Jaguars in the matrix: population, prey abundance and land-cover change in a fragmented landscape in western Mexico

Víctor H. Luja, Diana Jatziri Guzmán-Báez
Oyólsi Nájera and Rocío Vega-Frutis

Abstract Habitat fragmentation threatens biodiversity worldwide, particularly affecting large-bodied species that require vast territories and move across long distances, including most large felids. The jaguar *Panthera onca* has lost more than half of its habitat throughout its range and its subpopulations are becoming isolated, making them susceptible to local extinction. Knowledge about the status of its subpopulations in highly fragmented environments is lacking but urgently needed. Using camera traps during 2019–2020, we estimated number of individuals, age classes and sex ratio, occupancy, relative abundance and density of jaguars in Nayarit, western Mexico. We also determined the relative abundance of potential prey and estimated the land-cover change rate during 1999–2019, using GIS. We found that a resident subpopulation of five adult females, two adult males and one cub, at a high density (5.3 individuals/100 km^2), is supported by at least 14 wild prey species. Natural habitat in the area is rapidly decreasing because of expanding agriculture and shrimp farming: agricultural areas increased from 39 to 50% and mangroves decreased from 35 to 26% of the study area over 20 years. The high jaguar population density and the diversity and relative abundance of remaining wild prey are remarkable, considering that natural habitat in the area is highly fragmented, shrinking rapidly and embedded in a matrix of human-dominated land-cover types. Effective conservation actions are needed urgently, including the protection of patches with native vegetation, reforestation to maintain connectivity between these patches, and the involvement of local communities.

Víctor H. Luja (Corresponding author, orcid.org/0000-0001-7480-7278, lujastro@yahoo.com) Unidad Académica de Turismo, Universidad Autónoma de Nayarit, Ciudad de la Cultura S/N., C. P. 63000, Tepic, Nayarit, Mexico

Diana Jatziri Guzmán-Báez Maestría en Ciencias Biológico Agropecuarias, Unidad Académica de Agricultura, Universidad Autónoma de Nayarit, Xalisco, Nayarit, Mexico

Oyólsi Nájera (orcid.org/0000-0002-8637-9482) Cuerpo Académico Recursos Naturales, Secretaría de Investigación y Posgrado, Universidad Autónoma de Nayarit, Tepic, Nayarit, Mexico

Rocío Vega Frutis (orcid.org/0000-0002-3393-5860) Programa Académico de Biología, Unidad Académica de Agricultura, Universidad Autónoma de Nayarit, Xalisco, Nayarit, Mexico

Received 12 April 2021. Revision requested 29 July 2021.
Accepted 29 October 2021. First published online 24 May 2022.

Keywords Conservation, felids, fragmentation, jaguar, Mexico, *Panthera onca*, population dynamics, wild cats

Supplementary material for this article is available at doi.org/10.1017/S0030605321001617

Introduction

Humans have modified more than 50% of terrestrial ecosystems (Hooke et al., 2012; Jacobson et al., 2019), with severe negative effects on biotic communities (Klein et al., 2011; Nagendra et al., 2013). Impacts vary depending on the type of ecosystem and biotic community, and can include the local extirpation and extinction of wild populations (Newbold, 2018; Bradshaw et al., 2021). Large carnivores have been particularly affected by habitat modification and loss (Loyola et al., 2008; Ripple et al., 2014; Zanin et al., 2015), and are suffering from synergistic effects of hunting and retaliatory killing (Ripple et al., 2014; Jędrzejewski et al., 2017).

