density jaguar population since Rabinowitz and Nottingham (1986). Recent data about the jaguar population sustains that the population in CBWS is stable and based on long term monitoring there is a maximum age record of fourteen years (Harmsen et al., 2017). Jaguar and ocelot capture rates are highly male biased and though ocelots have been monitored in the area, they are been rarely studied until recently with SECR (Davis, 2009; Satter, 2016; Satter et al., 2019). Ocelot studies have been carried out in neighbouring protected areas, such as Dillon (2005), Dillon and Kelly (2007) and Dillon and Kelly (2008), which provided home range data, densities on two sites with differing forest types and camera trap methodology for ocelots. Camera trap studies usually survey for short periods to comply with the closure assumption of closed population models and are usually combined with other limitations (Silver et al., 2004; Tobler and Powell, 2013). Lengthier surveys allow the detection of possible trends across a continuous time gradient which would be impossible to detect in short-term surveys (Barlow et al., 2009). This is the second study known to carry a lengthier camera traps survey and the first to apply closed population SECR method on two sympatric felid species and compare density estimates (Jędrzejewski et al., 2017). Gutiérrez-González et al. (2015) monitored for twelve years of year-long surveys consecutively but used open population models on periods with higher capture rates.

Due previous results in these studies, it is hypothesised that densities for both jaguar and ocelots would remain stable through the year independent of season. Sharing space through the use of trail infrastructure, to move through the forest matrix, is a habitat characteristic used by the three species, therefore it is hypothesised that the smaller ocelot and puma would be coerced to exploit this characteristic in less extent to enable coexistence with the jaguar in a high density felid system. And, between pumas and ocelots, pumas would exhibit higher

dominance through increased use of the trails therefore ocelots would tend to avoid using the same area and time where pumas are detected. The first objective is to estimate density of jaguars and ocelots, compare it with rainfall, a proxy for seasonality, to assess their relationship within a year. The second objective is to assess coexistence of the three felid species through activity patterns across the season, differential trail use in combination with time of consecutive captures between pairs of felids to determine spatial and temporal patterns that enable their coexistence across the year.

METHODS

Study area

Cockscomb Basin Wildlife Sanctuary (CBWS) (16° 42' 58.32" N, 88° 39' 38.88" W) is the first and only reserve worldwide established for the purpose of protecting jaguars after findings by Alan Rabinowitz of a healthy population in this area. It was heavily logged until it was declared a reserve in 1986. The Belize Audubon Society is co-manager for the reserve with ~ 51,700 hectares comprised of lowland broadleaf moist tropical forest (Figure 1-2). There is a series of river branches: perennial, intermittent and ephemeral flowing streams, which feed into South Stann River (E. Sanchez. pers.obs). The current trails used for camera trapping and tourist travelling routes were previously logging roads (Harmsen et al., 2017) (Figure 3). As part of the National Protected Areas System Revised Edition (2015), CBWS has limited human activities to which include research, education, tourism, and conservation management.

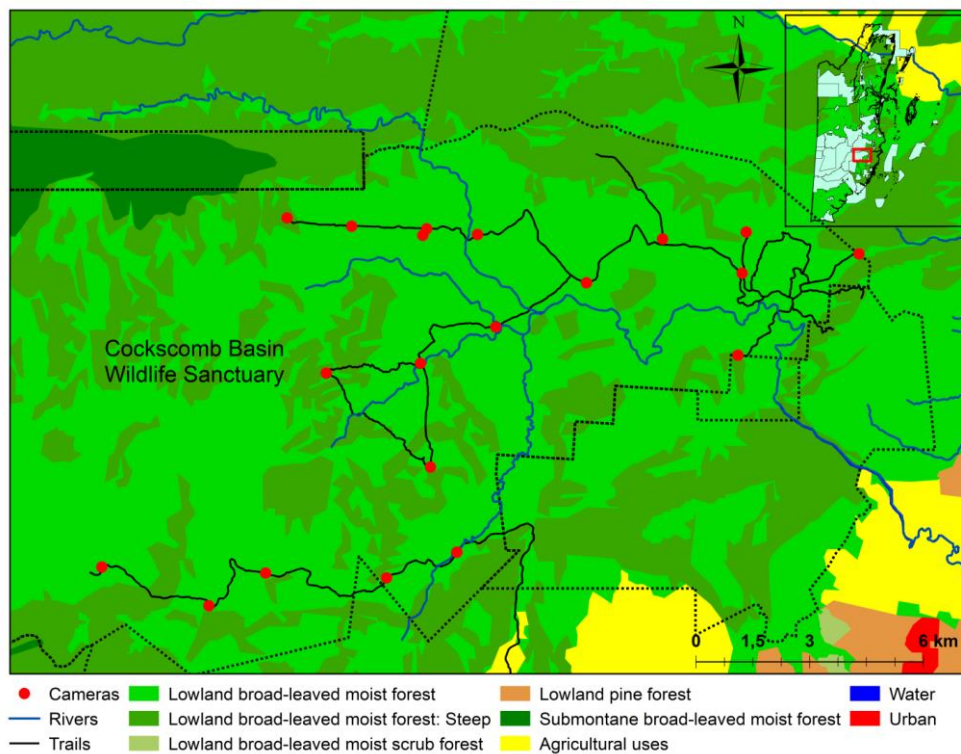


Figure 1. Forest types in Cockscomb Basin Wildlife Sanctuary and surrounding areas.

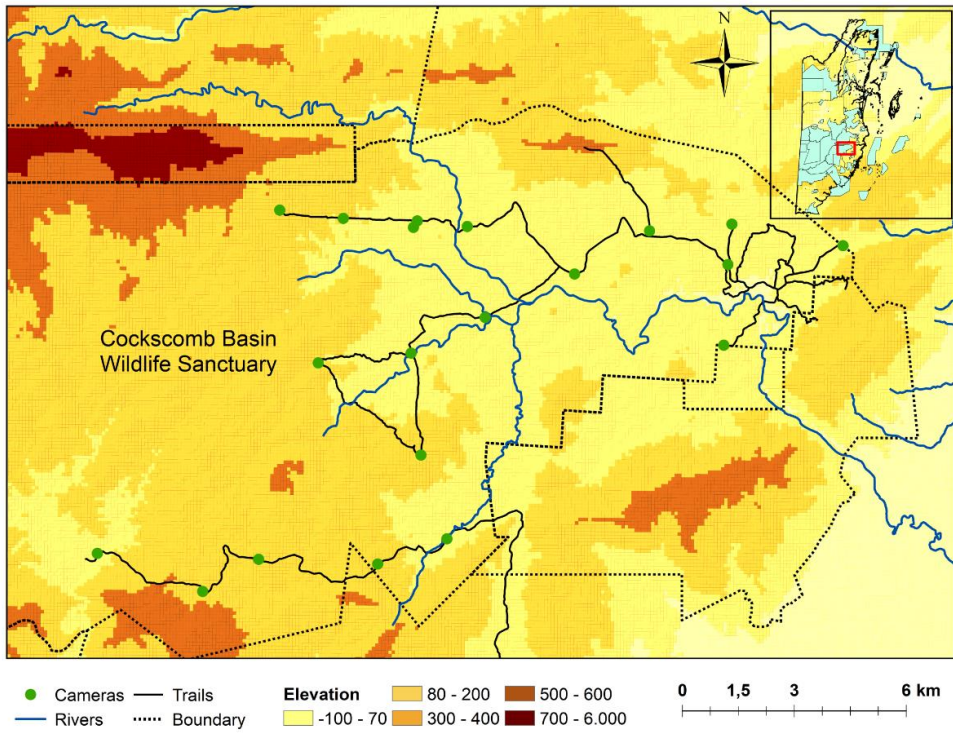


Figure 2: Elevation map for Cockscomb Basin Wildlife Sanctuary.

~117.4

km²

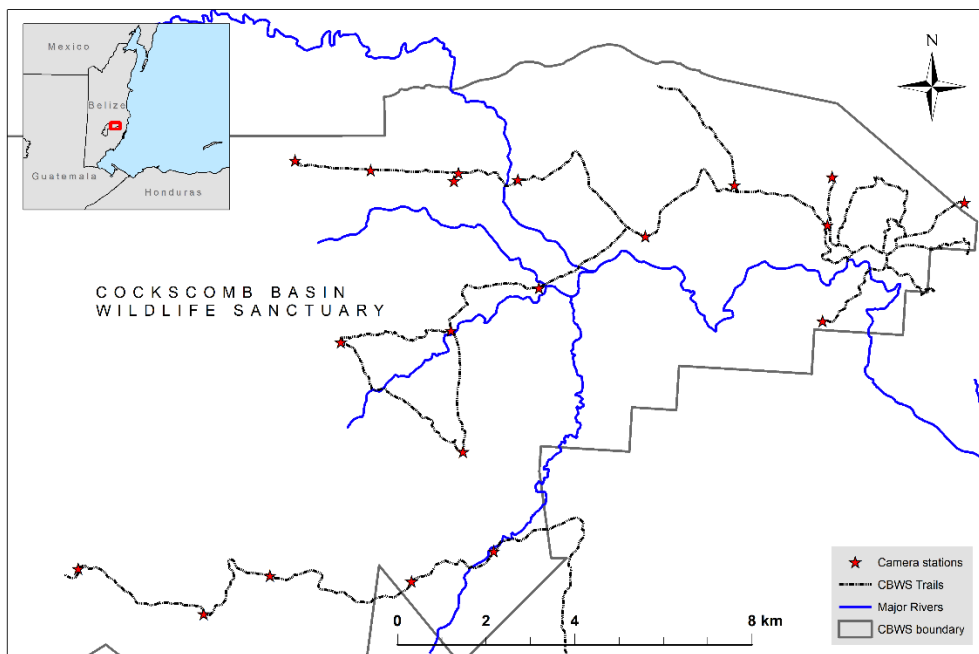


Figure 3: Cockscomb Basin Wildlife Sanctuary, Belize, including major rivers, trails and camera trap stations.

There are 163 species of mammals reported in Belize of which 96 are found in CBWS (Walker and Walker, 2006). Though research has mainly been focused on a limited number of species in CBWS, there is a reported 58%, 56%, and 69% of mammals, birds, and amphibians of the species reported nationwide (Walker and Walker, 2006). These include five species of felids: jaguar (*Panthera onca*), puma (*Puma concolor*), ocelot (*Leopardus pardalis*), jaguarundi (*Herpailurus yagouaroundi*), and margay (*Leopardus weidii*).

Camera Trapping

The camera trapping survey took place from March 2013 to March 2014 with monthly camera checks. The study area consisted of twenty camera stations with Panthera cameras (Panthera Corporation; V3 and V4) covering an area of 117.4 km² (100% Minimum Convex Polygon, MCP) (Karanth and Nichols, 1998; Harmsen et al., 2017). Cameras were deployed year-round at the same locations along existing trails. Cameras were mounted on trees along the trail about 30-40 cm from the ground. Each station consisted of a pair of cameras placed on either side of the trail to capture both flanks of our target species. They were angled away from each other to avoid interference by the flash when captures are triggered producing overexposed photos. All photo captures were automatically stamped with date, time, and station name after downloading them on-site from the cameras.

When cameras were mounted, the sensors were tested to ensure they could reach across to the other side of the trail to minimize missed captures. Cameras were placed at an average distance apart of 2.5 km, while the farthest distance between the farthest cameras in the grid was 21.6 km.

Data Processing

Captures from target species were grouped and given an individual identification in the database. Both jaguars and ocelots were uniquely identified by their pelt pattern which is easily contrasted through photo captures (Trolle and Kéry, 2003b; Silver et al., 2004). Individual's whose sex was unable to be determined were referred to as unknowns and kept as "NA" (Not available) in the capture histories. An album containing both flanks of individuals was kept to cross-reference any future re-captures.

The 12 month data was divided into four survey sessions of three months according to total rainfall. Consistent with the assumption of closed populations models and comparability with low rainfall sessions, the six consecutive months of high rainfall was split in two sessions (Karanth & Nichols, 1998). This resulted in four periods, early and late wet season and early and late dry season, defined by total rainfall in the following order: March - June, June - September, September - December and December - February. For analysis purposes we used one record per individual per trap within 24 hours (1 day) as independent captures (Satter et al., 2019). There was an average of 90.1 (± 1 SD) occasions with the ocelot data and 91.5 (± 1 SD) occasions with the jaguar data.

DENSITY ANALYSIS

Spatially Explicit Capture Recapture

We employed closed population, spatially explicit capture recapture (SECR) using the secr package (v 3.0.1) in R (R Core Team, 2013) and R Studio to estimate densities for each session throughout the year and to assess rainfall effects on density and capture probability (Efford, 2017). Individual core home

ranges (or hypothetical activity centres) are assumed to be distributed across an area study site and the number of activity centres defines number of animals in an area, SECR therefore, uses location and day of capture to estimate the most likely number of activity centres (Efford et al., 2009; Efford, 2017). In this case activity centres are unknown, however the locations of camera traps are known and are assumed to have the probability to capture at least one individual (Efford, 2004). An animal's capture probability (p) is a function of the distance (d) between its activity centre and the camera trap $P = f(d)$. Therefore, $P = f(d) = g(d)$ which requires two parameters: g_0 capture probability at the hypothetical activity centre and σ the spatial scale parameter over which detection declines away from the activity centre. $P = f(d) = g_0 * \exp \left[\frac{-(d+cov)^2}{2(\sigma+cov)^2} \right]$, where we used to covariates: sex (male and female) and season (high rain and low rain) (Efford, 2004).

In order to build capture histories two files are uploaded in the R environment. One file consists of the capture records of individuals over a series of occasions. The second file consists of detector names and locations with 1s and 0s indicating whether traps were functioning during the trapping session, where 0s indicate stolen, trap malfunction, or dried batteries.

Data for each species had a multi-session capture history with sex as a covariate consisting of the 12 month survey. In the case of jaguars, we used 20000 ha (200 km²) to create a jaguar state space with spacing of 300 m to delineate the potential location of activity centres. The largest home range recorded by an adult male jaguar in CBWS using GPS data is 169 km² (Harmsen et al. *unpublished data*). For ocelots a buffer of 9000 ha (90 km²) with spacing of 200 m was used to create the ocelot state space. The decision was made based

on the *suggest.buffer* function in *secr* package and the longest distance between two points of a home range polygon of a telemetry study in Belize (Dillon and Kelly, 2008).

Models in *secr.fit* used the half-normal detection function, denoted as 0, since this is the most commonly used in spatial modelling for either maximum likelihood or Bayesian models (Noss et al., 2012; Jůnek et al., 2015; Kane et al., 2015; Boron et al., 2016; Efford, 2017; Jędrzejewski et al., 2017). For more details on detection functions see Efford (2017) and Grente (2017). The underlying parameters in SECR consist of the probability of capture (g) of an individual i at a trap j on s occasion as a function of distance (d) from its activity centre (Borchers and Efford, 2008; Tobler and Powell, 2013). An occasion is defined as a 24 hour interval when traps j are open and has a coordinate (x,y) assigned (Higginbottom, 2012; Satter et al., 2019). The maximization method applied was Nelder-Mead as this is a relatively robust; however it is computationally complex (Boyd and Vandenberghe, 2004). Seasonality was included as precipitation (i.e. rainfall) as a covariate for each of four, 3 month periods to evaluate effects on density (Wilsterman et al., 2018). Using function *sessioncov* we included and labelled this covariate *season* with two levels, L and H, to represent low or high rainfall, respectively, for each period surveyed in the multi-session capture history. Therefore, sixteen (16) model combinations were run using constant, sex and season on both capture probability ($g0$) and the spatial parameter (σ). These included additive effects of sex and season applied on both $g0$ and sigma.

Unknowns were included by using the finite mixture models with the *hcov* function in *secr.fit* which randomly assigns sex variable to a capture of unknown sex and therefore include the capture in the model using the detection parameter

values that apply to the known class assigned (Efford, 2015). Finite mixture models were used and applied conditional likelihood (CL) as TRUE in *secr.fit* where density is a derived parameter (Borchers and Efford, 2008; Efford and Mowat, 2014). These components in *secr.fit* were applied to the full data set of independent records comprising of both sexes.

Model Selection

Akaike Information Criterion (AIC), available in the *secr* package, was used to select the best fitting model that explains the data (Burnham and Anderson 2002). AIC is used for selection of parsimonious models whereby a balance between bias and variation of parameters in a model is achieved (Mackenzie et al., 2017). Mackenzie *et al.*, (2017) further explains that this trade-off can favour models with fewer parameters because though bias is decreased with increased parameters in the model, variance increased thus there is lower precision. AIC is therefore a combination of a “relative measure” of the unexplained variance in the data by the model and a penalty on models which explain much of the variation using many parameters: $AIC = 2 \ln(L(\hat{\theta}|x)) + 2\delta$ (Mackenzie et al., 2017). The equation $(L(\hat{\theta}|x))$ is the log of the likelihood estimated for the parameters based on the data and δ (small delta) is the number of parameters estimated in the model (Mackenzie et al., 2017).

Best models with deltas values less than two ($\Delta AIC < 2$) are considered to have substantial level of support and values between 4 and 7 are substantially less supported (Burnham et al., 2002). Model averaging was done on competing models with the use of Burnham and Anderson (2004) formula on candidate

models to estimate average density and confidence intervals for each seasonal period.

We also applied SECR and model selection on male only data for both species. It is common for males of large solitary carnivores to have higher capture probability due to increased trail use and to comprise of a large proportion of captures (Tobler and Powell, 2013; Singh et al., 2014). These male-only models used only season (high and low rainfall) as a covariate. As a result, there were four models applied to these data, using a combination of the following parameters: $g_0 \sim \text{constant (1)}$, $g_0 \sim \text{season}$, $\sigma \sim 1$, $\sigma \sim \text{season}$. However, since these also included the unknown class (NA) which was inconsistent in all four periods an additional step was applied using the *shareFactorLevels*. This function coerced the factor covariate sex (M and NA) to be applied to all seasonal periods in the multi-session *capthist* rather than per period. The relationship of precipitation and densities was evaluated using spearman rank correlation in R (R Core Team 2015) which was applied to sex specific density estimates and overall estimates for both species of felids. We applied the “*alternative as greater*” in order to test our hypothesis for a positive relationship between density and precipitation. Welch t-tests were used for differences in number of captures and number of individual between the sexes for both target species. A chi-squared test (χ^2) was used to compare male and female densities for each species and to compare male and female capture and detection for each species. R and R Studio and Origin Pro 8 (v8.0724) were used for the generation of figures presented in this study.

