Spatial epidemiology of bovine leptospirosis in Veracruz, Mexico

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SUMMARY

Bovine leptospirosis is a bacterial disease that affects bovine herds, causing economic losses due to reproductive problems, which require expensive treatments. The main source of transmission for cattle is still uncertain, but it has been described that small wild mammals can play an important role in the transmission cycle by being maintenance hosts for the pathogenic species of the bacterium and spreading it through urine. In this study, we characterize possible risk areas for bovine leptospirosis in the state of Veracruz, Mexico; based on the geographical distribution of small wild hosts of *Leptospira* sp. reported in Mexico in addition with climatic, geographic, land use and human activities variables, and validated risk map with bovine seroprevalence data. We used a generalized linear regression model to understand the association between the appearance of bovine leptospirosis seroprevalences and the favorability of wild hosts of *Leptospira* sp. as well as environmental variables. The parameterized model explains 13.58% of the variance. The seroprevalence in cattle showed a negative relationship with elevation, geographic length and human population density, and a positive relationship with environmental favorability for the bats reservoirs and favorability for at least one rodent and opossum reservoir. The variation in seroprevalence is mainly explained by a longitudinal gradient (10.4% of the variance) and the favourability for bats (3.0% of the variance). Describing the possible risks of seroprevalence in an important and neglected livestock geographical region, we contribute to the selection of areas of strategies for diagnosis and prevention of this relevant disease.

Keywords: Biogeography, cattle, risk mapping , spatial epidemiology, wildlife.

INTRODUCTION

Bovine leptospirosis is a re-merging zoonotic disease with worldwide reports, whose highest incidence is recorded in tropical and subtropical areas (Adler & de la Pena Moctezuma, 2010; Costa et al., 2015). The causative agents of the disease are bacterias in the form of spirochetes of the *Leptospira* genus, within which the existence of at least 64 species is recognized along with over 300 serovars (Picardeau, 2017; Vincent et al., 2019). The appearance of this disease depends on the interaction between the infectious agent, the hosts (humans, domestic and / wild animals) and the environment, thus, its handling require a One Health perspective (Bierque et al., 2020; Grimm et al., 2020; Loureiro et al., 2020). In domestic animals, mainly in bovines, leptospirosis is characterized for producing reproductive problems such as abortions, stillbirths, and infertility, but it also leads to low production of milk and sometimes death of the adult animal (Delooz et al., 2018). The wild mammals, specifically rodents, marsupials and bats are considered hosts of pathogenic *Leptospira* species (Allan et al., 2018; Dietrich et al., 2015; Vieira et al., 2018). Wild animals may be possibly able to transmit bacteria to other hosts through contact with tissue or infected urine (Boey et al., 2019; Cordonin et al., 2020; Ko et al., 2009) or through the soil or water, depending on the conditions that prevail for bacteria to survive in the environment (Costa et al., 2015; Thibeaux et al., 2018). There is speculation that wild animals might play an important role as a source of infection for cattle, mainly when this is raised in extensive systems.

In recent years, the spread of infectious diseases such as the leptospirosis has integrated diverse tools from some other branches that strengthen pioneering fields such as health geography and spatial epidemiology (e.g. Jara et al., 2019). Health geography is the branch

of biogeography whereby epidemiology is linked to ecology with a view to study and understand the distribution patterns of infectious, emerging and/or endemic diseases (Escobar & Craft, 2016). These sort of models has led to a better understanding of a variety of transmission and distribution behaviors of diseases over large geographical areas as well as to the possibility to identify and quantify the key factors underpinning the presence and or emergency of disease (Brewer et al., 2020). From a cartographic point of view, such models offer the possibility of generating risk maps with a high level of potential for its use when it comes about the design of surveillance programs and the fight against diseases (Johnson et al., 2019; Peterson, 2008).

Via the Leptospirosis Burden Epidemiology Reference Group (LERG), the World Health Organization recommends the development and use of technological tools to generate risk maps in regions where data is not existent or scarce (Dhewantara et al., 2020; WHO, 2010). This, in order to predict, prevent, detect or intervene in the presence of leptospirosis and limit its impact, within One Health context (Durski et al., 2014). Even so, these approximations shall be interpreted and validated with available information for the area of study so as to be able to deliver interpretations and reliable predictions (WHO, 2010). Thus, leptospirosis risk maps have been generated globally (Torgerson et al., 2015), nationally (Nuñez-Gonzalez et al., 2020; Sanchez-Montes et al., 2015; Zhao et al., 2016) and at a more regional level (Gracie et al., 2014; Jara et al., 2019). The latter have had a high interest rate since such maps correspond to the actions of unit on many occasions, on an epidemiological level. Even though the use of this approach has been spreading in the last number of years, studies that include wild hosts information are few for the majority of the affected zones by the disease.