Most large felids are threatened by habitat fragmentation (Brodie, 2009; Holland et al., 2018). It has been estimated that the Asiatic lion *Panthera leo persica* and cheetah *Acinonyx jubatus* survive in just 2% of their historical range, the tiger *Panthera tigris* in 6% and the African lion *Panthera leo* in 17%. Some species have experienced dramatic population declines in the last 25 years: tiger 50% and lion 47% (Dalerum et al., 2008; Bauer et al., 2015; IUCN, 2019). In addition to habitat fragmentation, large felids are often subject to negative interactions with people, such as competition for land and prey, retaliatory killing or hunting for the increasing illegal trade (Krafte et al., 2018; Nijman et al., 2019). These combined threats make large felids particularly vulnerable to extinction. Therefore, to design effective conservation measures, we urgently need to improve our knowledge on the population dynamics of large felids, their prey, and the patterns of land-cover change in habitats fragmented by human activities.

The jaguar *Panthera onca* is the largest feline in the Americas. Historically it was distributed from the southern USA to northern Argentina (Seymour, 1989; Swank & Teer, 1989). Its current distribution in Mexico ranges from Sonora to Chiapas on the Pacific slope, and from Tamaulipas to Campeche and the Yucatan Peninsula on the Gulf of

Mexico slope. Its original range has decreased by 60%, with an estimated 4,800 individuals persisting in the wild (Ceballos et al., 2021). Jaguar subpopulations are becoming isolated and extirpated mainly because of illegal hunting, prey depletion, and habitat loss and fragmentation as a result of infrastructure development and expanding crop and livestock farming (Ceballos et al., 2012). At a global level, the species is categorized as Near Threatened on the IUCN Red List (Quigley et al., 2017), and in Mexico it is considered Endangered (SEMARNAT, 2010). The subpopulation of the Sierra de Tamaulipas and Gulf of Mexico has been assessed as Critically Endangered and those of the Mayan jungle and the Mexican Pacific as Endangered (De la Torre et al., 2017).

To effectively protect the jaguar in the Mexican Pacific area, accurate estimates of the size of its subpopulations are needed. Here we aimed to generate data (number of individuals, age classes and sex ratio, occupancy, relative abundance, density) on a jaguar subpopulation in Nayarit, western Mexico, in an area where natural habitats are highly fragmented and degraded by human activities. In addition, we sought to determine the relative abundance of the jaguar's potential prey, and to estimate the rate of land-cover change during 1999–2019 in this area.

Study area

The study area is in the Marismas Nacionales–Sierra San Juan corridor, in the Mexican state of Nayarit, within the Central Pacific region that has been identified as a priority area for jaguar conservation by the National Alliance for the Conservation of the Jaguar (Ceballos et al., 2018). The area used for camera trapping was between the towns of Toro Mocho (Municipality of Santiago Ixcuintla) and Boca del Asadero (Municipality of San Blas), Nayarit (Fig. 1). The climate is warm and humid, with a mean annual temperature of 31.7 °C, and the predominant native vegetation comprises mangroves *Avicennia germinans* and *Conocarpus erectus* with patches of deciduous forests. Other land use includes secondary vegetation, farmland and livestock pastures (Luja et al., 2017).

Methods

Camera trapping

We carried out camera-trap surveys during January–March 2019 and January–March 2020. During both surveys the sampling period did not exceed 60 consecutive days, to avoid violation of the assumption of a closed population

