INSTITUTO DE ECOLOGIA, A.C.

ECOLOGÍA ESPACIAL DEL COYOTE (*CANIS LATRANS*) EN UN BOSQUE TROPICAL CADUCIFOLIO DE LA COSTA DE JALISCO, MÉXICO

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DECLARACIÓN

Excepto cuando es explícitamente indicado en el texto, el trabajo de investigación contenido en esta tesis fue efectuado por el Biol. Mircea Gabriel Hidalgo Mihart estudiante de la carrera de Doctorado en Ciencias (Ecología y Manejo de Recursos Naturales) entre septiembre de 1998 y agostol del 2004, bajo la supervisión de los Drs. Alberto González Romero y Carlos Alberto López González.

Las investigaciones reportadas en esta tesis no han sido utilizadas anteriormente para obtener otros grados académicos, ni serán utilizadas para tales fines en el futuro.

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A mis padres

René Hidalgo Salinas

Magda Mihart Heisler

A mi Hermana Doina y su allegada Mónica

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Resumen

El área de distribución del coyote en México y Centroamérica se ha ampliado en los últimos 25 años, pues en los años 80´s y 90´s se reportaron por primera vez en áreas que anteriormente no ocupaban, como el norte de Panamá, el norte de Yucatán y Belice. Aunque no existen datos suficientes para asegurarlo, se ha sugerido que la expansión del coyote ha sido inducida fundamentalmente por la deforestación de los bosques tropicales para actividades agrícolas y ganaderas, pues esta acción crea áreas abiertas que son el hábitat ideal para una especie que evolucionó y esta adaptada zonas con baja cobertura vegetal como el coyote. La tendencia actual, en la cuál los bosques tropicales en México y Centroamérica se deforestan a elevadas tasas, muy probablemente traerá como consecuencia un aumento en el tamaño de las poblaciones de coyotes, así como la expansión del área de distribución de la especie. Como resultado de estas condiciones, es de esperarse que los conflictos entre humanos y coyotes se incrementen (principalmente daños a productos agrícolas y depredación de aves de corral y ganado). Ante esta situación se hace urgente el proponer planes de manejo y control de la especie en áreas tropicales que permitan tanto prever como responder a los posibles incrementos en las poblaciones de coyotes. Debido a la falta de información sobre respuesta de los coyotes a las áreas tropicales y la deforestación de las mismas, en este trabajo se pretendió generar información biológica básica sobre la especie (área de distribución actual e histórica, uso de hábitat en un ambiente tropical y respuesta de la especie a factores extremos de intervención humana como un basurero, en un área tropical), que puede ser útil como una herramienta en el diseño de planes de manejo para el coyote en zonas tropicales.

La información existente hasta hace poco tiempo indicaba que el límite sur de la distribución del coyote hacia el siglo XV alcanzaba únicamente el centro de México y que el cambio en las actividades productivas, sobre todo el arribo del ganado europeo, favoreció que el coyote invadiera el sur de México (con excepción de Yucatán), así como la costa del Pacífico y las tierras altas de Centroamérica hasta Costa Rica. Sin embargo, la revisión de registros fósiles e 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 provenientes de colecciones científicas de México y Estados Unidos 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 de una aproximación al nicho ecológico de la especie (GARP), muestra que además del área de distribución reconocida actualmente para el coyote, la especie también puede estar distribuida 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. 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.

El radio-seguimiento de dieciséis coyotes en un área cubierta principalmente por bosque tropical caducifolio con intrusiones de moderada extensión de áreas agrícolas y ganaderas (Reserva de la Biosfera Chamela-Cuixmala y zonas aledañas en la costa de Jalisco, México), mostró que los animales seleccionaban las áreas agrícolas y ganaderas sobre las cubiertas por bosque con relación a su disponibilidad. Esta observación permite concluir que muy probablemente, la ampliación de las áreas dedicadas a ganadería y agricultura en ésta región, favorecerá al crecimiento en el tamaño de las poblaciones locales de coyote, y consecuentemente, el incremento en los conflictos con los humanos por daños a cultivos, además de la depredación de aves de corral.

Finalmente, la observación de que la presencia de un basurero en un área tropical produce cambios importantes en el tamaño del área de actividad de los coyotes (coyotes que habitan en el área del basurero tienen áreas de actividad más pequeñas que las de los coyotes que viven en áreas alejadas del basurero) y el tamaño de grupo (coyotes que habitan en el área de basurero se organizan en un grupo, mientras que los coyotes que habitan áreas alejadas del basurero parecen organizase en parejas) indica que este factor de intervención humana extrema beneficia la presencia de coyotes.

I. INTRODUCCIÓN

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El coyote (*Canis latrans*) es un cánido de origen neártico que se cree que originalmente habitó en campos abiertos y pastizales (Bekoff, 1977). En la actualidad su área de distribución abarca desde Alaska, en América del Norte, hasta la región norte de la república de Panamá en América Central (Bekoff, 1977; Vaughan, 1983). En este extenso territorio, los coyotes habitan una gran variedad de ambientes, que incluyen tanto pastizales y matorrales desérticos como bosques templados y tropicales (Bekoff, 1977).

Los coyotes son de tamaño mediano siendo los machos más grandes que las hembras (machos de 8 a 20kg y hembras de 7 a 18kg; Bekoff, 1977). Se consideran depredadores generalistas (Bekoff, 1980; Vaughan, 1983; McCracken y Hannsen, 1987), debido a su amplio espectro trófico que va desde pequeños y medianos mamíferos (pocas veces grandes) hasta semillas y frutos pasando por aves, reptiles y carroña (Andelt, 1985; Leopold y Krausman, 1986; Vaughan y Rodríguez, 1986; Major y Sherburne, 1987). Son animales sociales que viven normalmente en parejas estables que perduran hasta 3 o 4 años. Son nocturnos, aunque presentan un alto porcentaje de actividad diurna, principalmente en lugares donde no existe presión humana (Andelt, 1985). El tamaño del área de actividad del coyote, definida como el área en la cual el animal encuentra los recursos necesarios para crecer, mantenerse y sobrevivir (Burt, 1943), varía notablemente entre un lugar y otro, desde menos de 4 km^2 en Texas (Andelt, 1985)) hasta más de 60 km^2 en Canadá (Bowen, 1982). Esta variación se atribuye a factores tales como la época del año, la condición reproductiva y la densidad de presas (Litvatitis et al., 1986).

El coyote es considerado como un competidor directo del ser humano, debido fundamentalmente a que en muchas ocasiones se alimenta de ganado, aves de corral, animales de importancia cinegética y de cultivos (Bekoff ,1977; McCCracken y Hannsen, 1987). Según estimaciones recientes, tan sólo en los Estados Unidos los coyotes producen pérdidas económicas superiores a los 100 millones de dólares anuales (National Agricultural Statistics Service 2000, 2001), razón por la cual, a través de intensivas campañas de envenenamiento y trampeo, más de 400,000 ejemplares son eliminados cada año. A pesar de estas medidas, y en contra de todo lo esperado, en los últimos 100 años el área de distribución del coyote, así como el tamaño de sus poblaciones, se ha incrementado notablemente tanto en los Estados Unidos como en Canadá (Voigth y Berg, 1987; Parker, 1995). Se cree que la causa de este fenómeno es resultado de la desaparición de los grandes depredadores y la degradación de los hábitats naturales por la actividad humana. se ha observado que por ejemplo el lobo (*Canis lupus*) es el controlador naturales de los coyotes, además de que la fragmentación de los hábitats naturales trae como consecuencia la creación de ambientes heterogéneos que favorecen la presencia de depredadores generalistas como el coyote (Litvaitis y Villafuerte, 1996).

Se ha demostrado que el coyote es una especie importante en muchos ecosistemas (Soulé et al., 1988; Vikery et al., 1992), pues en lugares donde son los depredadores dominantes, las variaciones positivas o negativas en el tamaño de las poblaciones de esta especie, producen efectos en cascada sobre las comunidades de depredadores medianos y presas (Crooks y Soulé 1999; Henke y Bryant, 1999).

Debido a la creciente importancia económica y ecológica de los coyotes y al fracaso en los programas de control y manejo de la especie en los Estados Unidos y Canadá, en la actualidad se considera que es necesario realizar investigaciones intensivas sobre su biología, ecología y comportamiento. De otra manera no se podrán llevar a cabo campañas efectivas para disminuir los daños producidos por este cánido (Parker, 1995).

