



Historical and present distribution of coyote (*Canis latrans*) in Mexico and Central America

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ABSTRACT

Aim Coyote (*Canis latrans*) distribution in Mexico and Central America has expanded recently reaching the Yucatan peninsula, Belize and Panama, probably promoted by deforestation of tropical areas. Historically, the southern distribution of coyotes prior to European settlement in America was described as reaching only as far south as central Mexico and that introduction of livestock favoured migration of coyotes to southern Mexico and Central America. However, coyote fossil records in Central America and Yucatan, as well as observational records of travellers during the sixteenth century suggest that the coyote's arrival to the region was earlier. Because of the uncertainty of past coyote distribution and the possible economic and ecological impacts due to recent range expansion, the objectives of this study were to confirm if paleontological and historical evidence support the hypothesis that the southernmost limit of coyote distribution before the arrival of European settlers was the centre of Mexico, to discuss the possible factors that have influenced historical shifts in coyote distribution, and to model the present distribution of the coyote in Mexico and Central America, determining the areas where they could invade in the near future.

Location The research area comprises continental Mexico and the Central American Isthmus countries: Guatemala, Belize, El Salvador, Honduras, Nicaragua, Costa Rica and Panama.

Methods The historical distribution (Pleistocene–Early Holocene, Pre-Columbian, sixteenth to nineteenth centuries and twentieth century) was established from coyote records obtained from museum collections and specialized literature. Present coyote distribution for Mexico and Central America was modelled using the Genetic Algorithms for Rule-set Prediction (GARP).

Results Historical coyote records show that this species was distributed in southern Mexico and Central America during the Pleistocene–Early Holocene, the Pre-Columbian period, and during the arrival of Europeans in the sixteenth century. Coyote records indicate a continuous range expansion during the twentieth century. Historical advance and regression of tropical forests in southern Mexico and Central America produced by natural and human events such as climatic changes and variation in human densities could help us understand the historical coyote distribution. The modelled present-day coyote distribution included the north of Belize, the north of Panama, the north of the Yucatan Peninsula and a corridor on the Gulf coastal plain of Campeche in Mexico. Also, the model predicted a region north of the Darien in southern Panama as appropriate for the presence of coyotes, although they have not been detected there so far.

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Main conclusion Coyote records in southern Mexico and Central America during the Pleistocene–Early Holocene, the Pre-Columbian period, and early arrival of European settlers to the area indicated that coyotes were probably already present there and did not recently disperse from the north of Mexico to the south due to livestock introduction.

Keywords

Coyote, *Canis latrans*, Mexico, Central America, distribution, Genetic Algorithms for Rule-set Prediction, range expansion.

RESUMEN

Objetivo La distribución del coyote (*Canis latrans*) se ha expandido recientemente en México y Centroamérica hasta alcanzar la península de Yucatán, Belice y Panamá, probablemente favorecida por la deforestación en regiones tropicales. Históricamente se ha creído que la distribución de esta especie a la llegada de los colonizadores europeos tenía su límite sur en el centro de México y que la introducción del ganado en el sur de México y Centroamérica favoreció la migración de los coyotes hacia estas áreas. Sin embargo, registros fósiles de coyotes en Centroamérica y Yucatán, así como registros visuales de esta especie por viajeros durante el siglo XVI, sugieren que la llegada de los coyotes a la región fue anterior a lo que previamente se creía. Debido a la controversia sobre la distribución anterior del coyote, así como por los posibles impactos económicos y ecológicos que los coyotes pueden provocar por su reciente expansión, los objetivos de este estudio fueron determinar si la evidencia paleontológica e histórica apoya la hipótesis de que la distribución de esta especie antes de la llegada de los colonizadores europeos llegaba hasta el centro de México, discutir los posibles factores que han influido sobre los cambios históricos en su distribución y modelar la distribución actual del coyote en México y Centroamérica, determinando las áreas que los coyotes pueden invadir en el futuro.

Área de Estudio El estudio comprendió la porción continental de México y los países del Istmo Centroamericano: Guatemala, Belice, El Salvador, Honduras, Nicaragua, Costa Rica y Panamá.

Métodos Se estableció la distribución histórica del coyote (Pleistoceno-Holoceno temprano, Precolombina, siglos XVI al XIX y siglo XX) a partir de registros de coyotes obtenidos de colecciones científicas de museos y literatura especializada. Se modeló la distribución actual del coyote en México y Centroamérica usando algoritmos genéticos (GARP).

Resultados Los registros históricos de coyote indican que la especie estuvo distribuida en el sur de México y Centroamérica durante el Pleistoceno-Holoceno temprano, la etapa Precolombina y a la llegada de los europeos en el siglo XVI. Los registros indican un incremento continuo en el área de distribución del coyote durante el siglo XX. El avance y contracción de los bosques tropicales en el sur de México y Centroamérica debido a causas naturales y humanas, tales como cambios climáticos o variación de las densidades humanas, pueden ayudar a entender la distribución histórica del coyote. La distribución actual de esta especie obtenida a través del modelo, reconoce que puede estar presente al norte de la península de Yucatán y la llanura costera del Golfo de Campeche en México, y en Centroamérica, el norte de Belice y el norte de Panamá. Además, el modelo muestra que, aún cuando la especie no ha llegado a la región norte de Darién en el sur de Panamá, dicho lugar es apropiado para ser invadido por los coyotes.

Conclusiones Principales Los registros de coyotes en el sur de México y Centroamérica en el Pleistoceno-Holoceno temprano, la época Precolombina y durante las primeras etapas de la Colonia Española indican que los coyotes probablemente ya estaban presentes en el área a la llegada de los colonizadores europeos, y no se dispersaron recientemente hacia el sur de México y Centroamérica desde el centro de México con la introducción de la ganadería en el área.