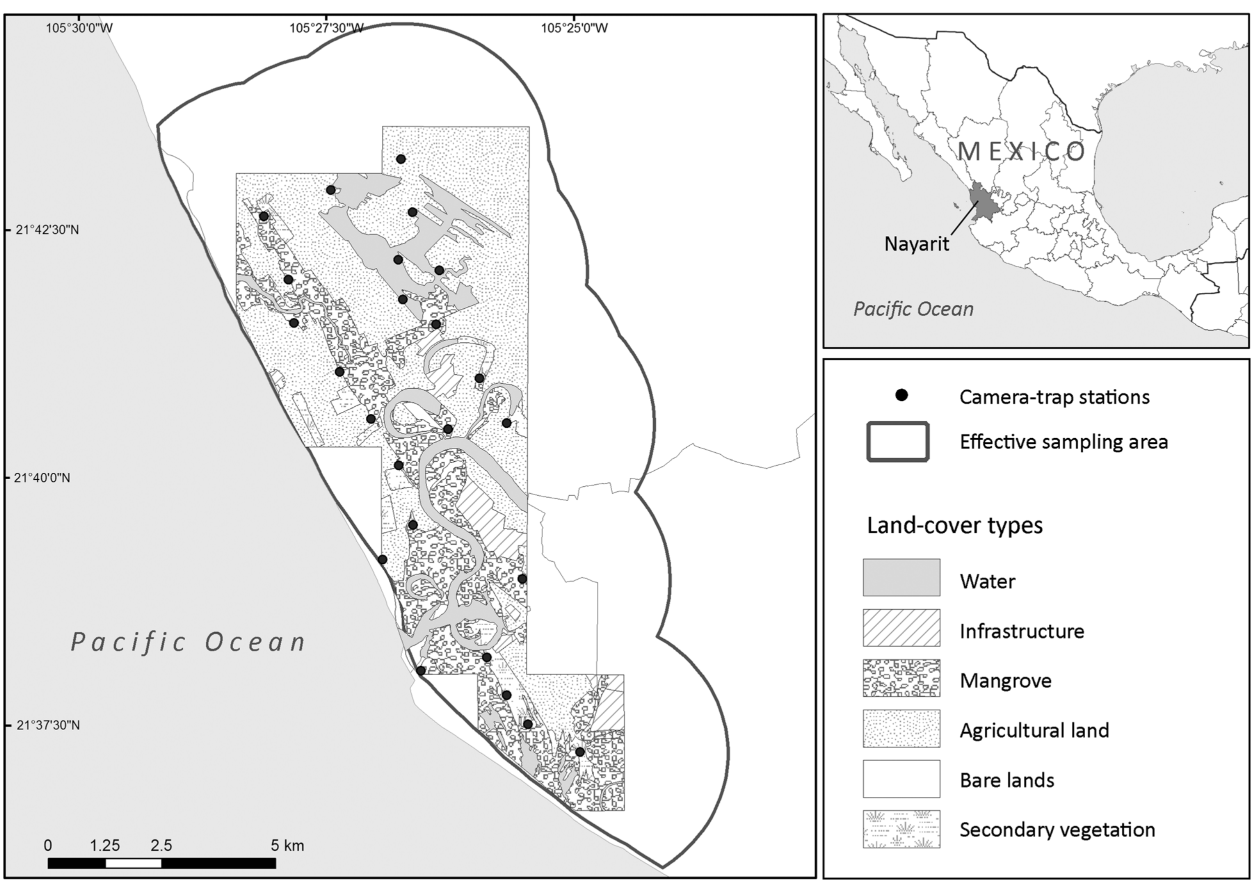

Fig. 1 The study area in the coastal plain of the state of Nayarit, western Mexico, showing the land-cover types and location of the camera-trap stations.

Oryx, 2022, 56(4), 546–554 © The Author(s), 2022. Published by Cambridge University Press on behalf of Fauna & Flora International doi:10.1017/S0030605321001617

(Karanth & Nichols, 1998). Camera trapping followed the protocol of the National Jaguar Census, a methodology created by Mexican scientists to standardize the collection of jaguar population data (Chávez et al., 2007). Using *QGIS 3.4.4.* (QGIS, 2020) and *Google Earth* (Google, Mountain View, USA), we divided the study area into seven quadrats of 9 km^2 each. In each quadrat, we placed three camera-trap stations (two with a single camera each, and one with two cameras facing each other, to obtain photographs of both flanks of jaguars passing between them), in locations with signs of jaguar presence such as tracks and scrapes. We installed a total of 25 camera stations, with a minimum distance of 1 km between stations. We used Cuddeback Colour X-Change camera traps (Cuddeback, De Pere, USA), attached to trees 40–50 cm above ground level, placed perpendicular to wildlife trails and programmed to take one picture with a trigger speed of 0.5 seconds.