Los coyotes en México

El coyote es quizá el carnívoro mejor estudiado en los Estados Unidos y Canadá, debido principalmente a su importancia económica como especie perjudicial. En contraste, en México y Centroamérica se han realizado muy pocos estudios sobre la ecología de este cánido (Hérnandez y Delibes, 1994), a pesar de que habita en casi todo el país (excepto el sur de la península de Yucatán) y es también comúnmente considerado como una plaga (Cuarón, 2000). La mayor parte de los estudios que existen para México son descripciones de los hábitos alimentarios, principalmente en zonas como bosques de pino (e. g. Aranda et al., 1995), bosques de pino-encino (e. g. 1986; Salas 1987; Delibes et al.,1989; Servin y Huxley, 1991), pastizales (List-Sánchez, 1998), y matorrales xerófilos (e. g. Pérez et al., 1982; Arnaud, 1993; Hernandez y Delibes, 1994; Sanabria et al., 1995). Así mismo, existen dos trabajos en áreas tropicales (Villa y Aguilar, 1992; Hidalgo-Mihart et al. 2001) y uno en bosque mesófilo (Esparza, 1991). En estos trabajos, se ha encontrado que los coyotes se alimentan principalmente de mamíferos pequeños y medianos, materiales vegetales, y conforme se vuelven más tropicales, se observa una marcada tendencia al incremento en el consumo de (Hernández et al., 1994).

El tamaño del área de actividad de los coyotes en México se ha estudiado únicamente para cuatro áreas, dos con matorrales xerófilos (Hernández et al., 1993; Carreón, 1998) donde se reportan áreas de 4 hasta 11 km^2 , una zona de pastizal donde se obtuvieron áreas de 30 a 70 km^2 (List-Sánchez, 1997) y un sitio de pino-encino (Servin y Huxley, 1994) en la que se encontró que los coyotes usan áreas de entre 3 y 13 km^2.

En cuanto al tipo de hábitat utilizado por los coyotes, este varía dependiendo de las condiciones locales de cobertura vegetal, abundancia de presas y exposición a depredadores (Bekoff, 1977). En los únicos dos estudios en México donde se ha analizado el uso de hábitat por los coyotes, se encontró que para un matorral xerófilo los coyotes usaban áreas con una espesa cobertura vegetal donde la densidad de presas era mayor (Hernández et al., 1993). En otro estudio realizado en un área de pastizales, se encontró que los coyotes prefieren áreas con abundante vegetación, pues es ahí donde pueden evitar ser cazados como parte de las medidas de control para mitigar daños a la ganadería (List-Sánchez, 1997).

La información existente para el país sobre los daños económicos producidos por el coyote son prácticamente inexistentes, pues con excepción del trabajo de Villa (1960) dónde se estima que los coyotes producían importantes daños económicos en el norte de Chihuahua, no se ha realizado ninguna otra estimación sobre las pérdidas producidas por esta especie.

LOS COYOTES EN ÁREAS TROPICALES

La información existente hasta hace poco tiempo indicaba que el límite sur de la distribución del coyote alrededor del siglo XV llegaba únicamente hasta el centro de México (Gier, 1975; Parker, 1995). De acuerdo a esa información, el cambio en las actividades productivas al arribo de los conquistadores españoles, sobre todo la entrada del ganado europeo, habría favorecido la expansión del coyote tanto hacia el sur y sureste de México (con excepción de Yucatán), como hacia la costa del Pacífico y las tierras altas de Centroamérica y cuyo límite alcanzaría a la actual Costa Rica (Young and Jackson, 1951). Nuevas informaciones provenientes del hallazgo de fósiles pleistocénicos de este cánido en la

República de Costa Rica (Lucas et al. 1997), así como del análisis detallado de informes de viajeros y religiosos europeos que mencionan la presencia de coyotes en el siglo XVI en ese mismo país, además de Nicaragua y Guatemala (Monge-Nájera y Morera-Brenes, 1986), muestran que muy probablemente el límite sur de la distribución de esta especie antes de la llegada de los europeos al continente americano era mucho más al sur de lo que anteriormente se pensaba.

Independientemente de esto, es un hecho que el área de distribución del coyote en México y Centroamérica se ha ampliado en los últimos 25 años, pues en las décadas que comprendieron los años 80 y 90 del siglo XX, se avistaron ejemplares de este carnívoro por primera vez en áreas en donde anteriormente no se habían observado, como es en el norte de Panamá (Méndez et al., 1981; Vaughan, 1983), el norte de Yucatán (Sosa-Escalante et al., 1997) y en Belice (Platt et al., 1998). Aunque no existen datos suficientes para asegurarlo, se ha sugerido que la expansión del coyote fue inducida fundamentalmente por la deforestación de los bosques tropicales causada por el crecimiento de las actividades agrícolas y ganaderas (Vaughan, 1983; Sosa-Escalante et al., 1997), pues esta acción probablemente crea ambientes similares a los hábitats abiertos dónde la especie evolucionó y a los cuáles está bien adaptada (Young y Jackson, 1951; Bekoff, 1977). En estos entornos, una especie generalista como el coyote fácilmente puede encontrar comida (Hidalgo-Mihart et al., 2001).

La tendencia actual, en la cuál los bosques tropicales en México y Centroamérica se deforestan a elevadas tasas (Challenger, 1998), muy probablemente traerá como consecuencia un aumento en el tamaño de las poblaciones de coyotes, así como la expansión del área de distribución de la especie (Cuarón 2000). Como resultado de estas condiciones, es de esperarse que los conflictos entre humanos y coyotes (daños a productos agrícolas y depredación de aves de corral y ganado; Hidalgo-Mihart et al., 2001) se incrementen (Méndez et al., 1981; Sosa-Escalante et al., 1997; Cuarón, 2000; De la Rosa & Nocke, 2000). Ante esta situación se vuelve urgente el planteamiento de planes de manejo y control de la especie en áreas tropicales que permitan tanto prever como responder a los posibles incrementos en las poblaciones de coyotes.

OBJETIVOS

Debido a que la generación de información básica del coyote en ambientes tropicales, puede ayudar a predecir la forma en que las poblaciones de la especie responderán a factores como la deforestación, el objetivo general de este trabajo, fue generar información que podría ser útil como una herramienta en el diseño de planes de manejo para el coyote en zonas tropicales.

Los objetivos particulares de éste estudio fueron:

1. Analizar desde un punto de vista histórico la expansión del coyote en las áreas tropicales, así como determinar la distribución actual de la especie en México y Centroamérica.
2. Determinar el uso de hábitat de los coyotes en un área tropical estacional.
3. Determinar la influencia que tiene un basurero sobre el área de actividad y el tamaño de grupo de coyotes en un área tropical estacional.

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II. ÁREA DE ESTUDIO

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El estudio se realizó en la Reserva de la Biósfera Chamela-Cuixmala y áreas desmontadas aledañas, en la costa del estado de Jalisco. La topografía del área se caracteriza por un sistema de lomeríos con altitudes máximas de 200 m.s.n.m. La característica climática más importante en la zona es que la precipitación presenta una estacionalidad marcada. El 80 % de esta ocurre entre julio y octubre, alcanzando en un año típico niveles de hasta 750mm (Bullock 1986), lo que provoca que en el sitio se presenten sequías prolongadas y la disponibilidad de agua se encuentre muy limitada sobre todo al final del estiaje.

En la zona se distinguen dos tipos principales de vegetación, el bosque tropical caducifolio y el bosque tropical subcaducifolio (Rzedowsky, 1983). El primero se presenta en los lomeríos y se caracteriza por perder casi en su totalidad las hojas durante la temporada seca. El segundo se presenta principalmente en los valles y a la orilla de los arroyos y se compone por árboles que no pierden en su totalidad las hojas durante la temporada seca (Bullock, 1986). Otros ambientes comunes en el área son las zonas desmontadas, que son utilizadas principalmente para la ganadería aunque también existen cultivos temporales de maíz, fríjol y sandía, así como cultivos permanentes de mango, papaya y cítricos. Junto a estas comunidades vegetales hay existen áreas cubiertas por bosques secundarios producto del abandono de áreas de cultivo y ganaderas.

En la costa de Jalisco, alrededor del 25% de los hábitats originales han sido transformados a pastizales y zonas agrícolas en los últimos 25 años (Miranda 2002). Además, la zona presenta un desarrollo turístico importante, existiendo varios hoteles distribuidos a lo largo de la costa.

Situación actual de los coyotes en el área de Chamela-Cuixmala

A pesar de que los coyotes no son habitantes nuevos de la Costa de Jalisco pues fue reportada su presencia desde finales del siglo XIX (Merriam, 1897 cit en Bekoff, 1977), es muy probable que la destrucción de los bosques tropicales en el área (Miranda 2002) haya creado las condiciones ideales para el incremento en el tamaño de las poblaciones locales de coyotes. Esta observación se ve apoyada por el hecho de que los coyotes en el área se alimentan principalmente de roedores asociados a zonas dónde los bosques tropicales han sido desmontados (rata algodonera; *Sigmodon mascotensis*), y de frutas cultivadas como la papaya y el mango (Hidalgo-Mihart et al. 2001). Además, monitoreos de la abundancia de carnívoros mediante el uso de estaciones olfativas, han mostrado que los coyotes son abundantes en zonas agrícolas y ganaderas y escasos en el interior del bosque tropical (Cantú-Salazar et al. 1998).

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CAPÍTULO III.- DISTRIBUCIÓN HISTÓRICA Y PRESENTE DEL COYOTE (*CANIS LATRANS*) EN MÉXICO Y CENTROAMÉRICA

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ORIGINAL ARTICLE

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 suggests 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 distribution included the north of Belize, the north of Panama, the north of the Yucatan Peninsula and a corridor on the Gulf costal plain of Campeche in Mexico in the coyote distribution. 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.

