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Authors: Luja, Víctor H., Navarro, Carlos J., Torres Covarrubias, Luis Alberto, Cortés Hernández, Mauricio, and Vallarta Chan, Ignacio Luis

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Víctor H. Luja¹, Carlos J. Navarro², Luis Alberto Torres Covarrubias³,
Mauricio Cortés Hernández³, and Ignacio Luis Vallarta Chan⁴

Abstract

The jaguar (*Panthera onca*) is one of the most endangered felids in the world. Its distribution has been reduced by 50% globally, and the species continues to be hunted illegally. We provide data on jaguar abundance, sex ratio, seasonal and daily activity, and site fidelity in La Papalota—a 368-ha natural protected area in Nayarit, western Mexico. La Papalota is located between two areas with high priority for the conservation of the jaguar: Marismas Nacionales Biosphere Reserve and the San Blas-San Juan area. Over a period of 4,240 trap nights (14 months), we collected 130 independent photos of six different individuals (one adult male, three adult females, one subadult female, and one cub). Jaguars use La Papalota all year round, and we were able to document three pregnancies. We suggest that, although a small protected area like our study site cannot provide an entire home range for even a single jaguar, it and similar reserves can play a crucial role as stepping-stones for jaguars moving across highly modified landscapes.

Keywords

camera trapping, corridor, fragmentation, predator, tropical forest

Introduction

The jaguar (*Panthera onca*) is the largest extant wildcat in the Americas, where it has lived for about one million years (Rabinowitz, 2014). Originally, this predator was widely distributed, from the arid mountains of the south-western United States through Mexico, Central America, and South America to Argentina (Seymour, 1989). In Mexico, its modern distribution includes the Gulf of Mexico, from Tamaulipas to the Yucatan Peninsula in the Caribbean; the Pacific coast, from Sonora to Chiapas (Chávez-Tovar, Aranda, & Ceballos, 2006); and the Central Plains in the states of Morelos, Mexico, and Hidalgo (Aguilar-López, Ramos-Frías, Rojas-Martínez, & Cornejo-Latorre, 2015; Monroy-Vilchis, Sánchez, Aguilera-Reyes, Suárez, & Urios, 2008; Valenzuela-Galván, Castro-Campos, Servin, Martínez-Barona, & Martínez-Montes, 2015).

Due to habitat loss and poaching, the jaguar's distribution in Mexico has decreased by 54% (Nowell & Jackson, 1996; Sanderson et al., 2002), with a current estimate of approximately 4,000 to 5,000 wild individuals (Chávez, Zarza, de la Torre, Medellín, & Ceballos, 2016). The species is classified as globally *near threatened* according to the International Union for Conservation

of Nature (IUCN; Caso et al., 2008), and it is listed in Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora. In Mexico, jaguars are listed as *in danger of extinction* and have been protected from hunting since 1987 (Secretaría de Medio Ambiente y Recursos Naturales, 2010). Recently, de la Torre, González-Maya, Zarza, Ceballos, and Medellín (2017) assigned the jaguar population from Sierra de Tamaulipas and Gulf of Mexico to IUCN's *critically endangered* category and from the Selva Maya and Mexican Pacific to IUCN's *endangered* category.

¹Coordinación de Investigación y Posgrado, Unidad Académica de Turismo, Universidad Autónoma de Nayarit, Tepic, Nayarit, México

²ONCA MAYA A.C., Monterrey, NL, México

³Pronatura Noroeste, Tepic, Nayarit, México

⁴La Papalota, Finca Ecológica A.C., Nayarit, México

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Corresponding Author:

Víctor H. Luja, Coordinación de Investigación y Posgrado, Unidad Académica de Turismo, Universidad Autónoma de Nayarit, Ciudad de la Cultura S/N. C.P., 63000 Tepic, Nayarit, México.
Email: lujastro@yahoo.com



