



Jaguar (*Panthera onca*) density and tenure in a critical biological corridor

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We estimated jaguar density and tenure, and investigated ranging behavior, using camera traps across the Maya Forest Corridor, a human-influenced landscape in central Belize that forms the only remaining connection for jaguar populations inhabiting two regional forest blocks: the Selva Maya and the Maya Mountain Massif. Jaguars were ubiquitous across the study area. Similar to the neighboring Selva Maya, mean density ranged from 1.5 to 3.1 jaguars per 100 km², estimated by spatial capture-recapture models. Cameras detected almost twice as many males as females, probably reflecting detection bias, and males ranged more widely than females within the camera grid. Both sexes crossed two major rivers, while highway crossings were rare and male-biased, raising concern that the highway could prevent female movement if traffic increases. Jaguars were more transient where the landscape was fragmented with settlements and agriculture than in contiguous forest. Compared with jaguars in the protected forests of the Maya Mountains, jaguars in central Belize displayed a lower potential for investment in intraspecific communication, indicative of a lower quality landscape; however, we did detect mating behavior and juveniles. Tenure of individuals was shorter than in the protected forests, with a higher turnover rate for males than females. At least three-quarters of reported jaguar deaths caused by people were male jaguars, and the majority was retaliation for livestock predation. Jaguars seem relatively tolerant to the human-influenced landscape of central Belize. However, intensification of game hunting and lethal control of predators would threaten population persistence, while increased highway traffic and clear-cutting riparian forest would severely limit the corridor function. Our results show that the viability of the corridor, and thus the long-term survival of jaguar populations in this region, will depend on appropriate land-use planning, nonlethal control of livestock predators, enforcement of game hunting regulations, and wildlife-friendly features in future road developments.

Keywords: camera trap, corridor, jaguar, *Panthera onca*, spatially explicit capture-recapture density

Utilizando trampas-cámara, se estimó la densidad, permanencia y desplazamiento de jaguares a través del Corredor del Bosque Maya, un paisaje dominado por humanos en la zona central de Belice y que actualmente representa la única posibilidad de conectividad para las poblaciones de jaguares que habitan en dos grandes bloques boscosos regionales: La Selva Maya y El Macizo de las Montañas Mayas. Los jaguares estuvieron presentes en toda el área de estudio. De igual forma que en la vecina Selva Maya, la densidad media varió de 1.5 a 3.1 jaguares por cada 100 km², estimada con modelos espaciales de captura-recaptura. Las cámaras detectaron casi el doble de machos que hembras, probablemente reflejando un sesgo de detección; y los machos se desplazaron más ampliamente que las hembras a lo largo de la cuadrícula de las cámaras. Jaguares de ambos sexos cruzaron dos ríos principales, mientras que el cruce de carreteras no fue común y estuvo sesgado hacia los machos, generando la preocupación de que las carreteras puedan impedir el movimiento de hembras si el tráfico vehicular aumenta. Los jaguares fueron más transitorios en paisajes fragmentados por asentamientos

humanos y agricultura que en áreas de bosque continuo. Comparando con los jaguares de los bosques protegidos de las Montañas Mayas, los jaguares de la zona central de Belice mostraron menor potencial para invertir en comunicación intraespecífica, indicador de un paisaje de menor calidad; sin embargo, se detectó comportamiento de apareamientos y la presencia de juveniles. La permanencia de individuos fue más corta que en los bosques protegidos, con una tasa de recambio más alta para machos que para hembras. Al menos las tres cuartas partes de las muertes reportadas de jaguares causadas por humanos correspondieron a jaguares machos, la mayoría como retaliación por la muerte de ganado. Los jaguares parecen relativamente tolerantes del paisaje dominado por humanos en la zona central de Belice. Sin embargo, el aumento de la cacería de especies presa y el control letal de predadores amenazaría la persistencia de la población, mientras que el aumento del tráfico vehicular y la deforestación de bosques de galería reducirían severamente la funcionalidad del corredor. Nuestros resultados muestran que la viabilidad del corredor y por lo tanto la sobrevivencia de jaguares a largo plazo en esta región dependerá de la planificación apropiada del uso del suelo, de un control no letal de predadores de ganado, una mejor regulación de la cacería, y de una infraestructura amigable con la vida silvestre en las futuras carreteras.

Palabras clave: captura-recaptura espacialmente explícita, corredor, densidad, jaguar, *Panthera onca*, trampas-cámara

Three-quarters of large carnivore species are experiencing population decline and range contraction due to habitat loss and degradation, depletion of wild prey, direct killing associated with livestock protection, and the use of body parts (Ripple et al. 2014; Benítez-López et al. 2019). In the case of the largest felids, tigers (*Panthera tigris*) and lions (*Panthera leo*) now occupy just 7% and 8% of their historic ranges, respectively (Dinerstein et al. 2007; Bauer et al. 2016), and the remaining populations are highly fragmented (Walston et al. 2010; Dolrenry et al. 2014). Jaguars (*Panthera onca*) have lost approximately half of their historic range, and have been extirpated from over three-quarters of their Mesoamerican range (Wulsch et al. 2016; de la Torre et al. 2017a; Quigley et al. 2017). Due to their wide-ranging behavior combined with shrinking areas of natural habitat, jaguars roam beyond boundaries of protected areas and natural wilderness into human-influenced landscapes, where they come into conflict with people (Woodroffe and Ginsberg 1998; Foster 2008; Inskip and Zimmermann 2009; Foster et al. 2010a). Although recent estimates of the global jaguar population size are contested, there is agreement that populations outside of Amazonia generally are small and fragmented (de la Torre et al. 2017a; Jędrzejewski et al. 2018). Further population decline could be averted by protecting source populations, enabling exchange between populations, and limiting population sinks throughout the landscape (Foster 2008). To ensure metapopulation persistence by informing land-use management and conservation strategies at the local and range-wide level, we need to understand jaguar population ecology across the whole landscape, including human-influenced areas.

All Mesoamerican jaguar subpopulations are considered endangered or critically endangered, with at least 75% experiencing population declines and fragmentation (Sanderson et al. 2002; Wulsch et al. 2016; de la Torre et al. 2017a). The landscape of central Belize is crucial for the movement of jaguars between the 42,300 km² Selva Maya which spans northern Belize, western Guatemala, and southern Mexico and is the largest tropical forest block north of Colombia (IUCN 2020), and the 5,000 km² Maya Mountain Massif in Belize, considered a jaguar stronghold in the region (Rabinowitz and Zeller 2010;

Doncaster et al. 2012; Kay et al. 2015; Harmsen et al. 2017). In turn, the jaguar population of the Maya Mountain Massif depends on connection with the rest of Central America via southern Belize (Petracca 2010, 2011; Rabinowitz and Zeller 2010). In this study, we use data from large-scale, long-term camera-trap surveys in central Belize to investigate jaguar ecology across a mosaic landscape of natural and modified habitats, human settlements, and agriculture.

Two large-scale genetic studies have highlighted the importance of a north-south movement corridor for jaguars across their geographic range (Roques et al. 2016; Wulsch et al. 2016). The Jaguar Corridor Initiative is a range-wide conservation strategy that has identified source populations (Jaguar Conservation Units, from here on “JCU”) and over 180 putative corridors that may facilitate movement among populations (Rabinowitz and Zeller 2010; Zeller et al. 2013). However, changes in human activities and land use threaten the integrity of the movement corridors. For example, agricultural encroachment threatens the connectivity of a 240-km unprotected corridor along the eastern coast of Nicaragua, which constitutes the only link between the two main JCUs in the country (Petracca et al. 2014). Degradation of movement corridors, to the extent that they lack sufficient habitat or prey to support or attract dispersing individuals across sufficient distances, will isolate already threatened source populations. This may increase their vulnerability to demographic fluctuations, environmental perturbations, and inbreeding depression (MacArthur and Wilson 1967; Westemeier et al. 1998; Griffen and Drake 2008). Monitoring of wild populations in JCUs and jaguar corridors will aid our understanding of how jaguars respond to anthropogenic and environmental disturbances, and thus help prioritize conservation efforts.