COEXISTENCE: SPATIAL-TEMPORAL INTERACTION

Activity Pattern and Rainfall

We investigated sympatric felids interaction and coexistence and any associated relationships with seasonality using temporal activity patterns across the year and frequency of events of felid pairs per trap. First, we used the package *overlap* (v 0.3.0) in R to determine activity pattern distribution for each session, described above, to assess relationship between seasonality and temporal competition by these species. The kernel density distribution and overlap, that is, the coefficient of overlap (Δ), for all three species (Ridout and Linkie, 2009). We used *dhat4* estimate to describe Δ as recommended in the *overlap* manual (v 0.3.0) for samples of 50 or larger and *dhat1* for smaller samples (Meredith and Ridout, 2017). For samples which were less than the recommended by the method we abstained from making overlap estimates, as is the case with females and male capture events. Females sample size were increased to apply the overlap method and made comparable between samples only when pooled within the High and Low categories for the entire year, that is, two samples for the year. In the case of males, overlap was estimated for each seasonal period, early and late dry and wet season. The 24 hour interval per individual per trap was considered an independent capture for all three species for this analysis.

The kernel density distribution was plotted using *densityPlot* in *overlap* for both species in all four sessions described above. The value of delta (Δ), i.e. coefficient of overlap, ranges between 0 and 1, where 0 means no overlap and 1 means complete overlap. Confidence intervals were calculated by bootstrapping the sample using the *bootCI* function in the *overlap* package. The values used were in “basic0” calculated as $perc - \text{mean}(bt) + t0$ where “perc” are percentiles of

the confidence interval, bt is mean of bootstrap of the sample, and $t0$ is the estimate for the original sample (Meredith & Ridout, 2017). The coefficients of overlap (Δ %). of felid species pairs were compared between high and low seasonal rainfall through a chi squared test (χ^2).

Spatial and Temporal coexistence

Coexistence of jaguars, pumas and ocelots was evaluated through their detection frequency on camera traps by pairs of species in a fixed interval in relation to seasonality periods. Time differences per trap between consecutive captures between same and different species, same sex and different sex pairs within same species and different species pairs were used to investigate sympatric interaction.

To evaluate seasonality effects on their coexistence, the 24 hour independent capture database was used to count the frequency of events with pairs per trap: jaguar-puma (JP), jaguar-ocelot (JO), and puma-ocelot (PO) within a 48-hour fixed interval. These frequencies were summed across all traps and then per pair for each of the four seasonal period with an average of 45 occasions each. Due to time differences calculated, 48 hour interval (2 days) is enough to suggest an interaction between any pair of felid species. Frequency of events were log transformed and a two-way ANOVA was applied using two factors: (a) pairs with three levels named above and (b) season was pooled into high and low rainfall factor levels and interaction of both. A Tukey HSD test was used on variables with significant effect in the ANOVA model. Thus, we hypothesize that frequencies per trap would be the same for all felid pairs, i.e. no differences, if

there was no interaction between any pair. And, therefore season would not affect this frequencies across the year.

A Two-way ANOVA was performed in R (version 3.5.0) and RStudio (version 1.1.447) with the *aov* command to build the model, which includes response of frequencies by combining effects of both season (high and low rainfall) and pairs of felids, and *TukeyHSD* command to determine for significance between factor variables that two-way ANOVA indicated were significant.

To further investigate the type interaction among the three felids, time differences between consecutive captures per trap for jaguar, ocelots and pumas were calculated using the complete dataset. The time differences were calculated in days per trap by taking into consideration the date and time of capture between consecutive captures between: jaguar-ocelot, ocelot-jaguar, jaguar-puma, puma-jaguar, puma-ocelot and ocelot-puma, where were defined as captures between different species, i.e. DIFFERENT. Time differences were also estimated in events of consecutive capture between same species, i.e. SAME, which includes ocelot-ocelot, jaguar-jaguar, and puma-puma consecutive captures per trap. Between these two categories, time differences were extrapolated for sexes, that is, male-male (MM), male-female (MF), female-male (FM) and female-female (FF). In the SAME category, FM and MF were merged due to small sample sizes of such events to carry analysis. Both DIFFERENT and SAME consisted time differences of unknown sexes but were not included in categories for sex. Unit time difference is expressed in decimals which is the sum of differences in day and time (Day:hours), when applicable.

Time differences for SAME and DIFFERENT consecutive captures were compared using two sample t-test for equal means and F-test equal variance. The following were merged into three categories: Jaguar-Ocelot and Ocelot-Jaguar, Jaguar-Puma and Puma-Jaguar, and Ocelot-Puma and Puma-ocelot, therefore order of captures was not considered when testing for equal means. The mean time differences of sex pairs within consecutive captures of different species was also compared. Equal means was tested in the SAME category between, ocelot-ocelot, jaguar-jaguar, and puma-puma consecutive captures. Means were also compared between sex pairs within the SAME category. These tests of equal means were performed using a One-way ANOVA and Tukey significant difference test when there was significant difference between groups. All samples are tested for normality using Shapiro-Wilks, and when samples are not normally distributed, the Kruskal-Wallis test for equality of medians between samples was used, and Mann-Whitney U post-hoc test when there is significant difference of medians between samples. Using the Levene's Test for equality of variance of samples, p-value <0.05 is indicative of unequal variance, then Welch test is reported instead of the ANOVA values. These tests used alpha as 0.05 for significance (p-value < 0.05) and were all performed in PAST (version 3.22, 2018). The hypothesis is that time differences between consecutive captures of sex pairs and felid pairs within the SAME and DIFFERENT categories, would not be significantly different because captures on trails occur at random suggestive of no interaction.

RESULTS

DENSITIES OF SYMPATRIC FELIDS JAGUAR (*PANTHERA ONCA*) AND OCELOT (*LEOPARDUS PARDALIS*) USING SECR

In total there were seven thousand, one hundred and seventy-five (7175) trap nights during the entire study period. Number of females, males and detections per period are summarized in (Table 1). There was a significant difference in male and female detections across the four sessions in both species (Jaguar: $t_w = 13.89$, $df = 4.05$, $p\text{-value} < 0.05$; Ocelot: $t_w = 2.70$, $df = 3.31$, $p\text{-value} < 0.05$). Jaguars had four mating events recorded with another four captures of cubs with their mothers. While ocelots recorded no mating events, however, there were three events of cubs with their mothers. Cubs were not included for any of the analysis presented here. Number of individuals captured per sex for ocelots and jaguars were significantly different, although ocelots were just marginally different (t-test = ocelots: $p\text{-value} < 0.05$; jaguars: $p\text{-value} < 0.001$). Jaguar state space used was estimated at $\sim 2,257 \text{ km}^2$ and for ocelots it was $\sim 765 \text{ km}^2$.

Figure 4 displays the order of the four seasons with their respective total rainfall. The first and last seasonal periods are categorized having low rainfall while the second and third consecutive seasonal periods are categorized as high rainfall. The distribution of detections and individuals captured per session is summarized in Table 1.

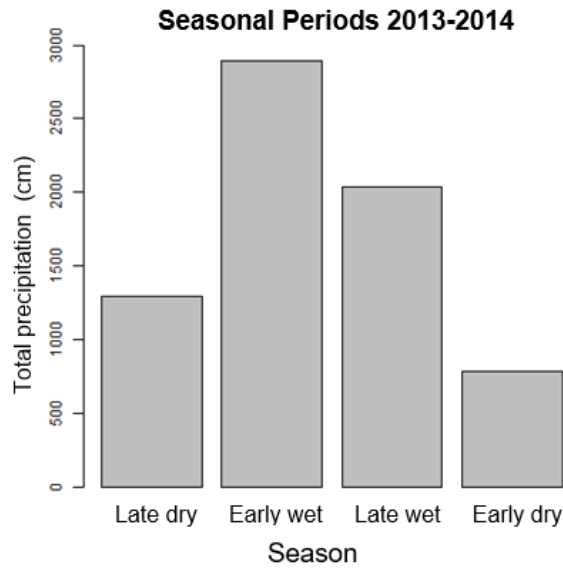


Figure 4. Barplot of the four seasonal periods showing the fluctuating rainfall (cm) recorded during the year of the survey.

Table 1. A summary of detection across four consecutive seasons for jaguars and ocelots in Cockscomb Basin Wildlife Sanctuary (CBWS), Belize. (1: Mar-Jun, 2013; 2: Jun-Sep, 2013; 3: Sep-Dec, 2013; 4: Dec, 2013-Mar, 2014).

Season	Ocelot					Jaguar				
	1	2	3	4	TOTAL	1	2	3	4	TOTAL
Occasions	89	92	90	92	363	90	92	92	92	366
Female Detections	22	16	15	18	71	7	17	22	22	68
Male Detections	26	29	35	56	146	132	146	164	127	569
Unknowns	0	0	2	6	8	0	4	0	0	4
Total Detections	48	45	52	80	225	139	167	186	149	641
Male Individuals	10	7	7	12	14	13	13	13	16	21
Female Individuals	6	7	6	7	10	3	6	7	6	12
Unknown	0	0	2	4	6	0	3	0	0	3
Total	16	14	15	23	30	16	22	20	22	36

Jaguar Density Estimation and Seasonality

The topmost competing model ($\Delta AICc$ 0) for jaguars supported constant (1) g_0 and sex variation on σ ($g_0 \sim 1$ $\sigma \sim \text{sex}$). The second competing model supported sex variation on both g_0 and σ ($\Delta AICc$ 1.26). While the third competing model supported seasonal variation on g_0 sex variation on σ in the jaguar data ($\Delta AICc$ 1.609). None of the models with additive effects (sex + season) were substantially supported ($\Delta AICc > 2$) (See Appendix I). Jaguar densities (individuals/ 100 km²) estimated from the first ranked model were 3.56, 7.13, 5.90, and 5.76, for periods 1, 2, 3 and 4, respectively. However, the other models with $\Delta AICc < 2$ although they presented a small variation in the values, were consistent with the density pattern among the different sessions (See Appendix III). Mean densities for each session estimated from the top three competing models were similar to the estimates of the topmost model (Table 2).

Table 2. Mean densities (individuals/100 km²) estimated from competing models for jaguars in CBWS, Belize.

Season	Mean	Variance	SE	L.C.I	U.C.I
1	3.56	1.36	1.17	1.28	5.84
2	7.09	3.7	1.92	3.32	10.86
3	5.87	2.86	1.69	2.55	9.18
4	5.76	2.61	1.62	2.6	8.92

The averaged sex specific densities show a significantly larger estimate for females than males (Welch: $t_w = -2.836$, $p\text{-value} < 0.05$, $df = 3.24$) (Table 3). Male densities remained constant across the year except in the last seasonal

period when density increased to 2.15 ind/ 100 km² (Table 3, Figure 5). Female increase in density after the first session where the first 30 days had zero captures of females. The highest abundance of females (N = 7) was recorded in the third seasonal period and for males this occurred in the following period (N = 16). The Spearman rank correlation test between overall density and precipitation was not significant, therefore, there was no relation between changes in density and fluctuations in precipitation in each season (Spearman: p-value >0.05).

Table 3. Mean sex specific density (individuals/100 km²) estimates of jaguar with confidence intervals and standard errors estimated from the top competing models.

Season	Female				Male			
	D	SE.est	low.CI	upper.CI	D	SE.est	low.CI	upper.CI
1	1.8	1.05	0.62	5.23	1.76	0.5	1.02	3.05
2	3.54	1.5	1.6	7.8	1.74	0.5	1.01	2.9
3	4.11	1.57	1.96	8.61	1.7	0.49	1.06	2.97
4	3.6	1.51	1.61	7.95	2.15	0.55	1.32	3.55

The third most supported model supported seasonal variation on $g0$ and variation on σ with sex (See Appendix I 2a). However, the spearman rank correlation test was not significant in either pairs, that is, male and female density and seasonality (Spearman: p-value > 0.05).

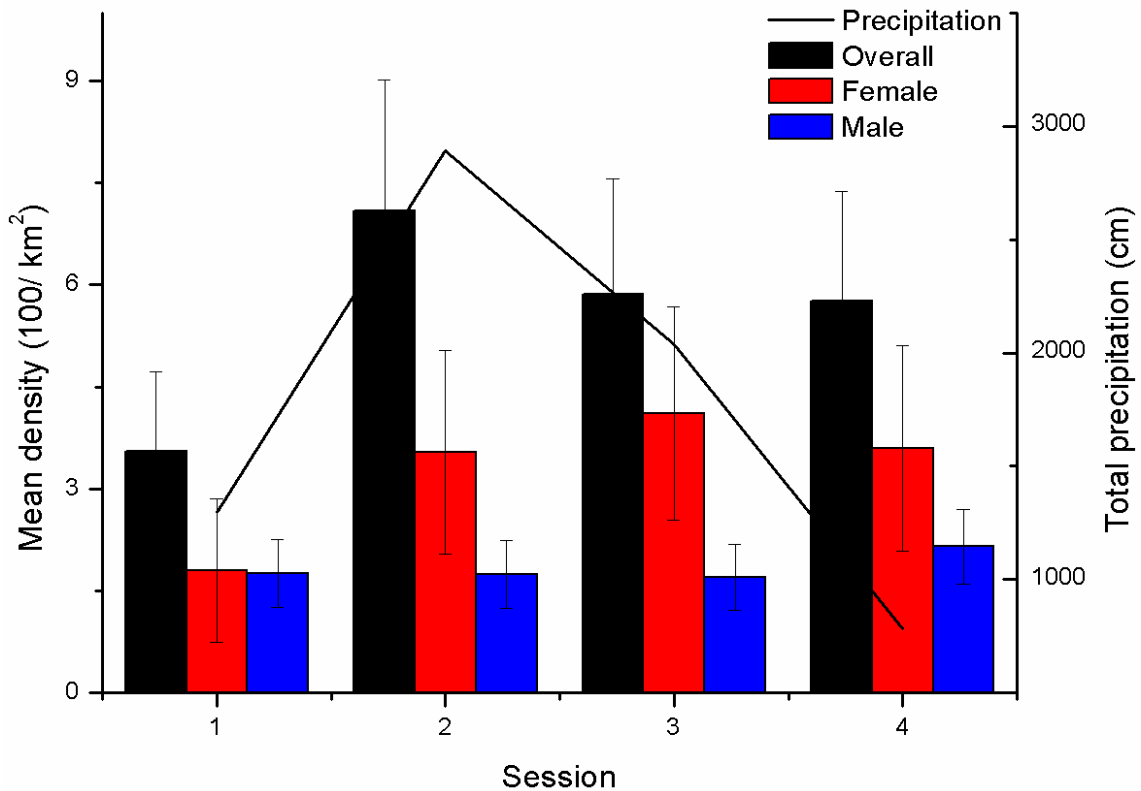


Figure 5: Mean overall and sex specific densities (individuals/100km²) for jaguars with standard errors estimated from the candidate model average using MLE for each seasonal period.

Jaguar Detection Probability and Spatial Parameter

Regarding the detection parameter, the first ranked model supported a constant $g0$ (0.05, SE = 0.52, 95% CI = 0.04-0.06) but the spatial parameter, σ , varied with sex (Female: 980.9 m; Male: 3555.3 m) (Figure 6). While the second competing model both parameters, $g0$ and σ , varied with sex. Therefore, the parameter $g0$ was not significant as a single effect when compared to the spatial parameter σ . Female $g0$ was 0.043 (SE = 0.56, 95% CI = 0.02-0.07) and male $g0$ was 0.056 (SE = 0.63, 95% CI = 0.21-0.14) (Figure 7). Both figures (6 and 7) display the difference in distance by sex where female movement is more restricted than males. Female movement away from the activity centre can reach

a maximum of ~3 km while males were detected up to a maximum of ~10 km away from their activity, indicating female home ranges to be smaller in size. The third competing model indicated variation with season on $g0$ only while σ varied with sex (Figures 8) which suggested a negative effect on $g0$ and sigma with decreased precipitation (Table 4). There was substantial support in these three models for differences on σ with sex, with females having smaller or more restricted activity centres (Table 4).

Table 4. Back transformed estimates of parameters ($g0$ and σ) for jaguar's competing models. Male (M) and female (F) estimates of parameters are provided when the model supported sex differences (σ = meters). Design of fitted models are available in Appendix 1.

Model	Parameters	Estimate	SE	LCI	UCI
FIT1	$g0$	0.055	0.521	0.047	0.064
	F. σ	980.87	1.09	827.69	1162.40
	M. σ	3555.30	1.20	2494.25	5067.71
FIT2	F. $g0$	0.043	0.565	0.026	0.070
	M. $g0$	0.057	0.631	0.021	0.146
	F. σ	1047.95	1.12	840.85	1306.06
	M. σ	3544.60	1.26	2248.04	5588.93
FIT3	High. $g0$	0.058	0.527	0.048	0.071
	Low. $g0$	0.051	0.566	0.031	0.084
	F. σ	986.76	1.09	829.29	1174.14
	M. σ	3565.06	1.20	2482.47	5119.77

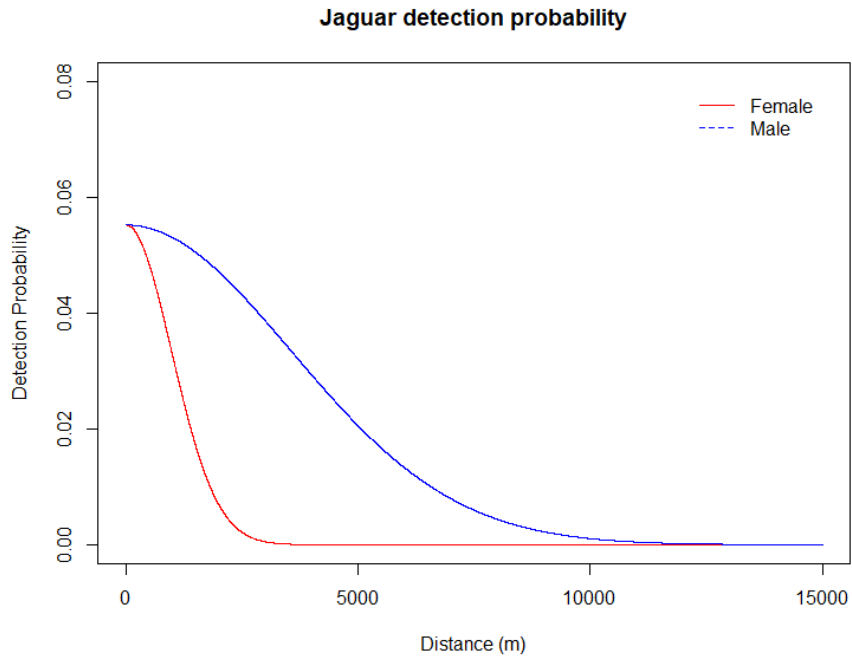


Figure 6. Jaguar sex specific detection probability as a function of distance estimated with first competing model, Fit 1 ($g_0 \sim 1$ $\sigma \sim \text{sex}$).