Concerning Mexico, leptospirosis has been described in humans (Sanchez-Montes et al., 2015; Zuñiga-Carrasco & Caro-Lozano, 2013), domestic (Carmona-Gasca et al., 2011; Zarate-Martinez et al., 2015) and wild animals (Ballados-Gonzalez et al., 2018; Espinosa-Martinez et al., 2015; Gutierrez-Molina et al., 2019; Torres-Castro et al., 2018, 2020). Human cases, just as the incidences in domestic and wild animals, are more frequent in the Southeast states of the country, which include: Tabasco, Yucatan and Veracruz (Ballados-Gonzalez et al., 2018; Pappas et al., 2008). The state of Veracruz is, among these, the main producer of bovine cattle of the country with an annual production of 479,077.518 tons of meat on the hoof and an inventory of 4,306,215 (SIAP, 2018), situation that could be threatened due to the leptospirosis (Allan et al., 2018). At this juncture, the main purpose of our study was to develop risk maps based on the environmental favorability for the main wild *Leptospira* sp. host species; a risk index was elaborated for the state of Veracruz through an analytical framework of the species distribution models, the function of favorability and fuzzy logic, same that were validated with seroprevalence data form bovine animals. Obtained results serve to improve the design of leptospirosis epidemiologic surveillance programs as well as for stimulating the development of directional hypothesis on the role small mammals can play in the transmission of bacteria to the bovine animal in this region, and potentially in other tropical regions where cattle is an important business driver.

MATERIAL AND METHODS

Study area

The study area corresponds to the southeastern coastal state of Veracruz, Mexico, with a total area of 72,410.05 km^2 (3.7% of Mexico). Half of the state is covered by natural

vegetation (grassland, woodland and jungle), however it is estimated that the remaining territory has been destined for agriculture, and urban areas (INEGI, 2017). It is considered that tropical and subtropical climates dominate the state from the sea level to about 1000 masl. Warm and humid, temperate and cold (in the mountains) complete the huge mixture of climates in this diverse state (INEGI, 2020; see also Figure 1).

For analytical purposes, a regular grid with 1km x 1km squares (n=78,612) was developed. This grid was used for spatially explicit modelling; both the initial species distribution models for wildlife hosts and the risk factor analyses carried out in a second step (see below). Thus, all the information handled in this study (wild host distribution data, ecogeographical predictors and *Leptospira* sp. seroprevalence in cattle herds) was transferred to this grid by using zonal statistics and join information by location in QGIS vs 3.10 (QGIS Development Team, 2020). The use of grids solves a large part of the spatial autocorrelation problems derived from sampling bias or observation spatial clustering (Romero et al., 2019).

Occurrences for potential wild hosts of *Leptospira* sp.

Five bat species (*Artibeus jamaicense, Artibeus lituratus, Chiroderma villosum, Desmodus rotundus* and *Pteronotus parnelli*), two rodents (*Mus musculus* and *Rattus rattus*) and two opossums (*Didelphis marsupialis* and *Didelphis virginiana*) were identified in previous studies, using serological approaches, isolation and/or genomic sequencing, as potential reservoirs of *Leptospira* sp. in Mexico (Ballados-González et al., 2018; Gutiérrez-Molina et al., 2019; Krijger et al., 2019; Ruiz-Piña et al., 2002; Vado-Solís et al., 2002; Valbuena-Torrealba & Pefaur-Vega, 2015). Thus, they were the wild species considered in this study. The raw information on distribution for these species was downloaded from GBIF April,

2020 (Global Biodiversity Information Facility, 2020). For a given species, a grid square was considered as "presence" when at least one occurrence was recorded in GBIF (see Table 1).