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 limite 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 debido a 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 distribuida 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 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 centre 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 distribution 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 actual 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/eco/), 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 km^2 cell in the Mexican states of Baja California Norte, Baja California Sur, Sonora, Chihuahua, Coahuila, Durango, Zacatecas and San Luis Potosi.

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).

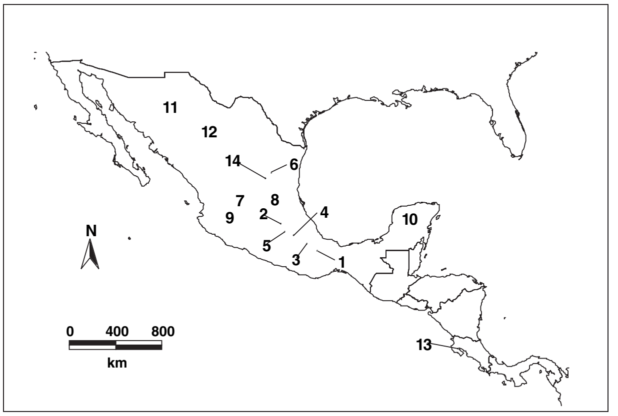

Figure 1 Location of Pleistocene coyote records for Mexico and Central America. Numbers specify the original citation of the record. The period of the record is cited when it was present in the original publication. (1) Monte Flor Cave, Valle Nacional, Oaxaca (Álvarez, 1963a); (2) Tequixquiac, Estado 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–Postglacial; 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 Tipu, 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-

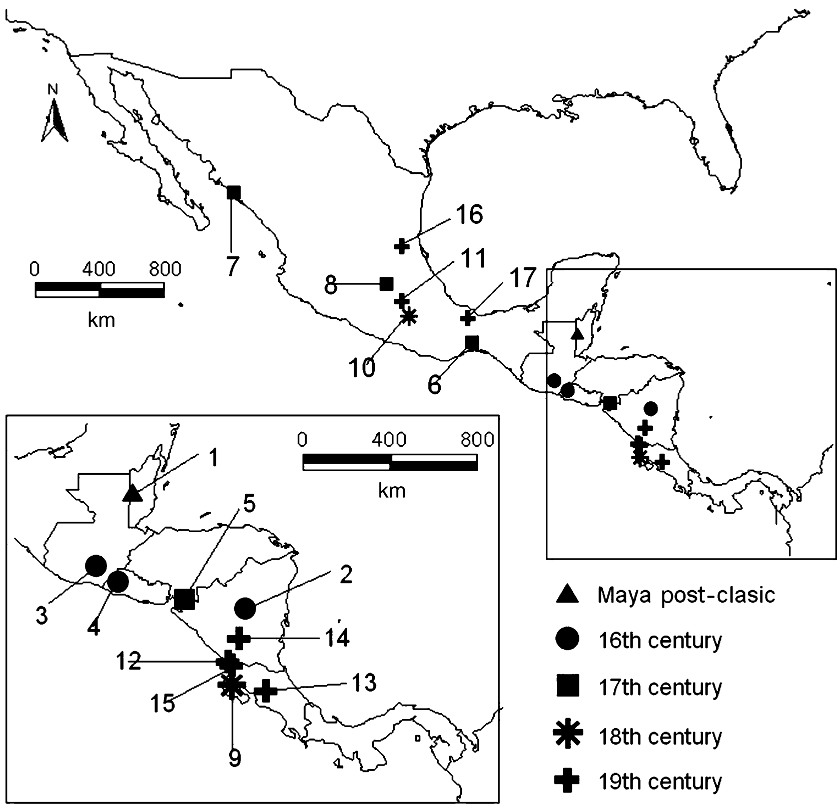

Figure 2 Approximate location of Pre-Columbine and Colonial coyote records for Mexico and Central America. Symbols indicate the time period where coyotes were recorded. The Mayan Post-Classic (1100–500 yr BP) record originated from zooarcheological excavations. Colonial records originated from chronicles 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 Choluteca (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,

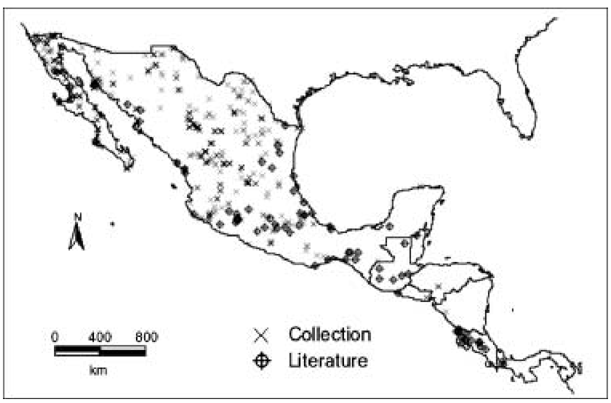

Figure 3 Locations of known occurrences of coyotes from Mexico and Central America. Symbols specify the origin of the data: collection (records originated from a mammal collection of Mexico or the USA) and literature (records obtained from lists of mammal faunas and coyote citations in literature).

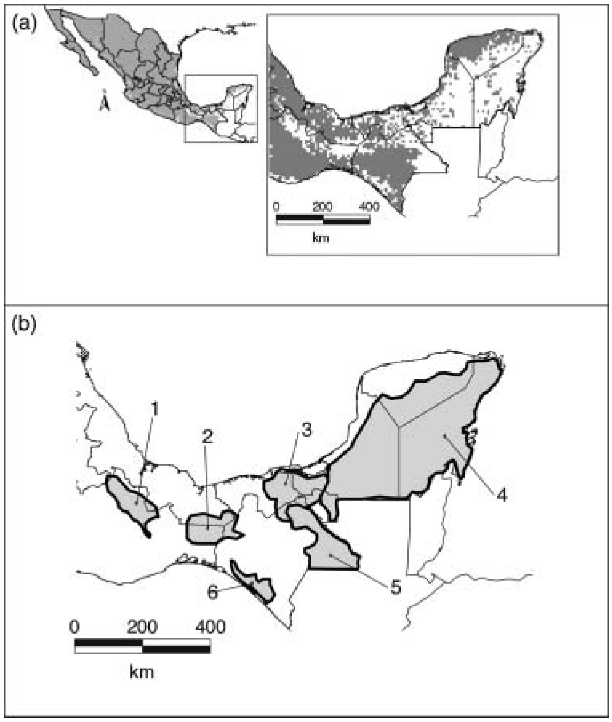

Figure 4 (a) Predicted geographic distribution of coyote in Mexico using GARP. Grey tone indicates presence of coyotes in seven or more of the 10 best subset models. White tone indicates absence of coyotes. A zoom to the south of Mexico is shown on the right side of the (b) general areas of the south 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 this 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

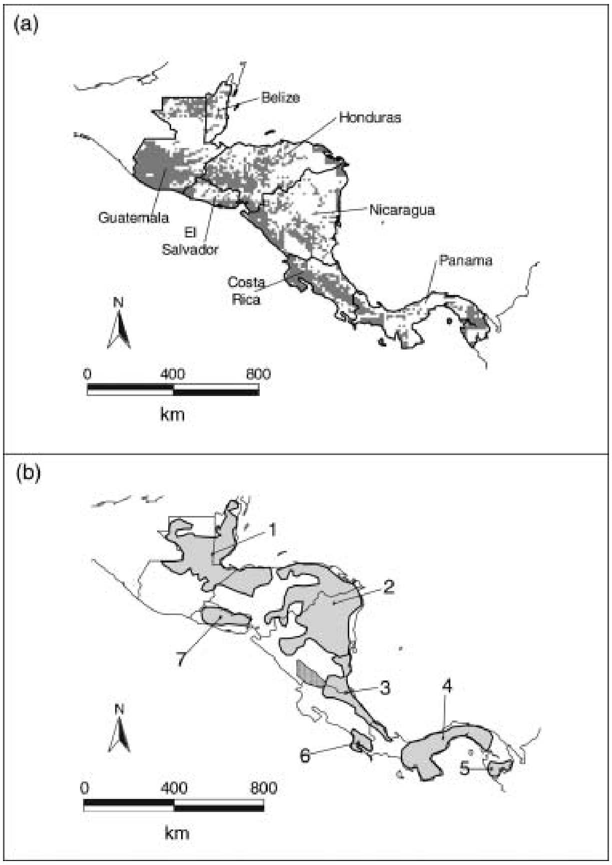

Figure 5 (a) Predicted geographic distribution of coyote in Central America using GARP. Grey tone indicates presence of coyotes in seven or more of the 10 best subset models. White tone indicates absence of coyotes. (b) General areas in Central America where the model indicates coyotes are absent: Belize-Petén-Maya 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 hatched 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 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-Caussel, 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 costal 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 coyote 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).

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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 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 Nacional 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); Uaxactun, 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 Paricutín (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); Higueras 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).