Palabras clave

Coyote, *Canis latrans*, México, Centro América, distribución, GARP, expansión.

INTRODUCTION

The size, shape, boundaries and internal structure of the distribution of any species is the manifestation of complex interactions between the intrinsic characteristics of the organisms (environmental tolerances, resource requirements, life history attributes, dispersal characteristics, etc.) and the characteristics of their extrinsic environment (in particular those features whose variation in space and time limit distribution and abundance; Brown *et al.*, 1996). The coyote's capacity to exploit clearings in the landscape caused by human settlements and the eradication of larger predators and competition are probably the key factors that have allowed coyotes to change the structure and dynamics of their geographic range and colonize most of North America over the past 100 years (Parker, 1995). These factors may explain changes in the distribution of coyotes in the USA and Canada, but there is little information on the causes that have favoured the expansion of coyotes in southern Mexico and Central America. The recent deforestation of tropical areas by human activities has been suggested as the key factor contributing to the establishment of new coyote populations in northern Panama (Méndez *et al.*, 1981; Vaughan, 1983), the north of the Yucatan peninsula (Sosa-Escalante *et al.*, 1997) and Belize (Platt *et al.*, 1998). This suggestion is based on the supposition that deforested areas are similar to open and semi-open habitats where coyotes evolved and to which they are well-adapted (Young & Jackson, 1951; Bekoff, 1977). In addition forests appear to be marginal habitats for coyotes probably because of their poor hunting abilities in dense forest vegetation, as perhaps reflected by malnutrition and low fecundity and population densities (Richer *et al.*, 2002; see Créte *et al.*, 2001 for a review).

The current distribution of coyotes, with almost every site between Alaska and Costa Rica being occupied (Bekoff, 1977; Hall, 1981), contrasts with the coyote hypothetical distribution prior to the arrival of Europeans in the sixteenth century, when coyotes were apparently restricted to the prairies of western North America and extended south only to central Mexico (Young & Jackson, 1951; Nowak, 1978). It was not until European settlement and livestock introduction radically changed patterns of land use that coyote expansion

occurred throughout North America, including southern Mexico, and Central America reaching the present-day distribution (Young & Jackson, 1951). However, this distributional hypothesis assumes a scenario in which the environment in the south of Mexico and Central America before the arrival of Europeans was stable and forests permanently covered the area preventing coyote colonization to the south. Recent findings indicate that from 30,000 yr BP. (when the first coyotes inhabited northern and central Mexico in the Pleistocene) through the European arrival, geological and historical events produced that enormous areas of forest in southern Mexico and Central America advanced and retreated in response to climatic changes and impacts of populations of Native Americans (Leyden, 1984; Whitmore & Turner, 1992; Metcalfe *et al.*, 2000; Brenner *et al.*, 2002). This dynamic scenario, in which open and semi-open habitats were present in southern Mexico and Central America before the arrival of the Europeans, suggests the hypothesis that coyotes might have moved to southern areas earlier than previously thought. Thus, we predicted that, after a review of the recent literature, paleontological and historical evidence would show that the southernmost limit of coyote distribution before the arrival of European settlers was farther south in Central America and not in the center of Mexico.

Understanding the processes that have affected the distribution of this predator in Mexico and Central America may yield insights into the consequences of coyote range expansion in the future. Such consequences are not trivial, given the observed extent of economic (i.e. National Agricultural Statistics Service, 2000, 2001) and ecological (i.e. Crooks & Soulé, 1999) impacts of this species in other areas of their range. Thus, our second objective was to attempt to identify the geological and historical events that influenced the historical distribution of coyotes in the area.

If recent coyote range expansion in southern Mexico and Central America has been influenced by the adaptation of coyotes to man and habitat destruction (Vaughan, 1983; Sosa-Escalante *et al.*, 1997), expansion is likely to continue in the future, especially with the accelerated deforestation rates (Kaimowitz, 1996; Challenger, 1998). Therefore, our third objective in this study was to determine the present distribu-

tion of coyotes in Mexico and Central America and the areas that this species could potentially invade in the future, by using an approximation of the fundamental ecological niche of the species – defined here as the complex of ecological conditions within which the species is able to maintain populations (Peterson *et al.*, 2001).

METHODS

Study area

The research area comprises continental Mexico (hereafter called Mexico) and the countries composing the Central American Isthmus: Guatemala, Belize, El Salvador, Honduras, Nicaragua, Costa Rica and Panama (hereafter called Central America).

Study design

We divided the historical distribution of coyotes in Mexico and Central America into four periods: Pleistocene–Early Holocene, Pre-Columbian, sixteenth to nineteenth centuries, and twentieth century. This division was based on the origin and magnitude of environmental changes that occurred during each period. During the Pleistocene, climatic variations resulted in extensive modification of the environments in Mexico and Central America (Leyden, 1984; Colinvaux, 1997, Metcalfe *et al.*, 2000). During the Pre-Columbian period, the expansion and collapse of several indigenous cultures had dramatic effects on the natural environment of the area (Whitmore & Turner, 1992; Leyden, 2002). During the period spanned by the sixteenth to seventeenth centuries, European settlers colonized Mexico and Central America, introduced livestock, and radically changed patterns of land use (Melville, 1994; Challenger, 1998). The twentieth century was characterized by severe human impacts on natural landscapes due to a continuous expansion agriculture and cattle grazing (Kaimowitz, 1996; Challenger, 1998). Due to the differences among literature sources containing coyote distributional records, we used different approaches to compile information for each of the historical periods.