Spatial explicit models

For each wild species, we followed a two-step modelling procedure: i) delimitation of geographical extent for species distribution modelling, and ii) modelling environmental favourability and transferability to overall Veracruz. As the extent of the geographical background has substantial effects on the outputs of species distribution models (e.g Acevedo et al., 2017; Barve et al., 2011), we delimited an adequate territory to study species distribution (one per species) by a first model in which the third-degree polynomial of the latitude and longitude (trend surface analysis) was considered as predictors (Acevedo et al., 2012). The geographical extent for distribution modelling was represented by the squares which, after carrying out the first model, had a predicted suitability higher than the minimum value assigned to a presence (for further details see Acevedo et al., 2012). This procedure allowed us to study the distribution range within the area that is accessible for the species and is aimed to provide more explanatory models (e.g. Acevedo et al., 2017). As a second step, and within the area selected for each species, we determined the environmental drivers for each species in basis on occurrence points in which the species has been recorded, using generalized linear models (binomial distribution and logit link function; GLM; Hosmer & Lemeshow, 1989). For modelling purposes, we considered all presences and randomly selected ten-times the number of presences as background. We forced this intermediate level of prevalence to avoid statistical artefacts known to produce results biased to the larger group in GLM (Hosmer & Lemeshow, 2000). The model was

parameterized using an 80% random sample of the species data (training dataset) and internally evaluated against the remaining 20% of the data (validation dataset). Twenty-nine variables, related with climate, land uses, topography and human activities were considered as predictors (see Table 2), all of them commonly used in spatial explicit modeling as potential drivers of wildlife distribution from local to large spatial scale (Hortal et al., 2010). To avoid multicollinearity-related problems, we quantified within a stepwise procedure the variance inflation factor (VIF) on the training datasets to exclude those predictors VIF>3 from the analyses prior to modelling (Zuur et al., 2009). The selected predictors after controlling for VIF were considered in the GLM and the most parsimonious model (final model) was selected following a forward-backward stepwise procedure based on Akaike's information criteria (AIC; Akaike, 1974).

Predictive performance of each final model was assessed on the evaluation datasets in terms of discrimination and reliability (e.g. Jiménez-Valverde et al., 2013; Pearce & Ferrier, 2000). Discrimination capability was quantified by the area under the receiver operating characteristic plot (AUC; see Lobo et al., 2008) that was computed using "ROCR" R package (Sing et al., 2005). Reliability of the predicted probabilities obtained from the final models (P) was estimated by exploring the calibration plot and H-L associated statistic (Lemeshow & Hosmer 2000). Calibration plots were constructed using "ggplot2" R package (Wickham, 2009) by plotting the proportion of occupied evaluation sites against the predicted probability of presence (for the ten equally sized probability intervals).

The P-values obtained from GLM were included in the favourability function (Acevedo & Real, 2012; Real et al., 2006): $F = [P/(1-P)] / [(n_1/n_0) + (P/(1-P))]$, were n_1 is the number of presences and no the number of absences in the training dataset. The favourability

function provides a measure of the degree to which local environmental conditions lead to a local probability higher or lower than that expected at random (*F*), being this random probability defined by the overall prevalence of the species in the training dataset. So, using the favourability function those localities with environmental conditions that favour the presence of the taxa ($F>0.5$) can be easily distinguished from those with detrimental characteristics ($F<0.5$) for its presence. The inherent quality of the favourability function of being expressed in relation to the species' prevalence enables direct comparison and combination when several of them are involved in the analytical design, as in this study. For example, this is needed when using models from different event prevalence as a basis for defining endemic areas for a diseases or exposure risk for a given disease (e.g. Boadella et al., 2010; Olivero et al., 2017), which cannot be built based on *P* because these are higher in common than in rare species, so the values for the former would prevail over those for the latter.

Risk indices and risks mapping

Using fuzzy logic operations on *F* values we estimated two different risk indices for flying (bats) and terrestrial wild host (rodents and opossums) (see also Boadella et al., 2010; Romero et al., 2019): i) minimum favourability (*minF*) per square for all involved species within each group (bats and rodents/opossums), and ii) maximum favourability (*maxF*) per square for all involved species within each group. The first one accounts for areas simultaneously favourable for all species and therefore the risk is defined by the presence of a broad community of *Leptospira* sp. potential hosts. The second index accounts for areas in which at least one of the species achieved a high favourability. The consideration