Habitat fragmentation is one of the most serious threats to the persistence of jaguar populations at the continental level (Medellín, de la Torre, Zarza, Chávez, & Ceballos, 2017). Top predators such as the jaguar may be particularly susceptible to habitat fragmentation given their low population densities, leading to small effective population sizes in local fragments (Haag et al., 2010). Connectivity between populations (the degree to which the landscape foment or limits the displacement of individuals between habitat patches) allows genetic turnover and prevents problems such as inbreeding from reducing the viability of populations (Chávez et al., 2016; Soulé & Mills, 1998; Stockwell, Hendry, & Kinnison, 2003). Corridors and stepping-stones have been proposed as landscape-level strategies to increase connectivity between fragmented and isolated populations (Baum, Haynes, Dilleuth, & Cronin, 2004). Although some studies have located potential sites that could act as corridors and stepping-stones for the jaguar (de la Torre et al., 2017; Rabinowitz & Zeller, 2010), field observations are required to confirm whether jaguars in fact use these areas.

The objective of this study is to determine whether La Papalota, a small protected area, is part of a biological corridor as a stepping-stone that contributes to connect the populations of jaguars of Marismas Nacionales Biosphere Reserve (north) with those of the San Blas-San Juan area (south). Both areas are considered *high priority jaguar conservation units* for the conservation of jaguar populations in Mexico (Medellín et al., 2017).

Methods

Study Area

La Papalota, the first private reserve in Mexico, is located in the municipality of Santiago Ixcuintla, Nayarit, in western Mexico (Figure 1), which is between 21.67° N and –105.45° W and 21.63° N and –105.44° W. This reserve lies on the western bank of the mouth of the Santiago River, facing the Pacific Ocean. The climate is warm and humid. The rainy season is between June and October, peaking in July and August, and rainfall varies from