Pleistocene–Early Holocene distribution

We defined this as the period from 30,000 to 3500 yr BP. Localities of Pleistocene–Early Holocene records of coyotes from Mexico and Central America were obtained from searching the *Journal of Vertebrate Paleontology*, the *Journal of Paleontology* and the *Journal of Mammalogy*, as well as other journals such as the *Southwestern Naturalist*, *Revista Mexicana de Historia Natural*, *Arqueología*, *Cuadernos de Trabajo del Departamento de Prehistoria del Instituto Nacional de Antropología e Historia*, and from other paleontological and natural history books (e.g. Flannery, 1967; Nowak, 1979; Polaco & Buitrón, 1997).

Pre-Columbian distribution

We defined this as the period from 3500 yr BP, until arrival of the European colonizers in the sixteenth century. Coyote presence in the highlands of northern Mexico during Pre-Columbian times has been previously confirmed (Young & Jackson, 1951). Consequently, we decided to search only for records in central and southern Mexico, and areas in Central America where the coyote's presence at that time has been disputed. We obtained localities and dates of coyote records from Mexico and Central America through an extensive bibliographic search of archeological excavation reports and books about Pre-Columbian civilizations in which archaeozoological observations were present.

Sixteenth to nineteenth century distribution

Coyote records after the European settlers' arrival were obtained from texts of naturalists and travellers, following Monge-Nájera & Morera-Brenes (1986). As in the Pre-Columbian distribution section, we only searched for coyote records from central and southern Mexico, and Central America.

Twentieth century distribution

Localities where coyotes were collected from Mexico and Central America during the twentieth century were compiled from museum collections of Mexico and the USA (see Acknowledgments). Coyote records deposited in the mammal collections of the University of Kansas, the University of California at Berkeley and Cornell University were obtained via Species Analyst (<http://speciesanalyst.net/index.html>). Records from the Colección de Mamíferos de la Sierra Volcánica Transversal de México (UAM- Iztapalapa), Museo Alfonso L. Herrera, Facultad de Ciencias UNAM, Colección de Aves y Mamíferos del Valle de Cuatrociénegas Coahuila and Mamíferos de Nuevo León were obtained using the World Biodiversity Information Network REMIB (http://www.conabio.gob.mx/remib_ingles/doctos/remib_ing.html). We supplemented these data with annotated mammal checklists, miscellaneous scientific reports, unpublished theses, and management plans of natural protected areas from Mexico and Central America (see Appendix). All coyote records from museums and literature localities were georeferenced to the nearest minute of latitude and longitude via direct consultation of various map series.

Current distribution

The current distribution is the area presently occupied by coyotes in Mexico and Central America. To predict the current potential distribution of coyotes in Mexico and Central America, we use the desktop version of the Genetic Algorithm for Rule-set Prediction (GARP; <http://www.lifemapper.org/desktopgarp/>). This is an iterative artificial-intelligence-based

algorithm used to approximate the fundamental ecological niche of a species. In GARP, individual approaches to approximate species fundamental niche, such as BIOCLIM (Nix, 1986) and logistic multiple regression (Austin *et al.*, 1990) among others, are used to produce component 'rules' in a broader rule set. Hence, portions of the landscape may be identified as inside or outside of the niche (Stockwell & Peters, 1999). GARP represents a superset of the other approaches (BIOCLIM, logistic multiple regression, etc.) and should generally have greater predictive ability than any one of them alone. Extensive testing of GARP has indicated excellent predictive ability for species geographic distributions (e.g. Peterson, 2001; Peterson & Vieglais, 2001).

To build the model of the current distribution with GARP, we used the georeferenced coyote records and localities obtained for the twentieth century. Due to differences in the origin and quality of the environmental layers available for model construction for Mexico and Central America, we decided to develop a different model for the two regions. For the distributional model of Mexico, we used digitized maps of potential vegetation, current vegetation, and categorical climate maps that summarized annual average temperature and precipitation, obtained from Conabio-México (<http://www.conabio.gob.mx>), and digital elevation models (processed into maps of elevation, slope, aspect, and solar radiation) obtained from the Defense Mapping Agency (<http://edcdaac.usgs.gov/gtopo30/hydro/namerica.html>). For Central America, we used the Leemans Holdridge Life Zones (Leemans, 1990) from the National Geophysical Data Center (<http://www.ngdc.noaa.gov/seg/ecosys/>), the digital elevation models from the Defense Mapping Agency (elevation, slope, aspect, and solar radiation), and the averages of mean annual temperature and precipitation (1960–90; New *et al.*, 1999) from the Intergovernmental Panel of Climate Change (<http://ipcc-ddc.cru.uea.ac.uk/>) as data layers. Because GARP requires all data to be at the same spatial resolution, we re-sampled the input environmental data for Mexico and Central America to a standard 10 × 10 km grid size, although the native resolution of the topographic data is finer (1 × 1 km) and that from the climatic data is coarser (30 × 30 km).

Because coyote records for extensive areas in the south of Mexico are limited, we decided to use all coyote occurrences in the distribution model building (training) as this increases the predictive capacity of GARP when the occurrence data are scarce (Anderson *et al.*, 2003). We developed 100 replicate models of ecological niches for Mexico and Central America. Since we used all coyote occurrences in model building, we selected the best 10 models for each area from the entire set of models using the intrinsic test proposed by Anderson *et al.* (2003). Selected models were saved in ASCII raster grid format, and imported into ArcView (version 3.2). Then all models were superimposed to create a composite prediction showing the number of optimal models predicting presence in each pixel across the study region. We considered a pixel to form part of the coyote distribution if seven or more of the

10 best models indicated the presence of coyotes in the pixel. To reduce bias obtained in the GARP model for Mexico due to excessive coyote records in the north of the country (550 of the 610 coyote records from collections are from areas over 21° of latitude), we decided to use only one randomly selected record per 500 km² cell in the Mexican states of Baja California Norte, Baja California Sur, Sonora, Chihuahua, Coahuila, Durango, Zacatecas and San Luis Potosí.