Jaguar population data

We derived occupancy and relative abundance of jaguars from the analysis of images obtained during both survey periods and following the methodology described by Sanderson & Harris (2012), which is detailed below for relative abundance potential prey. We determined the number of individuals, age classes and sex ratio by identifying individuals from their unique spot and rosette patterns (Karanth & Nichols, 1998). To estimate population size, we constructed a capture history matrix (1 = presence, 0 = absence) for each individual and each 10-day survey period (Chávez et al., 2013). We analysed the resulting matrix using *CAPTURE* (Rexstad & Burnham, 1992). To estimate population density, we divided the abundance estimated with *CAPTURE* by the effective trapping area (Silver et al., 2004). To estimate the effective trapping area, we generated a circular buffer area around each trapping station, with a radius equal to half the mean maximum distance moved. We estimated the maximum distance moved for each male individual captured at more than one station, as their home ranges are much larger than those of females. We then calculated the total area covered by the stations and their buffer areas, thus estimating the effective trapping area, using *QGIS* (Silver et al., 2004), and calculated jaguar population density by dividing the estimated population size by the effective trapping area. To generate abundance estimates for the sampled area, *CAPTURE* uses several different models based on the number of individual animals captured and the frequency of recaptures. The models consider different sources of variation in the probability of capture, including the variation between individuals, their probability of being captured, and others. *CAPTURE* also offers model selection to determine which estimator best fits the data.

Relative abundance of potential prey

We determined potential prey species based on available literature (Hayward et al., 2016; Luja et al., 2020; Perera-Romero et al., 2021) and followed the protocol described by Sanderson & Harris (2012) for the organization and analysis of camera-trap photographs. We calculated the relative abundance index (RAI) using the formula proposed by Maffei et al. (2004): RAI = (*C*/SE) × 100 where *C* is the number of photographic captures, SE is the sampling effort (number of cameras per monitoring day) per 100 camera days (standard correction factor). We considered photographs of the same species at the same camera station as independent if they were taken at least 60 minutes apart (Sanderson & Harris, 2012). We calculated naïve occupancy as the proportion of cameras by which a species was registered in relation to the total number of cameras used (O'Connell & Bailey, 2011).

Land-cover change

We analysed land-cover change across 6,276 ha, the approximate area of the terrain covered by camera traps, by visually interpreting digital orthophotos from 1999 (resolution of 1 m per pixel) obtained from the National Institute of Statistics, Geography, and Informatics (Instituto Nacional de Estadística, Geografía e Informatica, INEGI, Aguascalientes City, Mexico), and images from *Google Satellite* 2019 (Google, Mountain View, USA; resolution of 0.6–2.5 m per pixel), using *QGIS*. Firstly, we made a preliminary classification, distinguishing elements of the images by their shape, size, tone and colour, texture and distribution, supported by vegetation maps and the prior knowledge of the observer. Secondly, we verified land cover on the ground, validating or correcting the preliminary identification of land-cover types. We carried out an interpretation precision test and constructed a confusion matrix, obtaining the omission error values and the overall accuracy of the map (Cakir et al., 2006). We identified six land-cover types: water bodies, infrastructure, agricultural land, mangrove, bare land and secondary vegetation. We obtained the total area (in ha) for each land-cover type for the years 1999 and 2019, and determined the per cent of the study area covered by each type in each year and the change in the area covered by each type in 1999 compared to 2019. We calculated the annual change rate (Tasa) in ha/year for each land-cover type, using the equation proposed by the Food and Agriculture Organization of the United Nations in 1996 (Ruiz et al., 2013):

$$Tasa = \left[\frac{S_2}{S_1}\right]^{1/n} - 1$$

where S_2 is the area in year 2, S_1 the area in year 1, n is the number of years between the two dates, multiplied by 100 to express it as a percentage. We generated a transition matrix of the land-cover types by applying Markov chains, a stochastic model in which it is assumed that the change in the land-cover type depends on the state (type) immediately prior to the change (Balzter, 2000).