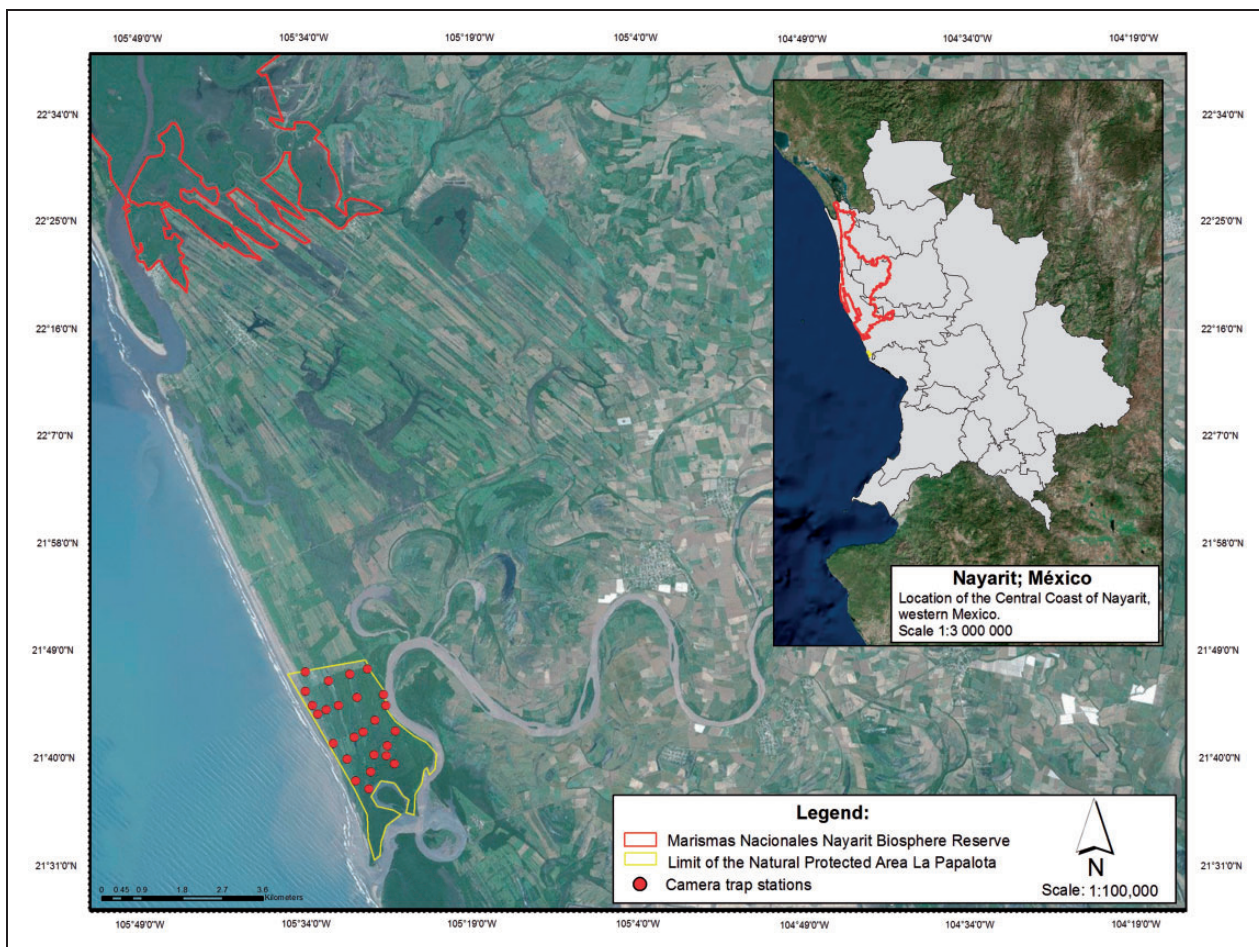


Figure 1. Natural protected area *La Papalota*, Nayarit, western Mexico. The yellow line delimits the 368-ha area of the reserve, and red dots indicate locations of camera trapping in this study.

Table 1. Geographic Locations of 25 Sites Where 10 Camera Traps Were Randomly Placed Every Month.

Station	Lat N	Long W	Sampling months	Number pictures
1	21°40'15.50"	105°27'35.33"	4,5,7,9	0
2	21°40'17.23"	105°26'50.33"	2,3,6,7,8,9,10	1
3	21°40'9.44"	105°27'18.30"	1,8,10,11	0
4	21°40'2.33"	105°27'35.08"	1,3,5,8,10,14	1
5	21°39'52.70"	105°27'29.95"	4,5,10,12,14	4
6	21°39'47.23"	105°27'26.17"	4,7,11,12,13,14	2
7	21°39'49.97"	105°27'20.00"	1,5,7,9,13,14	2
8	21°39'52.77"	105°27'11.39"	2,7,9,11,13,14	3
9	21°39'58.13"	105°26'58.07"	4,6,9,13	2
10	21°40'0.25"	105°26'38.69"	1,2,5,6,8,11,13,14	11
11	21°39'52.95"	105°26'37.12"	6,7,9,10	5
12	21°39'42.91"	105°26'44.99"	1,3,4,10,12,14	3
13	21°39'34.85"	105°26'53.41"	3,5,7,8,9,10,11,12,13	9
14	21°39'31.55"	105°26'59.83"	1,3,4,5,6,10,12,13	31
15	21°39'27.32"	105°27'15.12"	7,11	1
16	21°39'16.88"	105°27'5.11"	2,3,5,8	0
17	21°39'19.62"	105°26'45.42"	2,6,12,14	3
18	21°39'25.67"	105°26'35.91"	2,4,8,13	0
19	21°39'35.79"	105°26'30.03"	3,4,6,10,12	18
20	21°39'2.09"	105°26'59.07"	1,3,6,8,9,11	8
21	21°39'8.17"	105°26'48.05"	1,2,3,6,7,8	8
22	21°38'56.68"	105°26'49.22"	2,3,4,5,8,9,12,13,14	9
23	21°39'19.05"	105°26'36.60"	5,11,12,13	4
24	21°40'13.72"	105°27'3.21"	1,2,4,7,9,11,12	5
25	21°39'13.74"	105°26'30.84"	1,2,10,11,14	0

Note. Sampling month column indicate the number of month corresponding to the period from January 2016 (1) to February 2017 (14), and the last column shows the number of jaguar pictures on every site.