Ecological research on jaguars largely has focused on populations inhabiting protected areas. For example, of the 131 published and unpublished estimates of jaguar density from camera-trap data across 93 field sites, 79% (104/131) are for areas with designated protected status, with 64% (84/131) exclusively in protected areas; one-third (36%, 47/131) include unprotected sites, with 21% (27/131) occurring exclusively in unprotected areas (Supplementary Data SD1). Research

in protected areas is useful for identifying potential source populations, and for understanding population dynamics and behavioral ecology under natural, potentially optimal, conditions (Harmsen et al. 2009, 2010a, 2010b, 2017). However, the spatial and behavioral ecology of jaguars differs between protected wilderness and the neighboring areas of agriculture and human disturbance (e.g., Conde et al. 2010; Foster et al. 2010a, 2010b; Colchero et al. 2011), and remains understudied because the majority of studies focus on estimating density at a site. Of the density estimates exclusively from unprotected areas (27 studies, 26 sites), the majority of surveys were carried out in forest concessions (10 studies, 10 sites), biosphere reserves (five studies, five sites), or livestock ranches with extensive areas of wilderness (four studies, three sites). Well-managed selective logging operations where hunting is prohibited may have low impact on jaguar populations, with densities comparable to those in protected forests (Kelly and Rowe 2014; Tobler et al. 2018). Similarly, large-scale cattle ranches, such as those in the Pantanal and Los Llanos, with abundant domestic and native prey species and low human population density, support high-density populations of jaguars (Soisalo and Cavalcanti 2006; Jędrzejewski et al. 2017). Few data are available on jaguars occupying the mosaic of human settlements and agriculture that comprise typical unprotected landscapes, including jaguar movement corridors. In this study, we estimated jaguar density across such a mosaic landscape, adding much-needed data to the body of work that currently is biased toward protected areas. Density estimates from unprotected lands will contribute to a more representative sampling of regional populations for compiling global population estimates, which to date are largely based on data from protected areas (e.g., de la Torre et al. 2017a; Jędrzejewski et al. 2018).

Natural habitat supporting wildlife movement through jaguar corridor landscapes is under considerable threat (e.g., Zemanova et al. 2017). Across the current jaguar range, forest fragmentation increased in corridor landscapes between 2000 and 2012, associated with a reduction in forest cover of 4.4% (46,000 km²—Olsoy et al. 2016). During this period, corridors lost more forest than JCUs, with higher rates of deforestation in unprotected than protected areas (Olsoy et al. 2016). In an interview-based study of habitat use by jaguars in 12 putative corridors across Central America, Petracca et al. (2018) predicted the probability of occurrence to be highest in central and southern Belize (> 0.9). In contrast, the probability of jaguar occurrence was ≤ 0.5 in each of the 10 putative corridors surveyed in the rest of Central America (Petracca et al. 2018).

Forest cover per se is not the only feature dictating the permeability of a mosaic landscape. The extent to which a putative corridor facilitates large carnivore movement will be impeded by physical features and sensory disturbances. These may include rivers, roads, agriculture, and settlements that obstruct movement, and zones or periods of human activity that may deter movement at particular times. These features and zones become barriers if the species avoids them or suffers increased mortality when crossing them. For species in which the sexes

or age groups respond differently, we may observe sex- or age-specific habitat fragmentation in which one demographic group moves through the landscape more easily than the other (e.g., Conde et al. 2010; Elliot et al. 2014). In large carnivores, males generally are more risk-prone than females, dispersing further and ranging more widely (Linnell et al. 1999; Hunter 2011; Elliot et al. 2014). Identifying behavioral differences between sexes can inform about the results of demographic fragmentation in human-influenced landscapes. In the case of jaguars, research in the Selva Maya forest of Mexico and Guatemala has demonstrated sex-specific habitat fragmentation, wherein the landscape is more permeable to males, with females displaying greater aversion to roads, agriculture, and human settlements, than do males (Conde et al. 2010; Colchero et al. 2011). The wider-ranging and risk-prone sex will come into contact with humans more frequently, and thus be at greater risk of conflict with humans (e.g., road traffic accidents, lethal control). However, the further dispersing sex also will be more likely to traverse a corridor, successfully moving from one JCU to another.

In landscapes such as JCUs, which allow the establishment of home ranges, we find stable systems of long-term tenure, and investment in intraspecific communication for delineating ranges, defending resources, and/or maximizing mating opportunities (Harmsen et al. 2009, 2016, 2017; Wooldridge et al. 2019). Deviations from these characteristics, such as short tenures, little potential for interaction among individuals, and overall low occurrence in the landscape, may reflect a less productive system while being indicative of a functional corridor. Within a landscape that supports dispersers only (the minimum requirement of a corridor), we would expect a high proportion of transient individuals, and minimal investment in delineating ranges, territorial defense, or searching for mates, as individuals move through seeking areas of higher quality.

Using data from large-scale and long-term camera-trapping, we use maximum likelihood spatially explicit capture-recapture (SCR) models (Borchers and Efford 2008) to derive jaguar density across the landscape of the Maya Forest Corridor (formerly the Central Belize Corridor), a human-influenced and largely unprotected landscape in central Belize. We investigate the limits of a landscape's functionality as a corridor by comparing sex differences in ranging behavior, daily activity patterns, and the tendency to cross physical features in the landscape; and by assessing the potential for interaction between conspecifics, the level of transience, and tenure length in terms of landscape use and occupation through time, and human-induced mortality of jaguars. As the only remaining connection between the jaguar populations inhabiting the Selva Maya and the Maya Mountain Massif forest blocks, this area forms a critical link in the regional jaguar corridor network.

MATERIALS AND METHODS

Study Area

Our study focused on the central plains of Belize, a mosaic landscape of lowland secondary broadleaf moist forest, short-grass

savannah, shrubland, wetland, and agriculture (Fig. 1). Human activities include livestock farming, citrus and sugar cane plantations, multi-crop slash and burn farms (“milpa farms” hereafter), game hunting, logging, and tourism.

Our surveys spanned private, community, and national lands, including nominally protected areas. Illegal extraction (hunting and logging) is common across the entire landscape (R. J. Foster, pers. obs.). The study area included the Maya Forest Corridor, which has a human population density of approximately five people per km², and the more densely populated lands to the north of the corridor, where human population is at least twice as high (Fig. 1). The ~750 km² corridor forms a critical link for wildlife movement from the Selva Maya forest of northern Belize, Guatemala, and Mexico, to the Maya Mountain Massif forest of southern Belize (Rabinowitz

and Zeller 2010; Petracca 2011; Doncaster et al. 2012; Kay et al. 2015).

The study area is bisected by a 64-km-long, two-lane highway, stretching between the cities of Belmopan and Belize City. The highway has an approximately 7.3-m wide tarmac surface with 1.2-m wide gravel shoulders, and is bordered along the entire length by natural vegetation, agriculture, and settlements (Fig. 1). A 23-km section of the highway passes through the corridor. During the study period, agriculture and settlements bordered at least one side of the corridor along 8% and 22% of its length, respectively; 69% was bordered on both sides by natural vegetation (lowland broadleaf forest, shrubland, and lowland savannah with trees); and 22% had canopy cover on both sides, considered potential crossing points for terrestrial forest species. Low