208 of these two risk indices allows to disentangle the potential role of small mammals in the
209 bacteria circulation in the cattle farms.
210 Finally, we performed a risk analyses in order to identify the main factors explaining
211 variations in *Leptospira* sp. seroprevalence in cattle farms. Seroprevalence values for 306
212 herds (widely distributed in the study area; see Figure 1) were obtained from Cruz Romero
213 et al. (2013). These authors provide seroprevalence values per herd and, thus, it provides an
214 independent data for validating the risk indices as actual indicators of risk**.**
215 The risk analyses were performed at herd level (previously transferred to our territorial
216 units for modelling purposes). The four risk indices previously described and related with
217 wildlife were considered as predictors. In the case of those related to bats and due to the
218 high movement capability of these species (Ceballos, 2014; Esbérard et al., 2017) we
219 characterized each sampled 1km x 1km square with the *F* values within a buffer 10 km
220 radious. In addition to risk from wildlife, topography (elevation and slope), geography
221 (latitude and longitude), human activity (population density) and cattle density (SIAP,
222 2018), were also considered as predictors for their potential to explain variability in
223 seroprevalence. All potential risk factors were centered and standardized by subtracting the
224 mean and dividing by standard deviation, prior the modelling. *Leptospira* sp.
225 seroprevalence (log transformed) was the response variable and was modelled with a GLM
226 (normal distribution and identity link function). The final model was obtained following a
227 stepwise backward procedure based on AIC. VIFs of the predictors retained in the final
228 model were checked, as well model assumptions by the visual exploration of the residuals
229 (Zuur et al., 2009). The final model was transferred to overall study area in order to
230 represent the predicted seroprevalence in basis to the main risk factors.
231

RESULTS

The number of localities selected after step 1 are shown in Table S1 (Supplementary Material). VIF analyses excluded for the environmental models some predictors (Table S1). The results of the statistical models used to explain the distribution range of the selected species in basis to environmental predictors are summarized in Table S2 (Supplementary Material). Predicted favourability for each species is represented in Figure S1 (Supplementary Material). Models achieved a high predictive performance according to AUC (>0.7) and calibration plots (see Figure S2 in Supplementary Material).

Fuzzy logic operations allowed to combine specific favourability maps in order to estimate risk indices, independently for each group of species (Figure 2). Risk indices for each wild host group showed equivalent spatial pattern. It is characterized by achieving higher values in Centre and South of Veracruz, mainly in the western mountainous systems and in marshlands close to the Gulf of México (Figure 2). The model parameterized for explaining variations in *Leptospira* sp. seroprevalence in cattle explained 13.58% of the variance. The stepwise procedure selected a model with five predictors (see Table 3), all of them achieved VIF<3. The seroprevalence in cattle showed a negative relation with elevation (marginally significant), geographical longitude and population density (marginally significant), and a positive one with *minF* for bats and *maxF* for rodents and opossums, being the latter marginally significant. Figure 3 shows the relationships between seroprevalence and predictors retained in the final model with statistically significant relationships. Variation in seroprevalence is mainly explained by a longitudinal gradient (accounting for 10.4% of the variance) and the *minF* index for bats (accounting for 3.0% of the variance). The predicted pattern of cattle *Leptospira* sp. seroprevalence according to this model is shown in Figure 4.

DISCUSSION

The approach in this study allowed the drafting of various risk indexes for the *Leptospira* sp. base on the information on distribution of potential wild hosts and along the line of the analytical framework of species distribution models. Such indexes were incorporated in models so as to explain and predict the relative risk associated to the exposure to *Leptospira* sp. on bovine herds and its spatial variation. The model undertaken here revealed a significant role of small mammals, especially of bats previously highlighted as potential reservoirs for this pathogen. In addition to this, it explained the level of seroprevalence in combination with the geographic latitude in bovine livestock herds distributed along the state. Expected spatial patterns with higher index of seroprevalence were located in the central part of the state of Veracruz where areas specifically designated for livestock and farming prevail and the main water sources and important state cities are (INEGI, 2017).

