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# Jaguar conservation in the American continent: the role of protected landscape and human-impacted biomes

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## ABSTRACT

**Introduction:** Worldwide, expanding human activities continue to be a threat to many large-bodied species, including jaguars. As these activities continue, it is critical to understand how home range sizes will be impacted by human-modified landscapes.
**Objective:** To evaluate the importance of protected and unprotected land on home-range size across their range.
**Methods:** We used home range data from 117 jaguars in several habitat protection categories and human biome types. We used a Generalized Linear Mixed Model to test home range and spatial overlap with conservation categories and human biomes.
**Results:** Most home-ranges were in Jaguar Conservation Units (62 %), followed by Protected Areas (21 %), Indigenous People's Lands (10 %) and Jaguar Movement Corridors (3 %), where 76 % of the jaguars lived inside one the first three conservation types. However, outside of conserved land, Rangeland, Cropland, Seminatural land and other human biomes were also important (24 % of the individuals). Jaguars in Rangeland, Cropland and Seminatural land had the largest home ranges.
**Conclusions:** Although conservation land was dominant, human-impacted lands appear to play a considerable role in satisfying the spatial requirements of jaguars.

**Key words:** conservation planning; human biomes; Indigenous People's Lands; jaguar conservation units; jaguar movement corridors; *Panthera onca*; protected areas.

**RESUMEN**

**Conservación del jaguar en el continente americano: papel de las áreas protegidas y biomas con intervención humana**

**Introducción:** A nivel mundial, la expansión de actividades humanas continúa teniendo un riesgo para muchas especies de cuerpo grande, tal como los jaguares. Conforme continúen estas actividades, es crucial entender el impacto de paisajes modificados sobre el tamaño de su territorio.
**Objetivo:** Evaluar la importancia de terrenos protegidos y no protegidos sobre el tamaño de su territorio a lo largo de su rango.
**Métodos:** Usamos datos de tamaño de los territorios de 117 jaguares en varias categorías de protección de hábitats y biomas humanos. Usamos un Modelo Mixto Lineal Generalizado para probar traslapes espaciales y de territorios con categorías de conservación y biomas humanos.
**Resultados:** La mayoría de los territorios estaban en Unidades de Conservación de Jaguares (62 %), seguido por Áreas protegidas (21 %), Tierras de Pueblos Indígenas (10 %) y Corredores de Movimiento de Jaguares (3 %), en donde el 76 % de los jaguares vivían dentro de alguna de las primeras tres modalidades de conservación. Sin embargo, fuera de áreas protegidas, pastizales, tierras de cultivo, terrenos seminaturales y otros biomas humanos también fueron importantes (24 % de individuos). Jaguares en pastizales, tierras de cultivo, y terrenos seminaturales tuvieron territorios más grandes.
**Conclusiones:** Aunque las áreas de conservación fueron dominantes, áreas con impacto humano parecieron jugar un rol considerable en satisfacer los requerimientos espaciales de los jaguares.

**Palabras clave:** planeación de conservación; biomas humanos; tierras de los pueblos indígenas; unidades de conservación del jaguar; corredores de movimiento de jaguares; *Panthera onca*; áreas protegidas.

## INTRODUCTION

In recent decades, anthropogenic pressures (i.e., habitat destruction, climate change, chemical pollution, overharvesting, and land use change) on the natural environment and biodiversity have increased worldwide (Butchart et al., 2010). This has left a legacy of species range contractions and extinctions (Tilman et al., 2017; Torres-Romero et al., 2020). The world's mammalian large carnivores (Order: Carnivora) are disproportionately impacted by these pressures, and their remaining range is increasingly overlapping with human activities (López-Bao et al., 2017; Torres-Romero et al., 2020). Most large carnivore species have undergone extensive range contractions in recent human history and, are now listed as threatened with extinction (Ripple et al., 2014; Torres-Romero et al., 2020).

Variation in the ability of large carnivores to share the landscape with humans is important to both global and regional landscape conservation planning. Previous studies have demonstrated different evidence that illustrates coexistence scenarios between large carnivores and humans (Boron et al., 2016; Chapron et al., 2014; López-Bao et al., 2017). Land abandonment and/or conservation policies have facilitated coexistence between large carnivores and humans in different regions, such as Europe: i.e., the Eurasian lynx (*Lynx lynx*), brown bear (*Ursus arctos*) and wolf (*Canis lupus*) (Chapron et al., 2014; Cimatti et al., 2021). Sharing the landscapes with these carnivore species across many extensive human-dominated areas remains, however, one of the major barriers to large mammal's conservation (López-Bao et al., 2017; Lute et al., 2018).

Different conservation approaches have been proposed to protect large carnivores (Ripple et al., 2014). Some strategies have relied on the use of physical boundaries around protected areas, such as fences, to prevent conflicts and reduce threats (Packer et al., 2013); or have been focused on connecting core protected areas for these species using habitat corridors (Saura et al., 2019). Alternative strategies increasingly seek to incorporate the persistence of large carnivores into human-dominated landscapes (Chapron et al., 2014; Llaneza et al., 2018; Lute et al., 2018). This approach can sometimes lead to more frequent conflicts between people on how to conserve large carnivores, and consequently, greater local pressure threats on carnivores (i.e., retaliatory killings as retribution for livestock depredations, increased vulnerability to opportunistic but illegal hunting) (López-Bao et al., 2017). Regardless of the conservation strategy adopted, a lack of understanding regarding how large carnivores respond to these different conservation approaches (i.e., spatial use in relation to landscape protection) limits our ability to prioritize conservation planning efforts.