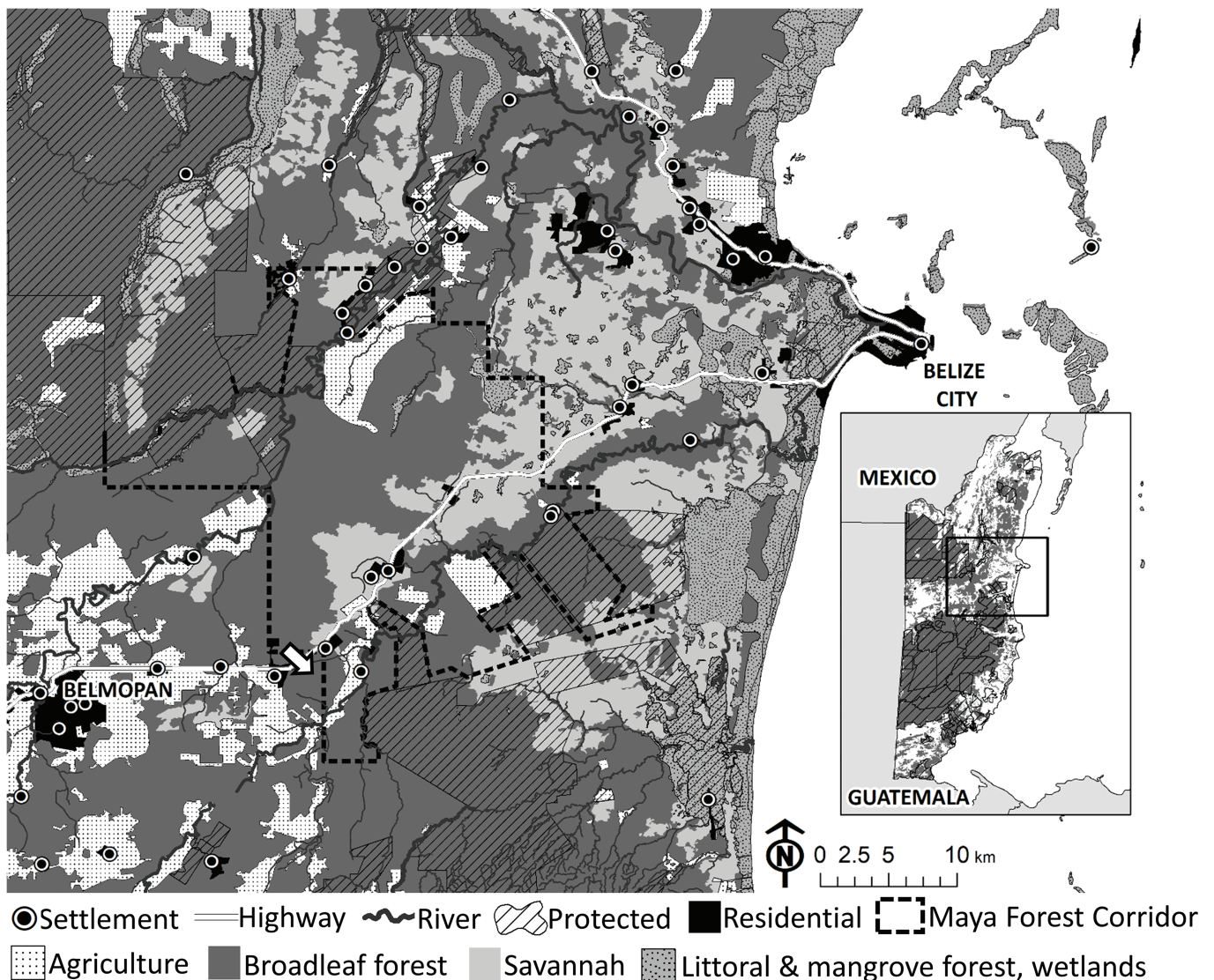


Fig. 1.—Study area in central Belize, showing broadleaf forest (lowland moist forest and moist scrub forest, and shrubland), lowland savannah (short-grass savannah with: dense trees or shrubs/scattered trees and or shrubs/seasonally waterlogged with broadleaf trees or shrubs), wetlands, mangrove and littoral forest, residential and agricultural lands, lands with protected status, rivers, the highway, settlements, and the delineation of the Maya Forest Corridor; white arrow with black outline on highway indicates the crossing point and direction of travel of an adult and juvenile jaguar (*Panthera onca*) observed on the highway in 2012; land cover shown is for 2011 from Meerman and Clabaugh (2017).

canopy vegetation along the northern side of the highway is periodically cleared up to about 30 m from the road for access to overhead cables, effectively widening the stretch of open space that an animal must be willing to traverse to cross the highway. Traffic volume through the study area along the highway is approximately 2,000 vehicles per day (McCarvell et al. 2012). The study area is bisected to the northwest by the Belize River and to the southeast by the Sibun River, approximately 50 m and 30 m wide, respectively (Fig. 1).

Belize experiences a dry season and a wet season, with most rain falling from June to November. The central plains are low-lying (≤ 60 m above sea level). Many areas experience low water availability during the dry season but become inundated with water during the wet season. In October 2010, a category 2 hurricane leveled approximately 163,000 ha of forest across central Belize (Meerman 2011). Large areas of dead wood from hurricane-downed trees burned extensively throughout the 2011 dry season (Meerman 2011). Most of the fires resulted from uncontrolled human-induced fires initiated for hunting or for clearing vegetation from below power lines (Meerman 2011). The damaged vegetation, fires, and partial recovery increased the spatial heterogeneity of the landscape.

Camera-Trap Data

Between 2008 and 2015, we collected data from camera traps deployed across the landscape. Camera locations were chosen to maximize the probability of detection of jaguars for density estimation, within the logistical constraints of accessing privately owned lands. We used Cuddeback (De Pere, Wisconsin) and Reconyx (Holmen, Wisconsin) from 2008 to 2011, and Bushnell (Overland Park, Kansas), Browning (Birmingham, Alabama), and Pantheracams (New York, New York), from 2012 onwards. We deployed cameras along artificial and natural funnels, including roads, pasture edges, man-made trails, game trails, cattle trails, and river banks. We used single or paired camera traps with either infrared or white flash depending on the location and risk of theft and/or flooding. All cameras were set to function continuously (24 h/day). We undertook “main” surveys in four areas: three in the core of the corridor, and one to the northeast (M1–M4; Fig. 2). Contiguous forest covered 90% and 76% of the M1 and M3 minimum convex polygon survey areas, respectively (Fig. 2). In contrast, for M2 and M4, forest patches covered 45% and 55% of the survey areas, respectively, fragmented by agriculture, settlements, the highway, and waterways (Fig. 2). The majority of cameras in M1 (95%), M2 (70%), and M3 (80%) sampled forest, while for M4, an equal proportion of cameras were distributed between forest and agriculture (each 39%; Fig. 2). Savannah comprised just 8% and 5% of the M1 and M3 survey areas, respectively, versus 45% and 20% for M2 and M4 (Fig. 2). Villages only were present in M2 and M4, covering 3% and 4% of the survey areas, respectively (Fig. 2). We ran each survey two or three times (total of nine surveys), for periods of 2–5 months each (Supplementary Data SD2). We collected additional camera data from two small-scale “supplementary” surveys along the banks of the Belize River (bordering the northern boundary of

the corridor) and along a logging road in the heart of the corridor (Fig. 2; Supplementary Data SD2). Main-survey camera stations were separated from nearest neighboring stations by $1,709 \pm 409$ m ($X \pm SD$, $n = 9$ surveys), and supplementary-survey camera stations were separated by 330 ± 76 m ($n = 2$ surveys). In total, across all survey grids and years, we collected data from 134 camera-trap locations spanning a minimum convex polygon of 718 km².

We identified jaguar individuals from their unique pelt pattern, and assigned sex based on the presence of testicles (following Silver et al. 2004 and Harmsen 2006). We assigned identities to 515 of the 542 jaguar detection events (the remaining 5% of photographs were too poor in quality to assign individual identities). For the majority of individuals, we used photographs of both flanks (“double-sided” individuals) to assign unique identities. However, for jaguars detected only at stations with one functional camera trap, either the right or left flank of the individual was photographed (“single-sided” individuals). If there are n single left flanks and m single right flanks within the data set, the conservative estimate of single-sided individuals is n or m , whichever is the greatest, and the maximum estimate of single-sided individuals is $n + m$. For analyses requiring individual identification (e.g., density estimation) we used all double-sided individuals plus either the left or the right single-sided individuals (whichever was greatest).

SCR density estimation.—For each of the nine main surveys, we selected survey periods of approximately 3.5 months ($X = 102$ days, range = 60–139; Table 1), excluded repeat detections of the same individual at the same location on the same day, and counted each 24-hour period as a trapping occasion for estimation of jaguar density using maximum likelihood SCR with the package “secr” in R (Efford 2016; R Development Core Team 2016). We modeled a half-normal detection function where the parameter g_0 is the capture probability if a detector were located at an individual’s activity center, and the spatial scale parameter, σ , relates to movement of individuals and describes the decline in capture probability with distance away from the activity center.

Across the jaguar’s geographic range, telemetry data estimate male ranges to be 1.1–3.1 times as large as female ranges (Cavalcanti and Gese 2009; Morato et al. 2016; de la Torre et al. 2017b; Kanda et al. 2019). Differences between the sexes in home range size and ranging behavior (such as the avoidance of trail systems; e.g., Sollmann et al. 2011) may result in sex-specific detectability by trail-based camera traps. Under these conditions, allowing g_0 and σ to vary by sex in SCR models can improve the accuracy of density estimates (Sollmann et al. 2011; Tobler and Powell 2013; Satter et al. 2019).

The scale parameter (σ) may be underestimated if the survey grid is small relative to home range size and/or if there are few spatial recaptures (Tobler et al. 2013; Tobler and Powell 2013). This in turn may positively bias the density estimate. If the average home range of the target population is known, the accuracy of density estimates can be improved by constraining σ to a fixed value (Tobler et al. 2013; Tobler and Powell 2013). In this