The results of the model showed a moderate level of expected seroprevalence of bovine leptospirosis in the state of Veracruz (Figure 4) and such findings partially differ from previous studies (Zarate-Martinez et al., 2015). These authors studied seven herds of the central zone of the state of Veracruz and had results with seroprevalences of 10 to 89%. Differences between previous prevalence and modeled values may be further detailed herein, at least partially given the fact that these include a higher number of strains of those used in our study (Cruz-Romero et al., 2013). This fact will support the idea that each region possess native serovars, many of them unknown when no insulations nor classifications were made in the majority of the cases (Carmona-Gasca et al., 2011; Delooz et al., 2018; Vincent et al., 2019). On the other hand, risk indexes that may derived for each group of *Leptospira* sp. wild, land and air hosts evidenced an equivalent spatial pattern

(Figure 2), at least in terms of showing a reduced favorability in the northern part of the state and highlighting the local patterns of greater favorability in the central zone. Even though spatial biases that may contain the GBIF data, might have had influence (e.g. Beck et al., 2014), results of internal validation, mainly the relation with the seropositivity indexes in bovine animals, suggest that the bias had no relevance. Moreover, indicators shown higher values in urban areas and water bodies where the presence of these species had not been reported. The foregoing makes sense in connection with its requirements of food and water, and on the other side, as a significant source of pathogens that subsequently can mobilize hosts and geographical areas (see Dobigny et al., 2015; Grimm et al., 2020; Schneider et al., 2018).

Geographical longitude and minimal favorability for concerned bats species were the most important factors explaining the spatial variation in the seroprevalence in bovine herds (Figure 3). Favorability for bats species that were described as reservoirs, identify the zones that possess environmental characteristics that favor the presence of these species. Such favorable zones, in this case the five species, are areas that will have a high abundance of bat species (e.g Weber & Grelle, 2012). This set – up enables a scenario in which the potential for establishing interactions among wild species and herds, are elevated. With the foregoing, the risk of transmission and levels of expected exposure (Ballados-Gonzalez et al., 2018; Dietrich et al., 2015). Conversely, geographical longitude is a gradient that mark big environmental contrasts within the state; to the east with the Gulf of Mexico, while in the west presents tow mountain ranges (Sierra Madre Oriental & Sierra Madre del Sur). This gradient markup has a high explanatory capacity in our model, given the fact that it might be possibly representing purely spatial inertia that can have the studied pattern (seroprevalence) such as the environmental particularities that might constrain differences

304 in the handling of cattle, in possible points of interaction with wild hosts and even in the
305 bacteria survival to temperature or pH in the environment (Schneider et al., 2018; Thibeaux
306 et al., 2018). More studies are needed so as to determine the processes behind the
307 longitudinal gradient so marked in the levels of seroprevalence that has been observed in
308 this research. In this respect, determination of interactions (contacts) among domestic and
309 wild reservoirs, both, based on studies of monitoring of points and/or individuals marked
310 and the analysis of molecular epidemiology, may result very illuminating (e.g. Triguero-
311 Ocaña et al. in press).
312 In turn, favorability for rodents and opossums that may act as hosts also contributed to the
313 risk of exposure when retained in the model (e.g. (Allan et al., 2018; Krijger et al., 2019).
314 The above permits to infer a possible transmission between bovine animals and rodents
315 when being present in studies of the same pathogenic *Leptospira* sp. in both hosts (Allan et
316 al., 2018). As Krijger et al. (2020) mentions, the rodents can be considered as indicator
317 species of *Leptospira* sp. in the environment, and therefore these could present a hazard for
318 the cattle. Hence, said outcome demonstrates once again, the importance of studying the
319 epidemiological relation between wild and bovine hosts, not only at a serovariety or illness
320 level but also at the level of circulating *Leptospira* species and validating findings through
321 genomic classification.
322 This research represents a great step forwards in veterinary medicine to understand the
323 behavior and geographic distribution of bovine leptospirosis at the serovariety level or more
324 effectively at the level of the *Leptospira* specie. It is crucial to know the circulating
325 leptospiras species in wild and bovine animals that interact on a specific area and to be able
326 to deeply observe the risks that may occur. The information presented herein has a keen
327 interest for its ability to stimulate the development of directional hypothesis over the factors

that explain the seroprevalence patterns in bovine cattle, situation that will promote further new studies to gain more in – depth knowledge concerning the *Leptospira* sp. epidemiology in domestic and wild animals, and mainly, in the interface between these. Apart from that, the carried-out risk assessment provides useful information for the development of prevention plans and disease control, based on the risk [sic] through which a more effective fight against the malaise could be reached.

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DATA AVAILABILITY STATEMENT

All the data used in the analyses come from public sources of information. The data that support the findings of this study are available from the corresponding author upon reasonable request.

CONFLICT OF INTEREST

Authors declare to have no conflict of interest.

All the data used in the analyzes come from public sources of information.