1,595.1 mm to 1,266.1 mm per year. The highest temperatures occur from May to October, and the annual average temperature is 31.7°C. La Papalota has an area of 368 ha. The area includes mostly mangrove forests (*Avicennia germinans* and *Conocarpus erectus*) in the southern part of the reserve that faces the sea, as well as a mosaic of tropical deciduous and secondary forests elsewhere. The continental margins of the protected area are surrounded by agricultural lands, particularly tobacco and sorghum fields. Most importantly, La Papalota represents an island of native vegetation located 9 km (straight line) south of the Marismas Nacionales Biosphere Reserve, and the whole region acts as a corridor for jaguar populations between northern (Sinaloa and Sonora) and southern (Jalisco to Chiapas) states (Ceballos, Chávez, & Zarza, 2012).

Fieldwork

The presence of jaguars in La Papalota was confirmed in 2009 when footprints were observed on the property. In July 2015, we started a biodiversity study using camera

traps. All the dirt roads of the reserve were searched for jaguar tracks. Between July and December 2015, five stations were set up in sites with the highest evidence of footprints, and we began camera trapping in January 2016. Each station included two cameras, one on each side of the road, to obtain photographs of both sides of the photographed individuals (O'Connell, Nichols, & Ullas, 2010). This allowed us to individually identify four adult specimens and one cub.

In January 2016, we divided the study area into 25 quadrants that were 300 m × 300 m using Google Earth Pro®. The size of the quadrant was established to maximize the probability of obtaining jaguar records from a small site; the minimum distance between cameras was 500 m (C. Chávez, personal communication, December, 2015). Every month from January 1, 2016 to February 28, 2017, we placed camera traps in each of 10 different quadrants (eight Cuddeback® cameras and two HCO Scoutguard® cameras). The quadrants were chosen randomly each month so that all areas of the reserve were equally likely to be sampled. Cameras were set for 24 hr



Figure 2. The six jaguars photographed in La Papalota between January 2016 and February 2017: adult females F01 (a), F02 (b), and F03 (c); adult male M01 (d); subadult female F04 (e); and a female cub C01 (f).

with standard sensitivity, and all photos that were taken captured the shooting time and date. Cameras were attached to trees 35 to 50 cm above ground and were placed perpendicular to dirt roads used by jaguars (confirmed by tracks), as described by Ceballos et al. (2012). We downloaded images and checked batteries on a monthly basis. Automatic data organization, storage and analysis of camera trap pictures were performed using the methods of Harris, Thompson, Childs, and Sanderson (2010).

Results

Our sampling efforts totaled 4,240 trap nights (424 nights \times 10 cameras) during the study period, with a total yield of 279 jaguar pictures. Of those, 130 shots (46.6%) were high quality and allowed us to unequivocally identify individuals. The remaining images were excluded from

analyses because individuals were not in position, blurry, or too far away ($N=36$), or because they represented duplicated individual records during the same 24-hr period ($N=113$). The location of each camera, sampling month, and number of jaguar pictures are summarized in Table 1.

Number of Jaguars and Sex Ratio

In our final set of 130 photos, we could identify six individuals, namely three adult females (F01, F02, and F03; Figure 2a, b, and c, respectively), one adult male (M01; Figure 2d), one subadult female (F04; Figure 2e), and one cub (C01; Figure 2f), resulting in a 1:4 male-to-female ratio. The number of individual pictures per jaguar was F01: 41 (30.1%); M01: 37 (27.21%); F02: 36 (26.47%); F03: 10 (7.35%); F04: 7 (5.1%); and C01: 5 (3.6%).