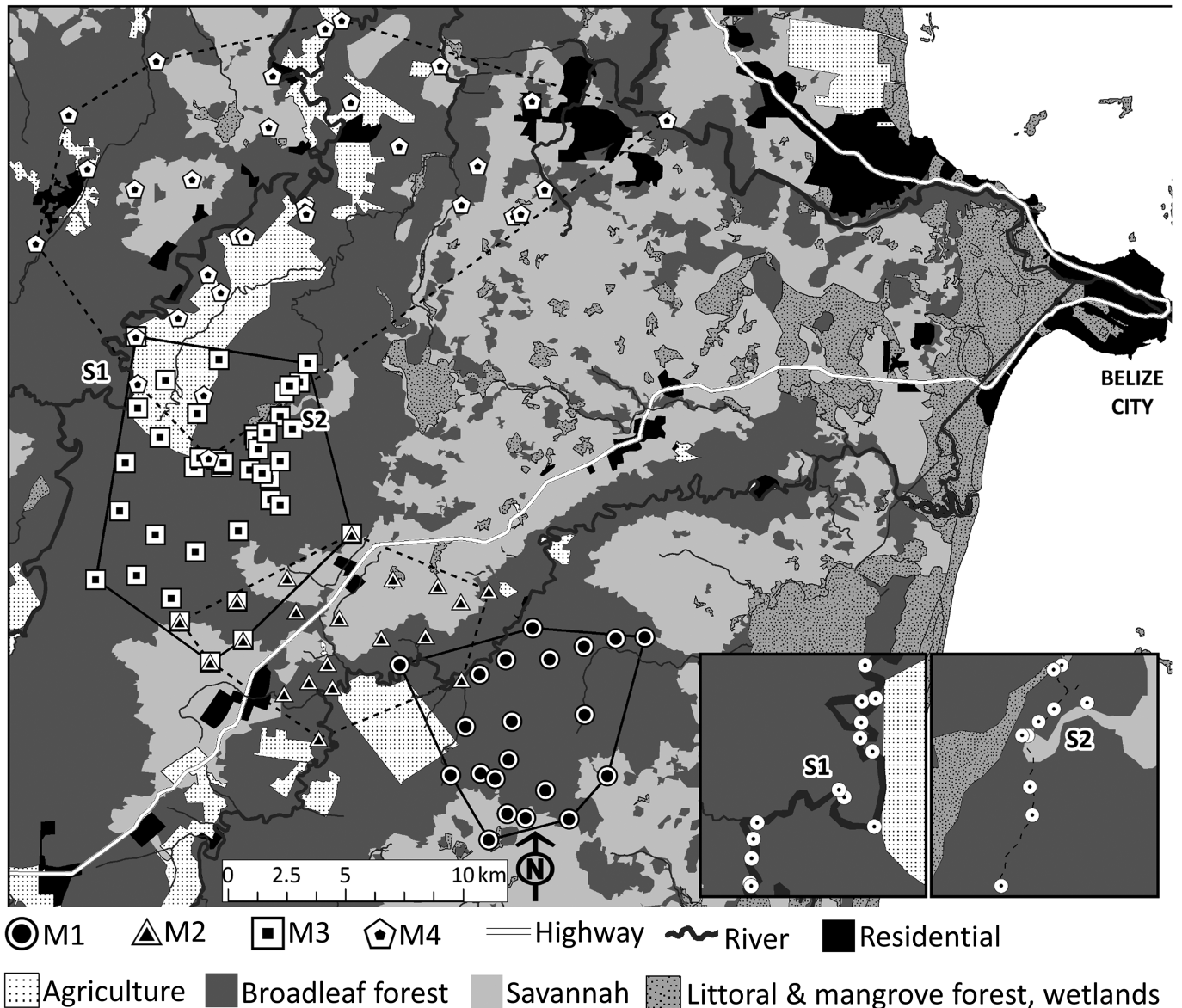


Fig. 2.—Distribution of cameras for four main surveys (M1–M4) in central Belize; locations of two supplementary surveys are indicated by S1 and S2, with insets showing camera distribution at these two sites. Note that some camera locations overlapped between M2 and M3 (triangle within square), and between M4 and M3 (pentagon within square).

Table 1.—Detections and spatial recaptures of jaguars (*Panthera onca*) in central Belize across nine camera-trap surveys conducted from 2008 to 2015 (M1A–M4B) showing number of occasions (Occ), number of stations (Stn), area of station grid as minimum convex polygon (Stn MCP), functional trap-nights (TN), the mean distance between nearest neighboring stations, individuals (Ind; numbers in parentheses are males M, females F, and individuals of unknown sex Unk), detections (Det), detections of the most frequently detected individual (Max det/ind), stations with jaguars detections, individuals with spatial recaptures (spt. recaps), and the median number of stations at which individuals with spatial recaptures were detected. Data are presented for the periods used for density estimation and overlap analysis only.

Survey	Occ (days)	Stn	Stn MCP (km ²)	TN	Mean (SD) dist neighbor stn (m)	Ind (M, F, Unk)	Det	Max det/ind	Stns with dets	Ind with spt. recaps	Median Stn/Ind (range)
M1A	124	20	62	1,876	1,581 (742)	9 (6, 3, 0)	45	16	18	6	4 (2–11)
M1B	60	21	62	1,248	1,491 (689)	9 (4, 4, 1)	52	22	12	7	4 (2–10)
M2A	104	20	68	1,723	1,643 (476)	9 (6, 2, 1)	18	5	8	2	2 (2–2)
M2B	100	20	68	1,865	1,643 (476)	10 (7, 2, 1)	17	5	7	1	3 (NA)
M3A	78	29	82	1,728	1,268 (867)	8 (4, 3, 1)	64	26	22	5	6 (2–10)
M3B	139	30	86	2,918	1,385 (719)	9 (7, 1, 1)	51	23	18	3	8 (3–10)
M3C	105	24	99	1,837	1,801 (532)	10 (8, 1, 1)	60	30	17	9	2 (2–10)
M4A	100	27	273	2,271	2,497 (1,088)	16 (11, 4, 1)	36	9	14	7	2 (2–4)
M4B	111	25	247	2,239	2,182 (1,172)	16 (8, 7, 1)	38	7	15	5	3 (2–4)

study, we used the SCR models to estimate σ , and also ran SCR models in which we constrained σ based on telemetry data.

We estimated σ from existing 95% kernel estimates of home range area (95HR, measured in km²), assuming a circular bivariate normal distribution of activity for which 95% of the activity is included within a radius of 2.45 σ meters (Efford et al. 2016):

$$\sigma = \sqrt{\frac{95HR}{\pi(2.45)^2}} \times 1,000$$

We used jaguar home range areas estimated from GPS collar data on six males and one female, which were tracked in the study area during the study period (Figueroa 2013). The mean 95HR = 250 \pm 21 km² ($X \pm SE$, from 464 \pm 34 locations per jaguar, range = 184 – 843, total = 3,246 locations; $n = 7$ individuals) yielded a universal spatial scale $\sigma_{uni} = 3,641$ m. We also estimated sex-specific σ values, with male $\sigma_m = 3,742$ m (from 95HR = 264 \pm 63 km², range = 127 – 531, $n = 6$) and female $\sigma_f = 2,993$ m (from 95HR = 169 km², $n = 1$), while recognizing that σ_f is based on the home range of only one individual.

For surveys with sufficient captures both of male and female individuals (> 30 detections and ≥ 3 individuals of each sex), we ran eight hybrid mixture models (Efford 2016). For four of these models, we constrained σ either to the sex-specific estimates (σ_m , σ_f) or to the universal estimate (σ_{uni}), and allowed $g0$ either to co-vary with sex ($g0_{sex}$), or not ($g0$). The other four models did not constrain σ , but allowed σ and/or $g0$ either to co-vary with sex (σ_{sex} , $g0_{sex}$) or not (σ , $g0$). For surveys with < 30 detections and ≤ 3 individuals of each sex, we ran only three models, excluding those with σ_{sex} or $g0_{sex}$. For each survey, we ranked the models using Akaike's Information Criterion (AIC) and assumed substantial support for those for which ΔAIC was < 2 relative to the minimum AIC (Akaike 1973; Burnham and Anderson 2002).

Ranging behavior.—GPS tracking of seven collared jaguars in central Belize showed a preference for broadleaf forest and shrubland over savannah and agriculture (Figueroa 2013). We therefore expected a higher level of transience in the areas of the landscape with savannah or fragmented by agriculture. We investigated the frequency of use of the landscape by calculating the mean detection rate per individual for each of the nine main surveys and comparing the estimates from the contiguous forest surveys (M1 and M3) with those carried out primarily in fragmented landscape (M2 and M4). We expected lower recapture rates per individual (greater transience, intermittent use) in the surveys spanning fragmented habitat versus contiguous forest.

For jaguars of known sex with ≥ 2 detections pooled across all surveys and years, we calculated the maximum distance moved (MDM) by each jaguar. We used MDM as a proxy for home range radius and compared it between males and females using a Student's t -test. We expected males to move larger distances than females.

Assuming that males range further than females, we expected to detect males more frequently and at more locations

than females. We used paired t -tests to compare the number of detections of males and females, and the number of male and female individuals detected, per location-month, where each location-month is the pooled data from a single camera-trap location for 1 month (Harmsen et al. 2009). We used only the location-months with at least one jaguar detection. Following Harmsen et al. (2009), we investigated the potential for dynamic interaction (communication) within and between the sexes at camera locations, by recording the number of males and females detected per location-month for all location-months with at least two jaguar detections and plotting a frequency distribution of individuals, per sex, per location-month. In the tropical environment of Belize, Wooldridge et al. (2019) showed that visual and olfactory marks of big cats degraded within 28 days, and suggested that beyond this time they no longer hold a signaling function. Thus, in this study, we assume that individuals associated with the same location-month (i.e., present at the same location during the same month) would have the potential for communication. Low potential for communication among conspecifics could be inferred from a high proportion of location-months with single individuals (Harmsen et al. 2009). For all the location-month analyses, we restricted the data set to the survey periods used for the SCR analyses ($X = 102$ days, range = 60 – 139). Because some camera stations contributed multiple location-months (range = 1 – 9), we checked for the effects of nonindependence by comparing the results from two data sets: one in which we averaged location-months from the same location, and one in which we treated all location-months separately (Harmsen et al. 2009). Because we found no difference between the results, we report only the results with highest sample size.

We counted the number of jaguar individuals that were detected on both sides of the highway and the two major rivers that cross the study area, and compared the proportion between males and females. Because males tend to be wider-ranging and more risk-prone than females (Linnell et al. 1999), we expected to detect more highway crossings among males than among females. Because jaguars are considered to be excellent swimmers (Sunquist and Sunquist 2002), we did not expect any difference between the proportion of males and females crossing rivers.