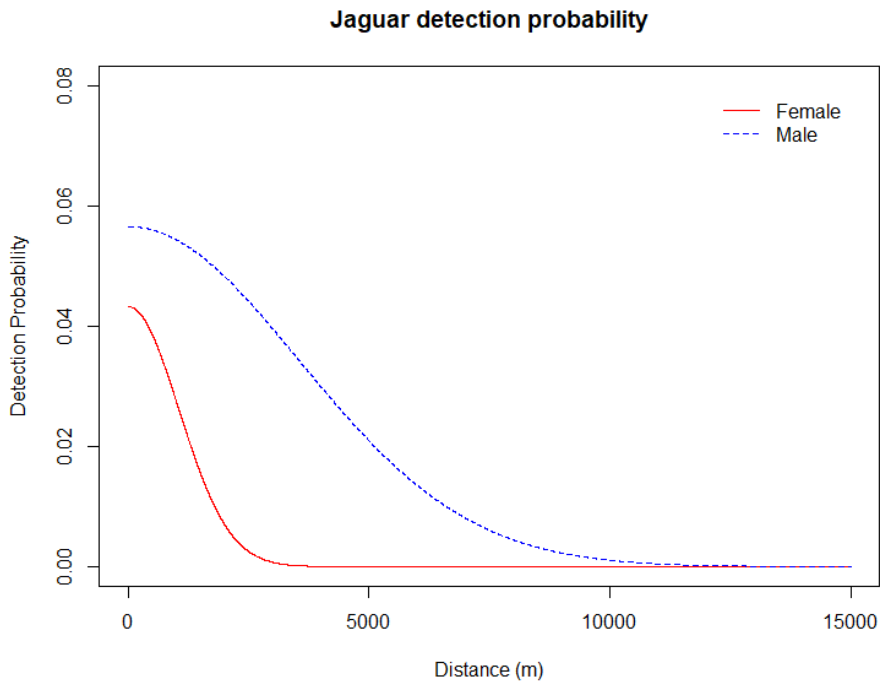


Figure 7. Jaguar sex specific detection probability as a function of distance as estimated with second competing model, Fit 2 ($g_0 \sim \text{sex}$ $\sigma \sim \text{sex}$).

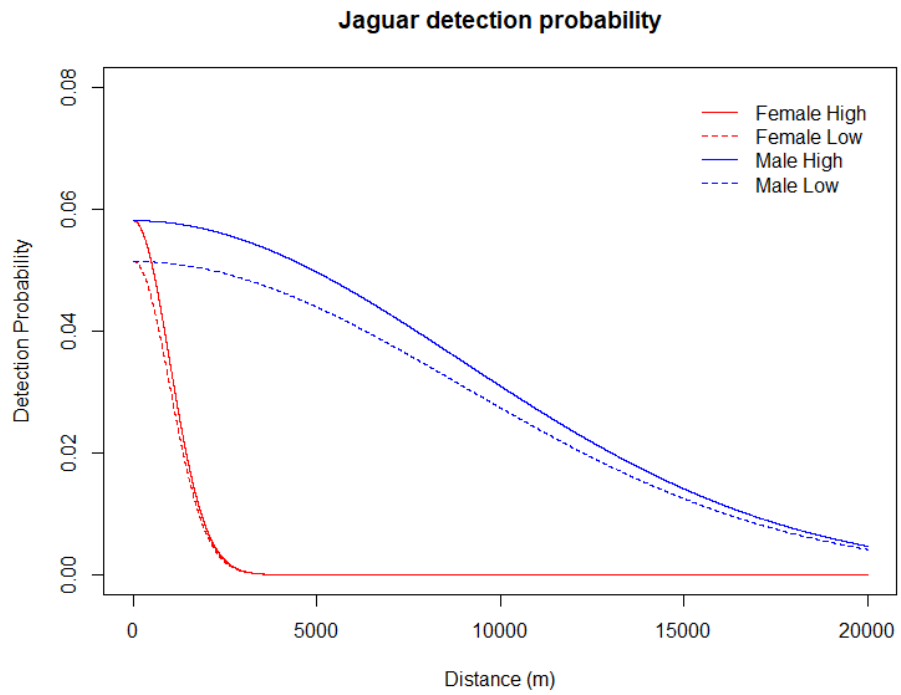


Figure 8. Jaguar sex specific detection probability as a function of distance estimated from the third competing model, Fit 3 ($g_0 \sim \text{season}$ $\sigma \sim \text{sex}$).

Ocelot density Estimation and Seasonality

There were only two competing models with the ocelot data, that is, $\Delta AIC < 2$. The first ranked model substantially supported sex variation on both parameters, $g0$ and the σ . While the second ranked model supported $g0$ as constant and σ varied with sex (See Appendix I). See Appendix II for density estimates for competing models with $\Delta AICc < 2$. Mean overall ocelot densities, estimated using both *competing* models, were between 6.82 ind/100 km² (95% CI: 3.01 - 10.63) to 11.16 ind/100 km² (95% CI: 6.25 - 16.08) (Table 5). Mean densities fluctuated between of 7.31 and 7.46 ind/100 km², with an increase in the last seasonal period to 11.20 ind/100 km², as estimated by the first ranked model ($g0 \sim \text{sex}$ $\sigma \sim \text{sex}$).

Table 5. Mean densities (individuals/100 km²) estimated from competing models for ocelots in CBWS, Belize.

Season	Mean	Variance	SE	L.C.I	U.C.I
1	7.34	3.81	1.95	3.52	11.17
2	6.82	3.78	1.94	3.01	10.63
3	7.44	4.29	2.07	3.38	11.5
4	11.16	6.3	2.51	6.25	16.08

Table 6. Mean sex specific density (individuals/100 km²) estimates of ocelots with confidence intervals and standard errors estimated from the top competing models.

Season	Female				Male			
	D	SE.est	low.CI	upper.CI	D	SE.est	low.CI	upper.CI
1	3.72	1.5	1.7	8.2	3.63	1.2	1.9	6.7
2	4.3	1.7	2.1	8.9	2.52	0.9	1.2	5.2
3	3.69	1.5	1.7	8.1	2.5	0.9	1.2	5.26
4	4.35	1.7	2.1	9.1	4.33	1.3	2.4	7.7

In contrast to jaguars, sex specific estimates of ocelots show narrower differences between male and female estimates (Table 6). In fact, the differences between male and female ocelots was not significant (Welch: p-value > 0.05, df = 3.70). Male ocelot densities were highest in the first and last session when precipitation was low. Similar to female jaguars, female ocelots displayed a similar pattern to the fluctuating precipitation except in the last session when density increased when rainfall was lowest producing the highest density in the last session (Figure 9). Both sexes presented wider confidence intervals due to the small sample size when compared to jaguar captures in the current study (Table 1). Spearman rank correlation for both overall (p-value > 0.05) and sex specific mean densities (p-value > 0.05) showed no relationship with seasonality due to rainfall changes.

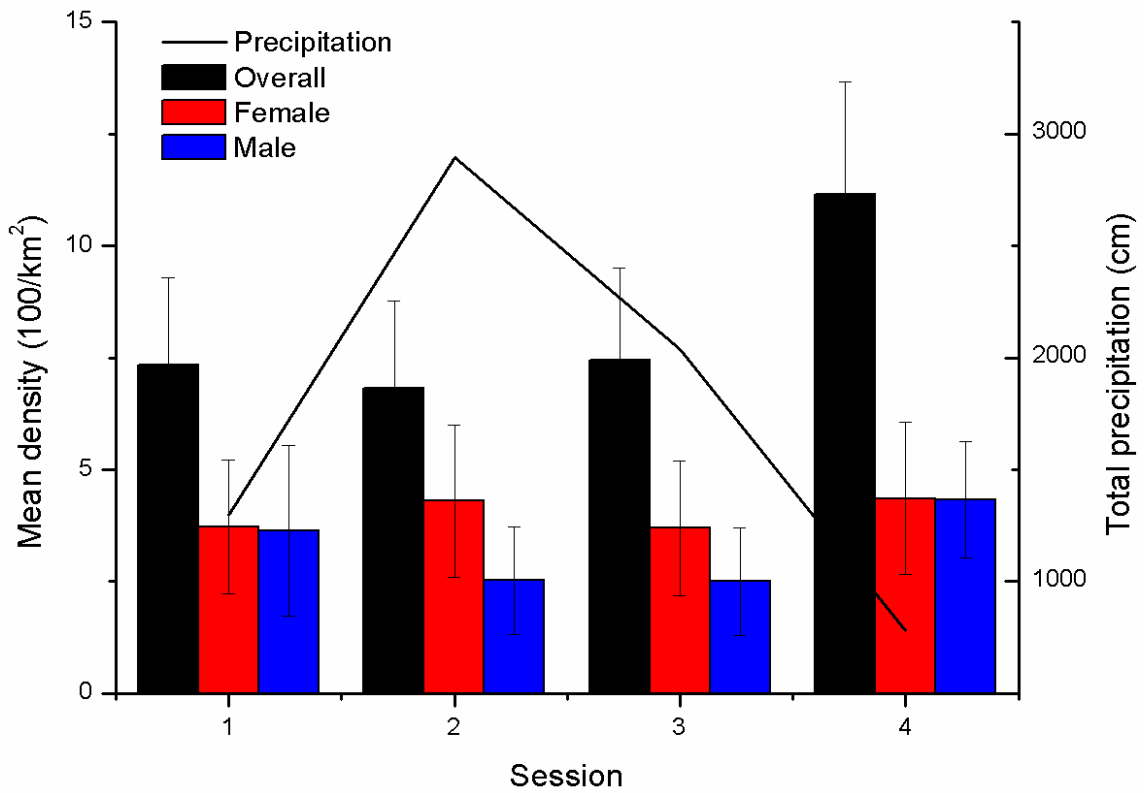


Figure 9. Mean overall and sex specific densities (individuals/ 100km²) for ocelots with standard errors estimated from the candidate model average using MLE for each session.

Ocelot Detection Probability and Spatial Parameter

According to the first ranked model, ocelot's detection and spatial parameter, $g0$ and σ , varied with sex. Figure 10 shows the sex specific detection probability changing over the distance moved away from their activity centres, derived with the first ranked model ($g0 \sim \text{sex}$ $\sigma \sim \text{sex}$, $\Delta\text{AICc} < 2$). Female detection (0.022, SE = 0.55, 95% CI = 0.015-0.034) was lower than males detection (0.036, SE = 0.62, 95% CI = 0.014-0.087) at their activity centre, similar to the second most supported model for the jaguar data (Table 7). Both male and female ocelots had an estimated lower $g0$ when compared to jaguars. The ocelot data also supported a second model, ($g0 \sim 1$, $\sigma \sim \text{sex}$, $\Delta\text{AICc} < 2$), therefore there was only one detection probability estimate for both males and females while this probability varied with sex, as they away from the activity centre (0.030, SE = 0.53, 95% CI = 0.024-0.039; Figure 11).

Table 7: Back transformed estimates of parameters ($g0$ and σ) for ocelot competing models. Male (M) and female (F) estimates are provided when the model supported sex differences of parameters ($\sigma = \text{meters}$). Design of fitted models are available in Appendix 1.

Model	Parameters	Estimate	SE	LCI	UCI
FIT1	F.g0	0.022	0.55	0.015	0.034
	M.g0	0.036	0.62	0.014	0.087
	F. σ	1218.84	1.10	1009.24	1471.97
	M. σ	1675.09	1.24	1083.22	2590.38
FIT2	g0	0.030	0.53	0.024	0.039
	F. σ	1,111.42	1.08	958.77	1288.38
	M. σ	1758.99	1.19	1255.46	2464.47

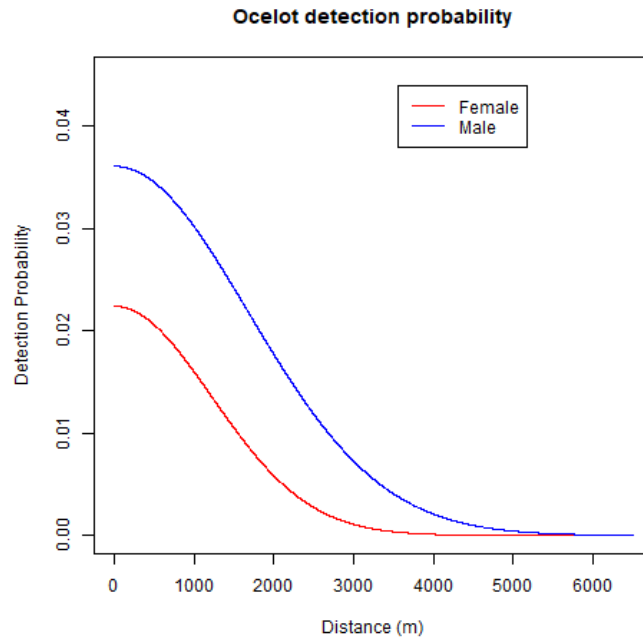


Figure 10. Ocelot sex specific detection probability as a function of distance estimated with the first ranked model, Fit 1 ($g0 \sim \text{sex}$ sigma $\sim \text{sex}$).

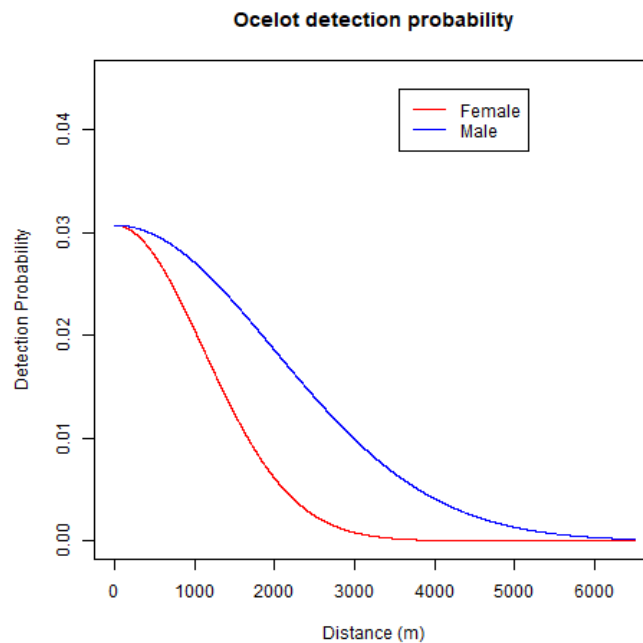


Figure 11: Ocelot detection probability as a function of distance from activity centre estimated with the second ranked model ($g0 \sim 1$ sigma $\sim \text{sex}$).

The data supports female detection probability for both sympatric species, jaguars and ocelots, decreases faster as they move away from their activity centre when compared to males. Models did not show clarity with the effect of seasonality on both detection and sigma. However, we did observe that density estimates in female jaguars varied across the seasonal periods within the year. In general, ocelot densities were higher than jaguar density estimates, and the range of estimates were more precise for male jaguar and female ocelots (Figure 12).

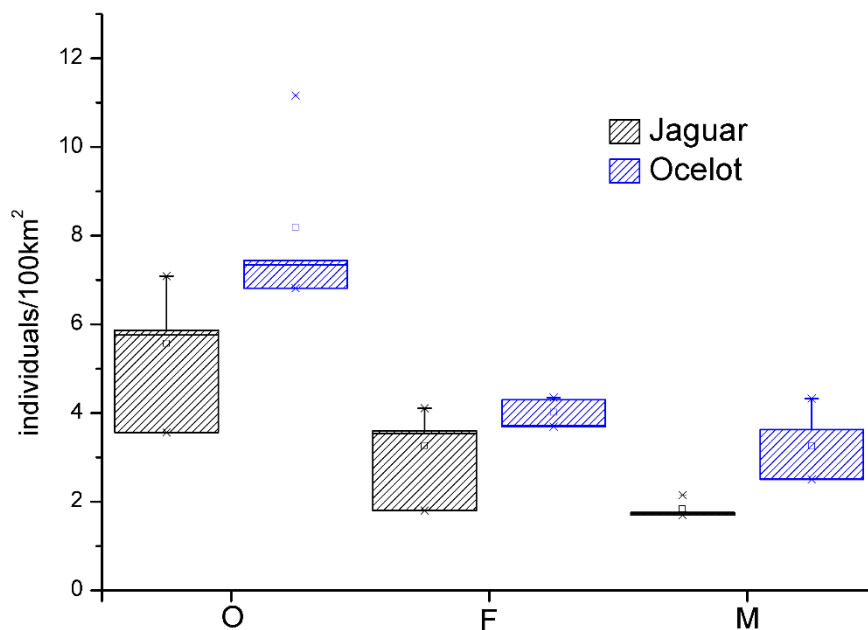


Figure 12. Boxplot comparing density estimates (O = Overall, F = Female, M = Male) for both jaguar and ocelots overall estimates and sex specific. These are mean estimates using competing model for each session.

Male only Models: Detection, Spatial Parameter and Season

Male only models used season as a covariate, as a result the top model for both species supported constant variation on $g0$ and sigma (See Appendix II). The AIC model selection test supported, for both, a second model ($\Delta AIC < 2$) in which it supported variation with season on $g0$ for male jaguars and σ for male

ocelots. For both species, the values estimated for the detection and spatial parameters were similar to those estimated using the full dataset (Table 8). The second ranked model for jaguar males, indicated $g0$ varied with season, with a higher detection probability in high rainfall season and lower detection in low rainfall season. The full data for ocelots, the first ranked model indicated male ocelot $g0$ was 0.036 (SE = 0.62, 95% CI = 0.014-0.087). Ocelot male only data's first ranked model where both parameters were constant, $g0$ estimate was 0.031 (SE = 0.53, 95% CI = 0.023-0.041) and sigma ~1.66 km (SE = 1.07, 95% CI = 1438.90-1914.94 m). The second substantially supported model for ocelots, suggested σ to be larger in high rainfall than lower rainfall season (Table 8).

Table 8. First and second ranked models. Back-transformed parameters, $g0$ and σ for jaguar and ocelot. S indicates when the parameter values correspond to high (H) and low (L) seasonal rainfall.

Males	Model	S	$g0$	SE	95% CI	S	σ (m)	SE	95% CI
Jaguar	$g0 \sim 1 \sigma \sim 1$	-	0.057	0.52	0.048-0.067	-	3543.8	1.04	3259.6-3852.9
	$g0 \sim \text{season}$				0.049-				3270.3-
	$\sigma \sim 1$	g0H	0.061	0.52	0.076	-	3559.2	1.04	3873.7
		g0L	0.052	0.48	0.030-0.086	-	-	-	-
Ocelot	$g0 \sim 1 \sigma \sim 1$	-	0.031	0.53	0.023-0.041	-	1656.4	1.07	1438.9-1914.9
	$g0 \sim 1$				0.024-				1436.7-
	$\sigma \sim \text{season}$	-	0.031	0.53	0.041	σ H	1742.6	1.1	2113.6
		-	-	-	-	σ L	1589.2	1.24	1027.1-2459.1

ACTIVITY PATTERN AND COEXISTENCE OF THREE SYMPATRIC FELIDS

The independent captures, including individuals with unknown sex, described for each seasonal period: late dry season, early wet season, late wet season, and early dry season were used to evaluate activity pattern. Table 9 summarizes the captures for each period for each species that will be referred to in this analysis. However, to examine females and male activity pattern, females were pooled to apply the method, therefore this resulted in 40 and 28 for jaguars, 32 and 39 for ocelots, and 16 and 13 for pumas in high and low seasons respectively. Overall, jaguars, pumas and ocelots species were primarily nocturnal-crepuscular in their activity pattern throughout the year.