CAPÍTULO IV.- USO DE HÁBITAT POR EL COYOTE (*CANIS LATRANS*) EN UN BOSQUE TROPICAL CADUCIFOLIO DEL OESTE DE MÉXICO

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RH: Coyote Habitat Use in a Tropical Area. *Hidalgo-Mihart et al.*

COYOTE HABITAT USE IN A TROPICAL DECIDUOUS FOREST OF WESTERN MEXICO

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Abstract: In tropical regions, information about coyotes (*Canis latrans*) is rather limited even though the species is widely distributed in these habitats and has recently expanded its range to new areas. It has been hypothesized that deforestation of tropical forests, produced by human activities, is the most important factor that has favoured coyote expansion; however, no empirical analysis has been achieved to probe such assumption. To test if coyotes are attracted to open and semi-open habitats created by the clearing of a tropical region, in an area of the coast of Jalisco, Mexico (covered by tropical forests and open habitats of human induced origin) we examined the habitat use of 16 radio-marked coyotes using compositional analysis at the study area and home range levels. No seasonal (dry season vs. rainy season) or gender (male vs. female) differences were observed in habitat use at any scale. Habitat selection was not detected at the study area level but selection for open habitats was observed at the home range level. At the home range level, results show that coyotes are attracted to open habitats, and at the study area level they indicate that coyotes are probably using tropical forests to travel between patches of open habitat. Continued deforestation for cattle grazing and agriculture in the area will result in the rise of local coyote populations, increasing their ecological impact and the extent of coyote-human conflicts.

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Key words: *Canis latrans,* Coyote, deforestation, habitat use, Jalisco, Mexico, tropical deciduous forest.

Coyotes are one of the most intensively studied carnivore species of the New World. However, most information on coyote ecology has been obtained from individuals living within the northern portion of their distribution. In their southern range (Mexico and Central America), home range estimations (e.g. Servín and Huxley 1995, Hernández et al. 1993) and food habits analyses (e.g.

Hernández et al. 1994, Sanabria et al. 1996) have been carried out in temperate areas or in subtropical deserts and scrublands. In tropical areas, information about coyotes is rather limited to some diet analyses (Vaughan and Rodríguez 1986, Hidalgo-Mihart et al. 2001) and recently home range estimation (Hidalgo-Mihart et al. in press). However, coyotes are widely distributed in these regions, and their presence have been recorded in areas where they were absent 25 years ago, such as northern Panama (Méndez et al. 1981, Vaughan 1983), the northern Yucatan peninsula (Sosa-Escalante et al. 1997), and Belize (Platt et al. 1998).

The exact causes contributing to the establishment of new coyote populations in tropical areas of Mexico and Central America are unclear, but it has been hypothesized that deforestation of tropical forests produced by human activities would be the most important factor (Vaughan 1983, Sosa-Escalante et al. 1997), probably because these cleared areas are similar to the open and semi-open habitats where the species seem to have evolved and is well adapted (Young and Jackson 1951, Bekoff 1977). Besides, it has been documented that forests are marginal habitats for coyotes, most likely because they are poor hunters in dense forest vegetation, which is perhaps reflected in malnutrition, low fecundity and low population densities (Richer et al. 2002).

In Mexico, tropical forests have been intensively during the last 30 years (see Challenger 1998 for a review). Therefore, in these areas it is necessary to get information on habitat selection by coyotes (*i.e.* habitat attributes selected for or against) in order to determine the role that human-opened areas play for this species and test if coyotes are attracted to these environments. Habitat selection by animals is considered an optimization process involving factors such as food supplies, density of co-specifics, body size, competitors, predators, landforms, etc. (Morrison et al. 1998), and consequently, research on coyote habitat selection in tropical areas is a fundamental tool to estimate future population trends of this predator, especially because current land transformation may lead to an increase in coyote-human conflicts (Cuarón 2000), such as damage to agricultural products, as well as poultry and livestock predation (Hidalgo-Mihart et al. 2001).

Thus, our objective was to determine habitat selection patterns of coyotes along the tropical deciduous forest (TDF) of the coast of Jalisco, Mexico. This ecosystem originally occupied 14% of the Mexican territory (Rzedowski 1983), but by the turn of the XX century, only 27% of it remained intact (Trejo and Dirzo 2000). In the coast of Jalisco, around 25% of the TDF has been transformed to croplands and induced grasslands for cattle ranching in the last 25 years (Miranda 2002). Even though coyotes are not new inhabitants of the coast of Jalisco (Merriam 1897 cit in Bekoff 1977), it is most likely that the clearing of the TDF in this area has created a suitable environment for the expansion of local coyote populations. This is supported by the fact that coyotes in the region feed mostly on rodents that invade areas where the TDF has been cleared, such as the Jaliscan cotton rat (*Sigmodon mascotensis*), and on cultivated fruits like papaya and mango (Hidalgo-Mihart et al. 2001). Also, scent station surveys have shown that coyotes are more abundant in croplands and induced grasslands than in the interior of forested areas (Cantú-Salazar et al. 1998).

Therefore, we predicted that, if coyotes are benefited by the open and semi-open habitats created by the clearing of the TDF, and if forests are marginal habitats for this species, then, along the Coast of Jalisco coyotes would select the open landscapes created by humans for cattle grazing and agriculture and would avoid the remaining tropical forests patches.

STUDY AREA

The study was conducted in a region of approximately 250 km^2, which included the Chamela-Cuixmala Biosphere Reserve and surroundings areas to the north and south (hereafter called Chamela). It was located on western Mexico in the coast of the State of Jalisco (19°30' to 19°33' N; 105°00' to 105°04' W). Climate in the region was warm sub-humid with an average temperature of 18 °C in the coldest month and 24 °C in the warmest. Annual average precipitation was approximately 750 mm, concentrated in a relatively short wet season. Elevation varies from 0 to 500 m above sea level (Bullock 1988). Tropical deciduous forest was the most abundant vegetation type. Dominant tree species of this system were *Cordia alliodora, Caesalpina eriostachys, Lonchocarpus* spp*., Jatropha chamelensis, Bursera* spp., *Guapira* spp. and *Croton* spp. (Bullock 1988, Lott 1993). The second most widespread natural vegetation type in the area was the tropical semi-deciduous forest, located in valleys and riparian areas. This system was dominated by *Brosimum alicastrum, Sciadodendron excelsum, Astronium graveolens, Tabebuia donnell-smithii, Ficus* spp. and *Thouindium decandrum* (Bullock 1988, Lott 1993). Around Chamela, some areas of the tropical deciduous forest has been converted to plantations of corn, papaya*,* mango and coconut. There are also open areas with induced grasslands for cattle grazing, covered mostly by exotic grasses (*Panicum maximum*), costal sand dunes dominated by *Opuntia excelsa*, *Acacia* spp. and *Mimosa* spp., and secondary tropical forests that resulted from the abandonment of croplands and induced grasslands, where dominant species are *Acacia* spp. and *Mimosa* spp. The area is turistically important, with several hotels and resorts distributed along the coast.

METHODS

Coyotes were trapped from January to May of 1996, 2000 and 2001 using number 3 “Victor” soft-catch leg-hold traps with neoprene protection to reduce damage to the animals (Olsen et al. 1986). Traps were placed in trails and road intersections and baited with commercial coyote attractants (coyote gland lure and coyote urine; Lenon Animal Lures, Manistique, Michigan). To avoid capturing small and non-target animals, we set trap pan tension devices to catch individuals > 8 kg. Traps were covered during the day and opened again at night to avoid capturing animals during diurnal hours, as recommended by the Animal Care and Use Committee of the American Society of Mammalogists (1997). Once captured, coyotes were immobilized with a mixture of Ketamine Hydrochloride (4.5 mg/kg) and Xilacine Hydrochloride (1.8 mg/kg; Servín et al. 1989). Conventional measurements and mass were obtained. Individuals were ear-tattooed with progressive numbers and fitted with radio-collar transmitters (Wildlife Materials, Inc., Carbondale, Illinois). After recovery from anaesthesia, coyotes were immediately released in the capture site.

Coyotes were radio-tracked using 4-element yagi handheld antennas and permanent null-peak systems. We obtained point locations at random times during day and night, and most radio-collared coyotes were located >5 times/week. We assumed independence of successive observations for locations separated by >6 hours (Swihart et al. 1988).

Because in the study site food resources for animals undergo substantial temporal and spatial fluctuations between seasons (wet and dry) and years (Lister and García 1992, Valenzuela and Macdonald 2002), and some carnivores (including coyotes) inhabiting this areas modify their habits as a response to seasonality (e.g., Nuñez et al. 2002, Valenzuela and Macdonald 2002, Hidalgo-Mihart et al. 2001), data were categorized by season to evaluate the possible consequences of seasonality on our prediction, even though it was not our main objective. The wet season (July-October) and dry season (November-June) corresponded to periods when resource abundance was high and low, respectively. We estimated seasonal home range size and boundaries by the Adaptive Kernel Method (Worton 1989) with 95% utilization distributions (Shivik and Gese 2000) using CALHOME software (Kie et al. 1996). We analysed only those coyotes that had >20 locations per season (for details of home range see Hidalgo-Mihart et al. 2004).