Twenty-four-hour activity patterns.—We investigated the daily activity pattern of male and female jaguars by pooling data across all camera locations. When the same individual was detected multiple times on the same day, we randomly selected one detection for inclusion in the data set and excluded the others, to ensure independence. We used the R package “overlap” (Meredith and Ridout 2016) to estimate the kernel densities of the temporal distribution of males and females, and then estimated the coefficient of overlap following Ridout and Linkie (2009). A value of 0 indicates no overlap and a value of 1 indicates identical activity patterns. We estimated the precision of the coefficient of overlap by bootstrapping with 999 simulations each for males and females (Meredith and Ridout 2016). Because females tend to be more risk-averse than males, we expected females to be less active than males during the

daytime, when the likelihood of sensory disturbance from human activities is greatest.

Length of tenure in the study area.—For individuals first detected prior to 2015, we calculated their “potential” tenure as the interval between the date of first detection and the last date of camera monitoring in the study area. Depending on the exact date of first detection, the maximum measurable tenure lengths were ~6 years for individuals first detected during 2008, ~5 years for those in 2009, ~4 years in 2010, and so on. Thus, all individuals detected between December 2008 and July 2014 had the potential to be detected 1 year after their first detection, while only the subset first detected between December 2008 and July 2009 had the potential to be detected during all years of camera surveys. As an index of the rate of “disappearance” of individuals from the study area, we calculated the proportion of individuals detected 1 year after first detection, 2 years after, 3 years after, ... up to 6 years after, as the actual number of individuals still detected x years after their first detection divided by the number of individuals that had the potential to be detected x years after their first detection. We calculated the proportions separately for males and females, and compared between the sexes. Because males tend to be wider-ranging and more risk-prone than females, we expected a higher turnover of males than females, reflecting their higher mortality rate and/or longer-distance dispersal (Sunquist and Sunquist 2002). If the landscape functions as a dispersal corridor and/or has high mortality, we would expect to detect a high turnover of individuals of both sexes. If the landscape supports a resident population, then we would expect to detect the same individuals over repeated surveys, with a higher tendency for philopatry in females versus long-range dispersal in males (Sunquist and Sunquist 2002). We recognize that our quantification of tenure will be an underestimate because we moved camera surveys across the landscape between years, with the result that some individuals may have escaped repeated detection simply because their ranges did not span multiple survey grids.

Human-induced mortality.—As part of an associated study of farm management and livestock predation, between November 2012 and February 2013, we interviewed all 71 livestock farmers in the central Belize landscape. The study was authorized by, and carried out in conjunction with, the government of Belize’s Forest Department. We asked each respondent how many jaguars had been killed on their farm since 2008 (the year in which we commenced the camera-trap surveys). The respondents varied in the detail they provided, but nearly always included the sex of the culled jaguar. We also kept records of opportunistically received reports of jaguar deaths in the study area (e.g., road traffic accidents, illegal hunting).

RESULTS

For the 6.5 years between December 2008 and July 2015, we collected data from 23,827 trap-nights across 134 camera locations. These data yielded 519 detections of jaguars (excluding repeat detections of the same individual at the same location on

the same day), comprising 52 – 61 adult jaguars (31 – 33 males, 14 – 16 females, and 8 – 12 of unknown sex), and 2 – 3 cubs.

SCR density estimation.—Five of the nine surveys met our criteria for inclusion of the sex covariate when estimating model parameters (> 30 detections and ≥ 3 individuals of each sex; surveys M1A, M1B, M3A, M4A, and M4B). For all surveys, we found substantial support for models of constant capture probability (g_0 ; [Supplementary Data SD3](#)). Three surveys (M3A, M4A, M4B) had competing models that allowed g_0 to vary with sex ([Supplementary Data SD3](#)). For those models, the estimate of g_0 was higher for males than for females, and density estimates were higher and generally less precise than for models of constant g_0 ([Table 2](#)). Estimates of g_0 generally were low and unstable, both within sites between repeat surveys and among survey sites. For the same models, estimates of g_0 varied by up to a factor of 3 within sites through time, and by up to 16.7 \times across survey sites and time ([Table 2](#)). The mean g_0 for the contiguous forest surveys (M1 and M3) was greater than for the surveys with fragmented land cover (contiguous M1 and M3, mean $g_0 = 0.03$, range 0.014 – 0.040, $N = 5$ surveys; fragmented M2 and M4, mean $g_0 = 0.007$, range 0.003 – 0.009, $N = 4$ surveys; [Table 2](#), model $\sigma_m\sigma_fg_0$).

For all surveys, we found substantial support for models for which we fixed σ according to the telemetry data from the study area (σ_{uni} or σ_m and σ_f ; [Supplementary Data SD3](#)). Density estimates were lower and generally more precise for models where σ was constrained to an average value across the sexes (σ_{uni}) rather than a separate male and female value ($\sigma_m\sigma_f$). Since σ_{uni} was derived from the home ranges of six males and only one female, we suspect that it was too large to be representative of a substantial proportion of the female population, and this may explain the lower density estimates for the σ_{uni} models versus the $\sigma_m\sigma_f$ models. Of note, for surveys M3B and M3C, which had a female:male ratio similar to the ratio of female and male home ranges used to estimate σ_{uni} , the density estimates from the σ_{uni} models are the same as those from $\sigma_m\sigma_f$ models ([Tables 1](#) and [2](#)). For two surveys (M2B and M4B), there also were competing models for which σ was estimated from spatial recaptures (σ and σ_{sex} , respectively; [Supplementary Data SD3](#)). For both these models, estimates of σ were lower than those estimated from telemetry data, and estimates of g_0 and density were higher and less precise ([Table 2](#)). In particular, for survey M2B, the estimate of σ from spatial recaptures had just one-third the magnitude of that derived from the telemetry data (1,209 m versus 3,641 m). The low value of σ contributed to a noticeably high and imprecise density estimate ([Table 2](#)).

Surveys M2A and M2B had few detections (< 20) and few spatial recaptures (1 – 2 individuals with spatial recaptures; [Table 1](#)), giving relatively imprecise density estimates when compared with the other surveys ([Table 2](#)). Overall, the only model with substantial support ($\Delta\text{AIC} < 2$ relative to the minimum AIC) across all survey years and sites had constant g_0 and σ fixed according to telemetry data from males and females ($\sigma_m\sigma_fg_0$). Using this model and excluding survey M2A and M2B gives densities that were stable both within sites between repeat surveys, and between sites; with a mean \pm SD estimate

Table 2.—Estimates of capture probability (g_0), spatial scale parameter (σ), density (D), and the effective sampling area (ESA) of the best-fitting spatially explicit capture-recapture (SCR) models (ΔAIC_c is < 2 relative to the minimum AIC_c) for jaguars (*Panthera onca*) for each of nine camera-trap surveys conducted in central Belize from 2008 to 2015 (M1A–M4B); constrained σ based on telemetry data shown in italics (Uni = universal; M = males; F = females). σ_{uni} (σ constrained to 3,641 m); σ_m (σ constrained to 3,742 for males); σ_f (σ constrained to 2,993 for females); σ_{sex} (σ allowed to co-vary with sex); $g_{0_{sex}}$ (g_0 allowed to co-vary with sex).