The jaguar (*Panthera onca*) is the largest felid in the Western hemisphere. It was historically distributed from the Southern United States, southward into Northern Argentine Patagonia (Sanderson et al., 2002). Over the past century, habitat destruction, poaching for illegal trade in body parts (i.e., skins, claws), depletion of the predator's prey base, and retaliatory killings following livestock depredations (Quigley et al., 2017), have contributed to the range contraction of the species, disappearing across more than half of its original geographic range (Sanderson et al., 2002). As land use intensifies and expands across Americas, this threat to jaguars will be compounded further by human population growth, illegal hunting, medicine markets, livestock production, fragmentation, road and other anthropogenic factors, all of which will only accelerate extinction risk (Cullen et al. 2016; Torres-Romero et al., 2020), and thus, effective policies are desperately needed to curb these threats. A review of suitable landscapes across Central and South America, highlighted that protected areas are too small and few to effectively protect jaguar populations (Rabinowitz & Zeller, 2010). Because jaguars range over relatively large territories (i.e., average home ranges of 128.6 ± 49.5 km$^2$; González-Borrajo et al., 2017), they are increasingly overlapping with human activities in human biomes (Figel et al., 2019; Payan et al., 2013), which are biomes predominantly anthropogenic, the product of human population growth, land use and land cover change, croplands and other human influence on ecosystems (Ellis et al., 2010).

One conservation approach to ensure viable populations of this large felid conservation is land-sharing (Johansson et al., 2016). Although, protected areas can be critical to the viability of low density, wide-ranging species such as jaguars, private and communal lands with high-quality habitat and sustainable land use practices can be important to ensuring long-term population viability and connectivity (Sanderson et al., 2002). In Colombia, for example, recent studies have highlighted the importance of unprotected areas across human-modified landscapes to the conservation of jaguars and their prey (Boron et al., 2016; Payan et al., 2013). Similarly, private lands appear to be playing a significant role in the persistence of jaguars in the Gran Chaco near the Paraguay-Argentina border (Giordano et al., 2014; McBride & Thompson, 2018), south of which jaguars are considered "functionally extinct" (Quiroga et al., 2014). Understanding how jaguars use core habitat areas and mixed-use landscapes across the range of the species could be used to improve our understanding of which landscapes might benefit from more sustainable practices, as well as to identify key areas essential to jaguar persistence in human-dominated landscapes.

In this study, we evaluated the relative importance of different landscapes towards the extent of jaguar home-ranges across the Americas, including human biomes (Fig. 1). We did this by examining different spatial layers of land use relevant to jaguar conservation, including: (a) Jaguar Conservation Units; (b) Jaguar Movement Corridors; (c) Protected Areas; (d) Indigenous People's Lands, (e) a layer combination of *potential core habitats* as Jaguar Conservation Units, Protected Areas and Indigenous People's Lands, all layers pooled together, and (f) a layer related to landscape transformations caused by direct human interaction classified as anthropogenic biomes, also known as "anthromes" or "human biomes" (henceforth, human biomes; see., Ellis et al., 2010). Here, we analyze the home range of

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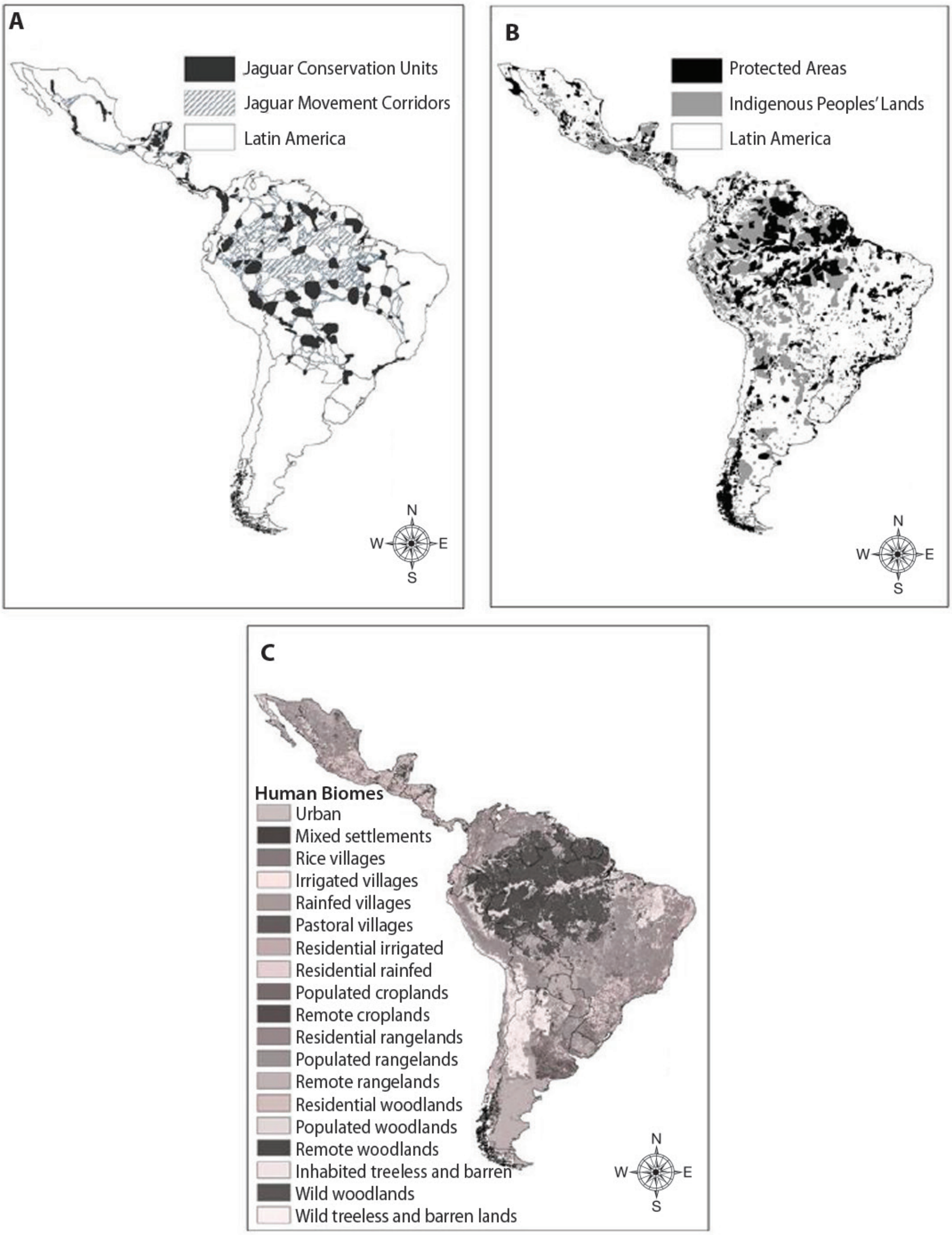


**Fig. 1.** Habitat protection categories and human biomes evaluated on spatial home range of jaguars (*Panthera onca*) in Latin America. Abbreviations are: **A.** jaguar conservation units and corridors network, **B.** protected areas and indigenous peoples' lands, and **C.** human biomes.