From a series of 1:75000 black and white georeferenced aerial photographs of the study area (1996, Instituto Nacional de Estadística, Geografía e Informatica, Aguascalientes, México), we developed a Geographic Information System (ArcView 3.2; ESRI, Redlands, California, USA) and classified the area in 9 vegetation types (in order of importance according to the area covered in the study region: tropical deciduous forest, induced grasslands and seasonal crops, tropical semi-deciduous forest, secondary tropical forests, mango plantations, beach and sand dunes, coconut plantations, aquatic vegetation and urban areas). Structurally, the areas covered by induced grasslands and seasonal crops, sand dunes and beach, mango and coconut plantations operate as open landscapes, thus, we decided to classify these areas in a single habitat type named open habitat. We classified the urban areas as unsuitable for coyotes, due to the persecution by local inhabitants. Aquatic vegetation was also classified as unsuitable. After eliminating the unsuitable habitats and pooling the areas covered by open habitats we had a final classification of 4 vegetation types: tropical deciduous forest, open habitat, tropical semi-deciduous forest and secondary tropical forest.

Habitat selection was investigated following the framework developed by Johnson (1980) and Aebischer el al. (1993) under the assumption that animals make decisions about habitat use at hierarchical stages, namely selection of home range within a study area (second-order selection) and selection of patches within home range (third-order selection). First-order selection (selection of a species´ geographic range) was beyond the scope of this study. To determine second-order selection (hereafter called study area selection), habitat use was defined as the percentage of total area occupied by each habitat type within the boundaries of the seasonal home range of each coyote, and habitat availability as the total area occupied by each habitat type within the boundaries of the study area. For each season, we defined our study area as the boundaries of the home range obtained with all radio-telemetry locations of all coyotes present during that particular season, estimated by the Adaptive Kernel Method with 95% utilization distribution. For the third-order selection (hereafter called home range selection), we defined habitat use as the number of radio-telemetry locations of each coyote in each habitat type, and habitat availability as the percentage of the total area occupied by each habitat type within the boundaries of the home range of each coyote.

We used compositional analysis (Aebisher et al. 1993) to examine seasonal habitat selection. We tested for differences of log-ratio habitat use and availability across seasons at each habitat selection order with a repeated measures multivariate analysis of variance (MANOVA) using Statistica for Windows ver. 98 (Statsoft Inc., Tulsa, OK). Small sample size precluded us from only using data of coyotes present in consecutive seasons; therefore we combined data of coyotes that were present in different years of the study.

Studies on coyotes have found mixed results on the effect of gender in habitat selection. Some authors indicate that differences in habitat selection exist due to gender (e.g. Gridner and Krausman 2001), meanwhile others have been unable to detect differences (e.g. Chamberlain et al. 2000). Even though it was not our primary objective to evaluate the possible consequences of gender in our prediction, we tested for differences of log-ratio habitat use and availability, between males and females with a one-way MANOVA using Statistica for Windows ver. 98.

When habitat use was significantly non-random ($P < 0.05$), we calculated the mean and standard deviation for all log-ratio differences and constructed a matrix, ranking habitat types in their order of use (Aebischer et al. 1993). To assess differences between ranks, we used a paired t-test to compare mean utilization between all pairs of habitats. When seasonal or gender differences were detected by the MANOVA, we created a separate ranking matrix for each gender or season. If gender or seasonal differences in habitat selection were not detected, we pooled all radio-telemetry locations of each coyote to determine a single ranking matrix of habitat use and habitat availability.

RESULTS

Sixteen coyotes (10 males and 6 females) were radio-tracked during the study, but the number of animals varied during years and seasons. Four of the radio-tracked animals died during the research. One was predated and the other three were poisoned by farmers (2 of them after poultry predation and the other one because of damage on papaya plantations).

We found that 4 of the coyotes (2 males and 2 females) were part of the same group (for details see Hidalgo-Mihart et al., 2004). Aebisher et al. (1993) indicate that caution is needed with gregarious animals, because one of the most important assumptions of compositional analysis is that each animal provides an independent measure of habitat use within populations, and group dynamics may influence the position of an animal’s home range with respect to the overall study area (study area selection). For this reason, at the study area selection level we pooled the data of these 4 coyotes and considered them as 1 in the analysis. On the contrary, at the home range selection level the comparison of utilized vs. available habitat may not be affected by group formation (Aebisher et al. 1993), thus at this level we considered the 4 coyotes as independent samples.

Ten animals (6 males and 4 females) had enough data for the dry and wet season. For the study area level, after pooling locations of the grouped coyotes, we had a sample size of 7 animals. We did not find significant differences in the repeated measures MANOVA of the log-ratios between seasons, either at the study area level (Wilks´ $\lambda = 0.59$, $F_{3,4} = 0.92$ $P = 0.51$) or at the home range level (Wilks´ $\lambda = 0.83$, $F_{3,7} = 0.47$ $P = 0.71$).

For the gender analysis, due to the lack of seasonal differences, we pooled data for both seasons. At the study area level we did not included the data of the grouped coyotes because the pack was composed by females and males. We did not find differences in habitat selection between females and males either at the study area level (Wilks´ $\lambda = 0.73$, $F_{3,8} = 0.98$ $P = 0.44$) or at the home range level (Wilks´ $\lambda = 0.65$, $F_{3,12} = 0.59$ $P = 0.86$).

Because no seasonal nor gender differences were found, we pooled all data for all coyotes for each level of analysis. We found that coyotes at the study area level were using all the habitats in proportion to their availability ($\chi^2 = 2.05$, df = 3, $P = 0.56$). In contrast, proportional use of vegetation types at the home range level was significantly different from availability ($\chi^2 = 13.51$, df = 3, $P = 0.004$). In order of relative selection at this level, coyotes selected open habitats, tropical semi-deciduous forest, tropical deciduous forest and secondary tropical forests (Table 1).

DISCUSSION

The results partially supported our prediction that coyotes in the study area were selecting open habitats. The fact that habitat selection at the study area level was not different from availability, contrasts with the observed selection of open habitats at the home range level.

Chamberlain et al. (2000) explain the lack of habitat selection at the study area level as a result of coyotes being omnivorous animals and using a variety of habitats. In our case, we consider that the lack of habitat selection is probably a reflex of the local deforestation patterns that have occurred in Chamela, where, as in other temperate and tropical areas of Mexico, they do not occur as a continuous process in time and space but are defined by the complex interactions between land tenure, environmental conditions and economic alternatives, which determine where and how much forest will be transformed and which productive activity will be undertaken (e.g. Ochoa-Gaona 2001). Therefore instead of large individual patches of different vegetation types, areas of TDF in Chamela are mixed up with patches of induced grasslands and croplands of various sizes, most of them in areas of gentle slopes where agriculture and cattle grazing activities are more favourable. As a response to this patchiness, coyotes probably have to travel through the forested areas that separate one cleared patch from another. These movements create home ranges that include the areas of TDF where coyotes move, and therefore habitat composition of coyotes home range was not different from the habitat composition of the study area.

The highly significant selection for open habitats at the home range level by coyotes indicates that the clearing of the TDF benefited this species. Habitat selection by coyotes varies across their range, but in general they tend to prefer open habitats in an area (Kamler and Gipson 2000), as these facilitate their cursorial hunting strategy (Kleiman and Eisemberg 1973). Thus, our observation that coyotes in Chamela used open habitats more than expected at this level could be because of the greater suitability of this habitat type for hunting. Also, habitat selection by coyotes is influenced by prey availability (i.e. coyotes usually select habitats containing the most abundant prey [see Gosselink et al. 2003 for a review]) and human pressure (i.e. coyotes avoid humans in areas where coyote hunting is a common practice [e.g. Roy and Dorrance 1985, Neale and Sacks 2001]). In Chamela coyotes feed on prey items typicallyof open areas like the Jaliscan cotton rat and cultivated fruits, such as papaya and mango (Hidalgo-Mihart et al. 2001); so it is possible that selection of open habitats would be a response to the presence of their primary food items in these habitats. During this research, human-related coyote fatalities were low compared to other studies (e.g. Althoff and Gipson 1981, Roy and Dorrance 1985). This probably had an effect on our results of coyote habitat selection in Chamela, because low persecution possibly facilitated the use of human-influenced areas like induced grasslands and cropland.

Important aspects of habitat selection could be masked by a study confined to only 1 scale. The observed divergence in the coyote habitat selection at the different scales (i.e. study area level not different from availability and home range level selection to open habitats) is probably a consequence of a process that involves coyote adaptability to open areas, landscape configuration, prey availability and human pressure among others. This class of discrepancy has been previously reported (e.g. Chamberlain et al. 2000). However, the response of coyotes is not constant, and the absence of divergence between scales is usual (habitat selection observed at the home range and study area levels [e.g. Gosselink et al. 2003]) or even in some cases the contrary situation occurs (habitat selection at the study area level but not at home range level [e.g. Gridner and Krausman 2001]), indicating that this result may be a response to local conditions. In our study, the most plausible hypothesis to the divergence between both scales, could be that coyotes are selecting open habitats but, due to the spatial configuration of the land cover, they must travel across the forest in order to reach other open areas to fulfil their requirements. If this interpretation is true, the observed lack of selection at the study area level would be supporting our prediction that coyotes are selecting the open habitats in the study area.