Survey	Model	g_0 (95% CL)	σ (95% CL, in meters)	D (95% CL) (individuals/100 km ²)	ESA (km ²)
M1A	$\sigma_m \sigma_f g_0$	0.015 (0.010–0.023)	$M = 3,742; F = 2,993$	2.33 (1.19–4.55)	387
	$\sigma_{uni} g_0$	0.016 (0.010–0.024)	<i>Uni = 3,641</i>	2.14 (1.10–4.15)	421
M1B	$\sigma_m \sigma_f g_0$	0.050 (0.028–0.087)	$M = 3,742; F = 2,993$	2.01 (1.03–3.93)	448
	$\sigma_{uni} g_0$	0.053 (0.030–0.094)	<i>Uni = 3,641</i>	1.75 (0.09–3.39)	515
M2A	$\sigma_m \sigma_f g_0$	0.005 (0.002–0.013)	$M = 3,742; F = 2,993$	3.12 (1.44–6.78)	288
	$\sigma_{uni} g_0$	0.005 (0.002–0.013)	<i>Uni = 3,641</i>	2.96 (1.37–6.40)	304
M2B	$\sigma_m \sigma_f g_0$	0.011 (0.004–0.030)	$M = 3,742; F = 2,993$	10.10 (4.79–21.35)	99
	$\sigma_{uni} g_0$	0.011 (0.004–0.030)	<i>Uni = 3,641</i>	3.97 (1.76–8.99)	252
M3A	$\sigma_m \sigma_f g_0$	$M = 0.047$ (0.026–0.084)	$M = 3,742; F = 2,993$	2.34 (0.96–5.67)	352
	$\sigma_{uni} g_0$	$F = 0.005$ (0.001–0.014)	<i>Uni = 3,641</i>	1.37 (0.68–2.76)	584
	$\sigma_{uni} g_{0_{sex}}$	$M = 0.046$ (0.026–0.079)	<i>Uni = 3,641</i>	2.03 (0.87–4.74)	402
		$F = 0.004$ (0.001–0.013)			
M3B	$\sigma_m \sigma_f g_0$	0.036 (0.023–0.057)	$M = 3,742; F = 2,993$	1.54 (0.76–3.14)	519
	$\sigma_m \sigma_f g_0$	0.014 (0.009–0.020)	$M = 3,742; F = 2,993$	1.68 (0.87–3.27)	535
M3C	$\sigma_{uni} g_0$	0.014 (0.010–0.021)	<i>Uni = 3,641</i>	1.67 (0.86–3.23)	540
	$\sigma_m \sigma_f g_0$	0.040 (0.025–0.063)	$M = 3,742; F = 2,993$	1.68 (0.89–3.16)	596
M4A	$\sigma_{uni} g_0$	0.040 (0.025–0.064)	<i>Uni = 3,641</i>	1.67 (0.89–3.13)	598
	$\sigma_m \sigma_f g_{0_{sex}}$	$M = 0.013$ (0.007–0.025)	$M = 3,742; F = 2,993$	3.22 (1.53–6.78)	501
		$F = 0.003$ (0.001–0.012)			
	$\sigma_m \sigma_f g_0$	0.009 (0.005–0.016)	$M = 3,742; F = 2,993$	2.69 (1.57–4.59)	596
	$\sigma_{uni} g_{0_{sex}}$	$M = 0.013$ (0.007–0.026)	<i>Uni = 3,641</i>	3.04 (1.50–6.16)	530
		$F = 0.002$ (0.001–0.010)			
M4B	$\sigma_m \sigma_f g_0$	0.009 (0.005–0.016)	$M = 3,742; F = 2,993$	3.06 (1.79–5.20)	524
	$\sigma_{sex} g_0$	0.016 (0.008–0.031)	$M = 3,257$ (2,304–4,602)	4.13 (2.28–7.50)	389
		$F = 1,679$ (1,179–2,390)			
	$\sigma_m \sigma_f g_{0_{sex}}$	$M = 0.018$ (0.006–0.050)	$M = 3,742; F = 2,993$	3.10 (1.76–5.43)	519
		$F = 0.006$ (0.003–0.013)			

of density of 2.1 ± 0.5 individuals/100 km², ranging from 1.5 to 3.1 across the landscape of central Belize (from seven surveys and three sites over 7 years; Table 2).

Ranging behavior.—Individual recapture rates were higher within surveys comprising primarily contiguous forest versus fragmented forest (mean detection rate per individual: contiguous = 2.0 – 4.6 detections per individual per 1,000 trap-nights, $N = 5$ surveys; fragmented = 0.9 – 1.2, $N = 4$ surveys) suggesting lower site fidelity in the more fragmented landscape. In every survey, the most frequently detected individual was male, responsible for more than one-third (36–50%) of the total detections in the contiguous forest surveys but less than one-third (18–29%) in the fragmented forest surveys (Table 1). Conversely, individuals that were recorded once during a survey comprised only 2 – 10% of detections in the contiguous forest surveys, and 18 – 41% of detections in the fragmented forest surveys, suggesting greater transience in the latter.

The maximum distance between any two stations in the study area was 36.8 km. The maximum distance between any two stations at which the same jaguar was detected (MDM) was 16.2 km over 5.8 years for a female, and 28.2 km over 5.2 years for a male. The average MDMs were almost twice as large for males as for females, suggesting that males tend to range further than females in this landscape (10.3 ± 6.4 km for 30 males, 5.7 ± 5.1 km for 14 females; two-sample t -test $t_{31} = -2.58$, $P < 0.05$).

Of the 729 location-months derived from 104 stations across nine surveys, we detected jaguars at 221 location-months, and assigned sex to jaguars at 215 location-months (78 stations). Males were more common across the landscape than females, detected 87% of location-months (188/215), versus 26% for females (56/215). We detected males more often than females (mean detections per location-month $\pm SD$: males = 1.4 ± 1.0 , range 0 – 6; females = 0.4 ± 0.7 , range 0–3; paired-sample t -test t -value = 11.71, $P < 0.001$, $N = 215$ location-months) and more males than females (mean individuals per location-month: males = 1.0 ± 0.6 , range 0 – 3; females = 0.3 ± 0.5 , range 0 – 2; paired-sample t -test t -value = 12.47, $P < 0.001$, $N = 215$ location-months), suggesting a detection bias between the sexes, probably associated with the longer range movements of males than females, such that males more frequently encountered camera locations than did females.

We recorded at least two jaguar detections for 82 of the location-months (43 stations), and used these to investigate overlap within and between the sexes. Our results suggest low potential for communication within the sexes: for both sexes, we most commonly detected single individuals, with single males at 62% (49/79) of location-months where we detected males, and single females at 84% (27/32) of location-months where we detected females (Fig. 3). We found the same pattern when we analyzed the contiguous and fragmented surveys separately,

suggesting that the potential for communication did not vary across the mosaic landscape. We detected individuals of both sexes at only 35% (29/82) of location-months, accounting for 55% (29/53) of the location-months with multiple individuals.

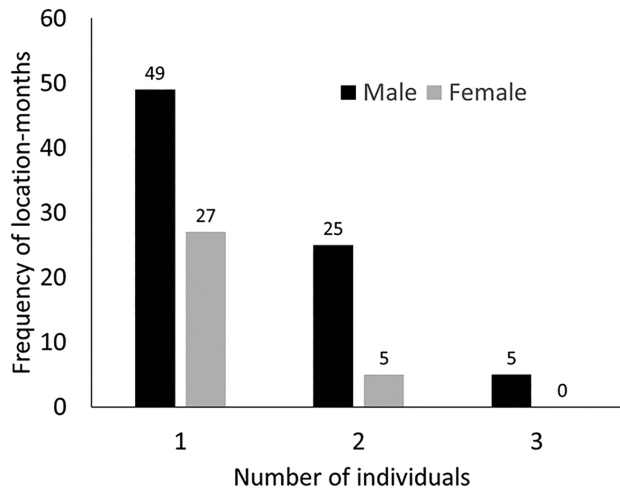


Fig. 3.—Frequency of shared or single occupancy per camera location per month (“location-month”) within the sexes by jaguars (*Panthera onca*) at location-months with ≥ 2 jaguar detections and for which sex could be assigned ($N = 82$ location-months representing 43 camera locations); the data are derived from nine camera-trap surveys which sampled a total of 104 locations in the central Belizean landscape between 2008 and 2015, with an average survey length of 102 days (range 60–139), and an average of 24 locations per survey (range 19–30), producing a total of 729 location-months; black bars indicate males ($N = 79$ location-months), gray bars indicate females ($N = 32$ location-months).

These results suggest the potential for male–female communication and thus mating opportunities within the corridor landscape. The relatively low proportion of location-months in which we detected individuals of both sexes may be attributable partially to the detection bias of males over females. Where the sexes overlapped, we detected up to three males and up to two females but more commonly, the number of males equaled the number of females (equal sex ratio 69%, male-biased 17%, female-biased 14%; [Supplementary Data SD4](#)).

Of the 42 “double-sided” jaguars (individuals for which we had records of both flanks, $n = 28$ males, 11 females, and three of unknown sex), we detected four jaguars (10%) on both sides of the highway, and 14 jaguars (33%, including one single-sided female) on both sides of either of the major rivers (eight for Belize River and six for Sibun River). Of the jaguars that crossed a river, nine were male (32% of males), four were female (33% of females), and one was of unknown sex. In contrast, all four jaguars that crossed the highway were male (14% of males). We found no evidence that any of the 11 females crossed the highway. In 2012, however, an adult female and juvenile were observed crossing the highway during the middle of the day at a place where the highway was bordered by forest on both sides (B. Martinico and R. Bourbour, University of California Davis, pers. comm.; [Figs. 1 and 4](#)). Since the photograph was taken, the forest has been cleared from one side of the highway section shown in [Fig. 4](#).

Twenty-four-hour activity patterns.—Jaguars were detected at all hours of the day and night, and most frequently detected at night between 1800 and 0600 h ([Fig. 5](#)). Detection rate increased sharply from approximately 1500 h, peaking between 1930 and 2000 h, and then declined steeply from approximately



Fig. 4.—Juvenile jaguar (*Panthera onca*) crossing the Western Highway in central Belize in 2012; the two-lane highway is 7.3 m wide with gravel/rough stone shoulders (~1.2 m wide) grading into natural vegetation, with an additional verge up to 30 m wide of vegetation cleared seasonally for access to overhead cables on the northern (left-hand) side of the highway. (Photo credit: Breanna Martinico and Ryan Bourbour 2012).