117 jaguars to address the following questions: (1) What is the role of Protected Areas, Jaguar Conservation Units, Jaguar Movement Corridors, and Indigenous People's Lands in facilitating the movement of jaguars?; (2) What role do human biomes play in facilitating movement by jaguars?; (3) Can strategies that encompass land-sharing across human biomes also play an important role and if so, to what degree?

## MATERIALS AND METHODS

**Spatial and Landscape Data:** We acquired the most recent database on jaguar movement from a database compiled by Morato et al. (2018). This database contains 134 690 spatial locations from 117 jaguars (54 males and 63 females) tracked using GPS technology. These individuals were monitored in five different countries: Brazil (N = 82), Paraguay (N = 23), Mexico (N = 8), Argentina (N = 3) and Costa Rica (N = 1), representing diverse parts of the jaguar's range. The majority of jaguars (N = 111) were adults (> 2 years old), four jaguars were juvenile, and two jaguars had undetermined age (see., Morato et al., 2018).

We used information on six layers conservation land protection categories considered important for jaguar conservation, including broad categories of human biomes. The six major spatial layers we considered included: (1) Jaguar Conservation Units (JCUs), defined by Sanderson et al. (2002) as "core" habitat areas of across the jaguar's range, representing ~2 million km$^2$ and believed to have stable prey and capable of supporting at least 50 breeding jaguars; (2) Jaguar Movement Corridors (JMCs), which delineate potential routes of dispersal, immigration, and emigration among jaguar conservation units as described by Rabinowitz and Zeller (2010) (Fig. 1); (3) Protected Areas (PAs), which constitute ~7 million km$^2$ of lands in Americas formally protected for their natural, ecological or cultural values as defined by the International Union for Conservation of Nature (UNEP-WCMC, 2020), and (4) Indigenous People's Lands (IPLs), which include terrestrial lands that are managed or co-managed by Indigenous Peoples (Garnett et al., 2018), and represented over ~4 million km$^2$ across Latin America. Together, PAs and IPLs constitute most of the recognized terrestrial conservation land, habitat protection, and ecologically intact landscapes on Earth (Garnett et al., 2018) (Fig. 1). We used seven distinct PAs sub-categories, which differ in number and category of protection depending on the enabling laws of each country (see., International Union for Conservation of Nature, 2020 for further details of levels and regulatory protection), including: Ia–Strict Nature Reserves, Ib–Wilderness Areas, II–National Parks, III–Natural Monument or Features, IV–Habitat/Species Management Areas, V–Protected Landscape/Seascapes, and VI–Multiple Use Management & Protected Areas, whereby the sustainable use of natural resources is permitted.

We also examined (5) the combination of the three largest aforementioned conservation land layers together (i.e., JCUs, PAs and IPLs pooled; henceforth, "Lyr-COMB"), as this overlap may indicate areas particularly important to regional biodiversity, or larger core habitat. Finally, we evaluated the effectiveness of (6) human biomes (HBs) layer, which constitute at least some measure of human modification, pressure, or footprint on the land via development. We examined this last category, which included different level and classes of development activities such as dense settlements, villages, croplands, rangeland, semi-natural lands, and various other land uses (Fig. 1) (see., Ellis et al., 2010 for further details of classification and description).

**Spatial data analyses and home range estimate:** Because temporal autocorrelation or serial correlation in the radiotelemetry can underestimate the true home range size for each animal (Swihart & Slade, 1985), as well as bias home range size estimates due to different collection schedules, monitoring periods, and sampling frequencies among individuals and years, we randomly sampled one spatial location/day per individual (Börger et al., 2006). This helped to mitigate against spatio-temporal autocorrelation, resulting in a total dataset of 19 622 independent spatial locations for subsequent analyses. We then calculated annual home ranges for each jaguar, incorporating probabilistic estimators using kernel density estimation (KDE, via 95 % isopleth as a representative area; we refer hereafter to those results obtained using this metric) using the Home Range Tools module for ArcGIS (ESRI, 2012) a commonly used method to estimate an animal's home range (Laver & Kelly, 2008; Worton, 1989).

Next, we evaluated how each jaguar's home range overlapped with the different habitat protection categories and land uses, previously described. For each jaguar home-ranges (JHR) in our dataset, we calculate the percentage of the home range overlap where it occurred for each individual with every selected land category. In those cases where > 90 % of the KDE home range was occupied by a single landscape category (i.e., JCUs, JMCs, PAs, IPLs or Lyr-COMB) only that spatial category was considered. Then, when KDE jaguar home-ranges did not overlap with any formal conservation land or habitat protection categories, we identified the main human biomes (i.e., croplands, rangeland or seminatural lands) overlapping totally within each home range.

We then tested for differences in jaguar home-ranges between those located inside conservation lands, and the ones being outside or called "unprotected" areas. In order to determine if a significant difference in KDE home-range size exists between jaguars within any land categories, we built a generalized linear mixed model (GLMM) with gaussian distribution error and identity link to test differences in home range size in relation to the spatial overlap of jaguars with the different land conservation categories considered in this study. We also included the interaction terms between sex and land conservation categories. The number of locations was included as a covariate in the model to control for potential bias associated to different sampling efforts. The country was included as a random factor in the model (grouping factor, several jaguars sampled by country and mean home range size). We used the "glmmAMDM" package to run the model (Skaug et al., 2013).

Finally, we tested spatial variation in those cases where KDE home ranges overlapped in human-modified landscapes or human biomes (i.e., croplands, rangeland and seminatural lands); we compared differences of home-range size between females and males in relation to each human biome using linear mixed model (GLMM). All statistical analyses were performed in program R 3.4.0 (R Core Team, 2014) while spatial analyses, land use mapping and spatial comparative assessments were performed using ArcGIS (ESRI, 2012).