ETHICAL STATEMENT

The authors confirm that the ethical policies of the journal, as noted on the journal's author guidelines page, have been adhered to. No ethical approval was required as this is a review article with no original research data.

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Figure legends

Figure 1.- A) Location of the study area, Veracruz state (Mexico), and distribution data obtained for B) bats and C) terrestrial mammals (rodents and opossums) considered in this study due to their potential in Leptospirosis maintenance (see text for details). D) Seroprevalence of Leptospirosis in 316 cattle herds that was considered for validating risks mapped in this study (data obtained from Cruz-Romero et al., 2013).

Figure 2.- A) Minimum favourability for bat species, B) Maximum favourability for bat species, C) Minimum favourability for rodent and opossum species, D) Maximum favourability for rodent and opossum species.

Figure 3.- Relationships between predicted *Leptospira* sp. seroprevalence in cattle herd from Veracruz, México, and the most relevant risk factors namely geographical longitude and minimum favourability (*minF*) for the selected bat species.

Figure 4.- Predicted *Leptospira* sp. seroprevalence in cattle herds from Veracruz, Mexico, according to the model showed in Table 3. Main risk factors were latitudinal gradient and favourability for selected bat species that were described as reservoirs.

636 **SUPLEMENTARY**

637 **Figure S1.-** Host species favourability. Bats: A) *Artibeus jamaicensis*, B) *Artibeus*

638 *lituratus*, C)*Chiroderma villosum*, D) *Desmodus rotundus*, E) *Pteronotus parnellii*;

639 Rodents: F) *Mus musculus*, G) *Rattus rattus*; and Opossums: H) *Didelphis marsupialis*, I)

640 *Didelphis virginiana*.

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642 **Figure S2.-** Calibration plots showing relationships between predicted probability of

643 occurrence from the models and the observed proportion of evaluation localities occupied

644 by each species. Summary of the statistical tests used to validate the models: AUC values

645 and Hosmer–Lemeshow goodness-of-fit statistic values. Significance codes: $P < 0.001$:

646 ***, $P < 0.01$: **, $P < 0.05$: *, n.s.: non-significant.

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Tables

Table 1.- List of the small mammals considered in this study. Raw distribution data obtained from GBIF and their transference to the territorial units considered for modelling is provided (raw/territorial units). A brief description of the role of the species in *Leptospira* sp. epidemiology and associate reference/s is also shown.

Group	Specie	Distribution data		Leptospirosis carrier evidences	Reference
		Occurrences	squares		
Bats	*Artibeus jamaicensis*	1148	189	Identificado en estados del sureste de México.	(Torres-Castro et al., 2020)
	Artibeus lituratus	250	69	Reportado en el estado de Veracruz, México.	(Ballados-González et al., 2018)
	Chiroderma villosum	45	22	Identificado en estados del sureste de México	(Torres-Castro et al., 2020)
	Desmodus rotundus	606	151	Reportado en el estado de Veracruz, México.	(Ballados-González et al., 2018)
	Pteronotus parnellii	199	73	Identificado en estados del sureste de México	(Torres-Castro et al., 2020)
Rodents	*Mus musculus*	104	46	Reportado con alta frecuencia de presencia en el estado de Veracruz, México	(Gutiérrez-Molina et al., 2019)
	Rattus rattus	53	20	Reportado con alta frecuencia de presencia en el estado de Veracruz, México.	(Gutiérrez-Molina et al., 2019)
Opossums	*Didelphis marsupialis*	217	114	Detección de anticuerpos anti leptospira en estados del sureste de México.	(Ruiz-Piña et al., 2002)

	Dedelphis virginiana	198	97	Detección de anticuerpos anti leptospira en estados del sureste de México.	(Ruiz-Piña et al., 2002)

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654 **Table 2.-** Variables used to model the distribution of small mammals (see Table 1) in