Results

The 25 camera-trap stations generated a combined sampling effort of 2,740 camera-trap days (2019 = 1,367; 2020 = 1,373), recording 2,337 independent captures (2019 = 1,293; 2020 = 1,044) of 28 species (16 mammals, 11 birds and one reptile) including people and domestic animals (cattle and dogs; Table 1).

Jaguar population data

We obtained a total of 120 independent photographs of jaguars (2019 = 64; 2020 = 56), of seven individuals in 2019 (four females, two males, one cub) and eight in 2020 (five females, two males, one cub). There were no unidentified individuals, and all individuals from 2019 where recaptured in 2020, with the addition of a new adult female in 2020. Jaguars were recorded at 21 of the 25 stations (2019 = 18;

TABLE 1 Survey effort, jaguar population data, and relative abundance index of all species recorded by our camera traps, including potential jaguar prey, by survey period (2019 and 2020) in the study area in coastal Nayarit, Mexico. Species marked with asterisks (*) are those that have been previously reported as jaguar prey (Hayward et al., 2016; Luja et al., 2020; Perera-Romero et al., 2021).

	Survey period		Conservation category[1]	
	2019	2020	Mexican law	IUCN
Survey effort				
Camera stations	25	23		
Camera-days	1,367	1,373		
Jaguar population				
Individuals identified	7	8		
Population estimate ± SE	6–10 ± 0.92	6 ± 0.18		
Density ± SE (individuals/100 km^2)	5.3 ± 0.92	5.3 ± 0.18		
Relative abundance index				
Nine-banded armadillo *Dasypus novemcinctus**	1.01			LC
Black vulture *Coragyps auratus**		0.18		LC
Bare-throated tiger-heron *Tigrisoma mexicanum*		0.10	Pr	LC
Black-crowned night-heron *Nycticorax nycticorax*	0.23	0.19		LC
Bobcat *Lynx rufus*	1.86	0.57		LC
Collared peccari *Pecari tajacu**	0.39	0.57		LC
Common green iguana *Iguana iguana**	0.08			LC
Crested caracara *Caracara cherywai*		0.29		LC
Domestic cattle *Bos taurus**	19.03	20.69		
Coyote *Canis latrans**	3.63	2.97		LC
Domestic dog *Canis familiaris**	2.94	1.63		
Grey fox *Urocyon cinereoargenteus**	0.08			LC
Human *Homo sapiens*	33.95	48.18		
Jaguar *Panthera onca*	4.95	5.36	P	NT
Jaguarundi *Herpailurus yagouaroundi*	0.23		A	LC
Limpkin *Aramus guarauna*	0.08			LC
Mexican cottontail *Sylvilagus cunicularius**	16.09	6.61		LC
Northern raccoon *Procyon lotor**	1.01	0.29		LC
Ocelot *Leopardus pardalis**	3.17	4.69	P	LC
Rufous-bellied chachalaca *Ortalis wagleri*	1.08	0.77		LC
Snail kite *Rostrhamus sociabilis*		0.10		LC
Tricolored heron *Egretta tricolor*		0.10		LC
Turkey vulture *Cathartes aura*		0.19		LC
Virginia opossum *Didelphis virginiana**	1.78	0.10		LC
White ibis *Eudocimus albus*	1.31	0.38		LC
White-nosed coati *Nasua narica**	2.32	1.82		LC
White-tailed deer *Odocoileus virginianus**	4.80	4.12		LC
Willet *Tringa semipalmata*		0.10		LC

[1]Category according to Mexican laws (NOM-059-SEMARNAT-2010): P, in danger of extinction; A, threatened; Pr, subject to special protection; and IUCN Red List of Threatened Species (IUCN, 2019): LC, Least Concern; NT, Near Threatened.