MANAGEMENT IMPLICATIONS

As in other parts of their range, coyotes in Chamela are considered pests, because they are frequently in conflict with human interests. Although coyote elimination is a common practice in the area, it is not a coordinated action and it mainly takes place when predation or damage to agricultural products occurs, and frequently, the ranchers absorb the damage without taking any action. Confirmation that coyotes are selecting open habitats suggests that, if current land transformation trends persist, local coyote populations in Chamela will increase, probably growing the extent of coyote-human conflicts. Under this scenario, new research will have to be focused on quantifying the amount of damage by this predator and the potential ways to manage it.

The increase in coyote populations will probably have ecological impacts too. Coyotes are competitors with, and predators of, a wide array of species. In other areas, top-down coyote dominated communities have been documented (e.g. Crooks and Soulé 1999), besides negative effects on endangered species or populations (e.g. Crête and Desrosiers 1995). This is of great importance in the Chamela area, where coyotes will most likely become the top predator in the agricultural and cattle grazing areas, because other big predators of the region (e.g. jaguar [*Pantera onca*], cougar [*Puma concolor*] or ocelot [*Leopardus pardalis*]) are adapted to forest environments. Thus, it is important to determine the impact of coyotes on open-habitat communities and the possible consequences on forest species.

Even though it is difficult to conclude patterns for the entire distribution of coyotes in tropical areas from a local study, the observed results lead us to speculate that the range expansion of this carnivore in the tropics may be a result of human activities, and the enlargement of the agriculture and cattle ranching frontier will probably have as a consequence the invasion of new areas by this predator.

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Table 1. Mean habitat selection ranks and relation of use between the 4 habitat types at the home range level for coyotes in a tropical deciduous forest of western Mexico. Values for mean rank of habitat selection goes from 0 (least selected habitat type) to 3 (most selected habitat type). The relation column indicates how coyotes were using the habitat type A in comparison to habitat type B. Each relation was replaced by its sign; a triple sign represents significant deviation from random at $P < 0.05$.

Mean rank of habitat selection	Habitat type A	Relation	Habitat type B
0	Secondary tropical forest	-	Tropical deciduous forest
		-	Tropical semi-deciduous forest
		-	Open habitats
1	Tropical deciduous forest	-	Tropical semi-deciduous forest
		+	Secondary tropical forest
		---	Open habitats
2	Tropical semi-deciduous forest	+	Tropical deciduous forest
		+	Secondary tropical forest
		---	Open habitats
3	Open habitats	+++	Tropical deciduous forest
		+++	Tropical semi-deciduous forest
		+	Secondary tropical forest

CAPÍTULO V.- EFECTO DE UN BASURERO SOBRE EL ÁREA DE ACTIVIDAD Y EL TAMAÑO DE GRUPO DE COYOTES (*CANIS LATRANS*) EN UN BOSQUE TROPICAL DECIDUO

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Effect of a landfill on the home range and group size of coyotes (*Canis latrans*) in a tropical deciduous forest

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Abstract

The effect of an open landfill and the seasonality of a tropical deciduous forest in Jalisco, Mexico, was tested on the home range and group size of coyotes *Canis latrans* under the Resource Dispersion Hypothesis (RDH), which proposes that in social carnivores dispersion of patches of limited resources determines home-range size, whereas independently, abundance of resources affects group size. The predictions in this study were that coyotes using the landfill, where food is available all year due to the continuous arrival of food wastes that are concentrated in a single patch, would have smaller, seasonally constant home ranges than coyotes living outside, where food is distributed in several patches. In this area, coyotes would increase their home ranges during the dry season due to seasonal changes in resource availability. Also, a larger coyote group size should exist in the landfill, where food abundance is greater. Home-range size and group size of coyotes living in and outside the landfill were estimated by radio-tracking. Home ranges of coyotes in the landfill varied from 0.9 to 9.5 km^2, whereas home-range sizes of coyotes outside the landfill varied from 10.9 to 43.7 km^2. Seasonality had no effect on the home-range sizes. We identified a group of four adult coyotes in the landfill and no group formation in coyotes outside. These results support the predictions about home-range and group size of coyotes in relation to landfill presence, and indicate that under the circumstances of our study, coyotes follow the postulates proposed by the RDH.

Key words: *Canis latrans*, home range, group size, landfill, tropical deciduous forest

INTRODUCTION

Coyotes *Canis latrans* exhibit great intraspecific variation in their home-range size and social behaviour, both between populations and within the same population, seasonally and annually (Moehlman, 1989). The adult breeding pair is the typical social unit in most coyote populations, where subadults usually disperse in their first year. In some populations, however, subadult coyotes delay dispersal until subsequent litters are born, favouring the formation of packs composed of three or more members (Bekoff, 1977). This group size variation has been linked in canids to allometric traits (Bekoff, Diamond & Mitton, 1981; Moehlman, 1989) and to patterns of resource availability (Geffen *et al.*, 1996). For coyotes, this behaviour has been usually explained as an adaptation for food defence (Bekoff & Wells, 1981; Bowen, 1981), as a response to high coyote densities that produce habitat saturation (Andelt, 1985) and sometimes as a consequence of food resource abundance and distribution (Gese *et al.*, 1988*a*,*b*; Mills & Knowlton, 1991 but see Patterson & Messier, 2001).

Typically in social carnivores, when group size increases via recruitment of additional members, home range must be enlarged to meet the increased metabolic requirements. However, contrary to these theoretical predictions, under some circumstances territory size does not increase when more members are added to the group (e.g. red fox *Vulpes vulpes*; Macdonald, 1983). This phenomenon has been explained by the Resource Dispersion Hypothesis (RDH; Macdonald, 1983), which states that there is no correlation of territory or home-range size with group size – i.e. home range is constrained by the distribution of patches of available food (or other resources), increasing its size when resource patches are more spread out, whereas the number of group members that can be sustained in a group is limited

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independently by richness of available patches and its pattern of availability (see Johnson *et al.*, 2001; 2002 for a review). Several studies have tested the RDH under the assumption that blocks of different habitat types in the environment can be interpreted as resource patches (e.g. Geffen *et al.*, 1992). Such an assumption is rarely tested satisfactorily because it may be false that overall food availability is necessarily different between habitat types, and resources may be spatially aggregated within one habitat type (Johnson *et al.*, 2001). Because coyotes are opportunistic carnivores known to feed on food discarded by humans (e.g. McClure, Smith & Shaw, 1995; Fedriani, Fuller & Sauvajot, 2001) and receive a direct benefit in areas where carrion protein, and consequently energy, is abundant (Rose & Polis, 1998), a small habitat patch with substantially more concentrated resources compared to the surrounding ones, like an operational landfill, can be used as a practical model to test the RDH. Additional food can change the spatial ecology of coyotes, as documented by Shrago (1988, cited in Bounds & Shaw, 1997), or increase their densities (Fedriani *et al.*, 2001) probably because they have access to a wide range of foods of human origin, including garbage.

Opportunistic tropical carnivores may vary the way resources are used relative to availability (Ray, 1998). According to the RDH, our first prediction was that if group and home-range sizes of coyotes in a tropical area are determined by availability of food resources, then coyotes living in a landfill area, where food is abundant and clumped in a single patch that could cover their metabolic needs, would have smaller home-range sizes than coyotes living outside the landfill, where food is dispersed in several patches. In relation to group size, coyotes in the landfill area would live in a larger group than coyotes outside the landfill, because the abundance of food in the landfill patch is greater than in any other patch outside.

In the tropical deciduous forests of our study area, the net primary productivity (Martínez-Yrízar & Sarukhán, 1990), and therefore the food resources for animals undergo substantial temporal and spatial fluctuations, between seasons (wet and dry) and years (Lister & García, 1992; Valenzuela & Macdonald, 2002). Carnivores inhabiting this area modify their home-range size as a response to resource scarcity of the dry season (e.g. Nuñez, Miller & Lindzey, 2002; Valenzuela & Macdonald, 2002). Because coyotes may respond to changes in resource abundance as documented in other areas (Mills & Knowlton, 1991), our second prediction was that coyotes outside the landfill would increase their home-range size during the dry season due to the seasonal changes in resource availability, but that home ranges of landfill coyotes would not change due to the continuous arrival of food resources during that season.

Most information on coyote home-range size has been reported from individuals living within the northern range of this species. In Mexico, studies on coyote home-range size have been conducted in temperate areas like pine-oak forests and grasslands (Servín & Huxley, 1995; List, 1997) or in subtropical deserts and shrublands (Hernández, Delibes & Ezcurra, 1993; Carreón, 1998). Very little is known about coyotes in tropical forests, even though this species is distributed widely in these areas, and coyote populations are likely to expand with deforestation and other human activities (Vaughan, 1983; Sosa-Escalante *et al.*, 1997). Our paper represents the first analysis of home range and group size of coyotes in a tropical environment.