RESULTS

Pleistocene–Early Holocene distribution

We found 14 coyote records for Mexico and Central America in the literature (Fig. 1). Most of the records were located in northern and central Mexico, but two of them were found in the southern portion of the present coyote distribution: one in the Yucatan peninsula (Álvarez, 1982) and the other in the Nicoya peninsula in Costa Rica (Lucas *et al.*, 1997).

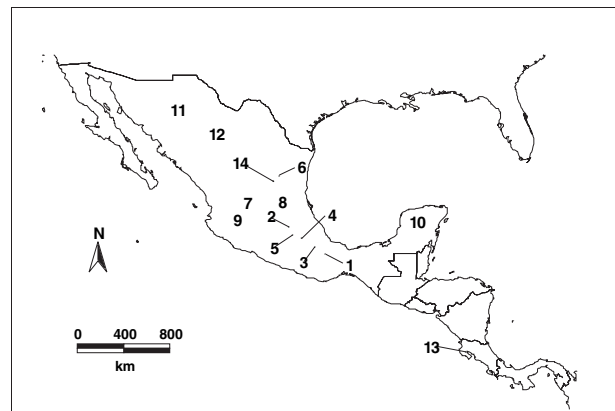


Figure 1 Location of Pleistocene coyote records for Mexico and Central America. Numbers specify the original citation of the record. The period of the record is cited when it was present in the original publication. (1) Monte Flor Cave, Valle Nacional, Oaxaca (Álvarez, 1963a); (2) Tequiquiac, Estado de México (Late Pliocene–Pleistocene; Álvarez, 1965); (3) Tehuacán valley, Puebla (Late Pleistocene–Early Holocene; Flannery, 1967); (4) Valsequillo, near Puebla (Late Pleistocene; Kurtén, 1967 cited in Nowak, 1979); (5) Tlapacoya, Estado de México (Pleistocene–Recent; Álvarez, 1969); (6) San Josecito Cave, Nuevo León (Rancholabrean–Post-glacial; Kurtén, 1974); (7) El Cedazo, Aguascalientes, México (Middle Pleistocene; Mooser & Dalquest, 1975); (8) Laguna de la Media Luna, San Luis Potosí (Late Pleistocene; Hernández-Junquera, 1977); (9) Chapala-Zacoalco, Jalisco (Late Pleistocene; Ferrusquia-Villafranca, 1978); (10) Loltún Cave, Yucatán (Late Pleistocene–Early Holocene; Álvarez, 1982); (11) Yepómera, Chihuahua (Late Pleistocene; Lindsay, 1984); (12) Jiménez, Chihuahua (Late Pleistocene–Holocene; Messing, 1986); (13) Barra Honda, Río Nacaome, Nicoya, Costa Rica (Lucas *et al.*, 1997); (14) La Presita, San Luis Potosí (Polaco & Buitrón, 1997).

Pre-Columbian distribution

The search of coyote records in the archaeozoological publications from the south of Mexico and Central America revealed only one record in Tipú, now Belize (Emery, 1999; Fig. 2). Dated during the Maya Post-Classic period (1100–500 yr BP), this record was based on the presence of coyote remains from the excavation and were clearly distinguished from domestic dog (*Canis familiaris*) remains.

Sixteenth to nineteenth century distribution

We found 15 mentions of coyote sightings for Mexico and Central America in the literature (Fig. 2). We found two mentions of wolves (*Canis lupus*; Fernández de Oviedo, 1856 cited in Monge-Nájera & Morera-Brenes, 1986; Cockburn,

1976) in Central America. Since in several texts coyotes are indifferently named coyotes or wolves (Ximenez, 1967; Belt, 1985), or recognized as small wolves (Sahagún, 1975), we decided to classify these observations as coyotes. Other coyote records were found, but due to the lack of accuracy in the location of the sighting (e.g. Sahagún, 1975) or because the sightings were located in the desert areas of the northern Mexico, we did not include these data in the analysis. Coyote records for this period were located mostly in central Mexico, southern Nicaragua and northern Costa Rica. Guatemala, El Salvador, and Honduras had one record each.

Twentieth century distribution

We obtained 802 coyote records for Mexico and Central America. Only 693 had enough information to be georefer-