TABLE 2 Land-cover change during 1999–2019 in the study area.

Land cover	1999 Area (ha)	1999 % of total area	2019 Area (ha)	2019 % of total area	Change (ha)	Annual change rate (ha/year)
Agricultural land	2,331.34	39	2,881.36	50	550.02	27.501
Bare land	117.67	2	65.96	1	−51.71	−2.586
Mangrove	2,065.31	35	1,510.12	26	−555.19	−27.760
Infrastructure	58.83	1	262.59	5	203.76	10.188
Water bodies	1,017.44	17	827.17	14	−190.27	−9.514
Secondary vegetation	376.67	6	266.83	5	−109.84	−5.492

TABLE 3 Transition matrix (area in ha) of land-cover changes between 1999 and 2019. Note that some land-cover change involved marine areas, which are not included here as these were not relevant for our analysis.

	Land-cover type in 2019					
Land-cover type in 1999	Water bodies	Infrastructure	Mangrove	Agricultural land	Bare land	Secondary vegetation
Water bodies	666.86	0.66	160.37	109.79	19.56	18.55
Infrastructure	0.04	57.66	0.02	0.92	0.00	0.00
Mangrove	118.06	58.99	1,283.83	285.07	19.17	163.26
Agricultural land	32.15	53.67	47.56	2,168.10	0.02	25.33
Bare land	5.94	11.45	9.43	60.56	27.19	2.75
Secondary vegetation	3.29	78.80	7.33	229.96	0.00	56.70

2020 = 13), with a naïve occupancy of 0.84. Relative abundance index was 4.95 independent records/100 camera-trap days in 2019 and 5.36 in 2020. For 2019 the estimated population was 6–10 individuals (SE = 0.92, CI = 95%) under the model that best fit the data (M_{th}; population estimate under temporal variation and individual heterogeneity in the capture probabilities), and for 2020 it was six individuals (SE = 0.18, CI = 95%) under the model M_o (the probability of capture is the same for all individuals and is not influenced by environment, time or response of individuals). Half of the mean maximum distance moved was 3 km, and the effective trapping area was 111.57 km^2. Mean jaguar density (D) was 5.3 ± SE 0.92 individuals/100 km^2 in 2019, and 5.3 ± SE 0.18 individuals/100 km^2 in 2020.

Relative abundance of potential prey

Of all species recorded during this study, 14 (11 mammals, two birds, one reptile) have been reported as potential prey of the jaguar in scientific literature. The relative abundance index during both survey periods was highest for the domestic cattle *Bos taurus* (2019 = 19.03; 2020 = 20.69 independent records/100 camera-trap days), followed by the Mexican cottontail *Sylvilagus cunicularius* (2019 = 16.69; 2020 = 6.91 independent records/100 camera-trap days) and white-tailed deer *Odocoileus virginianus* (2019 = 4.80; 2020 = 4.12 independent records/100 camera-trap days; Table 1).

Land-cover changes

The image interpretation precision test returned a value of 81.89%, with a concordance measure (kappa value) of 82.17 (see matrices in Supplementary Material 1). In 1999, agricultural land covered 39% (2,331 ha) of the study area, followed by mangroves with 35% (2,065 ha). In 2019, agricultural land had increased to 2,881 ha (50% of the study area) and mangroves decreased to 1,510 ha (26% of the study area; Table 2). With the transition matrix, which shows the change in the area covered by each land-cover type between 1999 and 2019, we determined that 1,283 ha of mangroves remained unchanged over this 20-year period, but 285 ha were replaced by agricultural land (Table 3).