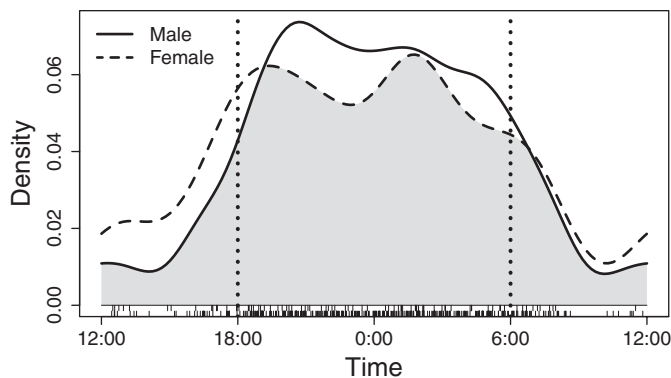


Fig. 5.—Kernel densities of the temporal distribution of male and female jaguars (*Panthera onca*) detected by camera traps in central Belize; gray shaded area shows overlap; vertical black dotted lines indicate approximate times of sunrise (0530–0630 h) and sunset (1730–1830 h); upper and lower vertical lines along x-axis indicate female and male detections, respectively, $n = 327$ independent male detections and 81 independent female detections.

0600 until 1000 h. Male and female activity patterns were similar but not identical, having an overlap coefficient of 0.86 (95% $CI = 0.82 - 0.97$, $n = 327$ male detections and 81 female detections). Females were more active than males between 1200 and 1800 h, while males were more active than females between 1800 and 0600 h. Overall, the females had a longer active period over the course of the night, starting earlier than males, but finishing at the same time.

Length of tenure in the study area.—Longevity in the study area differed between males and females (Fig. 6), such that 70% (7/10) of females and 58% (15/26) of males that had the potential to be detected 1 year after their first year of detection were detected; while half (3/6) of females but only 8% (1/12) of males that had the potential to be detected 5 years after their first detection were detected. None of the four females or 10 males that had the potential to be detected 6 years after their first detection were detected during the final year of study. Females appeared to have longer tenure than males, despite their smaller ranges and the moving survey grids, strengthening the argument that females are more philopatric than males in this landscape.

Human-induced mortality.—Respondents in our survey of 71 farms reported that at least 15 jaguars were killed in response to livestock predation in the study area between 2008 and 2012, of which at least nine were male and three were female. In addition, we know of one male jaguar that appeared to have been killed opportunistically by hunters, and two male jaguars that were killed in road traffic accidents on the 23-km stretch of highway that bisects the corridor (all three deaths reported in Figueroa 2013).

DISCUSSION

Our study has shown that jaguars are ubiquitous, and predominantly nocturnal, across the mosaic landscape of central Belize, and provides new data on the ecology and dynamics of jaguars

using a critical movement corridor. Within our camera grids, male jaguars moved larger distances than females, and we detected more males than females, and more frequently. A male bias in the detection of jaguars often is documented in data from camera-trap surveys, and likely is an artifact of the males ranging more widely, exacerbated by females avoiding trail systems dominated by males, and the tendency for researchers to deploy camera traps on trails (Maffei et al. 2011; Foster and Harmsen 2012; Boron et al. 2016; Harmsen et al. 2017).

Our estimates of jaguar density across the landscape of central Belize are within the range of those from the neighboring Selva Maya Forest JCU. There, the mean jaguar density across two protected tropical moist lowland forest sites surveyed annually from 2009 to 2013 was 3.3 individuals/100 km² (range 0.6–6, $n = 10$ —Kelly and Rowe 2014), compared to a mean of 2.1 individuals/100 km² in this study (range 1.5–3.1, $n = 7$). Estimates of jaguar density outside of Belize range between 0.5 and 5.6 individuals/100 km², differing with habitat, land use, and human activities. In tropical moist lowland forests outside of Belize, jaguar density estimates are similar to those reported in this study, ranging from 1.0 to 4.5 individuals/100 km², with higher estimates from areas with no human activities or logging concessions only, and lower estimates at sites with settlements and hunting (Petit et al. 2017; Pierre et al. 2018; Tobler et al. 2018). In other habitats, the highest jaguar densities have been estimated on an expansive conservation-friendly cattle ranch and nature reserve in Venezuela, a mosaic of open lowland savannah, pastures, open marshes, and deciduous and dry forests (3.7–5.6 individuals/100 km²—Jędrzejewski et al. 2017). The high density was attributed to the high prey availability and productivity, and prohibition of hunting in this area, and contrasted with the lower estimate (2.2 individuals/100 km²) obtained from a similar landscape in Colombia where there is livestock but hunting of jaguars and their prey is common (Boron et al. 2016; Jędrzejewski et al. 2017). Similarly, low density (2.0 individuals/100 km²) has been estimated for a mosaic landscape of tropical dry forest with settlements, crops, and hunting in Mexico (Figel et al. 2016). The lowest estimates are from sites in the transitional Chaco/tropical dry forests of Bolivia, with livestock and hunting (0.5–1.0 individuals/100 km²—Maffei et al. 2002; Cuéllar et al. 2003a, 2003b; Peña et al. 2004; Montaña et al. 2010; Noss et al. 2012). Overall, sites with livestock and hunting of wild prey tend to have the lowest jaguar densities.

The protected forest of the Maya Mountain Massif JCU is situated approximately 50 km from our study area in central Belize and supports stable populations of wild prey and one of the highest jaguar densities in the region (Harmsen et al. 2010b). In this JCU, the average weight of prey animals consumed by jaguars was 7.1 kg (Foster et al. 2010b; Harmsen et al. 2010b). In contrast, jaguar scats collected primarily in the contiguous forest of central Belize revealed smaller prey, averaging 4.6 kg (Figueroa 2013), suggesting that larger ungulate prey species are less common in this landscape than in the JCU. At both sites, the nocturnal nine-banded armadillo was the most commonly consumed prey, associated with the predominantly

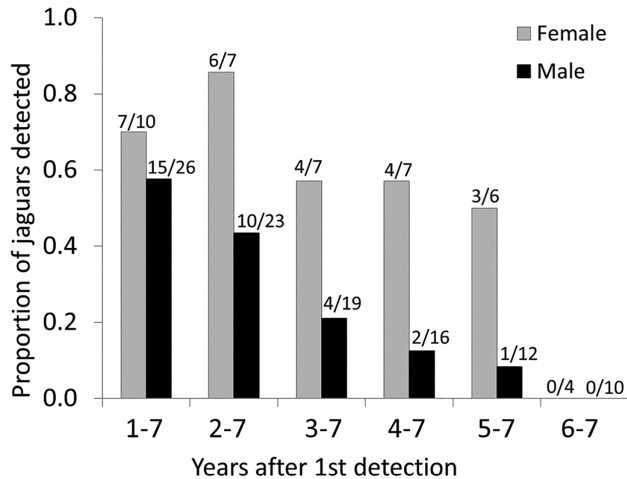


Fig. 6.—Jaguar individuals detected as a proportion of those that had the potential to be detected x years (1, 2, ..., up to 6.6 years) after their first detection by camera traps in central Belize (1 December 2008 to 21 July 2015); shown separately for males (black) and females (gray); $n = 36$ jaguars; fractions indicate sample sizes, e.g., seven female jaguars were actually detected at least 1 year after their first detection, out of 10 that had the potential to be detected at least 1 year after their first detection; three female jaguars were detected at least 5 years after their first detection, out of six that had the potential to be detected at least 5 years after their first detection.

nocturnal activity of jaguars in both areas (Foster et al. 2010b; Harmsen et al. 2011; Figueroa 2013). The scarcity of larger prey is not unexpected: game hunting is prolific throughout central Belize, and loosely regulated, with hunters rarely seeking to obtain hunting licenses, and no mechanism in place for the authorities to regulate or monitor harvest (R. J. Foster and Y. L. Urbina, pers. obs.). In areas with unsustainable harvests, jaguars will be forced into competition with hunters for wild prey, and exposed to persecution when searching for alternative domestic prey (Foster et al. 2016). Although the carrying capacity of jaguars may increase if large domestic ungulates are abundant, retaliatory killings by farmers protecting their livestock may subsequently decrease jaguar survival. The development of such a situation in the Maya Forest Corridor would be detrimental to its critical function of connecting habitats if low survival impedes jaguar movement between JCUs.

On average, individual jaguars were recaptured less often in the fragmented landscape than in areas of contiguous forest. Detection patterns of jaguars in contiguous forest were similar to those in the undisturbed protected forests of the Maya Mountain Massif JCU in southeastern Belize, in which a minority of individuals comprised the majority of detections (local residents), and the majority of individuals were detected at a low level (local transients—Harmsen et al. 2017). This pattern of detections was not observed in the fragmented survey sites, where all detected individuals were more transient, perhaps reflecting the higher levels of human activity and/or lower prey availability in these areas.