Table 9: Summary of independent captures of sympatric felids used to evaluate activity pattern.

Session	Ocelot	Jaguar	Puma
1	48	139	131
4	80	144	93
2	46	162	124
3	54	190	133

Sample size between male and females among species were significantly different (p -value < 0.05) thus comparison between sexes within each species was excluded, female captures were pooled into high and low seasons for comparison. Female activity pattern between high and low rainfall for all three cat species suggested similar activity patterns between seasons with overlap estimated greater than 80% (Figures 13-14). Female jaguars and pumas displayed cathemeral activity, with increased activity in crepuscular hours, while female ocelot's activity decreased to zero during daylight hours. The lowest overlap estimate was for pumas at 68% due to high oscillation of activity in high

rainfall (Figure 15). However, using the large portion of the sample (Figure 16, N = 211) with unknown sex, a coefficient of overlap was above 80%. Increased diurnal activity of pumas was observed in low rainfall using puma unknown sex sample, a pattern observed in late dry season (Figures 18 and 19).

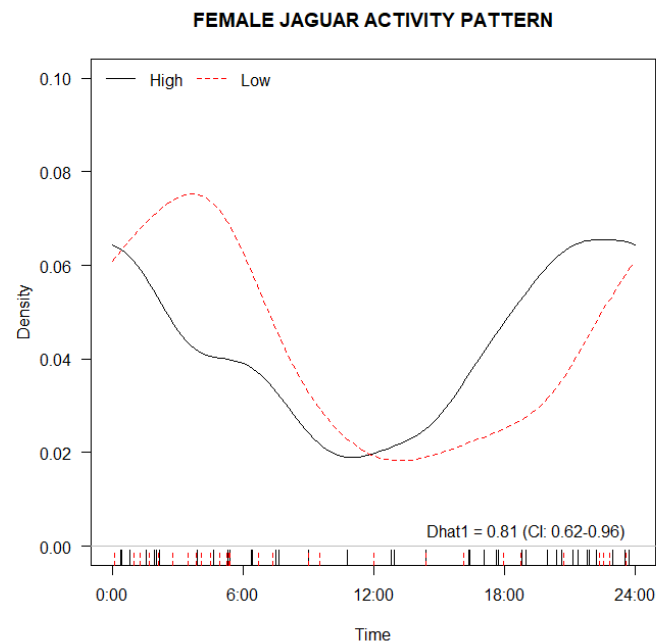


Figure 13: Female jaguar activity pattern in CBWS compared between high and low seasons.

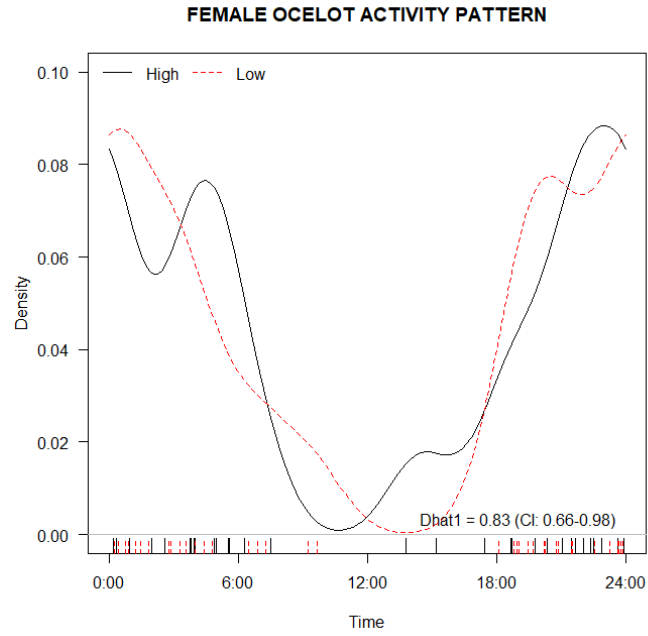


Figure 14: Female ocelot activity pattern in CBWS compared between high and low seasons.

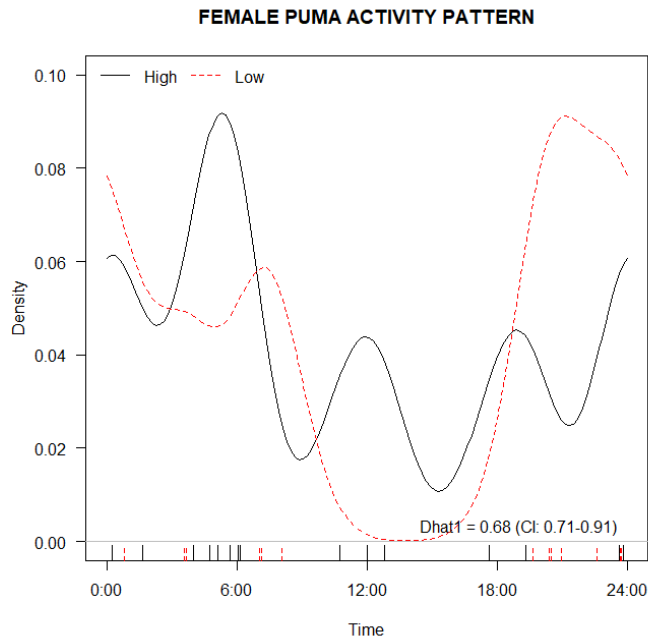


Figure 15: Female puma activity pattern in CBWS compared for high and low seasons.

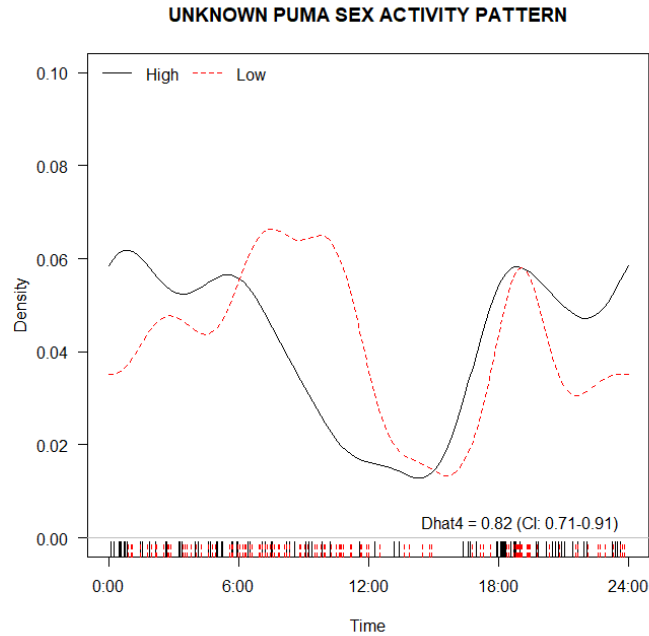


Figure 16: Activity pattern of pumas of unknown sex in CBWS compared between high and low seasons.

Table 10. Percent overlap (95% CI) for each felid species pair between wet and dry season in CBWS, Belize.

Pairs	% OVERLAP (95% CI)	
	Wet	Dry
Jag-Oce	71 (57-84)	86 (74-96)
	85 (72-95)	88 (77-96)
Oce-Pum	79 (66-91)	91 (79-100)
	80 (65-92)	66 (54-77)
Pum-Jag	86 (76-94)	88 (78-97)
	88 (78-96)	70 (60-79)

Felid Pairs Overlap

Felid pairs, jaguar-ocelot, puma-jaguar and ocelot-puma shared considerable overlap temporally. All three exhibited nocturnal-crepuscular patterns, but could be active during day-light hours at lower frequencies. There was no association related to activity patterns overlap and seasonality between any felid species pairs ($\chi^2 = 5.1504$, $df = 6$, $p\text{-value} > 0.05$).

Jaguar and ocelot overlap ranged between 71% - 88% in which the lowest overlap was recorded in the early wet season (Figure 17). Puma and jaguar temporal activity overlap 70% - 88%, with the lowest happening in the late dry season (Figure 18). Ocelot and puma activity overlap ranged between 66% - 91%, the lowest and highest percentages of temporal overlap between the three pairs (Figure 19).

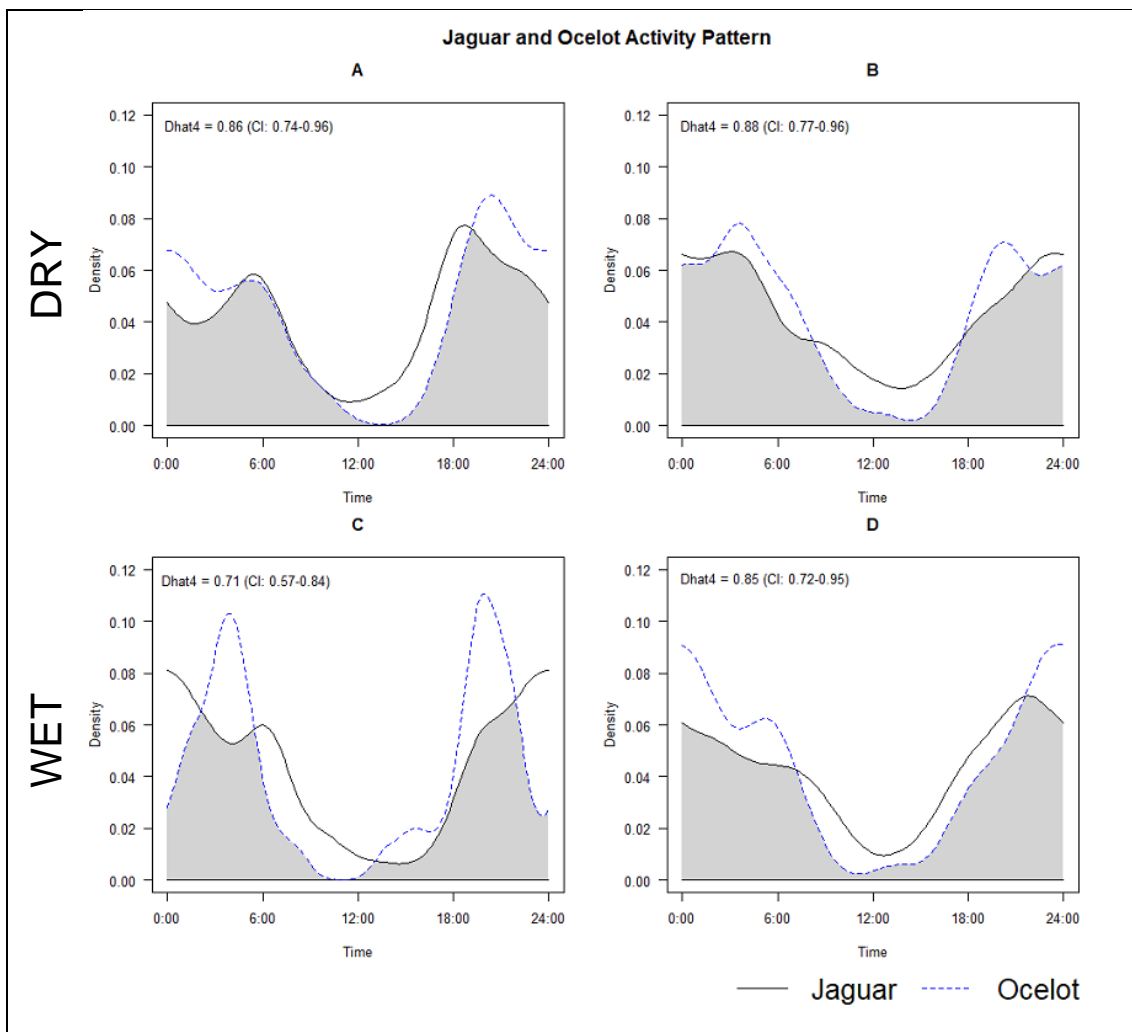


Figure 17: Activity of jaguars and ocelots across the survey presented into seasonal periods for dry (A and B) and wet (C and D) seasons.

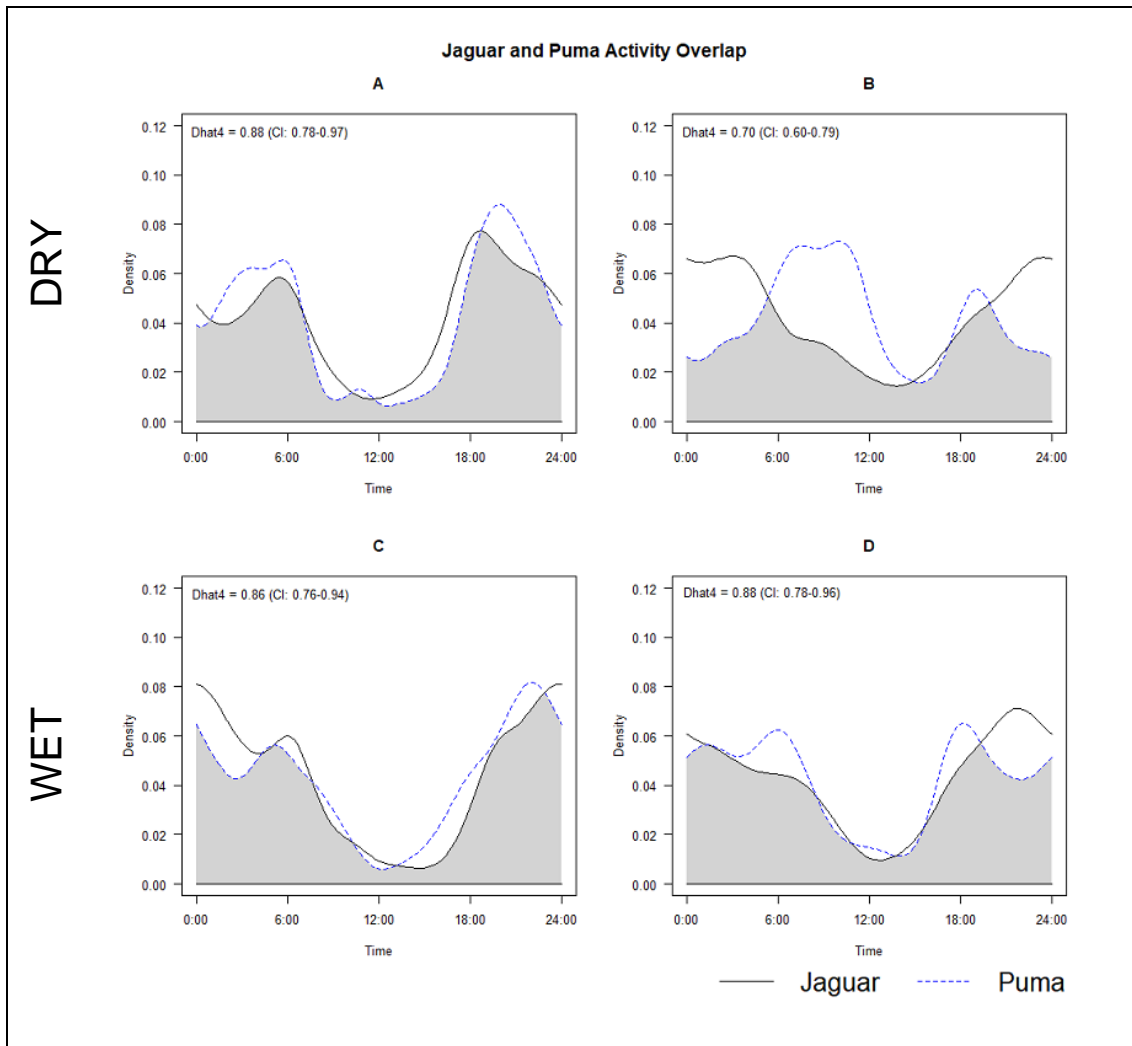


Figure 18. Jaguar and puma activity patterns across the survey presented seasonal periods of dry (A and B) and wet (C and D) season rainfall.

Jaguar and puma and ocelot and puma least overlap occurred in fourth seasonal period, the period of early dry season, plots B in all overlap figures. This period showed that pumas' temporal activity was mostly diurnal in comparison to the other two felids. However, between these three felid species there is little to no temporal activity segregation.

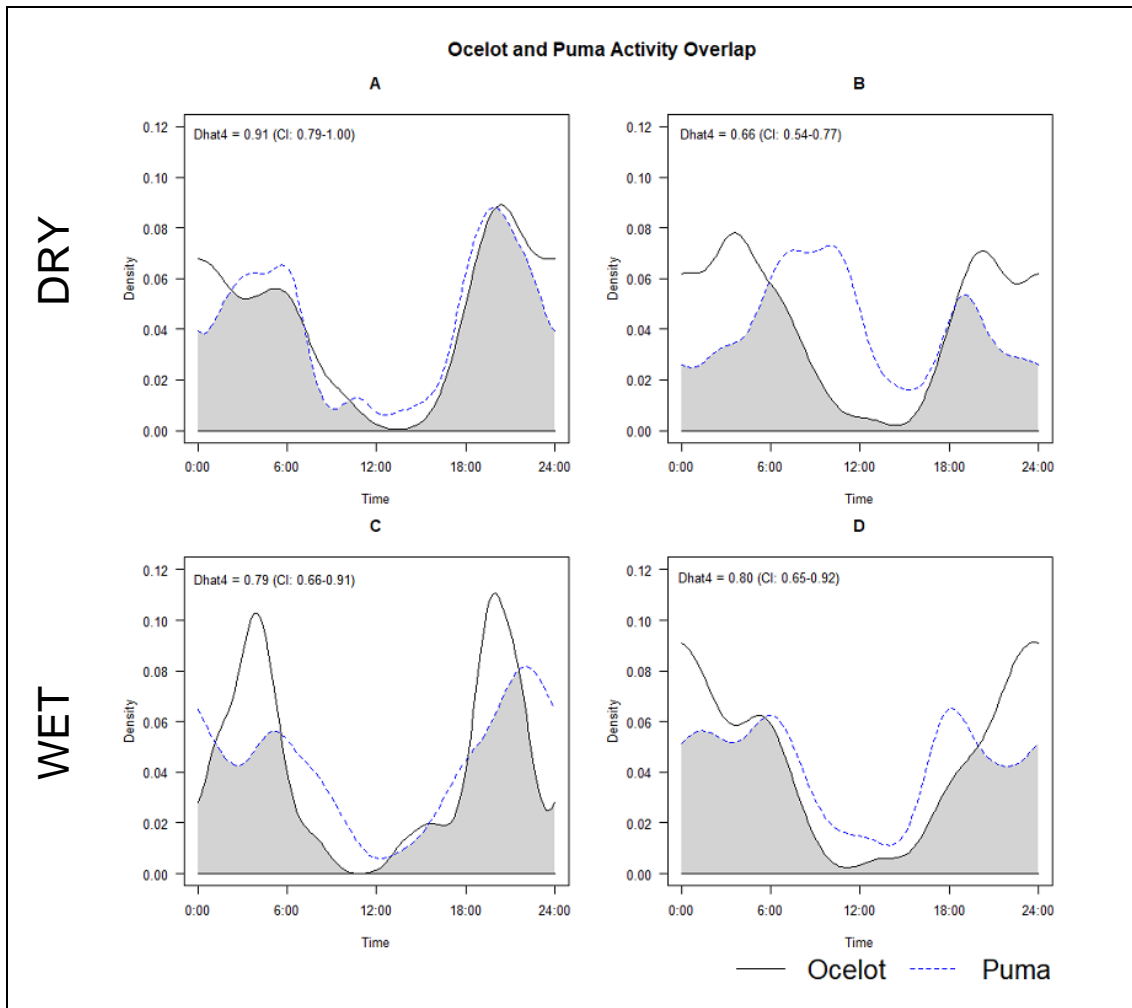


Figure 19: Ocelot and puma activity patterns across the survey presented into seasonal periods of dry (A and B) and wet (C and D) season.