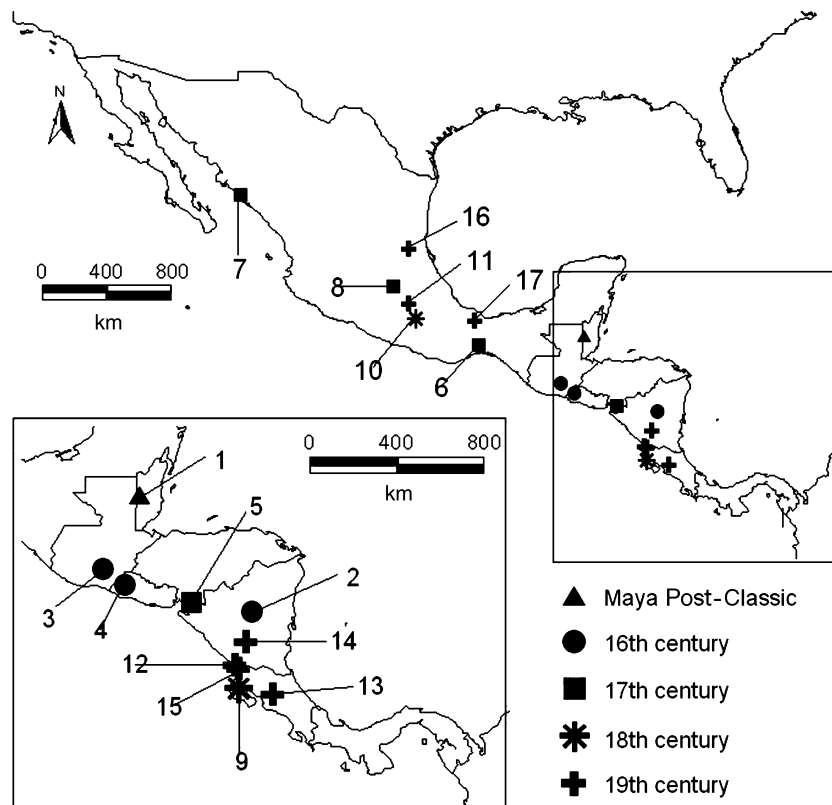


Figure 2 Approximate location of Pre-Columbian and Colonial coyote records for Mexico and Central America. Symbols indicate the time period where coyotes were recorded. The Mayan Post-Classic (1100–500 yr BP) record originated from zooarchaeological excavations. Colonial records originated from chronicles of travelers and priests of the centuries sixteen to nineteen. Numbers specify the original citation of the record. Maya Post-Classic: (1) Tipú, Belice (Emery, 1999). Sixteenth century: (2) Río de la Plata, Gobernación de Castilla y Oro (Fernández de Oviedo, 1856 cited in Monge-Nájera & Morera-Brenes, 1986); (3) San Raymundo las Casillas, Valle de Guatemala (Ximenez, 1967); (4) Santa Ana la Grande, Provincia de el Salvador (Ximenez, 1967). Seventeenth century: (5) El Salvador close to Cholulteca (Wafer, 1934); (6) Tehuantepec, Oaxaca (Gage, 1986); (7) Provincia de Sinaloa (Pérez de Rivas, 1985); (8) Jilotepec, Estado de México (Torquemada, 1986). Eighteenth century: (9) Golfo de Herradura, Valle de Bagaces (Cockburn, 1976); (10) Chinantla, Alto Papaloapan, Oaxaca (Ajofrín, 1986). Nineteenth century: (11) Amecameca, Estado de México (Ladensio, 1868 cited in Iturriaga, 2003); (12) Turracaras near Alajuela (Alfaro, 1897); (13) Tamarindo and Junquillal near Bay of Salinas (Alfaro, 1897); (14) San Ubaldo, Nicaragua (Belt, 1985); (15) Guanacaste, Costa Rica (Meléndez, 1974 cited in Monge-Nájera & Morera-Brenes, 1986); (16) Huasteca Potosina, San Luis Potosí (Lyon, 1984); (17) Istmo de Tehuantepec, Sur de Veracruz (Sainte-Croix, 1992).

enced to the nearest minute of latitude and longitude. Of these, 610 records were obtained from mammal collections of the USA and Mexico and 83 from local mammal faunas and miscellaneous scientific reports (Fig. 3).

Current distribution

After reducing the number of collection points to decrease the bias in the GARP distributional models for Mexico, we developed our final model for the country with 298 spatially unique records. For Central America, we developed the distribution model with 29 spatially unique records. The model for Mexico showed that coyotes present a continual distribution in the north and centre of the country (Fig. 4a), with major gaps in the distribution present in the south of the country. Large areas where the model indicated the absence of coyotes are located in what is known as the Chimalapas, Selva Lacandona, Sierra Norte de Oaxaca, Tabasco-Campeche wetlands, the Coast of Chiapas, and the Yucatan peninsula (Fig. 4b). For Central America, the model predicted the occurrence of coyotes mostly on the Pacific coast of Guatemala, Honduras, Nicaragua, Costa Rica, northern Belize, and northern Panama, including potentially northern Darien (Fig. 5a). Major gaps of coyote distributional predictions were in Belize-Peten-Maya Forest, the Mosquitia coast, the Atlantic forests of Nicaragua and Costa Rica, eastern and central Panama, southern Darien, the Osa Peninsula, and central and northern El Salvador (Fig. 5b).

DISCUSSION

Past coyote distribution

During the Pleistocene, fossils indicate that coyotes roamed in extensive areas of north and central Mexico. However, coyote records found in the Yucatan peninsula and Costa Rica show that coyotes lived farther south than previously reported,

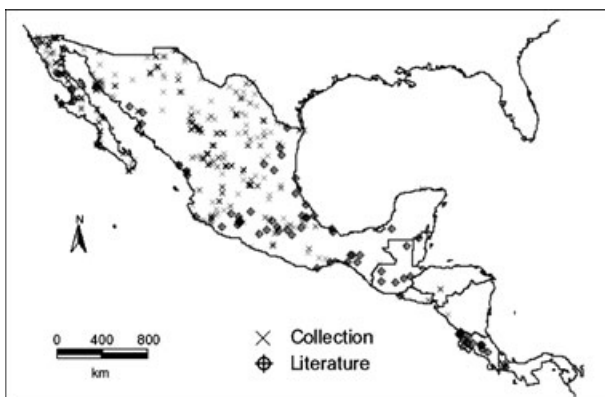


Figure 3 Locations of known occurrences of coyotes from Mexico and Central America. Symbols specify the origin of the data: collection (records originated from a mammal collection of Mexico or the USA) and literature (records obtained from lists of mammal faunas and coyote citations in literature).