Across the landscape, jaguars of the same sex tended not to use the same location during the same month, suggesting low investment in resource defense and/or range delineation

within the sexes. In comparison, within the undisturbed protected forest of the Maya Mountain Massif JCU there was a higher tendency for shared occupancy among conspecific males: in this study 62% of location-months with single males, versus 24% in the JCU protected forest (Harmsen et al. 2009). Male jaguar ranges in central Belize are approximately twice the size of those of the protected forest of the JCU (Figueroa 2013; Harmsen et al. 2020). Large transient ranges and minimal investment in communication between individuals of the same sex suggest a landscape that is of lower quality for jaguars compared to the protected forest: this may reflect a lower availability of prey, greater sensory disturbances, and/or less suitable habitat. While investment in communication within the sexes was relatively rare, use of the same location during the same month by both sexes was more common (males and females detected at 55% of the location-months with multiple individuals despite an overall negative bias in the detection of females in this study). Our camera data also revealed evidence of mating events and juvenile jaguars in the study area. Together, these results suggest residency for some females in the area.

Evidence suggests that jaguars avoid roads with vehicular traffic; for example, Foster et al. (2010a) found that jaguar use of the road leading into the protected forest of the Maya Mountain Massif JCU decreased during peak tourist months, when motor-vehicle intensity along the road and human activity both were high. In this study, recorded highway crossings by jaguars were infrequent and male-biased, with 14% of males detected on both sides. Compared to males, female jaguars may be more risk-averse and sensitive to anthropogenic disturbances such as paved roads and traffic. Analyses of GPS telemetry locations have shown that female jaguars in the Selva Maya forest of Guatemala and Mexico avoided roads, whereas this relationship was not observed for males (Conde et al. 2010). Despite a relatively low frequency of motor traffic, especially at night, the highway may be already impacting movement of individuals, particularly females, in central Belize. A decade since this study began, the length of corridor highway with canopy cover on both sides has diminished from approximately 5 km to 2.8 km. The clearance of forest from both sides of the highway and an increase in traffic volume associated with development and human population increase likely will lead to the highway becoming a movement barrier for jaguars and other terrestrial vertebrates. In comparison, one-third of jaguars in this study crossed a major river, with no difference between the proportion of males and females that crossed. These rivers, which are three to four times wider than the highway, still are partially bounded by riparian forest, aiding jaguar movement throughout the study area. However, the ongoing conversion of fertile riparian forest to agricultural croplands could convert these rivers to barriers. In combination with the highway, such activity has the potential to sever the corridor into three parallel segments from north to south.

Our estimates of tenure length in the study area are conservative due to moving our sampling grids across the landscape over time; at minimum, nevertheless, half of the females that

were detected in the central Belize landscape at least 5 years before our final year of study remained there for at least 5 years. The photographic evidence of mating events and juvenile jaguars in the study area, combined with the long tenure of some individuals, are signs of population health, and may suggest the landscape currently is functioning as more than a movement corridor, with some individuals breeding and remaining in the area rather than merely traveling through. However, male tenure within the study area was short, with only 8% of the males remaining for at least 5 years. In comparison, within the protected forest of the Maya Mountain Massif JCU, 50% of detected male jaguars remained for at least 10 years (Harmsen et al. 2017). Within this comparison, we recognize that tenure in the JCU was derived from a camera grid that was permanent in space, while the quantification of tenure in central Belize will be an underestimate because each of the four camera grids were not sampled every year. In this study, we cannot distinguish between emigration and death events. The shorter tenure of males in the central Belize landscape may reflect male-biased dispersal and the corridor function of the area. Alternatively, or in addition, the wider ranging of male than female jaguars will raise their probability of contact with people and highways, hence of human-induced mortality. Our data support this premise. At least three-quarters of the reported jaguar deaths caused by people were male jaguars, and the jaguar for which we recorded the longest distance moved between camera stations (28.2 km), was shot on a farm. Regional populations can remain viable with lower survival in corridors compared to JCUs, as long as there is movement between JCUs. Future work will need to focus on mortality and movement within a metapopulation framework.

The landscape of central Belize is changing and threats to the natural habitat and wildlife are intensifying (Kay et al. 2015). Although the wildlife corridors in Belize have been identified as having the highest probability of jaguar occurrence of any corridors in Central America, both the Maya Forest and Southern Belize Corridors also have experienced the highest percentage of deforestation over the last 5 years (Petracca et al. 2018). Forest is being cleared for agricultural expansion, the cattle industry is growing, the hunting of wild prey is not adequately regulated (no monitoring of populations and harvests, or enforcement of hunting legislation), and the potential for predation and conflict with people is increasing (Foster et al. 2016; Foster 2018; Roberson 2018). Our study has shown that jaguars are ubiquitous across central Belize, demonstrating a degree of tolerance to the human-influenced landscape. Similarly, jaguars were detected throughout the human-matrix neighboring the Maya Mountain Massif JCU in southeastern Belize. There, density declined with distance from the protected forest along a gradient of increasing human disturbance and reduced canopy cover, with comparatively low detection rates in forest patches, savannah, pasture, and milpa farms, when compared to the protected forest and its contiguous unprotected forest buffer (Foster 2008; Foster et al. 2010a). In the protected forests of the Selva Maya JCU in northern Belize, a 5-year multisite study found no evidence that jaguars are impacted negatively by selective logging in areas where hunting

is prohibited (Kelly and Rowe 2014). However, opening up roads for logging or other activities in forests where hunting is improperly regulated may lead to the depletion of wild prey and “empty forest” syndrome (Redford 1992; Benítez-López et al. 2019), thereby encouraging predation on livestock and retaliatory lethal control of carnivores. Thus, while the moderate human activity in the current mosaic landscape of central Belize may not impede jaguar use of the area, the expansion of infrastructure and intensification of its use, allowing easy access for unregulated hunting and associated retaliatory killing of livestock predators, will be counterproductive to a sustainable jaguar population. If the minimum conservation goal is that the area functions as a corridor, rather than sustaining a population, then of greater concern is the creation of permanent barriers to movement, such as high-traffic roads and large-scale forest clearance. Our findings support the premise that the highway already is restricting jaguar movement through the corridor. Increases in traffic volume, and deforestation along the highway, as well as clearance of riparian forest for agricultural expansion along the two rivers, likely will further reduce the critical corridor function of central Belize.

Ensuring the long-term persistence of the jaguar will require conservation efforts in JCUs and jaguar movement corridors. This means that monitoring of wild populations must take place both inside and outside protected areas. A powerful approach is to make use of existing camera-trap data from multiple long-term study sites. With the advances and reduction in costs of camera-trap technology, researchers, government agencies, conservation NGOs, and private individuals, are increasingly deploying camera traps. Bringing together these data under one umbrella has the potential for monitoring across large spatial and temporal scales, and detecting large-scale dispersal movements. This strategy is underway in Belize, through the implementation of a government-endorsed national jaguar monitoring program, and the creation of a national jaguar album documenting all jaguar individuals identified from camera traps and carcasses (Harmsen 2019). These data will reveal the extent to which jaguars use the corridors, and move between human-influenced landscape and protected areas, improving our understanding of metapopulation dynamics. Our results will inform range-wide conservation and management strategies. Efforts to maintain jaguars in this landscape will require improving management of livestock to reduce predation, regulation of hunting for wild prey of jaguars, regulating forest clearance including riparian zones, and ensuring wildlife-friendly road development.

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Published (peer-reviewed articles) and unpublished (reports/theses) density estimates of jaguars (*Panthera onca*) based on capture-recapture data from camera-trap surveys: ad hoc density estimates based on a buffer of half the mean maximum distance moved ($\frac{1}{2}$ MMDM), spatially explicit (SECR) density estimates using Bayesian (Bay) and Maximum Likelihood (ML) methods; also showing the country, survey site, camera polygon area, the effective trapping area (ETA), habitat, land use, land status (P = protected, U = unprotected), and references.

Supplementary Data SD2.—Camera-trap surveys conducted in central Belize from 2008 to 2015, showing start and end dates, duration, number of camera stations (Stn), number of trap-nights (TN; accounting for functional failure), and the mean distance between nearest neighboring camera stations. M1–M4 were main surveys used for density estimation; S1 and S2 provided supplementary data for other analyses.

Supplementary Data SD3.—Spatially explicit capture-recapture models of jaguar (*Panthera onca*) density in central Belize across nine camera-trap surveys conducted from 2008 to 2015 (M1A–M4B) ranked in order of best fit using Akaike's Information Criteria corrected for small sample sizes (AIC_c), where ΔAIC_c is the difference in AIC_c between the best model and each of the other models, and AIC_{cwt} is the relative likelihood of the model (the probability that a given model is the best model in the set).

Supplementary Data SD4.—Frequency of jaguar sex ratios per location-month*; $N = 82$ location-months where jaguars were detected at least twice and for which sex could be assigned, representing 43 camera locations; derived from nine surveys that sampled a total of 104 locations in the central Belizean landscape between 2008 and 2015, with an average survey length of 102 days (range 60–139), and an average of 24 station locations per survey (range 19–30). Black indicates that one sex was detected, gray indicates biased sex ratio, and white indicates sex ratio of 1:1. *Location-month refers to a camera station location during a survey; therefore, the same camera station may be included more than once.

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