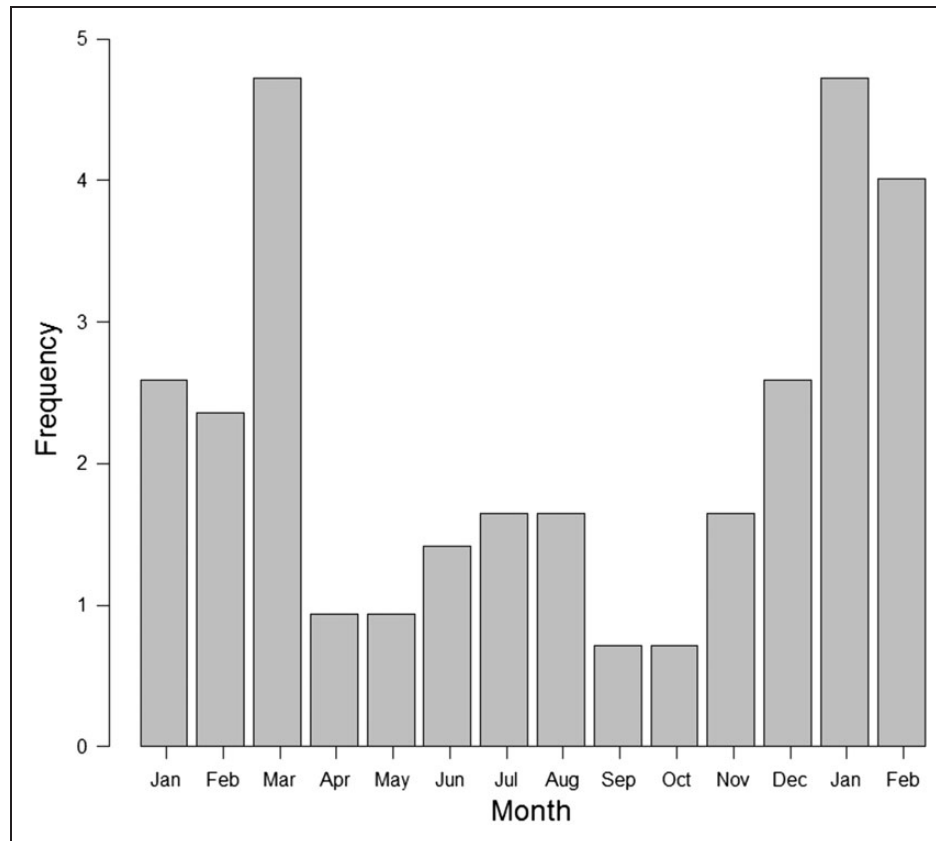


Figure 3. Monthly frequency (# of monthly pictures / # total pictures) of jaguar records captured by camera traps in La Papalota in 2016 and 2017.

Seasonal Activity

We obtained jaguar pictures in all of the 14 months of the study with a mean of 9.2 pictures per month, 95% confidence interval (CI) [6, 12.5]. The highest number of records (Figure 3) occurred in March 2016 (20 pictures), January 2017 (20 pictures), and February 2017 (17 pictures); the lowest number of records (Figure 3) occurred in September and October 2016 (3 pictures each).

Daily Activity

Fifty-three (40.7%) and 77 (59.3%) photographs were obtained during the day (7:00 a.m. to 6:30 p.m.) and at night (6:30 p.m. to 7:00 a.m.), respectively. Diel activity peaked from 10:00 p.m. to 11:00 p.m. (15 pictures, 11.5%) and from 6:00 p.m. to 7:00 p.m. (12 pictures, 9.2%) and was lowest at 11:00 a.m. to 12:00 noon and 12:00 noon to 1:00 p.m. (2 photos each, Figure 4).