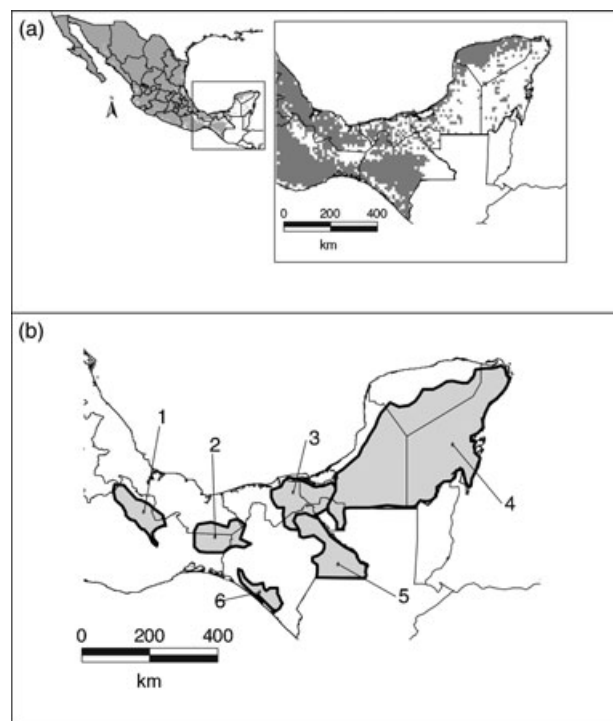


Figure 4 (a) Predicted geographic distribution of coyote in Mexico using GARP. Grey tone indicates presence of coyotes in seven or more of the 10 best subset models. White tone indicates absence of coyotes. A zoom to the south of Mexico is shown on the right side of the figure. (b) General areas of the south of Mexico where the model indicates coyotes are absent: Sierra Norte of Oaxaca (1), Chimalapas (2), Tabasco-Campeche wetlands (3), Yucatan Peninsula (4), Selva Lacandona (5) and Chiapas coast (6).

suggesting that environmental conditions during this time allowed them to survive in these areas. Quaternary Paleoclimatological data for Yucatan and Central America have shown that cyclical dry conditions transformed extensive areas covered with tropical forests to open forests or grasslands with some exceptions such as the Darien in Panama, where tropical forests were present during the whole period (Leyden, 1984; Colinvaux, 1997; Metcalfe *et al.*, 2000). These open environments in Central America favoured the arrival and expansion of many North American mammals associated with grasslands, like canids, and their posterior invasion to South America (Webb, 1977; Berta, 1987). It is likely that these conditions also favoured coyote survivorship in areas as far south as Costa Rica.

The Post-Classic Maya coyote record in Tipu (Emery, 1999) indicates that coyotes lived in the southeast of the Yucatan Peninsula in that time. During Pre-Columbian period, human civilizations in southern Mexico and Central America converted widespread areas of forest to agricultural lands (e.g. Behling, 2000; Brenner *et al.*, 2002). This effect, combined with the fact that during this period global climatic changes also had important effects on forest distribution in the area (Whitmore *et al.*, 1996; Brenner *et al.*, 2002; Leyden, 2002), resulted in large extensions of open landscapes. It is probable

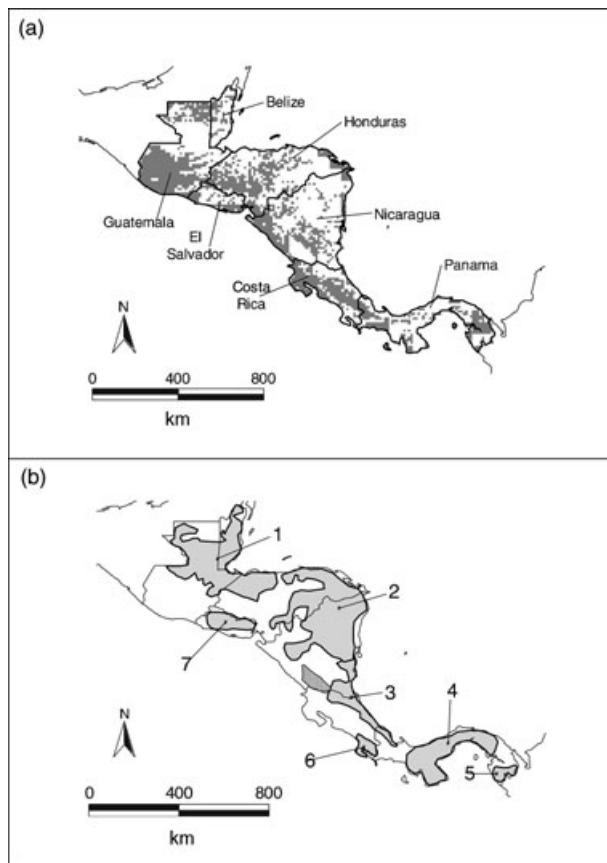


Figure 5 (a) Predicted geographic distribution of coyote in Central America using GARP. Grey tone indicates presence of coyotes in seven or more of the 10 best subset models. White tone indicates absence of coyotes. (b) General areas in Central America where the model indicates coyotes are absent: Belize-Petén-Maya Forest (1), Mosquitia coast (2), Nicaragua and Costa Rica Atlantic forest (3), East Panama (4), Darien (5), Osa Peninsula (6) and North of El Salvador (7). Lake Nicaragua is represented by the dashed area.

that the Tipu record came from coyote populations that subsisted in these open-environments. Another possible explanation for the origin of these remains is trade, although commercial activities in the Tipu area were highly reduced during the Post-Classic period (Emery, 1990 cited in Emery, 1999).