Spatial-temporal Interaction: Felid pairs and Season

Maximum traps used in the low season were 19, 16 and 19 and in high season were 18, 17, and 19 for puma, ocelot and jaguar, respectively. Table 11 summarizes the frequency of events in which pairs were found sharing a trap in a 48-hour interval. The two-way ANOVA indicated a significant effect between pairs (p -value < 0.05 , $df = 6$, $F = 4.811$) and also indicated that seasonality was not a significant effect on the frequencies (p -value > 0.05 , $df = 1$, $F = 0.08$). Therefore, the significant effect variable between felid pair groups was further investigated, which indicated a difference in mean frequency of events on traps

shared by pairs between Puma – Ocelot (PO) and Jaguar – Puma (JP) (Figure 20).

Table 11: Frequency of events in which pairs were recorded on the same trap within 48-hrs interval in CBWS, Belize.

Frequency of events		
Pairs	H-Rainfall	L-Rainfall
Jag-Oce	17	22
Jag-Pum	40	32
Pum-Oce	8	7

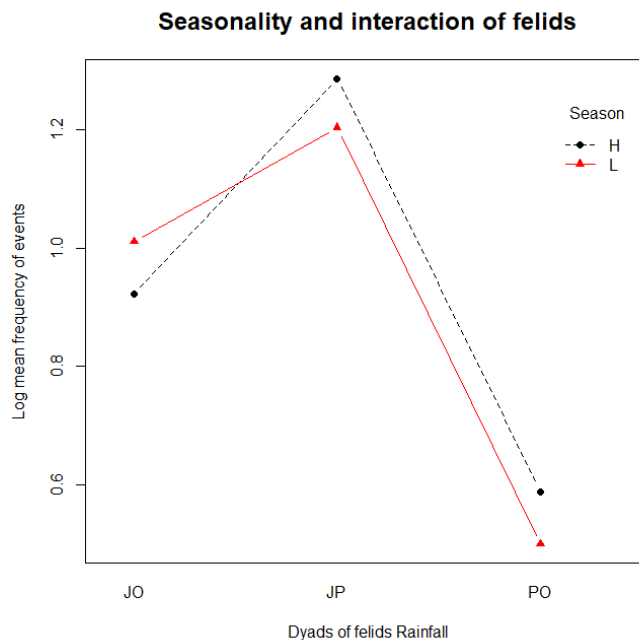


Figure 20: Interaction effects plot of mean frequency of events of pairs and seasonal (H= High, L=Low) rainfall. Pairs: JO (Jag-Oce); JP (Jag-Pum); PO (Pum-Oce).

The Tukey Honest Significance Difference (HSD) indicated that Puma-Ocelot pair mean frequency was significantly different to Jaguar-Puma and Jaguar-Ocelot but not between the latter two pairs (Figure 21). The Tukey DSH results also show the interaction model of multiple comparisons of pairs across

seasons. Season was omitted from further analysis since it was not a significant variable to explain interaction.

Consequently, the time differences between consecutive captures between felid pairs were estimated trap and are presented on Figure 22. One trap (6) was used only by pumas and another (9) was used by jaguars and ocelots only. Traps used with similar frequencies by all three felid species show a shorter time difference between consecutive captures.

```
Tukey multiple comparisons of means
95% family-wise confidence level

Fit: aov(formula = DF.LOG$log.freq ~ DF.LOG$Pairs +
DF.LOG$Season + DF.LOG$Pairs:DF.LOG$Season)

$`DF.LOG$Pairs`
      diff          lwr          upr      p adj
JO-PO 0.4537837  0.07965664 0.8279108 0.0229414*
JP-PO 0.7248639  0.35073686 1.0989910 0.0024520**
JP-JO 0.2710802 -0.10304684 0.6452073 0.1453307

$`DF.LOG$Pairs:DF.LOG$Season`
      diff          lwr          upr      p adj
PO:H-PO:L 0.13650064 -0.549787155 0.8227884 0.9590716
JO:H-PO:L 0.47100403 -0.215283765 1.1572918 0.1980507
JO:L-PO:L 0.57306402 -0.113223773 1.2593518 0.1020978
JP:L-PO:L 0.76573946  0.079451667 1.4520272 0.0310345*
JP:H-PO:L 0.82048903  0.134201237 1.5067768 0.0226373*
JO:H-PO:H 0.33450339 -0.351784401 1.0207912 0.4608359
JO:L-PO:H 0.43656338 -0.249724409 1.1228512 0.2472876
JP:L-PO:H 0.62923882 -0.057048969 1.3155266 0.0713331
JP:H-PO:H 0.68398839 -0.002299399 1.3702762 0.0507112
JO:L-JO:H 0.10205999 -0.584227800 0.7883478 0.9878162
JP:L-JO:H 0.29473543 -0.391552359 0.9810232 0.5707528
JP:H-JO:H 0.34948500 -0.336802789 1.0357728 0.4228786
JP:L-JO:L 0.19267544 -0.493612351 0.8789632 0.8586221
JP:H-JO:L 0.24742501 -0.438862780 0.9337128 0.7105091
JP:H-JP:L 0.05474957 -0.631538221 0.7410374 0.9993144
```

Figure 21. Tukey test results used to comparing pairs, which was the most significant variable of the interaction model. Significance is indicated for p-value <0.05.

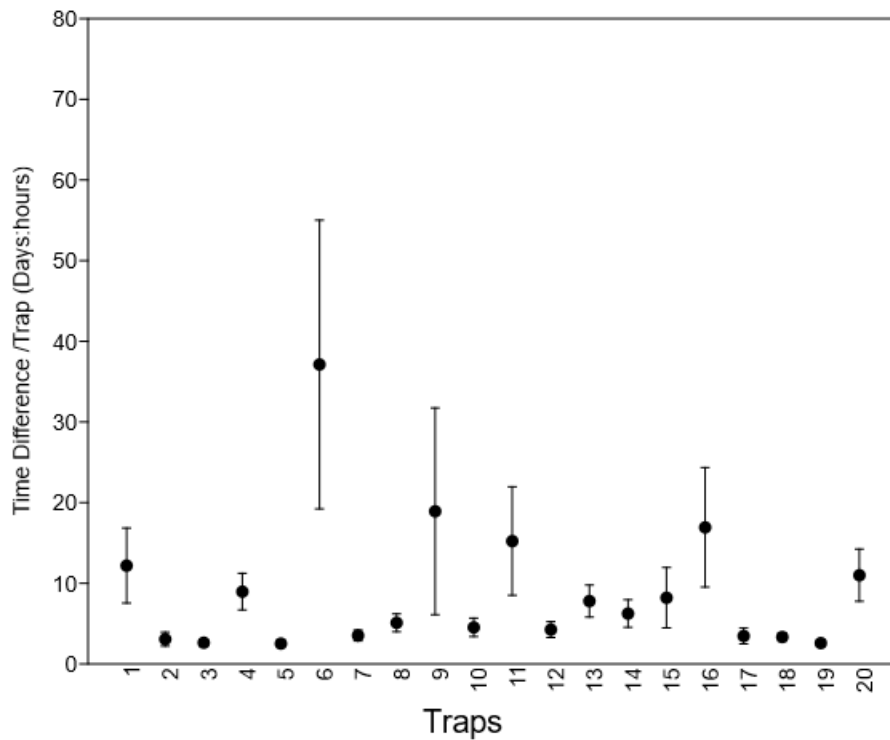


Figure 22. Mean time differences and (95%) CI between consecutive captures per trap throughout the year.

Overall mean time differences between consecutive captures per trap of SAME (i.e. same species consecutive capture) (Mean = 4.66, 95% CI = 4.07-5.25) and DIFFERENT (i.e. different species consecutive captures) (Mean = 5.26; 95% CI = 4.7-5.83) pairs were not significantly (p -value > 0.05; Figure 23). The one way ANOVA used to compare time differences between the three groups, Jaguar - Puma, Jaguar - Ocelot, and Puma - Ocelot, indicated significant differences between groups (p -value < 0.05, $df = 2$, $F = 4.029$) and the Tukey Test indicated a significant difference between Jaguar - Puma and Puma-Ocelot pairs (p -value < 0.05; Figure 24). Jaguar - Puma species pair (p -value > 0.05, mean = 4.776 days, 0.95 CI = 4.1699 - 5.3821) and Jaguar - Ocelot (p -value > 0.05, mean = 4.938 days, 0.95 CI = 3.8267-6.0504) pairs were not significantly different

however, Puma - Ocelot difference between captures were significant (p-value <0.05, mean = 7.0453 days, 0.95 CI = 5.04 – 9.0507) (Figure 24).

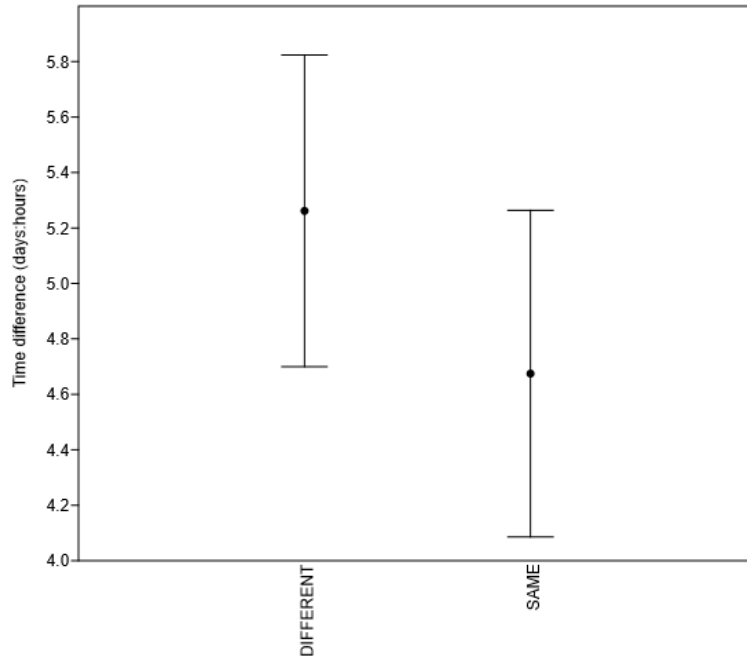


Figure 23. Comparison of Different and Same pairs of species' time difference between consecutive capture per trap across the year.

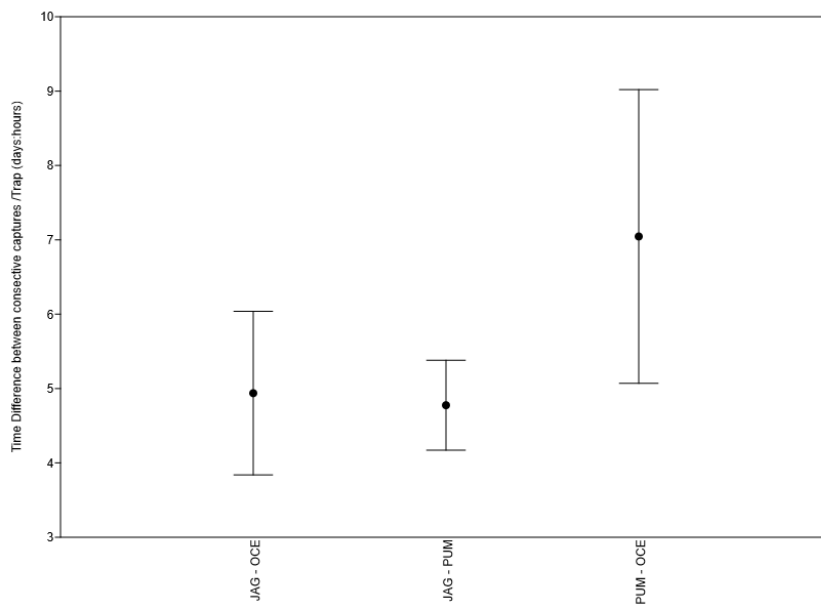


Figure 24. Time difference per trap between unlike pairs of species.

In the “Same” category, species consecutive time difference between captures of sex pairs were compared. The FF sample was not normally distributed (N = 25) therefore the Kruskal-Wallis test and Mann-Whitney post hoc tests were used. The Kruskal-Wallis test indicated unequal medians between samples (p-value < 0.05; Hc = 9.42). The Mann-Whitney U test indicated a significant difference between FM and MM consecutive captures (p-value < 0.05; Figure 25). However, mean differences between same species consecutive captures was not significantly different between groups, (p-value > 0.05; df = 2; F = 2.243; Figure 26), although between ocelot captures time differences tend to be in longer periods than between jaguars and between pumas.

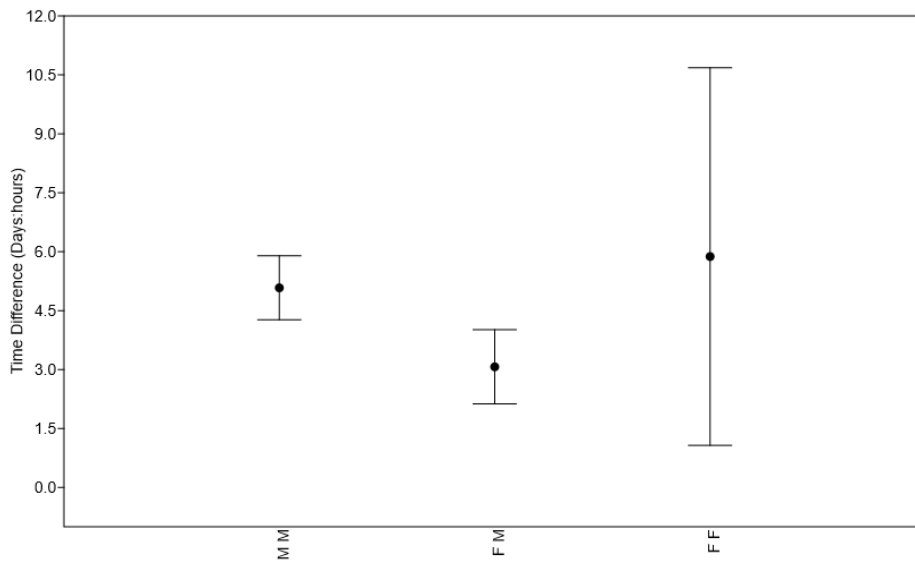


Figure 25. Time differences between sex pairs within consecutive captures between same pairs.

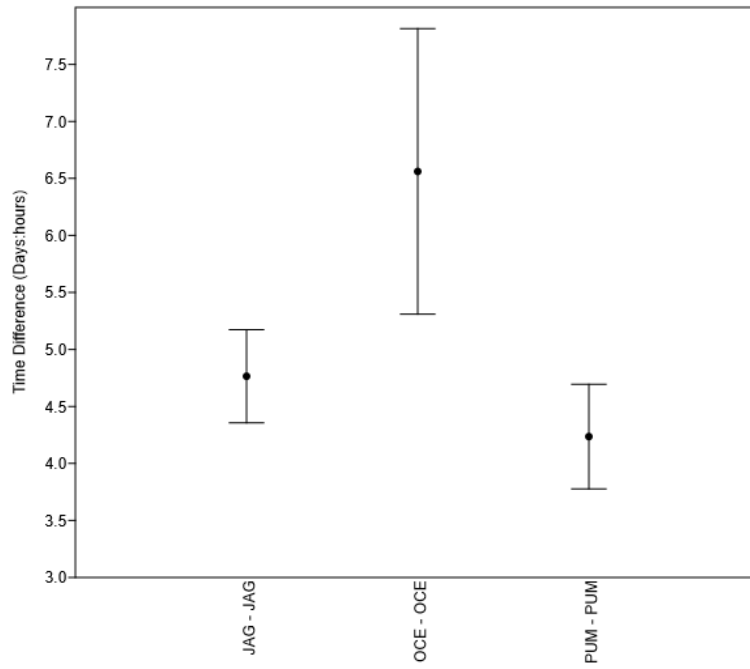


Figure 26. Time difference between consecutive captures per trap for same species pairs across the year.

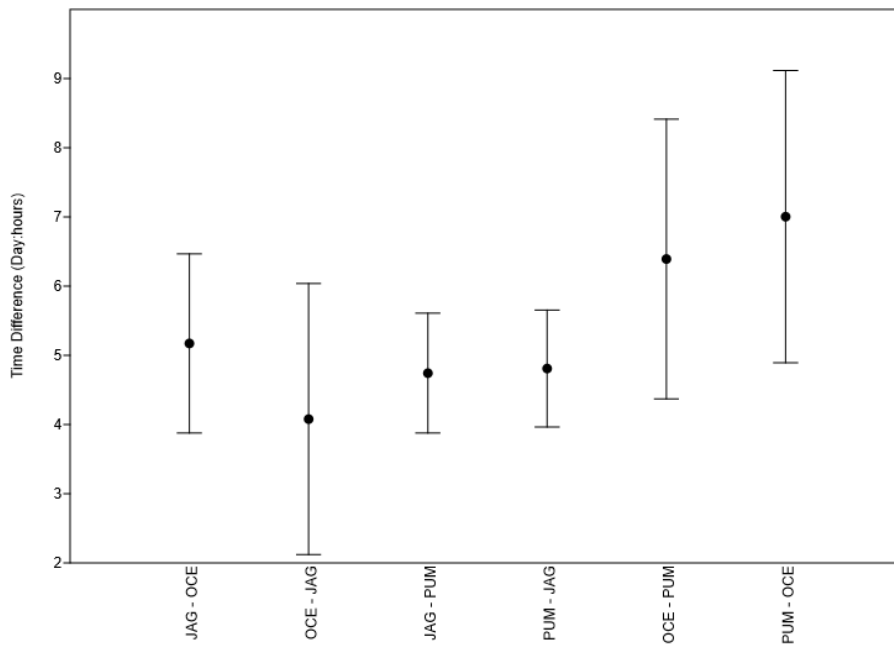


Figure 27. Comparison of time differences between consecutive captures per trap for each pair of felid species.