## RESULTS

Our results identified that 89 of 117 individuals (76 %; 49 females: 40 males) had a home range size ranging from 155 ± 19 $km^2$ and, overlapped with the combination of land protection areas together (i.e., Lyr-COMB). Among these 89 jaguars, the size of home range of females and males ranged from 99 ± 14 to 224 ± 38 $km^2$, respectively (Table 1). However, 28 of 117 jaguars (24 %; 13 females: 15 males) utilized "unprotected" lands, i.e., outside the boundaries of all land with some protected status combined. Of these jaguars (N = 28), the size of home ranges was generally larger though still varied considerably, with females and males ranging from 211 ± 59 to 762 ± 219 $km^2$, respectively (Table 1). The size of home ranges varied depending on whether the home ranges were inside or not of the combination conservation lands ($P < 0.05$) (Table 1).

The number of individuals is indicated as *n*, and jaguar home-ranges are indicated as *JHR*. Mean home range sizes ($km^2$) for females, males and both sexes, and the results as mean ± standard error (SE) are shown. In each case (P) in bold represent the level statistically significant. Abbreviations are: Jaguar Conservation Units (JCUs), Indigenous People's Lands (IPLs), Protected Areas (PAs), Jaguar Movement Corridors (JMCs), and (Lyr-COMB) represent three layers categories combined (JCUs,

TABLE 1
Individual jaguars that occurred inside (in) and outside (out) of each land protection category

| | JCUs | P | IPLs | P | PAs | P | JMCs | P | | Lyr-COMB | | | P | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | in | out | | in | out | | in | out | | in | out | | in | out | |
| | females | | females | | females | | females | | | females | | | | | |
| JHR | 101 ± 18 | 157 ± 35 | > 0.05 | 157 ± 31 | 118 ± 19 | > 0.05 | 105±15 | 127 ± 22 | > 0.05 | 83 | 122±18 | | 99±14 | 211±59 | <0.05 |
| n | 38 (32.48 %) | 24 (20.51 %) | | 7 (5.98 %) | 55 (47.01 %) | | 13 (11.11 %) | 49 (41.88 %) | | 1 (0.85 %) | 60 (51.28 %) | | 49 (41.88 %) | 13 (11.11 %) | |
| | males | | males | | males | | males | | | males | | | | | |
| JHR | 232 ± 41 | 614 ± 163 | > 0.05 | 384 ± 45 | 370 ± 76 | > 0.05 | 258 ± 57 | 403 ± 86 | > 0.05 | 473 ± 202 | 373 ± 70 | >0.05 | 224±38 | 762±219 | <0.05 |
| n | 35 (29.91 %) | 20 (17.09 %) | | 5 (4.27 %) | 50 (42.73 %) | | 12 (10.25 %) | 43 (36.75 %) | | 2 (1.71 %) | 54 (46.15 %) | | 40 (34.18) | 15 (12.82 %) | |
| | both sexes | | both sexes | | both sexes | | both sexes | | | both sexes | | | | | |
| JHR | 164 ± 23 | ± 83 | > 0.05 | 251 ± 42 | 238 ± 39 | > 0.05 | 179 ± 32 | 256 ± 44 | > 0.05 | 343 ± 174 | 241 ± 36 | >0.05 | 155±19 | 507±123 | <0.05 |
| n | 73 (62.39 %) | 44 (37.60 %) | | 12 (10.21 %) | 105 (89.74 %) | | 25 (21.37 %) | 92 (78.63 %) | | 3 (2.56 %) | 114 (97.43 %) | | 89 (76.07 %) | 28 (23.93 %) | |

IPLs and PAs). See main text for details on how jaguar home-ranges occurred inside and outside were depicted.

Seventy-three of 117 (62.4 %; 38 females: 35 males) JHR occurred in some part of JCUs, where females and males JHR ranged from 101 ± 18 to 232 ± 41 km$^2$, respectively. While 44 of 117 (37.6 %; 24 females: 20 males) individual home ranges occurred outside the designated boundaries of JCUs, where the sizes of JHR ranging from 157 ± 35 to 614 ± 163 km$^2$ for males and females, respectively, but jaguar home-ranges do not show significant differences ($P > 0.05$) between inside and outside of JCUs (Table 1).

We found fewer individuals (10 %; 7 females: 5 males) that overlapped with the IPLs, which presented home range areas ranging from 157 ± 31 to 384 ± 45 km$^2$, respectively. While more individuals (N = 105) occurred outside of IPLs, we did not find significant differences ($P > 0.05$) in range size both inside and outside of IPLs (Table 1).

Twenty-five of 117 jaguar home-ranges (21 %; 13 females:12 males) occurred within PAs, where ranged from 105 ± 15 to 258 ± 57 km$^2$, respectively. While 92 individuals (~79 %; 49 females: 43 males) were outside of PAs. The JHR both females and males increased their home ranges outside the boundaries of PAs, but we did not find significant differences ($P > 0.05$) both inside and outside of PAs (Table 1). On the other hand, only three individual jaguars (2 males: 1 female) (2.56 %) overlapped with potential JMCs; stated differently, the overwhelming majority of individual jaguar movements did not overlap at all with any part of a JMCs (97.43 %; 54 males: 60 females) and, in both overall, we did not find significant differences comparisons (Table 1).

Our results show that male and female jaguars in protected landscapes averaged smaller home ranges than male and female jaguars outside these conservation lands, respectively (Table 1). Thus, some individuals did not overlap their home ranges at all with some categories of conservation lands considered in this study. For example, we found that 28 jaguars

(24 %; 15 males and 13 females) occurred in some human biomes lands such as rangelands (i.e., lands used mainly for livestock grazing and pasture), followed by croplands (i.e., lands used mainly for annual crops) and seminatural lands (i.e., inhabited rural lands, with minor use for permanent agriculture and settlements) (Table 2). Based on our dataset, male jaguars that occurred in human biomes lands showed the largest home ranges compared with females with significant differences in rangelands (females 249 km$^2$ and males 685 km$^2$; P = 0.015) and croplands (females 8 km$^2$ and males 28 km$^2$; P = 0.049), but non-significant was found in seminatural lands (females 7 km$^2$ and males 21 km$^2$; P = 0.699).