Observations of coyotes by travellers during the sixteenth century in southern areas as far as Costa Rica suggest that if coyotes dispersed from central Mexico to southern Mexico and Central America after the European arrival, it was during the early stages of the colonization. However, the impact of livestock introduction from sixteenth to nineteenth centuries in tropical ecosystems of Mexico and Central America was fairly minor (Aguilar-Robledo, 2001; Castro-Herrera, 2001; Sluyter, 2001), and human depopulation after the European arrival (from 80% to 99% in some areas, Lovell & Lutz, 1995; Whitmore, 1996) favoured a shift in large areas that used to support intensive agriculture during the fifteenth century to forests by the middle of the seventeenth century (Denevan,

1992). This scenario in which open-habitats that should favour coyotes were reduced suggests that the most likely explanation for coyote presence in Central America in the sixteenth century was that they were already there at the arrival of the Europeans. The differentiation of three modern coyote subspecies in the south of Mexico and Central America (*C. latrans goldmani*, *C. latrans dickey* and *C. latrans hondurensis*) after migration from central Mexico following the arrival of the Europeans is questionable (Nowak, 1978), and thus does not provide evidence to support the alternative hypothesis that coyotes arrived after the settlers. Cranial similarities between *C. latrans hondurensis* and the Pleistocene subspecies *C. latrans harriscrooky* (now extinct) suggest that the time of origin of Central American coyotes was earlier than previously thought (Nowak, 1978). A phylogeographic analysis of the coyotes of Mexico and Central America will probably help to determine if this hypothesis is true and if modern coyotes are related to those who lived during the Pleistocene in the area or are emigrants from northern populations.

The distribution of coyotes in the tropical forests of southern Mexico and Central America during the first half of the century is difficult to determine. However, during this time historical events like the agrarian reform in Mexico and the opening of new areas for agro-exportation in Central America contributed to the reduction of important areas of forest in Mexico and Central America (Heckadon-Moreno, 1997; Challenger, 1998). These events may have benefited the expansion and establishment of coyote populations in the area. In the second half of the century, the area was characterized by the continuous expansion of agriculture and especially cattle grazing (Heckadon-Moreno, 1997; Challenger, 1998). Human-induced pasture expansion in tropical dry areas of the Pacific and central regions of Costa Rica and Panama from 1950 to 1980 (Kaimowitz, 1996) probably allowed coyotes to invade new territories in the south of Costa Rica by the end of the 1970s and the north of Panama in the beginning of the 1980s (Méndez *et al.*, 1981; Vaughan, 1983).

The path that coyotes followed to colonize the Yucatan Peninsula was probably the costal plain of Campeche (Sosa-Escalante *et al.*, 1997) where recent reports established coyote presence (Platt *et al.*, 1998) and where extensive deforestation occurred during the 1980s and 1990s (Mas-Causel, 1996). The new coyote record from the north of Belize (Platt *et al.*, 1998) was probably a result of the deforestation processes carried out in the Peten and in the southern portion of the Yucatan peninsula, where road construction and forest concessions recently caused substantial forest losses (Turner *et al.*, 2001; Hayes *et al.*, 2002).

Current and future coyote distribution

The ecological niche model of the distribution of coyotes in Mexico and Central America included areas not recorded before as part of the range of the species, although it is similar to previously reported distribution (Hall, 1981). For Mexico, the model indicated that the north of the Yucatan Peninsula

and a corridor on the Gulf coastal plain of Campeche are areas with potential habitat for coyotes. For Central America, the model included new areas in the north of Belize and the north of Panama as regions where coyotes might be present. Also, although the model showed that the region north of Darien is appropriate for the presence of coyotes, they have not been recorded in areas that far south.

The distribution model excluded most of the areas where extensive patches of tropical moist forests persist such as the Yucatan Peninsula–Belize–Petén–Maya Forest complex, the Selva Lacandona, Chimalapas, the Central America Atlantic forests, the Osa Peninsula, and the eastern Panama–Darien. This result indicated that among all the landscape variables used in the construction of the model, the most important factor limiting coyote distribution was the presence of large patches of tropical moist forests, which is coincident with the hypothesis that recent deforestation of tropical areas by human is the key factor contributing to the coyote range expansion (Vaughan, 1983; Sosa-Escalante *et al.*, 1997; Platt *et al.*, 1998).

In the near future it is likely that coyotes will continue to expand their range in southern Mexico. Intense human pressure exists in the Selva Lacandona, Yucatan Peninsula, the Petén, and the Selva Maya to open new areas for agriculture and cattle grazing (Cuarón, 2000; Hayes *et al.*, 2002). The prediction that coyotes will invade the Selva Lacandona in the short time due to increasing deforestation (Cuarón, 2000) could be supported by recent reports of coyotes in the surroundings (March *et al.*, 1996). Coyote colonization of other areas, such as the north of Belize and south of Yucatan, will probably continue in the coming years due to the opening of new areas to agriculture and the arrival of new settlers (Turner *et al.*, 2001; Hayes *et al.*, 2002). In Chimalapas, deforestation trends are less severe (Arriaga *et al.*, 2000; Caballero, 2000) and coyotes will probably not be able to invade the area in the near future.

The scenario in Central America is similar to southern Mexico. Areas such as the Osa Peninsula and central and southern Panama will probably be invaded by coyotes in the future because strong human population pressures are expected in these areas (Kaimowitz, 1996; Rosero-Bixby *et al.*, 2002). New reports of coyotes at the province of Cocle in central Panama (V. H. Tejera, Museo de Vertebrados, Universidad de Panamá, pers. comm.) are probably result of this pressure. The possible invasion of coyotes into South America following the completion of the Pan-American Highway that will connect Panama and Colombia is an old concern among naturalists (Monge-Nájera & Morera-Brenes, 1986; De la Rosa & Nocke, 2000). The argument that a new road through the Darien in Panama will favour the clearing of large areas of forest and open a corridor for coyotes to enter into Colombia is supported by our distribution model in which areas north of Darien are suitable habitats for this species. However, the road project is detained provisionally (Webster *et al.*, 1996), and the large extension of preserved forest (more than 150 linear km) will probably prevent coyote expansion, at least temporarily.