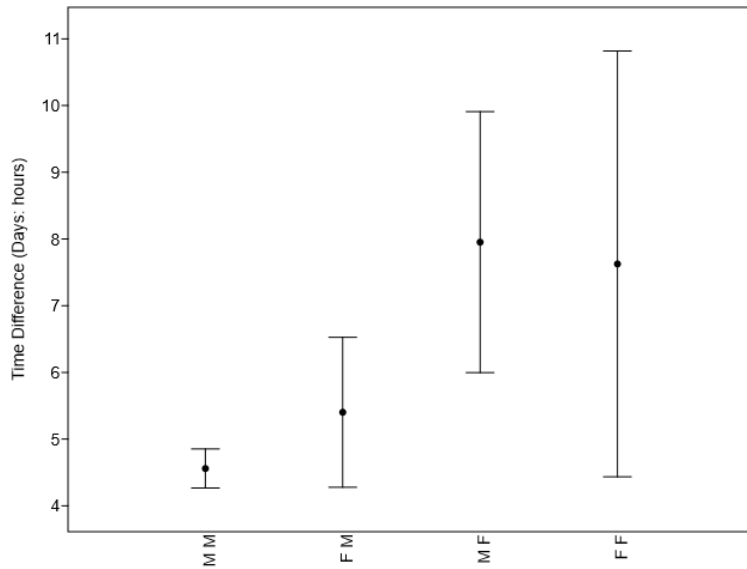


Figure 28. Overall time difference between sex pairs of consecutive captures of different species of felids, per trap in CBWS, Belize.

The one way ANOVA test indicated that mean time difference between consecutive felid captures of different species were not significant between groups or within groups (Figure 27). The Levene's test for equality of variance was significant (p -values < 0.05) for sex pairs, therefore the Welch F test was used, $F = 1.323$, $df = 151.1$, p -value > 0.05). The comparison between groups of sex pairs within different felid species was significant between groups of different species (p -value < 0.05 ; $F = 3.504$, $df = 3$; Figure 28). The time differences used for each felid pair are on Table 12. The post-hoc Tukey test indicated MM and MF sex pairs within different species groups had significantly different mean time differences, followed by FM and MF (Table 13).

Table 12. Number of time differences in which consecutive pairs of different species were observed.

	Jag - Oce	Oce - Jag	Jag - Pum	Pum - Jag	Oce - Pum	Pum - Oce
N	92	25	204	199	59	69

Table 13. Tukey Pairwise test of mean differences for sex pairs between captures of different species in CBWS, Belize.

Tukey Pairwise test	MM	MF	FM
MM		0,004395	0,9896
MF	4,505		0,04752
FM	0,1947	3,354	

DISCUSSION

Density and Detection of Sympatric Felids

Extending the survey period increased female capture rates, detection of individuals and therefore spatial explicit capture recapture method made it possible made it possible to estimate sex specific densities. Sex specific densities across the year were estimated even though competing models were uncertain towards sex effects on g_0 and σ . Ocelot densities were similar those reported by Satter et al. (2019) for this site using a shorter period survey. Densities for jaguar were lower, however, female densities were higher than expected as Harmsen et al. (2017) reported smaller abundances for females. There was no relationship between density estimates and seasonality however, female jaguar densities and male ocelot densities fluctuated across the year.

Even though we obtained a smaller sample size of females than male jaguars, the possibility to integrate sex variables on SECR parameters, the estimated female densities were significantly higher than male jaguars in all seasonal periods. Female movement parameter for both species suggested that their detection probability decreases quicker away from their activity centres when compared to males. Therefore, for both species female small activity centres in the area produced larger estimates of density. Solitary carnivores, such as jaguars and ocelots, female densities are expected to be larger with smaller home ranges when compared to males so that male home ranges cover as many females as possible to increase chances of reproduction (Schaller and Crawshaw, 1980; Ludlow and Sunquist, 1987; Sandell, 1989) and thus affect detection (Conde et al., 2010).

Jaguar top model supported equal and unequal detection between sexes. This study does not discard the possible difference in detection that may exist between male and female jaguar even though the first ranked model suggested equal detection probability between male and female (Sollmann et al., 2011; Boron et al., 2016) It is known that trails are male dominated and that females potentially prefer other routes of travel to avoid males and by lengthening the survey it increased the opportunity for higher detection of females (Jędrzejewski et al., 2017). For both species, female would only become detectable if they decided to use trails to move within the landscape while high captures and recaptures of males suggest more presence of males using trails within the grid. Female to male consecutive captures were rare events within the same species of felids and overall among the species male and female consecutive captures were at lengthier periods. Females are smaller than males and can harassed or potentially suffer attack towards both mothers and cubs therefore avoid use of trails (Sunquist and Sunquist, 2002; Soares et al., 2006).

Harmsen et al., (2017) used a robust design of open population models on jaguar data, through long term monitoring of CBWS, however, yearly female detection was sporadic. Using an extended period of camera trap surveys we increased female detectability, especially in latter seasonal periods, therefore increasing their sample size (N = 12) than previously obtained through shorter one off surveys, similar to Jędrzejewski et al. (2017). Srbek-Araujo (2018) suggested that females may be actively avoiding camera traps after it was observed that a decreased number of female captures occurred after the first six months of the first year of a five-year survey. This would not be the case in the study area when yearly monitoring has been conducted and female individuals

are being recaptured year while others appear sporadically. However, the data showed that most female captures occurred in the second half of the year. From a sample size of twelve females, four female individuals were captured in both wet and dry season, another three were captured only in the wet season and the remaining 6 were in the dry season while most males were present all year round. Captures of individual female ocelots varied between 6 and 7 across seasonal periods. This behaviour can be attributed to females avoiding trails to prevent infanticide, thus leading to shifts in home range similar to that reported by Soares et al. (2006) of a tracked female with cubs.

A watercourse only camera trap survey produced similar sex ratios captured to a concurrent survey in the same area (Higginbottom, 2012) suggesting no selection to watercourse routes by females. However, that study did not provide details of other riverine characteristics that were used, such as width of river, seasonal river, and height of water, just to name a few, which may play a role in female use (Higginbottom, 2012). Moreover, sporadic captures of rare individuals, referred to as transients, and low capture-ability of females (when compared to males) reportedly do not influence density estimates precision when using SECR when compared to conventional methods of estimation, unlike the total number of individuals in the sample (Higginbottom, 2012).

In the case of ocelots, densities were similar to those reported in other studies using SECR models, for example Satter (2016), but lower than those reported for the conventional methods reported for the same area in Davis (2009) and Higginbottom (2012). While we estimated higher female densities for this study area, using SECR, Gomez-Ramirez et al. (2017) estimated higher densities

of male ocelots, except in one year where female density was higher. These studies generally support sex differences in detection and the use of SECR especially support sex differences in sigma, that is, movement within activity centres. Satter (2016) found male ocelots to move further than females, a similar movement behaviour observed for our ocelot sampled population across the year in this study. However, sex specific densities have not been reported recently and our results estimated generally higher female densities although not significantly different to males. According to Higginbottom (2012) density is more sensitive to number of individuals captured and identified when using SECR which is reflected in our density estimates and the number of individuals reported for each seasonal period.

The spearman rank correlation suggested no relationship to seasonality in either species but their densities fluctuated across the year. This can be caused by capture probability that is influenced through individual movement in the landscape and number of individuals captured. Nuñez et al. (2019) using a single 70-day survey where the camera grid was blocked into three to estimate density produced similar densities. The block with the higher number of individuals captured produced a higher density estimate than the other adjacent two blocks with smaller number of individuals within the same period. Jaguar and ocelot density does not remain stable across time and space as individuals move within the landscape, and this space is possible not used evenly by all individuals. CBWS camera grid using Tobler and Powell (2013) can be regarded a small grid, while Morato et al. (2016) suggested that jaguar home range might be larger than initially thought, possibly this variation across the year reflects periodic individuals' shift within their larger home range.

The jaguar male only strongly supported constant $g0$ and σ but it also supported seasonal negative effects on $g0$, however the densities remain similar as with the full data. Seasonal effects were also supported using the full data set (as the third ranked model) with sex effects on sigma. On the other hand, seasonal effects on sigma were the second ranked model on the ocelot male only data but season was not substantially supported using the full data (AICc >2). It is possible that although there is a stable male population, potentially their trial used by different number of individuals varied in time. The effect of season on sigma in the male only ocelot data is potentially reflecting movement changes within home ranges between seasons found with telemetry in ocelots (Dillon and Kelly, 2008) and jaguars (Cavalcanti and Gese, 2009). SECR density estimates are sensitive to number of individuals, surveying the entire year provided an insight of when density can be inflated or negatively affected by number of individuals detected, which was suggested to occur at the onset of the rainy season (Higginbottom, 2012).

Detection and movement differences between male and female for both jaguar and ocelots between seasons may not be influenced by rainfall directly. Harmsen et al. (in prep) suggests that the latter part of the year can be an artefact of jaguar social change between male and females present during this period of the year. The study area is large enough to study ocelots however we are aware that mean distances between neighbouring camera traps are not the recommended (Dillon and Kelly, 2007; Dillon and Kelly, 2008) however, this study density estimates are consistent with a previous study (Davis, 2009). Considering their differences in size between ocelot and jaguars, movement and densities were as we expected.

Density estimates of females were higher than male densities for both species and were different across the four periods surveyed. Using a year-long survey we were able to determine fluctuations in density and how much variation there can be within the year. Therefore, studies that employ one-off short surveys to estimate densities can be sampling a period when capture of individuals are low. It is important to identify this characteristic within a study area as densities estimates can fluctuate as an effect to individuals captured. To obtain between estimates of elusive species such as jaguars and ocelots, we recommend extending periods of surveys to increase detection of individuals, especially females. It is difficult to define a specific period as this can be specific to study site, however, if number of individuals increase or decrease density, selecting two periods with different number of individuals can be combined to estimate density in either a consecutive or individually separated survey periods in time.

Males and females in both species displayed difference in SECR spatial parameter, which was consistent with other camera trapping (Sollmann et al., 2011) and telemetry studies (Morato et al., 2016) that indicate differential distance moved. A larger camera grid that covers an area with greater variety of microhabitat in which individuals which avoid using trails but used game trails to move within the landscape can be detected, for example, watercourses, trails, and elevations (Higginbottom, 2012) . Moreover, the linear grid maybe favouring male jaguars who appear to have more directional movement when compared to females tortuous short movements (Tobler et al., 2018). Using newly developed autocorrelated kernel density estimate (AKDE), Tobler et al. (2018) suggest current home range estimates maybe underestimated and movement behaviour still needs further research.

Temporal Activity Pattern

Jaguar and ocelot were mostly nocturnal – crepuscular, however could be active anytime of the day. Puma activity was observed to sharply shift mostly diurnal in the fourth seasonal period of low rainfall, although they were observed to have similar activity pattern as jaguars and ocelot. Female jaguars and female pumas were cathemeral, while female ocelot were nocturnal. Overlap between ocelot and jaguars was least in the first period of the wet season when there were less ocelot captures. While percent overlap in temporal activity by both jaguar and ocelots with puma was lowest when pumas' activity was mostly diurnal. There was no association with the observed overlap activity pattern between pairs of felid species and seasonality. This is consistent with other studies where these three sympatric felids are reported to be primarily nocturnal-crepuscular in their activity patterns (Di Bitetti et al., 2010; Harmsen et al., 2011; Foster et al., 2013; Pratas-Santiago et al., 2016) while pumas can be cathemeral (Gómez et al., 2005).

Carnivores in a South African reserve use temporal partitioning as a mechanism of coexistence in which the subordinate predator, cheetah and wild dog, avoid the dominant lion and hyena to minimize kleptoparasitism (Hayward and Slotow, 2009) or interspecific killing (Palomares and Caro, 1999). Herrera et al. (2018) argue that competing pairs of species had greater temporal separation, which in the study were jaguar and puma and puma and ocelot. Astete et al. (2017) suggested that pumas in their southern range avoid the dominant jaguar by preferring a different habitat type. A study in Brazil had suggested water sources and elevation to be the main variables shaping habitat suitability of both jaguars and pumas (Astete et al., 2016). However, our study area can be

described relatively homogeneous in relation to elevation and water availability across the grid. Similarly, Higgingbottom (2012) found no difference in activity in waterways-only surveys between jaguars and ocelots but puma captures were significantly lower in waterways, a characteristic found across the study site. Similarly, Davis et al. (2011) found that ocelot activity was positively related to jaguar captures in a pine forest type where puma detection was rare. The evidence of these data suggest that temporal segregation among these felids is not an important driving force promoting coexistence in CBWS tropical rainforest, and season does not affect this pattern.

Spatial-Temporal Interaction

There was no significant effect of seasonality between event frequencies of species sharing the same trap within the 48 hour interval. However, between pairs a significant difference between puma - ocelot pairs and jaguar-puma but to a lesser extent jaguar-ocelot. This relationship was further explored using time differences between captures.

Time differences per trap showed that not all traps were used at similar proportions by all three species, jaguar, ocelot and pumas. The trap used by pumas only had the highest mean time difference between captures, suggestive that there was no need for constant visits as no other competitor used the area. Although there was no significant differences in mean between the pooled time differences between consecutive captures of the same and different felid species, there was a tendency for different species to take longer between captures. However, among ocelots, jaguar and pumas, captures between ocelots took longer than between jaguars and between pumas. Even though this difference is

potentially an artefact of low capture rates of ocelots, there is reportedly a fatal case which suggested intraspecific killing of a male ocelot in Suriname (Thompson, 2011), suggestive of the potential aggressiveness between ocelot conspecifics. Taking into account the differences in time between captures of the different pair of species, ocelots avoid using the same space with pumas thus the longer time differences, and seem constantly be looking out for jaguars on trails. It is possible that ocelots would avoid, to a greater extent, the use of trails and thus the longer time between ocelot captures. Herrera et al. (2018) suggest greater competition between puma and ocelots and Di Bitetti et al. (2010) found supporting evidence that puma and ocelot co-occurrence decrease but mostly on trails than roads. However, due to size differences pumas are expected to be dominant over ocelots, and jaguars dominant over pumas (Donadio and Buskirk, 2006; Harmsen et al., 2009; Elbroch and Kusler, 2018).

This study found time difference between captures of pumas and jaguar and vice-versa were equal, potentially following each other but avoiding physical contact in time but using the same space because of abundance prey (Foster et al., 2010; Harmsen et al., 2011). However, pumas are potentially exploiting streams to move within the forest matrix (Higginbottom, 2012) and also to increase hunting of preferred prey, paca (*Cuniculus paca*), associated to watercourses (Goulart et al., 2009; Foster et al., 2010; de Matos Dias et al., 2018). While the results of time differences between puma and ocelot further support the finding that suggested they don't share same areas within a short interval of 48 hours. Their size differences might be playing a role between pumas and ocelots (Kiltie, 1984), and ocelot and jaguars association poses certain risks to ocelots, for example attacks (González-Maya et al., 2010).

Sex pair's consecutive captures within the same species of felids were significant between male – male and female – male. Male to male consecutive capture of the same species has a mean time difference lower than the other sex pairs. This was expected since this study estimated higher male detection rates than female in both ocelots and jaguars (See section on density estimates) and territorial defence by carnivores is more evident between males (Boydston et al., 2001), though this has not been documented in the reserve it has been reported in another area (Figueroa, 2013). Trail marking behaviour of jaguar and puma appear to be intraspecific and male dominated (Harmsen et al., 2016), potentially a marking area can be used by multiple males when there is high overlap, for example pumas (Logan and Sweanor, 2001). Time differences of female to male consecutive capture and vice-versa were longer periods, though this could be an artefact of low capture rates of females on trails compared to males. Naturally a female in oestrus would attack potential mates, but presence on trails could be linked to an assessment of potential mates, for example pumas (Wittmer et al., 2014), but due to the limitations of fix point observations by camera traps on trails it is difficult to make a conclusion regarding this outcome.

In the case of different species pair's consecutive captures, time differences was significant between male to male and male to female. Sex pairs consecutive captures between same species and different species groups, male to male time differences were on average similar while female to female consecutive captures too longer periods between different felid species. In the case of pumas in North America, there is tolerance between females because they are usually related (Logan and Sweanor, 2001), territoriality disputes between females of different species of carnivores have not yet been reported.

Consistent with other studies, in CBWS temporal segregation alone is not a driving force that allows coexistence between the large jaguar and pumas and the medium sized ocelot. There is high overlap in activity patterns between pairs of these three felid species and it is not affected by season. Using both space (camera trap locations) and time (time of capture) variables, between pairs of species the pattern observed suggest puma and ocelot associate less than ocelot and jaguars. However, the greater associated to ocelot by jaguars may indicate harassment by jaguar or no interaction effect between the two. Similar mean time difference in puma to jaguar and jaguar to puma indicates similar dominance of trails but also higher frequency of intraspecific inspection between males.

MANAGEMENT IMPLICATIONS

CBWS has been protected since 1980 with the highest form of protection. Extraction of any kind is illegal and enforcement efforts between governmental departments and the co-managers are important in keeping infringements at minimum. This collaboration is important to maintain the integrity of protected areas and in turn what it represents for biodiversity and communities surrounding them. The position of CBWS within the larger Maya Mountain Massif is a potential source of prey for predators and game meat for surrounding communities. This protected area has proven to encourage a healthy and stable population of jaguars and ocelots.

The stable population of jaguars and ocelots suggests that the population of prey and pumas is also stable. There is room for more research to investigate the recent prey abundances and evaluate the puma population not studied here. There is a need to study other felid species not only in this study site but also in other neighbouring protected areas. In turn, evaluate the effects of healthy populations of carnivores and their prey in human dominated landscapes across Belize.