These 28 jaguars were outside the combination of the three lands with protected status (i.e., Jaguar Conservation Units, Protected Areas and Indigenous People's Lands pooled) can occur in more than one biome. Note: Human biomes were organized into groups according to Ellis et al. 2010 (see Ellis et al., 2010 for further details of classification).

## DISCUSSION

The results presented here correspond to the first continental-scale evaluation of how jaguar home ranges overlap with different land protection status, and anthropized systems, an important consideration given that previous jaguar studies have underscored the importance of protected and unprotected areas for the species (Boron et al., 2016; McBride & Thompson 2019; Payan et al., 2013; Thompson et al., 2021). Our results enlarge information in the sense of landscape conservation planning for species with large spatial requirements, which requires the political and financial commitment needed to implement ambitious local, regional and continental conservation and connectivity strategies (Keeley et al., 2019; McBride & Thompson 2019; Saura et al., 2019). Indeed, lands with some "protected" or conservation status have been shown to be important to jaguar populations and other large mammals (Pringle, 2017; Torres-Romero et al., 2020). Thus, PAs are arguably regarded as the most critical aspects of world conservation planning efforts, and they can be particularly critical to carnivore populations and other vertebrates (Di Minin & Toivonen, 2015; Wegmann et al., 2014).

On the other hand, indigenous lands are also crucial to the sustainability and conservation of wild animal and plant communities on Earth, occupying an even greater total area than existing protected areas (Fa et al., 2020; Schuster et al., 2019). Indigenous People's Lands are of course inclusive of land tenure rights for semi-autonomous and autonomous indigenous nations across ~38 million km$^2$ in 87 countries; they further intersect with and/or are adjacent to about 40 % of all terrestrial protected land area, enhancing the ecological functioning and landscapes intactness (Garnett et al., 2018). The IPLs, despite representing less important areas to space use and movement for jaguars, still represents approximately 10.50 % of ecologically intact landscapes. Over the past several decades, however, anthropogenic pressure on PAs, IPLs and, otherwise, intact forest habitats have been accelerating (Qin et al., 2019). In 2019, for instance, bushfires devastated approximately 308,048 km$^2$ of the Amazon Basin, nearly 70 % more than during the period of 2018; large portions of Brazil, Venezuela, Bolivia, and Colombia were affected (Lizundia-Loiola et al., 2020). Other ecoregions in South America, including the Gran Chaco and Pantanal, which include important JCUs for jaguars, similarly suffered devastating losses resulting from intentional but uncontrolled fires.

Rabinowitz and Zeller (2010) originally described 90 JCUs encompassing 1.9 million km$^2$, and ~98 % of JCUs overlaps with other conservation lands. In this sense, our results show that JCUs play a leading role in the spatial patterns of space and movement of jaguars in a human-dominated landscape. This conservation lands have been proposed as critical jaguar conservation landscapes because of their perceived importance to long-term jaguar population viability and connectivity (Rabinowitz & Zeller, 2010; Zeller, 2007; Zeller et

TABLE 2
Percent of contribution of each human biomes vs. 28 individual home range of jaguars

| | | | Percent of contribution | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | Croplands | | | Rangeland | | | Seminatural lands | |
| | | | Lands used mainly for annual crops | | | Lands used mainly for livestock grazing and pasture | | | Inhabited lands with minor use for permanent agriculture and settlements | |
| Sex | Country | # ind. | Residential rainfed croplands | Populated rainfed cropland | Remote croplands | Residential rangelands | Populated rangelands | Remote rangelands | Populated woodlands | Remote woodlands |
| Female | Paraguay | 1 | | | | | 9.73 | 90.27 | | |
| Male | Paraguay | 2 | | | | | 0.5 | 99.5 | | |
| Female | Paraguay | 3 | | | | | 5.15 | 94.85 | | |
| Male | Paraguay | 4 | | | | | | 100 | | |
| Male | Paraguay | 5 | | | | | 12.36 | 87.64 | | |
| Female | Paraguay | 6 | | | | | 33.61 | 66.39 | | |
| Female | Paraguay | 7 | | | | | | 100 | | |
| Female | Paraguay | 8 | | | | | 32.07 | 67.93 | | |
| Male | Brazil | 9 | | | | | 77.54 | 14.04 | 8.42 | |
| Male | Paraguay | 10 | | | | | | 100 | | |
| Male | Brazil | 11 | | | | | 79.29 | 20.71 | | |
| Female | Brazil | 12 | | 39.22 | | | | | | 60.78 |
| Female | Brazil | 13 | 21.63 | 19.23 | | | | | | 59.13 |
| Female | Mexico | 14 | | | | | 4 | 96 | | |
| Male | Paraguay | 15 | | | | | | 100 | | |
| Male | Brazil | 16 | 6.8 | 48.54 | | | | | | 44.66 |
| Male | Brazil | 17 | 10.37 | 23.89 | 5.55 | | 15 | | 33.34 | 11.85 |
| Male | Mexico | 18 | | | | | 44 | 56 | | |
| Female | Brazil | 19 | | | | | 81.25 | 18.75 | | |
| Female | Brazil | 20 | | 8.24 | | | 88.84 | 2.92 | | |
| Male | Brazil | 21 | | | | | 77.78 | 22.22 | | |
| Male | Paraguay | 22 | | | | | | 100 | | |
| Female | Paraguay | 23 | | | | | | 100 | | |
| Female | Paraguay | 24 | | | | | | 100 | | |
| Male | Brazil | 25 | | | | | 77.25 | 22.75 | | |
| Female | Brazil | 26 | | | | | 100 | | | |
| Male | Brazil | 27 | | 6.12 | | | 89.69 | 4.19 | | |
| Male | Brazil | 28 | | | | 41.72 | 5 828 | | | |

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al., 2011). We should reiterate here that JCUs are not formal designations by any country and, while many encompass national protected and management areas, they may contain a mix of habitat quality and land use categories.