Our objective in this paper was to evaluate the influence of a landfill and the seasonality of a tropical environment on the home range and group size of coyotes, under the RDH postulates.

MATERIAL AND METHODS

Study area

The study was conducted in an area of approximately 250 km^2 that included the Chamela-Cuixmala Biosphere Reserve (Ch-CBR) and surrounding areas to the north and south. The area is located on the Pacific coast of the State of Jalisco, Mexico (19°30′ to 19°33′ N; 105°00′ to 105°04′ W). Climate in the region is warm sub-humid with an average temperature of 18 °C in the coldest month and 24 °C in the warmest. Annual average precipitation is approximately 750 mm concentrated in a relatively short, wet season (July–October). Elevation varies from 0–500 m above sea level (Bullock, 1988). The most abundant tree species are *Cordia alliodora, Caesalpina eriostachys, Lonchocarpus* spp., *Jatropha chamelensis, Bursera* spp., *Guapira* sp. and *Croton* spp. (Bullock, 1988; Lott, 1993). Tropical deciduous forest is considered the most endangered tropical ecosystem in the world (Janzen, 1988). The second most widespread vegetation type in the area is the tropical semideciduous forest, located in valleys and riparian areas. This system is dominated by *Brosimum alicastrum, Sciadodendron excelsum, Astronium graveolens*, *Tabebuia donnell-smithii, Ficus* spp. and *Thouindium decandrum* (Bullock, 1988; Lott, 1993). Around the Ch-CBR, some areas of the tropical deciduous forest have been converted to plantations of corn *Zea mays*, papaya *Carica papaya*, mango *Manguifera indica* and coconut *Cocos nucifera*. Other important habitat types are open areas with induced grasslands for cattle grazing covered mostly by exotic grasses (e.g. *Panicum maximum*) and costal sand dunes dominated by *Opuntia excelsa*, *Acacia* spp. and *Mimosa* spp. Tourists are important to the area with several 5 star hotels distributed along the coast.

In the study area, coyotes are known to feed primarily on small mammals and cultivated fruits (Hidalgo-Mihart *et al.*, 2001). Scent station surveys have shown that coyotes are more abundant in induced grasslands and croplands, and scattered in the interior of forested areas (Cantú-Salazar, Hidalgo-Mihart & López-González, 1998).

The landfill area

In the central part of the study area an operational open landfill of approximately 2 ha surrounded by an area of induced grasslands of about 3 km^2 has been in use since 1980. The landfill receives trash from several sources including the town of Careyes, the recreational area of Rincón de Careyes and occasional discharges from other nearby towns. The landfill provides services every day to at least 110 local inhabitants (Instituto Nacional de Estadística, Geografía e Informática, 2000), and from November to April of each year, it receives the trash of more than 600 persons/day from the 2 resorts in the area. Estimated daily average garbage production in Mexico for 2000 was 1.03 kg/inhabitant. Of this, food remains make up 31.6 % (Instituto Nacional de Ecología, 1997). Using this figure as a base, we estimated that at least 35.8 kg of food remains become available to scavengers daily, and during the peak of the tourist seasons this could increase up to 231 kg of food remains per day. This elevated amount of food available for scavengers contrasts with the surrounding areas of tropical deciduous forest, where the net primary productivity has been calculated as 9500 kg per ha by year (Martínez-Yrízar *et al.*, 1996). Besides coyotes, the scavenger community of the landfill consists of a permanent group of at least 15 feral dogs *Canis familiaris* (M. Hidalgo pers. obs) as well as black vultures *Coragyps atratus* and feral cats *Felis cattus*.

Capture and radio-telemetry

Coyotes were trapped from January to May of 1996, 2000 and 2001 using number 3 'Victor' soft-catch leg-hold traps with neoprene protection to reduce damage to animals (Olsen *et al.*, 1986). Traps were placed in trails and road intersections and baited with commercial coyote attractants (coyote gland lure and coyote urine; Lenon Animal Lures, Manistique, Michigan). To avoid the capture of small and non-target animals, tension devices were fitted on the traps and set to catch animals larger than 8 kg. Traps were covered during the day and opened again at night to avoid capture of animals during diurnal hours, as recommended by the Animal Care and Use Committee of the American Society of Mammalogists (1997). Once captured, coyotes were immobilized with a mixture of Ketamine hydrochloride (4.5 mg/kg) and Xilacine hydrochloride (1.8 mg/kg; Servín, Huxley & Veneces, 1989). Conventional measurements and mass were obtained. Coyotes were aged (adult or subadult) depending on size, tooth wear and dental condition. Individuals were ear tattooed with progressive numbers and fitted with radio-collar transmitters recommended for coyotes by Wildlife Materials, Inc., Carbondale, Illinois. After recovery from the anaesthesia, coyotes were immediately released in the capture site. In the 3 coyotes that were re-captured, there were no abrasions caused by the collars.

In 1996 trapping efforts were concentrated inside an area of preserved tropical deciduous forest in the Ch-CBR, but due to low capture success (5 coyotes in 2050 trap/nights), during 2000 and 2001, traps were set in induced grasslands, coastal dunes and croplands. Trapping during these years was concentrated in 3 areas, the landfill and its vicinity (with an effort of 850 trap/nights), an area of induced grasslands and agricultural lands located 8 km north of the landfill (with 860 trap/nights), and a mosaic of coastal dunes and induced grasslands located 9 km south of the landfill (with a trapping effort of 1240 trap/nights).

Coyotes were radio-tracked using 4-element yagi handheld antennas and permanent null-peak systems. We obtained point locations at random times during the day and night, and most radio-collared coyotes were located > 5 times/week. Frequency of locations was similar in the landfill area and elsewhere. We assumed independence of successive observations for locations separated by > 6 h (Swihart, Slade & Bergstrom, 1988). Data were categorized by season, to reflect important changes in resource availability produced between them. For coyotes outside the landfill influence, the wet season (July–October) and dry season (November–June) corresponded to periods when resource abundance was high and low, respectively. We estimated home-range size and boundaries by the Adaptive Kernel Method (Worton, 1989) with 95% utilization distributions (Shivik & Gese, 2000) using CALHOME software (Kie, Baldwin & Evans, 1996). We only calculated home-range size for coyotes that had > 20 locations per season. Coyotes were classified as residents, transients or dispersals according to the movement pattern observed during the study. We considered resident coyotes those that remained within one main activity area for > 3 months. Transient coyotes were defined as coyotes that never remained in any area > 3 months (Atkinson & Shackleton, 1991). Dispersers were those that abandoned the area during the study period.

Statistical analyses

We divided the studied coyotes in 2 categories depending on their relationship to the landfill. Coyotes influenced by the landfill (hereafter called landfill coyotes) were those whose home ranges included any portion of the landfill, and coyotes not influenced (hereafter called outside coyotes) were those whose home ranges did not include any portion of the landfill.

To determine if there were differences in home-range sizes due to the seasonality of the study area, and presence of the landfill (dry season *vs*. rainy season; landfill coyotes *vs*. outside coyotes), we used a Repeated Measures Analysis of Variance (Zar, 1999). Small sample size precluded us from only using data of coyotes present in consecutive seasons; therefore we combined data of coyotes that were present in different years of the study. Even though these results allow us to determine if the seasonality of the area had an influence on the home-range size of the coyotes, it is important to note that differences resulting from inter-annual variations could not be tested and remained in the analysis as part of the mean square of the error.

Most studies on coyotes had not found differences in home-range sizes between males and females (see for a review Gridner & Krausman, 2001). However, to evaluate

Table 1. Seasonal home-range size (km^2) estimated with the 95% Adaptive Kernel (ADK) of coyotes *Canis latrans* radio-tracked on a landfill area and outside it during 1996, 2000 and 2001 in a tropical deciduous forest of Mexico. M, male; F, female; [a], transient during the season

			Home-range size (km^2)					
			1996		2000		2001	
Sex	Radio-tracking period	Status at the end of study	Dry season	Rainy season	Dry season	Rainy season	Dry season	Rainy season
			Coyotes outside the landfill					
M1	01/96–12/96	Death 12/96	17.7	10.0				
M2	01/96–12/96 06/00–11/00	Unknown	28.1[a]	23.9		16.8		
M3	01/96–6/96	Unknown	13.9					
M4	01/00–11/01	Alive			88.5[a]	111.5[a]	43.7	10.9
M5	01/00–10/01	Alive			18.0	35.5	22.8	18.0
M6	07/00–11/00	Dispersed				29.5		
M7	05/00–12/00	Death 12/00				32.8		
F1	01/96–06/96	Unknown	16.7					
F2	01/96–12/96	Death 12/96	13.4	19.1				
F3	02/00–08/01	Alive			14.1	29.1	40.9	
F4	03/01–07/01	Unknown					22.9	
			Coyotes inside the landfill					
M8	02/00–11/01	Alive			5.5	7.7	3.6	2.9
M9	12/00–11/01	Alive					2.5	0.9
M10	03/01–07/01	Death 07/01					21.3[a]	
F5	02/00–08/01	Dispersed			3.1	4.2	31.0[a]	
F6	06/00–11/01	Alive				9.5	7.1	2.2

the possible consequences of sex on our prediction of the effect of the landfill on the home-range size, we simultaneously determined the influence of the landfill and the sex of the resident coyotes, using an Unbalanced Factorial Analysis of Variance (landfill coyotes *vs*. outside coyotes; males *vs.* females), following the procedure described by Milliken & Johnson (1992). We used this method because the number of landfill coyotes was not equal to the number of outside coyotes.