There is a perceived harmony, observed through camera traps, in coexistence among these three felids but there is the need to assess eco-tourism activities effects within the reserve, and use of other methods to assess coexistence at finer scales of all sympatric felid species (Scognamillo et al., 2003). However, the implications of bordering communities leading to coexistence with domestic species are revealed through the incidence of ectoparasitic larvae infestation (*Dermatobia hominis*, Linnaeus, Jr.) and mange

on felids (eg. ocelots and pumas) (Hill and Connelly, 2008). Several captures of domestic dogs have also been document on locations bordering the protected area and nearby rural communities that have access to the reserve. Although the pathway of transmission is unknown, high overlap among felid species, their prey and presence of domestic dogs is possible contributing to the spread of the illness within and outside the reserve. While the infected domestic population can be controlled, the wildlife population is not.

APPENDIX I

AIC results for models applied to full jaguar data

Model name	Model	npar	logLik	AIC	AICc	dAICc	AICcwt
secr2	$g0 \sim 1$ sigma~sex pmix~h2	4	-3.300.149	6.608.297	6.608.831	0.000	0.3381
secr6	$g0 \sim$ sex sigma~sex pmix~h2	5	-3.299.645	6.609.289	6.610.100	1.269	0.1793
secr10	$g0 \sim$ season sigma~sex pmix~h2	5	-3.299.815	6.609.630	6.610.440	1.609	0.1513
secr4	$g0 \sim 1$ sigma~sex + season pmix~h2	5	-3.300.049	6.610.099	6.610.909	2.078	0.1196
secr14	$g0 \sim$ sex + season sigma~sex pmix~h2	6	-3.299.301	6.610.602	6.611.753	2.922	0.0784
secr8	$g0 \sim$ sex sigma~sex + season pmix~h2	6	-3.299.548	6.611.095	6.612.246	3.415	0.0613
secr12	$g0 \sim$ season sigma~sex + season pmix~h2	6	-3.299.795	6.611.589	6.612.740	3.909	0.0479
secr16	$g0 \sim$ sex +season sigma~sex + season pmix~h2	7	-3.299.282	6.612.563	6.614.119	5.288	0.0240
secr1	$g0 \sim 1$ sigma~1 pmix~h2	3	-3.323.880	6.653.759	6.654.075	45.244	0.0000
secr5	$g0 \sim$ sex sigma~1 pmix~h2	4	-3.322.832	6.653.663	6.654.197	45.366	0.0000
secr9	$g0 \sim$ season sigma~1 pmix~h2	4	-3.323.429	6.654.859	6.655.392	46.561	0.0000
secr13	$g0 \sim$ sex + season sigma~1 pmix~h2	5	-3.322.330	6.654.659	6.655.470	46.639	0.0000
secr3	$g0 \sim 1$ sigma~season pmix~h2	4	-3.323.877	6.655.754	6.656.288	47.457	0.0000
secr7	$g0 \sim$ sex sigma~season pmix~h2	5	-3.322.831	6.655.662	6.656.473	47.642	0.0000
secr11	$g0 \sim$ season sigma~season pmix~h2	5	-3.323.378	6.656.755	6.657.566	48.735	0.0000
secr15	$g0 \sim$ sex + season sigma~season pmix~h2	6	-3.322.289	6.656.579	6.657.729	48.898	0.0000

AIC results for models applied to full ocelot data.

Model name	model	npar	logLik	AIC	AICc	dAICc	AICcwt
secr6	$g0 \sim$ sex sigma~sex pmix~h2	5	-1.284.757	2.579.514	2.580.482	0.000	0.3386
secr2	$g0 \sim 1$ sigma~sex pmix~h2	4	-1.286.504	2.581.009	2.581.644	1.162	0.1894
secr8	$g0 \sim$ sex sigma~sex + season pmix~h2	6	-1.284.712	2.581.424	2.582.801	2.319	0.1062
secr14	$g0 \sim$ sex + season sigma~sex pmix~h2	6	-1.284.751	2.581.503	2.582.880	2.398	0.1021
secr4	$g0 \sim 1$ sigma~sex + season pmix~h2	5	-1.286.479	2.582.959	2.583.927	3.445	0.0605
secr10	$g0 \sim$ season sigma~sex pmix~h2	5	-1.286.497	2.582.995	2.583.962	3.480	0.0594
secr5	$g0 \sim$ sex sigma~1 pmix~h2	4	-1.287.776	2.583.551	2.584.186	3.704	0.0531
secr16	$g0 \sim$ sex +season sigma~sex + season pmix~h2	7	-1.284.708	2.583.417	2.585.283	4.801	0.0307
secr7	$g0 \sim$ sex sigma~season pmix~h2	5	-1.287.629	2.585.259	2.586.226	5.744	0.0192
secr12	$g0 \sim$ season sigma~sex + season pmix~h2	6	-1.286.479	2.584.959	2.586.336	5.854	0.0181
secr13	$g0 \sim$ sex + season sigma~1 pmix~h2	5	-1.287.764	2.585.527	2.586.495	6.013	0.0167
secr15	$g0 \sim$ sex + season sigma~season pmix~h2	6	-1.287.606	2.587.212	2.588.589	8.107	0.0059
secr1	$g0 \sim 1$ sigma~1 pmix~h2	3	-1.297.303	2.600.606	2.600.981	20.499	0.0000
secr3	$g0 \sim 1$ sigma~season pmix~h2	4	-1.297.104	2.602.208	2.602.843	22.361	0.0000
secr9	$g0 \sim$ season sigma~1 pmix~h2	4	-1.297.267	2.602.533	2.603.168	22.686	0.0000
secr11	$g0 \sim$ season sigma~season pmix~h2	5	-1.297.099	2.604.197	2.605.165	24.683	0.0000

APPENDIX II

MALE ONLY AIC RESULTS

Jaguar Male Only Models

	Model	npar	logLik	AIC	AICc	dAICc	AICcwt
FitsM1	g0~1 sigma~1	2	-2.883.424	5.770.848	5.771.079	0.000	0.4627
FitsM3	g0~season sigma~1	3	-2.882.793	5.771.587	5.772.058	0.979	0.2836
FitsM2	g0~1 sigma ~season	3	-2.883.340	5.772.681	5.773.151	2.072	0.1642
FitsM4	g0~season sigma ~season	4	-2.882.783	5.773.567	5.774.367	3.288	0.0894

Ocelot Male Only Models

	Model	npar	logLik	AIC	AICc	dAICc	AICcwt
oce.M1	g0~1 sigma~1	2	-9.067.793	1.817.559	1.817.838	0.000	0.5280
oce.M3	g0~1 sigma ~season	3	-9.064.658	1.818.932	1.819.503	1.665	0.2297
oce.M2	g0~season sigma~1	3	-9.067.657	1.819.531	1.820.103	2.265	0.1701
oce.M4	g0~season sigma~season	4	-9.064.210	1.820.842	1.821.818	3.980	0.0722

APPENDIX III

Figure 2A

Overall jaguar density estimates (animals/100km²) for the four sessions with standard error, 95% confidence intervals and standard errors for competing models (AICc <2).

Model rank	Session	D	SE.est	low.CI	upper.CI
Fit1 (<i>g0</i> ~1, <i>sigma</i> ~sex)	1	3.56	1.16	1.90	6.64
	2	7.13	1.93	4.23	12.01
	3	5.90	1.70	3.40	10.26
	4	5.76	1.61	3.36	9.87
Fit2 (<i>g0</i> ~sex, <i>sigma</i> ~sex)	1	3.53	1.16	1.89	6.6
	2	7.07	1.92	4.18	11.93
	3	5.85	1.69	3.37	10.18
	4	5.72	1.6	3.34	9.81
Fit3 (<i>g0</i> ~season, <i>sigma</i> ~sex)	1	3.59	1.18	1.92	6.73
	2	6.99	1.9	4.14	11.81
	3	5.8	1.67	3.33	10.09
	4	5.83	1.64	3.39	10

Figure 2B

Overall ocelot density estimates (animals/100km²) for the four sessions with standard error, 95% confidence intervals and standard errors for models with Δ AICc <2.

Model rank	Session	D	SE.est	Low.CI	Upper.CI
Fit1 (<i>g0</i> ~sex sig~sex)	1	7.37	1.96	4.41	12.31
	2	6.84	1.94	3.96	11.80
	3	7.46	2.10	4.40	12.70
	4	11.20	2.52	7.22	17.33
Fit2 (<i>g0</i> ~1 sig~sex)	1	7.31	1.94	4.38	12.19
	2	6.79	1.92	3.94	11.70
	3	7.41	2.03	4.37	12.60
	4	11.11	2.49	7.19	17.16

Figure 2C

Jaguar sex specific density estimates (animals/100km²) derived from the best

Session	Female				Male			
	D	SE.est	low.CI	upper.CI	D	SE.est	low.CI	upper.CI
1	1.80	1.05	0.62	5.21	1.76	0.5	1.02	3.03
2	3.58	1.5	1.62	7.89	1.75	0.5	1.02	3.02
3	4.16	1.6	1.99	8.7	1.75	0.49	1.01	3.01
4	3.6	1.52	1.63	7.95	2.15	0.55	1.32	3.53

model ($g0\sim 1$ sigma \sim sex) according to the AIC model selection test.

Figure 2D

Table 5: Sex specific density estimates of ocelots with 95% confidence intervals and standard errors derived using the first model ($g0\sim$ sex sigma \sim sex).

Session	Female				Male			
	D	SE.est	low.CI	upper.CI	D	SE.est	low.CI	upper.CI
1	3.72	1.56	1.69	8.2	3.65	1.19	1.96	6.78
2	4.30	1.68	2.06	8.99	2.54	0.98	1.22	5.27
3	3.69	1.55	1.68	8.13	2.54	0.98	1.22	5.26
4	4.35	1.7	2.08	9.1	4.36	1.3	2.45	7.73

BIBLIOGRAPHY

- Akenson, J., H. Akenson, and H. Quigley. 2005. Effects of wolf reintroduction on a cougar population in the central Idaho wilderness. In: R. A. Beausoleil and D. A. Martorello, editors. Proceeding of the Eight Mountain Lion Workshop. p. 177–188.
- Astete, S., J. Marinho-Filho, M. Kajin, G. Penido, B. Zimbres, R. Sollmann, A. T. A. Jácomo, N. M. Tôrres, and L. Silveira. 2017. Forced neighbours: Coexistence between jaguars and pumas in a harsh environment. *J. Arid Environ.* 146:27–34. doi:10.1016/j.jaridenv.2017.07.005.
- Astete, S., J. Marinho-Filho, R. B. Machado, B. Zimbres, A. T. A. Jácomo, R. Sollmann, N. M. Tôrres, and L. Silveira. 2016. Living in extreme environments: modeling habitat suitability for jaguars, pumas, and their prey in a semiarid habitat. *J. Mammal.* gyw184. doi:10.1093/jmammal/gyw184.
- Barlow, A. C. D., C. McDougal, J. L. D. Smith, B. Gurung, S. R. Bhatta, S. Kumal, B. Mahato, and D. B. Tamang. 2009. Temporal Variation in Tiger (*Panthera tigris*) Populations and its Implications for Monitoring. *J. Mammal.* 90:472–478. doi:10.1644/07-MAMM-A-415.1.
- Benson, J. F., M. J. Chamberlain, and B. D. Leopold. 2006. Regulation of space use in a solitary felid: population density or prey availability? *Anim. Behav.* 71:685–693. doi:10.1016/j.anbehav.2005.08.005.
- Bischof, R., H. Ali, M. Kabir, S. Hameed, and M. A. Nawaz. 2014. Being the underdog: an elusive small carnivore uses space with prey and time without enemies: Space and time use by Altai mountain weasel. *J. Zool.* 293:40–48. doi:10.1111/jzo.12100.
- Borchers, D. L., and M. G. Efford. 2008. Spatially Explicit Maximum Likelihood Methods for Capture-Recapture Studies. *Biometrics.* 64:377–385. doi:10.1111/j.1541-0420.2007.00927.x.
- Boron, V., J. Tzanopoulos, J. Gallo, J. Barragan, L. Jaimes-Rodriguez, G. Schaller, and E. Payán. 2016. Jaguar Densities across Human-Dominated

Landscapes in Colombia: The Contribution of Unprotected Areas to Long Term Conservation. PLOS ONE. 11:e0153973. doi:10.1371/journal.pone.0153973.

Boyd, S. P., and L. Vandenberghe. 2004. Convex optimization. Cambridge University Press, Cambridge, UK ; New York.

Boydston, E. E., T. L. Morelli, and K. E. Holekamp. 2001. Sex Differences in Territorial Behavior Exhibited by the Spotted Hyena (*Hyaenidae*, *Crocuta crocuta*). *Ethology*. 107:369–385. doi:10.1046/j.1439-0310.2001.00672.x.

Braker, H.E. and Greene, H.W., 1994. Population biology: life histories, abundance, demography, and predator-prey interactions. *La Selva: ecology and natural history of a Neotropical rain forest* (LA McDade, KS Bawa, HA Hespenheide, and GS Hartshorn, Eds.). University of Chicago Press, Chicago, Illinois, pp.244-255.

Brook, L. A., C. N. Johnson, and E. G. Ritchie. 2012. Effects of predator control on behaviour of an apex predator and indirect consequences for mesopredator suppression. C. Dickman, editor. *J. Appl. Ecol.* 49:1278–1286. doi:10.1111/j.1365-2664.2012.02207.x.

Burnham, K. P., D. R. Anderson, and K. P. Burnham. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer, New York.

Carbone, C., T. Coulson, S. Christie, K. Conforti, J. Seidensticker, N. Franklin, R. Tilson, J. R. Ginsberg, M. Kinnaird, R. Laidlaw, A. Lynam, T. O'Brien, W. N. Wan Shahrudin, M. Griffiths, J. Holden, D. Martyr, K. Kawanishi, M. Sunquist, D. W. Macdonald, L. Nath, C. McDougal, and D. J. L. Smith. 2001. The use of photographic rates to estimate densities of tigers and other cryptic mammals. *Anim. Conserv.* 4:75–79.

Carbone, C., and J. L. Gittleman. 2002. A common rule for the scaling of carnivore density. *Science*. 295:2273–2276.

Cavalcanti, S. M. C., and E. M. Gese. 2009. Spatial Ecology and Social Interactions of Jaguars (*Panthera Onca*) in the Southern Pantanal, Brazil. *J. Mammal.* 90:935–945. doi:10.1644/08-MAMM-A-188.1.

Conde, D. A., F. Colchero, H. Zarza, N. L. Christensen, J. O. Sexton, C. Manterola, C. Chávez, A. Rivera, D. Azuara, and G. Ceballos. 2010. Sex matters: Modeling male and female habitat differences for jaguar conservation. *Biol. Conserv.* 143:1980–1988. doi:10.1016/j.biocon.2010.04.049.

Coronel-Arellano, H., N. E. Lara-Díaz, and C. A. López-González. 2017. Abundancia y densidad de jaguar (*Panthera onca*) en el APFF meseta de Cacaxtla, Sinaloa, México. *ACTA Zool. Mex.* NS. 33. doi:10.21829/azm.2017.3311020. Available from: <http://azm.ojs.inecol.mx/index.php/azm/article/view/1020>

Davis, M. L. 2009. Densities, habitat-use, and mesopredator release of the ocelot in Belize [Master of Science]. Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA.

Davis, M. L., M. J. Kelly, and D. F. Stauffer. 2011. Carnivore co-existence and habitat use in the Mountain Pine Ridge Forest Reserve, Belize: Carnivore co-existence in a neotropical pine forest. *Animal Conservation.* 14:56–65. doi:10.1111/j.1469-1795.2010.00389.x.

Di Bitetti, M. S., C. D. De Angelo, Y. E. Di Blanco, and A. Paviolo. 2010. Niche partitioning and species coexistence in a Neotropical felid assemblage. *Acta Oecologica.* 36:403–412. doi:10.1016/j.actao.2010.04.001.

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

Dillon, A. 2005. Ocelot density and home range in Belize, Central America: camera-trapping and radio telemetry. Master of Science Thesis. Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA.

Dillon, A., and M. Kelly. 2008. Ocelot home range, overlap and density: Comparing radio telemetry with camera trapping. *J. Zool.* 275:391–398.

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

doi:10.1017/S0030605307000518. Available from:
http://www.journals.cambridge.org/abstract_S0030605307000518

Donadio, E., and S. W. Buskirk. 2006. Diet, morphology, and interspecific killing in carnivora. *Am. Nat.* 167:524–536.

Durant, S. M. 1998. Competition refuges and coexistence: an example from Serengeti carnivores. *J. Anim. Ecol.* 67:370–398.

Eaton, T. S. 2016. Abundance and activity patterns of the jaguar (*Panthera onca*) in the Mountain Pine Ridge, Belize. Master of Science Thesis. Northeastern State University.

Efford, M. 2004. Density estimation in live-trapping studies. *Oikos*. 106:598–610. doi:10.1111/j.0030-1299.2004.13043.x.

Efford, M. 2015. Finite mixture models in secr 2.10. *sigma*. 3:0–04491511.

Efford, M. 2017. A tutorial on fitting spatially explicit capture–recapture models in secr.

Efford, M. G., D. K. Dawson, and D. L. Borchers. 2009. Population density estimated from locations of individuals on a passive detector array. *Ecology*. 90:2676–2682. doi:10.1890/08-1735.1.

Efford, M. G., and G. Mowat. 2014. Compensatory heterogeneity in spatially explicit capture–recapture data. *Ecology*. 95:1341–1348. doi:10.1890/13-1497.1.

Elbroch, L. M., and A. Kusler. 2018. Are pumas subordinate carnivores, and does it matter? *PeerJ*. 6:e4293. doi:10.7717/peerj.4293.

Figueroa, O. A. 2013. The ecology and conservation of jaguars (*Panthera onca*) in Central Belize: Conservation status, diet, movement patterns and habitat use. Ph.D Thesis. University of Florida.

Foster, R. J. 2008. The ecology of jaguars (*Panther onca*) in a human-influenced landscape. Ph.D Thesis. University of Southampton, London.

Foster, R. J., B. J. Harmsen, B. Valdes, C. Pomilla, and C. P. Doncaster. 2010. Food habits of sympatric jaguars and pumas across a gradient of human

disturbance: Food habits of sympatric jaguars and pumas. *J. Zool.* 280:309–318. doi:10.1111/j.1469-7998.2009.00663.x.

Gerber, B. D., S. M. Karpanty, and J. Randrianantenaina. 2012. Activity patterns of carnivores in the rain forests of Madagascar: implications for species coexistence. *J. Mammal.* 93:667–676. doi:10.1644/11-MAMM-A-265.1.

Gómez, H., R. B. Wallace, G. Ayala, and R. Tejada. 2005. Dry season activity periods of some Amazonian mammals. *Stud. Neotropical Fauna Environ.* 40:91–95. doi:10.1080/01650520500129638.

Gómez-Ramírez, M., C. Gutiérrez-González, and C. López-González. 2017. Ocelots thrive in a non-typical habitat of northwestern Mexico. *Endanger. Species Res.* 32:471–478. doi:10.3354/esr00828.