Similarly, Rabinowitz and Zeller (2010) identified 182 least-cost path corridors JMCs connecting the 90 JCUs across the jaguar's range. We do note, however, that based on our results, there is little evidence to suggest that JMCs are effectively being used by jaguars. This sort of evidence, however, requires special attention, because JMCs are not resident range, and it is therefore not surprising to found that jaguars do not show a space use and movement on these landscapes. As such, we recommend that future field investigations turn their attention to this critical knowledge gap, and to evaluate their use by jaguars. Otherwise, we face the risk of a proliferation of -paper corridors- that are never validated in the field.

On the other hand, our study highlights the relative importance of human biomes to jaguars. Our analyses show that throughout their geographic distribution, jaguars include within their home range human biomes such as rangeland, cropland, semi-natural lands and even villages' lands that do not necessarily have recognized conservation programs, but that could be important to spatial movements of endangered species. This shows that in addition to the decree of protected areas, it is essential to recognize and promote the proper management that various societies have over their territory, a strategy to do this is by promoting the establishment of voluntary conservation areas, even in partially anthropized systems (for example: areas voluntarily designated for conservation in Mexico, Gutiérrez-Hernández et al., 2021).

In the Paraguayan Chaco, for instance, evidence of the presence of jaguars was encountered regularly in unprotected and/or privately-owned mixed forest, semi-natural, and rangeland landscapes; however, at greater distances from protected areas, their presence was detected less frequently than pumas (*Puma concolor*), a consideration that has different conservation planning implications for each species (Giordano, 2015). In parts of Colombia, where hunting of primary prey species and retaliation killings were limited, jaguars were able to use human-dominated agricultural landscapes (Boron et al., 2016; Payan et al., 2013). A previous study of female cheetahs (*Acinonyx jubatus*) showed they tended to prefer denser vegetation types than males; they thus seek to mitigate exposure to human pressure through greater protective cover (Broomhall et al., 2003). Consistent with our results, we found that jaguars might be present in different human-dominated land-use types more broadly such as croplands, rangeland and seminatural-lands (Table 2). This finding is congruent with growing evidence that jaguars occur in sites with higher prey biomass because there would be sufficient food, which would increase the human-carnivore conflict (McBride & Thompson, 2018) due to depredations on livestock and pets, especially when natural prey and habitat is lacking (Athreya et al., 2016; Majgaonkar et al., 2019).

Therefore, effective continental, regional and local jaguar conservation planning may integrate the different types of human biomes used by the species (either to favor dispersal and connectivity between protected areas, or to support the permanent presence of jaguars) in the human-dominated matrix (Llaneza et al., 2018), together with conservation lands, in order to achieve an effective landscape-scale conservation approach for the species.

Because of the origin of the dataset, it is not surprising to find that the ranges of the collared animals overlap with the categories of protected lands, but the use of anthropized systems by the jaguar highlights the opportunity to promote the participation of different types of land management at the local, regional, and continental level for the conservation of this species. It is also important to recognize the different conservation schemes in the territory where landowners carry out surveillance activities, even in places with anthropized environments; cooperation between different levels of land management and conservation is essential to facilitate jaguar mobility through the JMCs maximizing the effective protective potential of the JCUs.

Therefore, the dataset from which we carry out the analyses presented in this work come from research works that did not follow the same protocols, or they did not have the same telemetry equipment; it also evidently comes from places where the population characteristics of the jaguar allowed its capture and subsequent monitoring, often close to areas expressly designated for the conservation of biodiversity (Giordano, 2015; Thompson et al., 2021). In this sense, we recognize that the data cannot be used to make comparisons among sites or countries, which is not our aim, and that it would be necessary to carry out a monitoring effort on spatial analysis of jaguar home-ranges in areas where there are no previous efforts to monitor or conserve the species.

Finally, this continental network of PAs, IPLs, and JCUs, as well as the incorporation of HBs connected by JMCs, might theoretically facilitate the movement of jaguars, while simultaneously protecting other endangered species, and enhancing the functioning of extensive ecological communities or entire ecosystems. We further note that some core areas with respect to JCUs and JMCs may have changed with respect to land use change and human impact since Sanderson et al. (2002) and, Rabinowitz and Zeller (2010). Furthermore, long-term viability of jaguars across their range necessitates a strategy of developing functional connectivity among key areas for the species, on one hand, and reassesses JCUs and JMCs on the other. Our work here therefore must be continued by others and improved upon, so that we might better understand how jaguars move across fragmented and human-dominated landscapes at regional and continental scales.

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## REFERENCES

Athreya, V., Odden, M., Linnell, J. D., Krishnaswamy, J., & Karanth, K. U. (2016). A cat among the dogs: leopard *Panthera pardus* diet in a human-dominated landscape in western Maharashtra, India. *Oryx*, *50*(1), 156–162.

Boron, V., Tzanopoulos, J., Gallo, J., Barragan, J., Jaimes-Rodriguez, L., Schaller, G., & Payán, E. (2016). Jaguar densities across human-dominated landscapes in Colombia: the contribution of unprotected areas to long term conservation. *PLOS ONE*, *11*(5), e0153973.

Broomhall, L. S., Mills, M. G. L., & Du Toit, J. T. (2003). Home range and habitat use by cheetahs (*Acinonyx jubatus*) in the Kruger National Park. *Journal of Zoology*, *261*(2), 119–128.

Börger, L., Franconi, N., De Michele, G., Gantz, A., Meschi, F., Manica, A., Lovari, S., & Coulson, T. I. M. (2006). Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology*, *75*(6), 1393-1405.

Butchart, S. H., Walpole, M., Collen, B., Van Strien, A., Scharlemann, J. P., Almond, R. E., Braillie, J. E. M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K. E., Carr, G. M., Chanson, J., Chenery, A. M., Csirke, J., Davidson, N. C., Dentener, F., Foster, M., Galli, A., … Watson, R. (2010). Global biodiversity: indicators of recent declines. *Science*, *328*(5982), 1164–1168.

Cimatti, M., Ranc, N., Benítez-López, A., Maiorano, L., Boitani, L., Cagnacci, F., Cengic, M., Ciucci, P., Huijbregts, M. A. J., Krofel, M., López-Bao, J. V., Selva, N., Andren, H., Bautista, C., Cirovic, D., Hemmingmoore, H., Reinhardt, I., Marence, M., Mertzanis, Y., ... Santini, L. (2021). Large carnivore expansion in Europe is associated with human population density and land cover changes. *Diversity and Distributions*, 27(4), 602–617.