655 Veracruz, Mexico.

Code	Variable
Climate*	
BIO1	Mean annual temperature (°C)
BIO2	Mean diurnal range temperatures (°C)
BIO3	Isotermality (BIO2/BIO17)(*100)
BIO4	Seasonal temperatures (°C)
BIO5	Maximum temperatures of the warmest month (°C)
BIO6	Minimum temperatures of the coldest month (°C)
BIO7	Annual temperatures range (BIO5–BIO6)
BIO8	Mean annual temperatures of the wetter quarter
BIO9	Mean annual temperatures of the dry quarter
BIO10	Mean annual temperatures of the warmest quarter
BIO11	Mean annual temperatures of the coldest quarter (°C)
BIO12	Annual precipitation (mm)
BIO13	Precipitation of the wettest month (mm)
BIO14	Precipitation of the driest month (mm)
BIO15	Seasonal precipitation (coefficient of variation) (mm)
BIO16	Precipitation of wettest quarter (mm)
BIO17	Precipitation of dry quarter
BIO18	Precipitation of warmest quarter
BIO19	Precipitation of coldest quarter
Land use[$]	
LU1	Agriculture (surface occupied by the land use, %)

LU2	Woodland (surface occupied by the land use, %)
LU3	Water bodies (surface occupied by the land use, %)
LU4	Grassland (surface occupied by the land use, %)
LU5	Savana (surface occupied by the land use, %)
LU6	Jungle (surface occupied by the land use, %)
LU7	Urbane (surface occupied by the land use, %)
Topography*[#]	
ELEV*	Elevation (m.a.s.l.)
PEND[#]	Slope (%)
Human activities[#]	
POB	Human population (habitants km^{-2})

Data sources: [#] Portal de geoinformación de la pagine del Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO, 2020). http://www.conabio.gob.mx/informacion/gis/ (Accessed April 2020), [$]Instituto Nacional de Estadística y Geografía (INEGI, 2020) https://www.inegi.org.mx/datos/ (Accessed April 2020), and *WorldClim—Global Climate Data available. Described in: Fick, S. E. and R. J. Hijmans. Worldclim 2: New 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology (2017). In: http://www.world clim.org/ (Accessed April 2020)

Table 3.- Summary of the results of the general linear model used to identify the main risk factors explaining the pattern of Leptospira sp. seroprevalence in cattle farms in Veracruz, México. Estimates are provided for standardized predictors. *minF* for bats represents the minimum favourability that is achieved for all (selected bat) species and *maxF* the maximum favourability that they (now selected rodents and opossums) achieve. Both are considered as risk indicators related with wildlife.

Factors	**Estimate (SE)**	**t-value**	**p-value**
(intercept)	0.83 (0.07)	11.943	<0.001
Elevation	-0.15 (0.09)	-1.768	0.078
Human population	-0.12 (0.08)	-1.507	0.132
Geographic longitude	-0.59 (0.09)	-6.109	<0.001
minF for bats	0.42 (0.13)	3.342	<0.001
maxF for rodents and opossums	0.22 (0.14)	1.604	0.110

SUPLEMENTARY

684 **Table S1.-** Number of localities selected for species and environmental predictor models

	Species	Training dataset	Model
Bats	*Artibeus jamaicensis*	1648	-1.24 + 0.09*BIO3 - 0.51*BIO7 + 0.01*LU1 + 0.04*LU7 + 0.03*BIO15 - 0.13*LU5 - 0.01*LU2 + 0.07*PEND
	Artibeus lituratus	604	-3.27 + 0.15*BIO3 - 0.46*BIO7 + 0.01*LU1 + 0.03*LU7 - 6.06*LU5
	Chiroderma villosum	220	-4.85 -11.96*LU2 + 3.08e-01*PEND - 3.06e-02*LU6 + 4.81e-03*BIO18 + 1.88e-04*POB
	Desmodus rotundus	1312	-4.24 + 0.0004524*POB + 0.11*BIO3 + 0.03*LU7 - 0.29*BIO7 + 0.01*LU1
	Pterinotus parnelli	641	1.70 - 1.02*BIO7 + 1.764e-01*BIO3 + 5.46e-04*POB + 8.21e-03*LU1 + 4.45e-02*BIO15 - 2.05*LU5 - 1.85e-02*LU6 - 3.34e-02*LU2 + 1.44e-01*PEND + 2.68*LU7
Rodents	*Mus musculus*	401	-6.35 + 0.0006545*POB + 0.09*LU7 + 0.06*BIO3 - 0.02*LU6 - 0.0097463* LU4
	Rattus rattus	176	4.01 + 2.057e-03*POB + 4.529e-02*LU7 + 2.039e-02*LU1 - 4.05 LU2 - 4.850e-01*BIO7 + 1.587e-01*BIO3
Opossums	*Didelphis marsupialis*	994	5.104e-01 + 2.90e-04*POB - 0.41*BIO7 + 1.01e-02*LU1 + 3.81e-02*LU7 + 7.44e-02*BIO3 + 2.09*LU5 - 8.38e-03*LU6
	Didelphis virginiana	848	-2.07 +0.0004527*POB + 0.05*LU7 - 0.01*LU6 - 0.33*BIO7 + 0.09*BIO3 - 0.02*LU2 + 0.0060103*LU1

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691 **Table S2.-** Logistic regression models and corresponding statistics for each species.