Discussion

We found that a resident jaguar subpopulation comprising five adult females, two adult males and one cub persists in the study area. Population density is high (5.3 individuals/100 km^2), supported by at least 14 wild prey species, and despite the fact that natural habitat is rapidly being modified, with agricultural lands and shrimp farms replacing mangroves (agricultural land increased from 39 to 50% of the study area, and mangroves decreased from 35 to 26% of the study area during 1999–2019). Previous studies have documented that jaguar distribution is highly associated with availability of natural habitat and low levels of anthropogenic disturbance (Jędrzejewski et al., 2018), and that jaguars prefer forests and avoid human-dominated and open areas (Morato et al., 2018; Costa et al., 2021; Thompson et al., 2021). The high jaguar population density and the diversity and relative abundance of wild prey in the study area are thus remarkable, considering that the remaining natural habitat is highly fragmented and embedded in a matrix altered by human activities.

The known density of jaguars estimated by camera-trap surveys is variable throughout the species' range. The highest values have been reported in large areas that are little affected by human activities: 1–4.4 individuals/100 km^2 in the Brazilian Amazon (de Oliveira et al., 2012; Tobler et al., 2013), 2.27–5.37 individuals/100 km^2 in Bolivia (Maffei et al., 2004), 6.6 individuals/100 km^2 in the Brazilian Pantanal (Soisalo & Cavalcanti, 2006), 5.75 individuals/100 km^2 in the Maya Mountains of Belize (Silver et al., 2004), and for some Mexican subpopulations, with 4.6 individuals/100 km^2 in the Montes Azules Biosphere Reserve, Chiapas (De la Torre & Medellín, 2011), 4.76 individuals/100 km^2 in El Eden, Quintana Roo (Ceballos et al., 2021) and 3.5 individuals/100 km^2 in the Chamela-Cuixmala Biosphere Reserve, Jalisco (Núñez et al., 2002). In contrast, low jaguar densities have been reported in highly fragmented landscapes: 0.3–0.5 individuals/100 km^2 in the Caatinga biome, Brazil (De Paula et al., 2012) and 1.1 individuals/100 km^2 in the Caribbean and Mosquita regions of Honduras (Mora et al., 2016). Why then is there such a high density of jaguars in a highly fragmented landscape in western Mexico?

In conservation biology it is generally understood that large and continuous forests are crucial for the maintenance of key ecological processes, and thus for the conservation of biodiversity (Gibson et al., 2011; Watson et al., 2018). However, recent studies have shown that small patches of remnant habitat can be of high conservation value, particularly in heavily modified, human-dominated landscapes. Where no large areas of undisturbed habitat are left and small patches are all that remains, ecological processes that are not present in the altered matrix may be maintained there (Lindenmayer, 2019; Wintle et al., 2019). Small habitat patches can thus act as stepping stones that promote population connectivity in otherwise highly modified environments (Manning et al., 2006). They also can be nodal points for stimulating natural regeneration of modified ecosystems (Chazdon et al., 2009). The 368-ha private La Papalota Reserve lies in the core of our study area, with a mixture of well-preserved mangrove forest, deciduous tropical forest and secondary vegetation. La Papalota may act as a stepping stone for jaguars, connecting the southern subpopulations (San Blas and San Juan mountain) with the northern one in the Marismas Nacionales Biosphere Reserve (Luja et al., 2017). Additional factors that may contribute to the persistence of a viable subpopulation in the area are a permanent water source (the Santiago River), a sufficient supply of wild prey, and the fact that the jaguar is not hunted in the region, neither directly nor in retaliation for attacks on livestock.