Chapron, G., Kaczensky, P., Linnell, J. D., Von Arx, M., Huber, D., Andrén, H., López-Bao, J. V., Adamec, M., Álvares, F., Anders, O., Balciauskas, L., Bayls, V., Bedo, P., Bego, F., Blanco, J. C., Breitenmoser, U., Broseth, H., Bufka, L., Bunikyte, R., ... Boitani, L. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*, *346*(6216), 1517–1519.

Cullen, L. Jr., Stanton, J. C., Lima, F., Uezu, A., Perilli, M. L. L., & Akçakaya, H. R. (2016). Implications of fine-grained habitat fragmentation and road mortality for jaguar conservation in the Atlantic Forest, Brazil. *PLOS ONE*, *11*, e0167372.

Di Minin, E., & Toivonen, T. (2015). Global protected area expansion: creating more than paper parks. *BioScience*, *65*(7), 637–638.

Ellis, E. C., Klein Goldewijk, K., Siebert, S., Lightman, D., & Ramankutty, N. (2010). Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography*, *19*(5), 589–606.

ESRI. (2012). *ArcGIS* (version 10.1 for Desktop, software). Environmental Systems Research Institute, Redlands, CA, USA.

Fa, J. E., Watson, J. E., Leiper, I., Potapov, P., Evans, T. D., Burgess, N. D., Molnár, Z., Fernández-Llamazares, Á., Duncan, T., Wang, S., Austin, B. J., Jonas, H., Robinson, C. J., Malmer, P., Zander, K. K., Jackson, M. V., Ellis, E., Brondizio, E. S., & Garnett, S. T. (2020). Importance of Indigenous Peoples' lands for the conservation of Intact Forest Landscapes. *Frontiers in Ecology and the Environment*, *18*(3), 135–140.

Figel, J. J., Botero-Cañola, S., Forero-Medina, G., Sánchez-Londoño, J. D., Valenzuela, L., & Noss, R. F. (2019). Wetlands are keystone habitats for jaguars in an intercontinental biodiversity hotspot. *PLOS ONE*, *14*(9), e0221705.

Garnett, S. T., Burgess, N. D., Fa, J. E., Fernández-Llamazares, Á., Molnár, Z., Robinson, C. J., Watson, J. E. M., Zander, K. K., Austin, B., Brondizio, E. S., Collier, N. F., Duncan, T., Ellis, E., Geyle, H., Jackson, M. V., Jonas, H., Malmer, P., McGowan, B., Sivongxay, A., & Leiper, I. (2018). A spatial overview of the global importance of Indigenous lands for conservation. *Nature Sustainability*, *1*(7), 369–374.

Giordano, A. J., Mujica, N., Ramírez, F., & Nielsen, C. K. (2014). Jaguar (*Panthera onca*) records from the south central Paraguayan Chaco: Implications for transboundary surveys at the southern range edge. *Cat News*, *60*, 38–40.

Giordano, A. J. (2015). *Status, conservation and population genetics of the jaguar (Panthera onca) in Paraguay and the Dry Gran Chaco*. [Doctoral Dissertation]. Texas Tech University, Lubbock.

Gonzalez-Borrajo, N., López-Bao, J. V., & Palomares, F. (2017). Spatial ecology of jaguars, pumas, and ocelots: a review of the state of knowledge. *Mammal Review*, *47*(1), 62–75.

Gutiérrez-Hernández, R., Sahagún-Sánchez, F. J., Delgado-Sánchez, P., Castillo-Lara, P., Fortanelli-Martínez, J., Reyes-Hernández, H., & De-Nova, J. A. (2021). Reevaluación de los bosques tropicales estacionalmente secos de la Reserva de la Biosfera Sierra del Abra Tanchipa y áreas con potencial para su conservación. *Botanical Sciences*, *99*(4), 735–751.

International Union for Conservation of Nature. (2020). *The IUCN red list of threatened species*. https://www.iucn.org/. 2020.

Johansson, Ö., Rauset, G. R., Samelius, G., McCarthy, T., Andrén, H., Tumursukh, L., & Mishra, C. (2016). Land sharing is essential for snow leopard conservation. *Biological Conservation*, *203*, 1–7.

Keeley, A. T., Beier, P., Creech, T., Jones, K., Jongman, R. H., Stonecipher, G., & Tabor, G. M. (2019). Thirty years of connectivity conservation planning: An assessment of factors influencing plan implementation. *Environmental Research Letters*, *14*(10), 103001.

Laver, P. N., & Kelly, M. J. (2008). A critical review of home range studies. *The Journal of Wildlife Management*, *72*(1), 290–298.

Llaneza, L., Sazatornil, V., & López-Bao, J. V. (2018). The importance of fine-scale breeding site selection patterns under a landscape-sharing approach for wolf conservation. *Biodiversity and conservation*, *27*(5), 1239–1256.

Lizundia-Loiola, J., Pettinari, M. L., & Chuvieco, E. (2020). Temporal anomalies in burned area trends: satellite estimations of the Amazonian 2019 fire crisis. *Remote Sensing*, *12*(1), 151.

López-Bao, J. V., Bruskotter, J., & Chapron, G. (2017). Finding space for large carnivores. *Nature Ecology & Evolution*, *1*(5), 1–2.

Lute, M. L., Carter, N. H., López-Bao, J. V., & Linnell, J. D. (2018). Conservation professionals agree on challenges to coexisting with large carnivores but not on solutions. *Biological Conservation*, *218*, 223–232.

McBride, R. T., Jr, & Thompson, J. J. (2019) Spatial ecology of Paraguay's last remaining Atlantic Forest jaguars (*Panthera onca*): implications for their long-term survival. *Biodiversity*, *20*, 20–26.

McBride, R., & Thompson, J. (2018). Space use and movement of jaguar (*Panthera onca*) in western Paraguay. *Mammalia*, *82*(6), 540–549.