692 Variable codes as in Table 2. Significance codes: P < 0.001 :***, P < 0.01 :**, P < 0.05: *.

693 β parameter coefficient and its standard error *SE*, *Wald* Wald test statistics, *Sig.* significance.

Variable Code	*Artibeus jamaicensis*				*Artibeus literatus*				*Chiroderma villosum*				*Desmodus rotundus*				*Pterinotus parnelli*			
	B	SE	Wald	Sig	B	SE	Wald	Sig	B	SE	Wald	Sig	B	SE	Wald	Sig	B	SE	Wald	Sig
Intercept	-1.24	1.62	-0.77	n.s	-3.27	2.34	-1.39	n.s	-4.85	1.10	-4.40	***	-4.24	1.68	-2.52	*	1.70	2.81	0.60	n.s
BIO3	0.09	0.02	3.28	**	0.15	0.03	3.84	***					0.11	0.02	4.50	***	0.17	5e-2	3.29	***
BIO7	-0.52	0.08	-6.48	***	-0.46	0.11	-3.98	***					-0.29	0.07	-3.97	***	1.02	0.16	-6.28	***
BIO15	0.03	0.01	3.69	***													4e-02	1e-2	2.99	**
BIO18									4e-3	2.e-3	2.40									
LU1	0.01	2e-3	4.34	***	0.01	3e-^{3}	3.07	**					0.01	0.002	3.48	***	8e-3	4e-3	1.72	n.s
LU2	-0.02	0.01	-2.55	*					-12	1180	-0.01	n.s					-3e-2	1e-2	-2.57	*
LU5	-0.14	0.14	-0.99	n.s	-6.06	343	-0.01	n.s									-2.05	1e2	-0.01	n.s
LU6									-3e-2	1e-2	-2.25	*					-1e-2	6e-3	-2.67	**
LU7	0.05	0.01	3.59	***	0.03	0.01	2.04	*					0.03	0.009	4.06	***	2.68	4e2	0.006	n.s
PEND	0.07	0.03	2.34	*					3e-1	1e-1	2.81	**					0.14	5e-2	2.60	**
POB									1e-4	1e-4	1.60	n.s	4e-4	1e-4	3.38	***	5e-4	2e-4	1.91	n.s
Variable Code	*Mus musculus*				*Rattus rattus*				*Didelphis marsupialis*				*Didelphis virginiana*							
	B	SE	Wald	Sig	B	SE	Wald	Sig	B	SE	Wald	Sig	B	SE	Wald	Sig				
Intercept	-6.35	2.51	-2.52	*	-4.01	6.45	-0.62	n.s	0.51	2.04	0.250	n.s	-2.07	2.16	-0.95	n.s				
BIO3	0.06	0.04	1.71	n.s	1e-1	1e-1	1.49	n.s	7e-2	3e-2	2.41	*	0.09	0.03	3.07	**				
BIO7					-4e-1	2e-1	-1.63	n.s	-4e-1	9e-2	-4.39	**	-0.33	0.10	-3.37	***				
LU1					2e-2	9e-3	2.14	*	1e-2	3e-3	3.00	**	0.006	0.003	1.65	n.s				
LU2					-4.05	4e2	-8e-3	.n.s					-0.02	0.01	-1.75	n.s				
LU4	-9e-3	6e-3	-1.51	n.s																
LU5									-2.09	1e2	-0.01	n.s								
LU6	-0.02	0.01	-1.81	n.s					-8e-3	56e-3	-1.63	n.s	-0.01	0.006	-2.25	*				
LU7	0.09	0.25	0.37	n.s	4e-2	1e-2	2.28	*	3e-2	1e-2	2.97	**	0.05	0.01	3.36	***				
POB	6e-4	2e-2	2.31	*	2e-3	9e-4	2.28	*	2e-4	9e-5	3.16	**	4e-4	0.0001	2.35	*				

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