Frequency of Occurrence

Three of the four adult jaguars (F01, F02, and M01) were photographed between 37 and 41 times (independent records), resulting in average times to recapture of 9.5 days,

95% CI [5.5, 13.6], to 10.9, 95% CI [6.3, 15.5], over the study period. The Kruskal–Wallis test showed no significant differences ($H = 0.596$, $N = 14$, $p = .742$) in the average recapture times of the three most photographed jaguars.

Discussion

Current conservation actions for the jaguar have focused on establishing parks, reserves, and natural protected areas (Rabinowitz, 2014; Sanderson et al., 2002). However, to maintain the viability of populations in the medium and long term, it is necessary to ensure connectivity between them through the establishment of biological corridors (de la Torre et al., 2017; Rabinowitz & Zeller, 2010).

In this work, we confirm that at least four adult jaguars use La Papalota as a safe site and breeding area because we documented three pregnancies. With these data, we provide evidence that small reserves can act as stepping-stones (small patches linking otherwise isolated patches; Baum et al., 2004). Stepping-stones are crucial for long-distance dispersal of species such as jaguar and for its range expansion through habitat networks (Saura, Bodin, & Fortin, 2014). Thus, at a regional level,

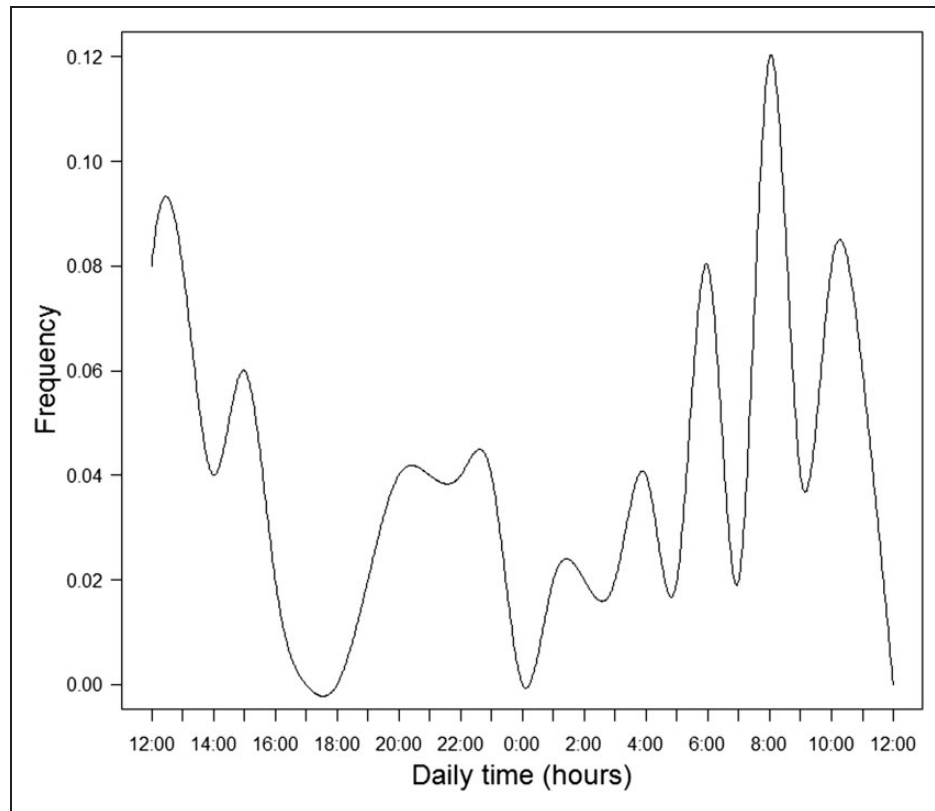


Figure 4. Frequency of jaguar daily activity according to photographic records in La Papalota between January 2016 and February 2017.

La Papalota contributes to the connectivity of two areas of importance for the conservation of the jaguar: Marismas Nacionales Biosphere Reserve and the San Blas-San Juan area.