Goulart, F. V. B., N. C. Cáceres, M. E. Graipel, M. A. Tortato, I. R. Ghizoni, and L. G. R. Oliveira-Santos. 2009. Habitat selection by large mammals in a southern Brazilian Atlantic Forest. *Mamm. Biol.* 74:182–190. doi:10.1016/j.mambio.2009.02.006.

González-Maya, J. F., E. Navarro-Arquez, and J. Schipper. 2010. Ocelots are prey items of jaguars: a case from Talamanca, Costa Rica. *CATnews.* 53:11–12.

Grente, O. 2017. Master thesis: Density variations of a jaguar population in Belize during long-term monitoring by camera-trapping: the influence of statistical models and home range size. Master of Science Thesis. University of the French West Indies, Pointe-à-Pitre, Guadeloupe, France. Available from: <http://rgdoi.net/10.13140/RG.2.2.31462.32320>

Gutiérrez-González, C. E., M. A. Gómez-Ramírez, and C. A. López-González. 2012. Estimation of the density of the Near Threatened jaguar *Panthera onca* in Sonora, Mexico, using camera trapping and an open population model. *Oryx.* 46:431–437. doi:10.1017/S003060531100041X.

Gutiérrez-González, C. E., M. A. Gómez-Ramírez, C. A. López-González, and P. F. Doherty. 2015. Are Private Reserves Effective for Jaguar Conservation? C. A. Hagen, editor. *PLOS ONE.* 10:e0137541. doi:10.1371/journal.pone.0137541.

- Hammer, Hammer, D.A.T., Ryan, P.D. 2001. PAST: Paleontological Statistics software package for education and data analysis. *Palaeontologia Electronica* 4(1): 9 pp
- Harmsen, B., R. Foster, S. Silver, L. Ostro, and C. Doncaster. 2009. Spatial and temporal interactions of sympatric jaguars (*panthera onca*) and pumas (*puma concolor*) in a neotropical forest. *J. Mammal.* 90:612–620.
- Harmsen, B., R. Foster, S. Silver, L. Ostro, and C. Doncaster. 2010. Differential use of trails by forest mammals and the implications for camera-trap studies: A case study from Belize. *Biotropica.* 42:126–133.
- Harmsen, B. J., R. J. Foster, E. Sanchez, C. E. Gutierrez-González, S. C. Silver, L. E. T. Ostro, M. J. Kelly, E. Kay, and H. Quigley. 2017. Long term monitoring of jaguars in the Cockscomb Basin Wildlife Sanctuary, Belize; Implications for camera trap studies of carnivores. M. S. Boyce, editor. *PLOS ONE.* 12:e0179505. doi:10.1371/journal.pone.0179505.
- Harmsen, B. J., R. J. Foster, S. C. Silver, L. E. T. Ostro, and C. P. Doncaster. 2011. Jaguar and puma activity patterns in relation to their main prey. *Mamm. Biol. - Z. Für Säugetierkd.* 76:320–324. doi:10.1016/j.mambio.2010.08.007.
- Harmsen, B. J., E. Sanchez, and R. J. Foster. 2016. Differential marking behaviour by sympatric felids in a Neotropical forest. *CATnews.* 8–12.
- Hayward, M. W., and R. Slotow. 2009. Temporal partitioning in activity in large African carnivores: tests if multiple hypotheses. *South Afr. J. Wildl. Res.* 39:109–125. doi:http://dx.doi.org/10.3957/056.039.0207.
- Heilbrun, R. D., N. J. Silvy, M. J. Peterson, and M. E. Tewes. 2003. Using automatically triggered cameras to individually identify bobcats. *Wildl. Soc. Bull.* 31:748–755.
- Hernández-SaintMartín, A. D., O. C. Rosas-Rosas, J. Palacio-Núñez, and L. A. Tarango-Arambula. 2013. Activity patterns of jaguar, puma and potential prey in San Luis Potosí, Mexico. 15.

Herrera, H., E. J. Chávez, L. D. Alfaro, T. K. Fuller, V. Montalvo, F. Rodrigues, and E. Carrillo. 2018. Time partitioning among jaguar *Panthera onca*, puma *Puma concolor* and ocelot *Leopardus pardalis* (Carnivora: Felidae) in Costa Rica's dry and rainforests. *Rev Biol Trop.* 66:10.

Higginbottom, P. A. 2012. Improving the reliability of jaguar abundance and density estimates from camera trapping surveys. Ph.D Thesis. Manchester Metropolitan University, Manchester, UK.

Hill, S. K., and C. R. Connelly. 2008. Human Botfly (*Dermatobia hominis*, Linnaeus Jr. 1781). *Featur. Creat. Entomol. Nematol.* Available from: http://entnemdept.ufl.edu/creatures/misc/flies/human_bot_fly.htm

Jędrzejewski, W., M. F. Puerto, J. F. Goldberg, M. Hebblewhite, M. Abarca, G. Gamarra, L. E. Calderón, J. F. Romero, Á. L. Vilorio, R. Carreño, H. S. Robinson, M. Lampo, E. O. Boede, A. Biganzoli, I. Stachowicz, G. Velásquez, and K. Schmidt. 2017. Density and population structure of the jaguar (*Panthera onca*) in a protected area of Los Llanos, Venezuela, from 1 year of camera trap monitoring. *Mammal Res.* 62:9–19. doi:10.1007/s13364-016-0300-2.

Jůnek, T., P. Jůnková Vymyslická, K. Hozdecká, and P. Hejcmanová. 2015. Application of Spatial and Closed Capture-Recapture Models on Known Population of the Western Derby Eland (*Taurotragus derbianus derbianus*) in Senegal. D. Russo, editor. *PLOS ONE.* 10:e0136525. doi:10.1371/journal.pone.0136525.

Kane, M. D., D. J. Morin, and M. J. Kelly. 2015. Potential for camera-traps and spatial mark-resight models to improve monitoring of the critically endangered West African lion (*Panthera leo*). *Biodivers. Conserv.* 24:3527–3541. doi:10.1007/s10531-015-1012-7.

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

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

- Kasper, C. B., A. Schneider, and T. G. Oliveira. 2016. Home range and density of three sympatric felids in the Southern Atlantic Forest, Brazil. *Braz. J. Biol.* 76:228–232. doi:10.1590/1519-6984.19414.
- Kelly, M. J., A. J. Noss, M. S. Di Bitetti, L. Maffei, R. L. Arispe, A. Paviolo, C. D. De Angelo, and Y. E. Di Blanco. 2008. Estimating Puma Densities from Camera Trapping across Three Study Sites: Bolivia, Argentina, and Belize. *J. Mammal.* 89:408–418. doi:10.1644/06-MAMM-A-424R.1.
- Kitchen, A. M., E. M. Gese, and E. R. Schauster. 1999. Resource partitioning between coyotes and swift foxes: space, time, and diet. *J. Mammal.* 77:12.
- Kiltie, R. A. 1984. Size ratios among sympatric neotropical cats. *Oecologia.* 61:411–416. doi:10.1007/BF00379644.
- Logan, K. A., and L. L. Swenar. 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press.
- Ludlow, M. E., and M. E. Sunkist. 1987. Ecology and behavior of ocelots in Venezuela. *Natl. Geogr. Res.* 3:447–461.
- MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2017. *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence*. Second Edition. Academic Press.
- Massara, R. L., A. M. de O. Paschoal, L. L. Bailey, P. F. Doherty, M. de F. Barreto, and A. G. Chiarello. 2018. Effect of humans and pumas on the temporal activity of ocelots in protected areas of Atlantic Forest. *Mamm. Biol.* 92:86–93. doi:10.1016/j.mambio.2018.04.009.
- de Matos Dias, D., C. B. de Campos, and F. H. Guimarães Rodrigues. 2018. Behavioural ecology in a predator-prey system. *Mamm. Biol.* 92:30–36. doi:10.1016/j.mambio.2018.04.005.
- McCarthy, J. L., H. T. Wibisono, K. P. McCarthy, T. K. Fuller, and N. Andayani. 2015. Assessing the distribution and habitat use of four felid species in Bukit Barisan Selatan National Park, Sumatra, Indonesia. *Glob. Ecol. Conserv.* 3:210–221. doi:10.1016/j.gecco.2014.11.009.

Meredith, M., and M. Ridout. 2017. Estimates of coefficient of overlapping for animal activity patterns.

Morato, R. G., J. A. Stabach, C. H. Fleming, J. M. Calabrese, R. C. De Paula, K. M. P. M. Ferraz, D. L. Z. Kantek, S. S. Miyazaki, T. D. C. Pereira, G. R. Araujo, A. Paviolo, C. De Angelo, M. S. Di Bitetti, P. Cruz, F. Lima, L. Cullen, D. A. Sana, E. E. Ramalho, M. M. Carvalho, F. H. S. Soares, B. Zimbres, M. X. Silva, M. D. F. Moraes, A. Vogliotti, J. A. May, M. Haberfeld, L. Rampim, L. Sartorello, M. C. Ribeiro, and P. Leimgruber. 2016. Space Use and Movement of a Neotropical Top Predator: The Endangered Jaguar. M. Stöck, editor. PLOS ONE. 11:e0168176. doi:10.1371/journal.pone.0168176.

Noss, A. J., B. Gardner, L. Maffei, E. Cuéllar, R. Montaña, A. Romero-Muñoz, R. Sollman, and A. F. O'Connell. 2012. Comparison of density estimation methods for mammal populations with camera traps in the Kaa-lya del Gran Chaco landscape: Density estimation with camera traps in the Chaco. R. Altwegg, editor. Anim. Conserv. 15:527–535. doi:10.1111/j.1469-1795.2012.00545.x.

Núñez Pérez, R., López González, C.A., Hidalgo Mihart, M., Gutierrez González, C., Gómez Ramírez, M., Rosas Rosas, O. 2018. Seguimiento a los esfuerzos de los censos del jaguar en México. Informe Final.

Ostfeld, R. S., and F. Keesing. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. Trends Ecol. Evol. 15:232–237. doi:10.1016/S0169-5347(00)01862-0.

Palomares, F., and T. M. Caro. 1999. Interspecific Killing among Mammalian Carnivores. Am. Nat. 153:492–508. doi:10.1086/303189.

Pratas-Santiago, L. P., A. L. S. Gonçalves, A. M. V. da Maia Soares, and W. R. Spironello. 2016. The moon cycle effect on the activity patterns of ocelots and their prey. J. Zool. 299:275–283. doi:10.1111/jzo.12359.

Quigley, H. B., R. J. Foster, L. S. Petracca, E. Payan, R. Salom-Pérez, and B. J. Harmsen. 2017. *Panthera onca*. doi:10.2305/IUCN.UK.2017-3.RLTS.T15953A50658693.en. Available from: <http://www.iucnredlist.org/details/15953/0>

Rabinowitz, A., and K. Zeller. 2010. A range-wide model of landscape connectivity and conservation for the jaguar, *Panthera onca*. *Biol. Conserv.* 143:939–945.

Ramesh, T., R. Kalle, and C. T. Downs. 2017. Staying safe from top predators: patterns of co-occurrence and inter-predator interactions. *Behav. Ecol. Sociobiol.* 71. doi:10.1007/s00265-017-2271-y. Available from: <http://link.springer.com/10.1007/s00265-017-2271-y>

Ramesh, T., R. Kalle, K. Sankar, and Q. Qureshi. 2012. Dietary Partitioning in Sympatric Large Carnivores in a Tropical Forest of Western Ghats, India. *Mammal Study.* 37:313–321. doi:10.3106/041.037.0405.

Rand, A. S. Stanley Rand, W. M. Rand 1985. Variation in rainfall on Barro Colorado Island. In Leigh, Egbert G., A. Stanley Rand, and Donald M. Windsor. *The Ecology of a tropical forest: seasonal rhythms and long-term changes.* No. 581.5 L528e. Washington, US: Smithsonian Institution, 1985.

Ridout, M. ., and M. Linkie. 2009. Estimating overlap of daily activity patterns from camera trap data. *J. Agric. Biol. Environ. Stat.* 14:322–337.

Sandell, M. 1989. The Mating Tactics and Spacing Patterns of Solitary Carnivores. In: J. L. Gittleman, editor. *Carnivore Behavior, Ecology, and Evolution.* Springer US, Boston, MA. p. 164–182. Available from: https://doi.org/10.1007/978-1-4613-0855-3_7

Sanderson, E. W., K. H. Redford, C.-L. B. Chetkiewicz, R. A. Medellin, A. R. Rabinowitz, J. G. Robinson, and A. B. Taber. 2002. Planning to Save a Species: the Jaguar as a Model. *Conserv. Biol.* 16:58–72. doi:10.1046/j.1523-1739.2002.00352.x.

Satter, C. B. 2016. Estimating population density and survival of ocelots (*Leopardus pardalis*) in six study sites over multiple years in Belize, Central America [Master of Science]. Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA.

Satter, C. B., B. C. Augustine, B. J. Harmsen, R. J. Foster, E. E. Sanchez, C. Wultsch, M. L. Davis, and M. J. Kelly. 2019. Long-term monitoring of ocelot

densities in Belize: Estimating Ocelot Density. *J. Wildl. Manag.* 83:283–294. doi:10.1002/jwmg.21598.

Schaller, G. B., and P. G. Crawshaw. 1980. Movement Patterns of Jaguar. *Biotropica*. 12:161. doi:10.2307/2387967.

Scognamillo, D., I. E. Maxit, M. Sunquist, and J. Polisar. 2003. Coexistence of jaguar (*Panthera onca*) and puma (*Puma concolor*) in a mosaic landscape in the Venezuelan llanos. *J. Zool.* 259:269–279. doi:10.1017/S0952836902003230.

Silver, S. C., L. E. T. Ostro, L. K. Marsh, L. Maffei, A. J. Noss, M. J. Kelly, R. B. Wallace, H. Gomez, and G. Ayala. 2004. The use of camera traps for estimating jaguar *Panthera onca* abundance and density using capture/recapture analysis. *Oryx*. 38:148–154.

Singh, R., Q. Qureshi, K. Sankar, P. R. Krausman, and S. P. Goyal. 2014. Evaluating heterogeneity of sex-specific capture probability and precision in camera-trap population estimates of tigers: Heterogeneity in Camera-Trapping of Tigers. *Wildl. Soc. Bull.* 38:791–796. doi:10.1002/wsb.471.

Soares, T. N., M. P. C. Telles, L. V. Resende, L. Silveira, A. T. A. Jácomo, R. G. Morato, J. A. F. Diniz-Filho, E. Eizirik, R. P. V. Brondani, and C. Brondani. 2006. Paternity testing and behavioral ecology: a case study of jaguars (*Panthera onca*) in Emas National Park, Central Brazil. *Genet. Mol. Biol.* 29:735–740. doi:10.1590/S1415-47572006000400025.

Sollmann, R., M. M. Furtado, B. Gardner, H. Hofer, A. T. A. Jácomo, N. M. Tôrres, and L. Silveira. 2011. Improving density estimates for elusive carnivores: Accounting for sex-specific detection and movements using spatial capture–recapture models for jaguars in central Brazil. *Biol. Conserv.* 144:1017–1024. doi:10.1016/j.biocon.2010.12.011.

Sollmann, R., M. Linkie, I. A. Haidir, and D. W. Macdonald. 2014. Bringing clarity to the clouded leopard *Neofelis diardi*: first density estimates from Sumatra. *Oryx*. 48:536–539. doi:10.1017/S003060531400043X.

Soto, C., and F. Palomares. 2015. Coexistence of sympatric carnivores in relatively homogeneous Mediterranean landscapes: functional importance of

habitat segregation at the fine-scale level. *Oecologia*. 179:223–235. doi:10.1007/s00442-015-3311-9.

Srbek-Araujo, A. C. 2018. Do female jaguars (*Panthera onca*, Linnaeus, 1758) deliberately avoid camera traps? *Mamm. Biol.* 88:26–30. doi:10.1016/j.mambio.2017.11.001.

Thompson, C. L. 2011. Intraspecific killing of a male ocelot. *Mamm. Biol.* 76:377–379. doi:10.1016/j.mambio.2010.10.011.

Sunquist, M., and F. Sunquist. 2002. *Wild Cats of the World*. The University of Chicago Press.

Tobler, M. W., and G. V. N. Powell. 2013. Estimating jaguar densities with camera traps: Problems with current designs and recommendations for future studies. *Biol. Conserv.* 159:109–118. doi:10.1016/j.biocon.2012.12.009.

de la Torre, J. A., P. Arroyo-Gerala, and L. Torres-Knoop. 2016. Density and activity patterns of ocelots in the greater Lacandona ecosystem. *Therya*. 7. doi:10.12933/therya-16-372. Available from: <http://132.248.10.25/therya/index.php/THERYA/article/view/372>

Trivellone, V., S. Bougeard, S. Giavi, P. Krebs, D. Balseiro, S. Dray, and M. Moretti. 2017. Factors shaping community assemblages and species co-occurrence of different trophic levels. *Ecol. Evol.* 7:4745–4754. doi:10.1002/ece3.3061.

Trolle, M., and M. Kéry. 2003b. Estimation of ocelot density in the Pantanal using capture–recapture analysis of camera-trapping data. *J. Mammal.* 84:607–614.

Vanak, A. T., D. Fortin, M. Thaker, M. Ogden, C. Owen, S. Greatwood, and R. Slotow. 2013. Moving to stay in place: behavioral mechanisms for coexistence of African large carnivores. *Ecology*. 94:2619–2631.

van Schaik, C.P., Terborgh, J.W. and Wright, S.J., 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of ecology and Systematics*, 24(1), pp.353-377.

Waide, R. B. 2008. Tropical Rainforest. In: S. E. Jørgensen and B. D. Fath, editors. *Encyclopedia of Ecology*. Academic Press, Oxford. p. 3625–3629. Available from: <http://www.sciencedirect.com/science/article/pii/B9780080454054003335>

Walker, Z., and P. Walker. 2006. *Cockscomb Basin Wildlife Sanctuary*. Wildtracks, Belize.

Weckel, M., W. Giuliano, and S. Silver. 2006. Jaguar (*Panthera onca*) feeding ecology: distribution of predator and prey through time and space. *J. Zool.* 0:060606025751038-??? doi:10.1111/j.1469-7998.2006.00106.x.

Wilsterman, K., N. L. McGuire, R. M. Calisi, and G. E. Bentley. 2018. *Seasonality: Hormones and Behavior*. In: *Reference Module in Life Sciences*. Elsevier. Available from: <http://linkinghub.elsevier.com/retrieve/pii/B9780128096338206882>

WB1:B111ittmer, H. U., M. L. Allen, and C. C. Wilmers. 2014. Puma communication behaviours: understanding functional use and variation among sex and age classes. *Behaviour*. 151:819–840. doi:10.1163/1568539X-00003173.