A good prey base is essential for the maintenance of healthy jaguar populations (Rabelo et al., 2019; Santos et al., 2019). In our study area, we recorded 14 species (11 mammals, two birds and one reptile) that have been reported as potential prey of the jaguar (Hayward et al., 2016). Previous studies showed that jaguars of this subpopulation prey mainly on medium-sized mammals such as the nine-banded armadillo *Dasypus novemcinctus*, northern raccoon *Procyon lotor* and white-nosed coati *Nasua narica*, but also on birds such as the black vulture *Coragyps auratus*, great egret *Ardea alba* and American stork *Mycteria americana* (Luja et al., 2020), and reptiles such as the ornate slider *Trachemmys ornata* (Luja & Zamudio, 2018). In other studies, jaguars have also been observed preying on medium-sized prey although large prey species are available (Novack et al., 2005; Cavalcanti & Gese, 2010). Low jaguar densities are often associated with lack of prey because of poaching, and persecution (Medellín et al., 2016; Rabelo et al., 2019; Ceballos et al., 2021). Our findings show that in this part of the Mexican Pacific jaguars still have a good base of wild prey and this subpopulation is apparently not subject to poaching or persecution. A social study found that attitudes of local people towards the jaguar are positive and conflict related to cattle predation is minimal (Zamudio et al., 2020).

Habitat fragmentation is a major threat to global biodiversity in general (Crutzen, 2006), and specifically to large felids (Ripple et al., 2014), including the jaguar (De la Torre et al., 2017; Thompson et al., 2021), which survives in only 40% of its original habitat (Ceballos et al., 2021). Our data showed an increase in habitat fragmentation over a 20-year period (2009–2019), with a high rate of mangrove replacement by agricultural lands and infrastructure, including rapidly expanding shrimp farms. Aquaculture has increased significantly in the region in recent decades (Berlanga et al., 2010), resulting in a reduction of natural wetland areas such as marshes. This is consistent with various locations in other countries, where shrimp farms are replacing mangroves, converting wetlands to wastelands (Thornton et al., 2003). The transformation of wetlands with natural vegetation to shrimp farms and agricultural areas results not only in habitat loss but also increases other threats to carnivores. We observed that some guards of shrimp farms were armed with shotguns and stated they would not hesitate to kill animals, including jaguars (VHL, pers. obs., 2019, 2020).

In a time when more than a half of the Earth's terrestrial area has been modified by human activities (Crutzen, 2006), we need to understand to what extent species such as the jaguar can persist in highly fragmented landscapes (Boron et al., 2016). The Mexican Pacific is considered an important area for jaguar conservation (Medellín et al., 2016) and is the last link connecting the subpopulations on the Pacific slope between Jalisco in the south and Sinaloa and Sonora in the north. Although our density estimate of the local subpopulation is high, the already highly fragmented habitat in the area is converted rapidly, making this subpopulation particularly vulnerable to extinction. Immediate and effective conservation actions must be taken, including the protection of patches with native vegetation and reforestation to maintain connectivity, and the involvement of local communities.

To share our findings more widely, we have created a social media page (Jaguares Sin Protección, 2017), published a children's book based on scientific information derived from this project (Luja & Zamudio, 2019) and conducted 10 workshops in four communities in the area during 2019–2021. As a result, several members of the local community have started to participate in jaguar monitoring and the conducting of workshops. However, improved law enforcement is required by the local environmental authorities as we have witnessed a variety of illegal activities such as logging, hunting, fishing and an increasing establishment of illegal shrimp farms.

Acknowledgements We thank M. Zamudio, I. Vallarta, A. Ponce, A. Guzmán, R. Virgen and volunteers and students for support with fieldwork; R. Thompson for constructive feedback and language review; and the National Council of Science and Technology (CONACyT) for funding project 3369 'Ecology and Conservation of the jaguar (*Panthera onca*) and its potential prey outside the Natural Protected Areas of Nayarit, Mexico'. DG-B received a Graduate Student Scholarship (no. 732522) from CONACyT Mexico. This manuscript is submitted in partial fulfilment of the requirements for the degree Maestría en Ciencias Biológico Agropecuarias of the graduate student programme at the Universidad Autónoma de Nayarit, Mexico.

Author contributions Study design, fieldwork: VHL, DJG-B; data analysis, writing: all authors.

Conflicts of interest None.

Ethical standards This research involved a non-invasive survey and otherwise abided by the *Oryx* guidelines on ethical standards.

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