Our study also provides data on the sex ratio, periods of activity, and reproduction of jaguars in western Mexico. Most studies of jaguars that use camera traps have reported a sex ratio biased toward males (2:1; Maffei, Noss, Silver, & Kelly, 2011). This bias differs for other large cats; females tend to outnumber males because the mortality rates of the latter are increased by intraspecific conflicts and during dispersal (Balme & Hunter, 2004; Goodrich et al., 2008; Logan & Sweanor, 2001). Nevertheless, males have larger home ranges and higher detection probabilities, and male-biased ratios seem to vanish when data are corrected for sex and encounter-rate probabilities (Tobler, Carrillo-Percestequi, Hartley, & Powell, 2013).

We found that jaguar activity increased from the hot and humid (April to November) to the cold and dry (December to March) months. This pattern agrees with previous studies carried out in areas with highly seasonal climates (Cavalcanti & Gese, 2009; Chávez-Tovar & Zarza, 2009; Núñez-Pérez, 2006). Low jaguar activity during the rainy season in La Papalota might indicate that jaguar home ranges track prey dispersal when fresh water is not a limitation.

Jaguars have been traditionally regarded as nocturnal with short bouts of daytime activity (Monroy-Vilchis, Rodríguez-Soto, Zarco-González, & Urios, 2009; Scognamillo, Maxit, Sunquist, & Farrell, 2002). However, a range of studies corroborate our finding that daytime activity is not infrequent (Maffei, Cuellar, & Noss, 2002; Núñez, Miller, & Lindzey, 2002), and nocturnal versus diurnal preferences can vary among individuals (Hoogesteijn & Mondolfi, 1992). Given that intensive hunting is often responsible for the shifting of nocturnal habits in jaguars and other large wildcats (de Almeida, 1990), we suggest that poaching pressure is relatively low in La Papalota.

With this small-scale study, data were obtained on reproductive aspects of jaguar along the Mexican Pacific coast. The subadult female (F04) was found to be the daughter of F01 and was born in the first months of 2015; cub and mother were photographed together in January, April, and July 2016, and the cub stayed in the area until the beginning of 2017 when she was recorded along with an adult male (M01). In addition, by December 2016, F01 was pregnant again and had given birth before February 2017; a 2-year period between consecutive pregnancies tallies well with published literature (Seymour, 1989). Finally, the other adult female (F02) was photographed pregnant in January 2016 and in company of her cub in December 2016.

La Papalota represents an island of primary tropical and mangrove forests bounded by the Pacific Ocean and agricultural fields. Freshwater reservoirs from the Santiago River are available to jaguars all year long, and potential prey species are diverse, including whitetail deer (*Odocoileus virginianus*), collared peccary (*Pecari tajacu*), white-nosed coati (*Nasua narica*), armadillo (*Dasybus novencintus*), raccoon (*Procyon lotor*), birds, reptiles, and crabs (Luja et al., unpublished data)—all of which are protected from hunting by La Papalota stakeholders. Overall, La Papalota could be a stepping-stone in a natural corridor for transient jaguars and other species transiting the large Marismas Nacionales Biosphere Reserve and the southern part of the western Sierra Madre mountain range (Navarro-Serment, López-González, & Gallo-Reynoso, 2005), through the Santiago and San Cristóbal rivers and the Matanchén Bay near San Blas (Figel, Ruíz-Gutiérrez, & Brown, 2016). Both the beach and the narrow corridors, which are host to healthy riparian vegetation, could be functioning as transit areas. To confirm this, we plan to expand the extent of our study area and complement camera trapping with telemetry studies.

Implications for Conservation

In a highly modified landscape dominated by human activities, it is urgent to identify those elements that can function as biological corridors or as stepping-stones that maintain connectivity between large populations. In this study, we found that a small patch of only 368 ha has adequate conditions for the jaguars to find shelter, food, and even reproduce. Although a small protected area like our study site cannot provide an entire home range for even a single jaguar, it and similar reserves can play a crucial role as stepping-stones for jaguars moving across highly modified landscapes.

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