As in other parts of their range, coyotes are considered pests in southern Mexico and Central America, because they are frequently in conflict with human interests (Cuarón, 2000). If current land transformation trends continue, there will most likely be a substantial increase in coyote populations and distribution with the consequent rise in human-coyote conflicts (Méndez *et al.*, 1981; Sosa-Escalante *et al.*, 1997; Cuarón, 2000; De la Rosa & Nocke, 2000). Coyote range expansion in the area will probably have ecological impacts, too. Coyotes are competitors with, and predators of, a wide array of species, and important effects of this predator have been documented in coyote dominated ecological systems (e.g. Crooks & Soulé, 1999). It is important to identify the range and magnitude of ecological effects produced by coyotes in tropical areas, especially because coyotes will probably become the top predators in the areas cleared for human activities (Cantú-Salazar *et al.*, 1998).

ACKNOWLEDGMENTS

We wish to thank all the curators and staff of the museums and mammal collections that kindly provided information about their coyote holdings: the American Museum of Natural History, the Harvard Museum of Comparative Zoology, the California Academy of Sciences, the Field Museum of Natural History, the Louisiana State University Museum of Natural History, the San Diego Natural History Museum (Bird and Mammal Department), the British Museum, the United States National Museum of Natural History, the Mammal Collection of the Instituto de Biología UNAM, the Mammal Collection of the Natural History Museum of Los Angeles County, the University of Michigan in Ann Arbor, the Michigan State University in Lansing and the Moore Laboratory of Zoology at Occidental College. We thank Rogelio Macías, Rurik List, Enrique Martínez-Meyer, Luis Hernández-Sandoval, Erin E. Boydston and two anonymous reviewers for helpful comments on the manuscript. We wish to thank the Instituto de Ecología A. C. for its support and CONACyT for the graduate scholarship to MGHM (Agreement 128761).

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APPENDIX

Coyote records for the twentieth century of Mexico and Central America obtained from annotated mammal checklists, miscellaneous scientific reports, unpublished thesis and management plans of natural protected areas. The name of the locality is followed by the name of the state or the province when it was available.

Belize: Golden Button Ranch, Orange (Platt *et al.*, 1998)

Costa Rica: Bahía de Salinas; Turrucaras near Alajuelas (Alfaro, 1897); Nicoya, Guanacaste; Bebedero, Guanacaste; Miravalles, Guanacaste (Goodwin, 1946); Highway Liberia to La Cruz; Playa Nancite; Santa Rosa National Park (Janzen, 1983); Highlands of the Braulio Carrillo National Park (Timm *et al.*, 1989); Palo Verde (Vaughan & Rodríguez, 1986); Cerro de la Muerte National Park; Monteverde National Park; San José Volcano National Park (Rodríguez & Chinchilla, 1996).

Guatemala: Northeast of Guatemala city; Quetzaltenango; Sierra los Cucumantes (Young & Jackson, 1951); Uxactun,

Petén (Platt *et al.*, 1998); Valle de Motagua (Valle *et al.*, 1999); Laguna Barrona (Dix & Fernández, 2001).

Mexico: Pochiutla, Guerrero (Leopold & Hernández, 1944); 15 mi northeast of Morelia (Hall & Villa, 1949); Escuinapa, Sinaloa (Young & Jackson, 1951); Reynosa, Tamaulipas; Tampico, Tamaulipas; Mazatlán, Sinaloa; Álamos, Sonora; Acatlán, Puebla (Ingles, 1958); Izúcar de Matamoros, Puebla (Van Gelder, 1960); Coalcoman, Michoacán (Brand, 1960 cited in Álvarez & Sánchez-Casas, 1997); Cráter Parícutín (Burt, 1961 cited in Álvarez & Sánchez-Casas, 1997); Nicolás, Tamaulipas; Sierra San Carlos, Tamaulipas; 9.5 mi SW Padilla, Tamaulipas (Álvarez, 1963b); Perote, Veracruz (Hall & Dalquest, 1963); Chapulco, Puebla (Flannery, 1967); Chamela, Jalisco (López-Forment *et al.*, 1971); Higuera de Zaragoza, Sinaloa; El Carrizo, Sinaloa; Tecapán, Sinaloa (Armstrong *et al.*, 1972); Arriaga, Chiapas; Cintalpa, Chiapas; Jiquilpas, Chiapas; Villaflores, Chiapas; Suchiapa, Chiapas (Álvarez, 1977); El Tuito, Jalisco (Nuñez-Garduño *et al.*, 1981); Sierra de Manantlán, Jalisco (González-Pérez *et al.*,

1992); Tocumbo, Michoacán (Lechuga & Nuñez-Garduño, 1992 cited in Álvarez & Sánchez-Casas, 1997); Ejido el Limón, Tepalcingo, Morelos (Sánchez & Romero, 1992 cited in Sánchez-Hernández & Romero-Almaráz, 1995); Salina Cruz, Oaxaca (Cervantes & Yépez-Mulia, 1995); Huautla, Morelos (Sánchez-Hernández & Romero-Almaráz, 1995); Zicuiran, Michoacán; La Salada, Michoacán (Álvarez & Sánchez-Casas, 1997); Ticumán, Morelos (Álvarez *et al.*, 1998); Los Tuxtlas, Veracruz (Coates-Estrada & Estrada, 1986) Sierra del Carmen (Mercado-Reyes, 1998); Escárcega, Campeche (Platt *et al.*, 1998); La Ciradilla, Michoacán; El Molino, Michoacán; El Mirador, Michoacán; Río el Huaco, Michoacán; Cerro de la Gallina, Michoacán (Reyna-Escaname, 1999); El Tajín, Veracruz (Gobierno del Estado de Veracruz, 2001); El Cielo, Tamaulipas (Vargas-Contreras & Hernandez-Huerta, 2001); Bahías de Huatulco, Oaxaca (Hernández-Hernández, 2002).

Panama: Guacala 70 km south of Costa Rica, Chiriquí; Boquete, Chiriquí (Méndez *et al.*, 1981).