Majgaonkar, I., Vaidyanathan, S., Srivathsa, A., Shivakumar, S., Limaye, S., & Athreya, V. (2019). Land-sharing potential of large carnivores in human-modified landscapes of western India. *Conservation Science and Practice*, *1*(5), e34.

Morato, R. G., Thompson, J. J., Paviolo, A., de La Torre, J. A., Lima, F., McBride Jr., R. T., Paula, R. C., Cullen Jr., L., Silveira, L., Kantek, D. L. Z., Ramalho, E. E., Maranhao, L., Haberfeld, M., Sana, D. A., Medellin, R. A., Carillo, E., Montalvo, V., Monroy-Vilchis, O., Cruz, P., Jacomo, A. T., … Riberio, M. C. (2018). Jaguar movement database: a GPS-based movement dataset of an apex predator in the Neotropics. *Ecology*, *99*(7), 1691.

Packer, C., Loveridge, A., Canney, S., Caro, T., Garnett, S. T., Pfeifer, M., Zander, K. K., Swanson, A., MacNulty, D., Balme, G., Bauer, H., Begg, C. M., Begg, K. S., Bhalla, S., Bissett, C., Bodasing, T., Brink, H., Burger, A., Burton, A. C., ... Polasky, S. (2013). Conserving large carnivores: dollars and fence. *Ecology Letters*, *16*(5), 635–641.

Payan, E., Carbone, C., Homewood, K., Paemelaere, E., Quigley, H. B., & Durant, S. (2013). Where will jaguars roam? the importance of survival in unprotected lands. In M. Ruiz-Garcia, & J. Shostell (Eds.), *Molecular Population genetics, Phylogenetics, Evolutionary Biology and Conservation of the Neotropical Carnivores* (pp. 603–628). Nova Science.

Pringle, R. M. (2017). Upgrading protected areas to conserve wild biodiversity. *Nature*, *546*(7656), 91–99.

Qin, S., Golden Kroner, R. E., Cook, C., Tesfaw, A. T., Braybrook, R., Rodriguez, C. M., Poelking, C., & Mascia, M. B. (2019). Protected area downgrading, downsizing, and degazettement as a threat to iconic protected areas. *Conservation Biology*, *33*(6), 1275–1285.

Quigley, H., Foster, R., Petracca, L., Payan, E., Salom, R., & Harmsen, B. (2017). *Panthera onca*. *The IUCN Red List of Threatened Species 2017: e.T15953A50658693*. International Union for Conservation of Nature and Natural Resources.

Quiroga, V. A., Boaglio, G. I., Noss, A. J., & Di Bitetti, M. S. (2014). Critical population status of the jaguar *Panthera onca* in the Argentine Chaco: camera-trap surveys suggest recent collapse and imminent regional extinction. *Oryx*, *48*(1), 141–148.

R Core Team. (2014). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Rabinowitz, A., & Zeller, K. A. (2010). A range-wide model of landscape connectivity and conservation for the jaguar, *Panthera onca. Biological Conservation*, *143*(4), 939–945.

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M. P., Schmitz, O. J., Smith, D. W., Wallach, A. D., & Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. *Science*, *343*, 1241484.

Sanderson, E. W., Redford, K. H., & Chetkiewicz, C. L. B., Medellin, R. A., Rabinowitz, A. R., Robinson, J. G., & Taber, A. B. (2002). Planning to save a species: the jaguar as a model. *Conservation Biology*, *16*(1), 58–72.

Saura, S., Bertzky, B., Bastin, L., Battistella, L., Mandrici, A., & Dubois, G. (2019). Global trends in protected area connectivity from 2010 to 2018. *Biological Conservation*, *238*, 108183.

Schuster, R., Germain, R. R., Bennett, J. R., Reo, N. J., & Arcese, P. (2019). Vertebrate biodiversity on indigenous-managed lands in Australia, Brazil, and Canada equals that in protected areas. *Environmental Science & Policy*, *101*, 1–6.

Skaug, H., Fournier, D., Bolker, B., Magnusson, A., & Nielsen, A. (2013). *Generalized linear mixed models using AD model builder*. *R package version* 0.7, 7. https://rdrr.io/rforge/glmmADMB/

Swihart, R. K., & Slade, N. A. (1985). Testing for independence of observations in animal movements. *Ecology*, *66*(4), 1176–1184.

Tilman, D., Clark, M., Williams, D. R., Kimmel, K., Polasky, S., & Packer, C. (2017). Future threats to biodiversity and pathways to their prevention. *Nature*, *546*(7656), 73–81.

Torres-Romero, E. J., Giordano, A. J., Ceballos, G., & López-Bao, J. V. (2020). Reducing the sixth mass extinction: Understanding the value of human-altered landscapes to the conservation of the world's largest terrestrial mammals. *Biological Conservation*, *249*, 108706.

Thompson, J. J., Morato, R., Niebuhr, B., Bejarano Alegre, V., Oshima, J., de Barros, A., Paviolo, A., de la Torre, J. A., Lima, F., McBride, R., Cunha de Paula, R., Cullen Jr., L., Silveira, L., Kantek, D. L. Z., Ramalho, E. E., Maranhao, L., Haberfeld, M., Sana, D. A., Medellin, R. A., … Ribeiro, M. (2021). Environmental and anthropogenic factors synergistically affect space use of jaguars. *Current Biology*, *31*, 3457–3466.

UNEP-WCMC (2020). *Protected Planet: The World Database on Protected Areas (WDPA) and World Database on Other Effective Area-based Conservation Measures (WD-OECM).* www.protectedplanet.net

Wegmann, M., Santini, L., Leutner, B., Safi, K., Rocchini, D., Bevanda, M., Latifi, H., Dech, S., & Rondinini, C. (2014). Role of African protected areas in maintaining connectivity for large mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*(1643), 20130193.

Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, *70*, 164–168.

Zeller, K. (2007). *Jaguars in the new millennium data set update: the state of the jaguar in 2006.* Wildlife Conservation Society.

Zeller, K. A., Nijhawan, S., Salom-Perez, R., Hernandez-Potosme, S., & Hines, J. E. (2011). Integrating occupancy modeling and interview data for corridor identification: A case study for jaguars in Nicaragua. *Biological Conservation*, *144*(2), 892–901.