To assess the level of association between coyote pairs and its pertinence to a group, we examined the temporal interactions among coyotes with overlapping home ranges using the Dynamic Interaction Test proposed by Doncaster (1990). This is a non-parametric procedure that evaluates the simultaneous movements of 2 individuals. The test determined if 2 coyotes radio-tracked simultaneously during a time interval were located within a critical distance more or less often than expected if the 2 animals were moving independently (Doncaster, 1990). Observed separation distances between pairs of coyotes were calculated from paired *x, y* coordinates within a 15-min interval. Expected differences were estimated from all possible combinations of unpaired coordinates. The distance at which coyotes become aware of conspecifics is unknown; therefore, we established 500 m as the critical distance to the test as done by Chamberlain, Lovell & Leopold (2000) for coyotes in a forest environment. A significant positive interaction occurred if observed frequencies (paired) were significantly greater than expected (unpaired) frequencies for each distance interval. A significant negative interaction occurred if expected frequencies (unpaired) were significantly greater than observed (paired) frequencies. Two coyotes were considered to be associated with each other when the observed frequencies of locations were significantly greater ($P < 0.05$) than the expected frequencies. We used Chi-square 2×2 test to identify positive and negative interactions. We classified the interactions between coyotes depending on their status to the landfill as interactions of landfill coyotes, interactions of outside coyotes and interactions between landfill coyotes with outside coyotes. We determined that coyote pairs with significant positive dynamic interaction were part of the same group.

RESULTS

Home-range size and landfill presence

Sixteen coyotes were radio-tracked during the study (five in the landfill and 11 outside it), but the number of animals varied during years, sites and seasons (Table 1). Seasonal home ranges of coyotes in the landfill varied from 0.9 to 9.5 km^2, whereas home-range sizes of coyotes outside the landfill varied from 10.9 to 43.7 km^2 (Table 1, Figs 1 & 2).

The coyote's home-range size exhibited an intense effect of the landfill ($F_{(1,8)} = 42.99$, $P < 0.001$) and no effect of the seasonality of the area ($F_{(1,8)} = 0.05$, $P = 0.99$) or the interaction between the seasonality and the landfill ($F_{(1,8)} = 0.02$, $P = 0.99$). Similarly, the home-range size differed markedly between the landfill and the outside ($F_{(1,10)} = 15.68$, $P = 0.003$), but there was no effect of

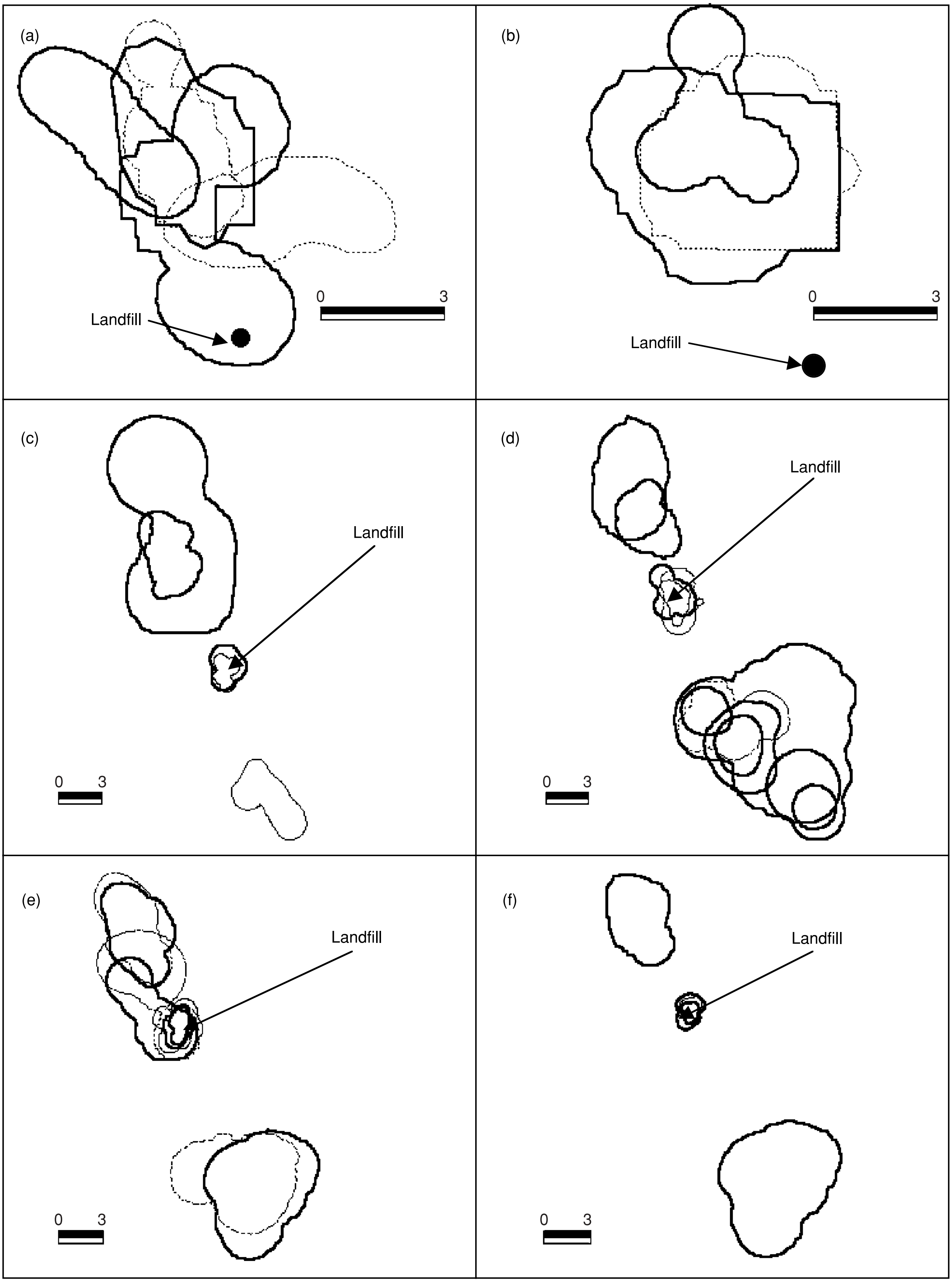

Fig. 1. Home range configuration of coyotes *Canis latrans* radio-tracked during 1996, 2000 and 2001 relative to the presence of a landfill in a tropical deciduous forest of Mexico. (a) Dry season 1996; (b) rainy season 1996; (c) dry season 2000; (d) rainy season 2000; (e) dry season 2001; (f) rainy season 2001. Bold lines represent males and dashed lines females. Scale is 0–3 km.

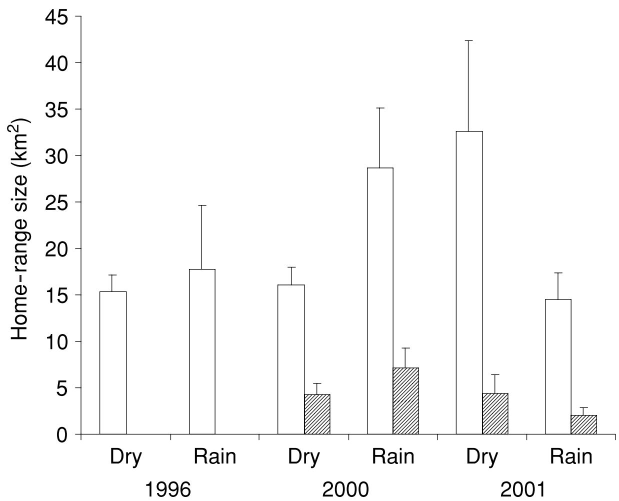

Fig. 2. Mean seasonal home-range size (km^2), estimated with the 95% Adaptive Kernel, of coyotes *Canis latrans* radio-tracked on a landfill area and outside it during 1996, 2000 and 2001 in a tropical deciduous forest of Mexico. Lines on the top of the bars represent one standard deviation. White bars represent the coyotes outside the landfill and dashed bars the coyotes inside the landfill area.

sex ($F_{(1,10)} = 0.02$, $P = 0.96$), and no interaction between sex and the landfill (ANOVA $F_{(1,10)} = 0.28$, $P = 0.61$).

Coyote group size and landfill presence

To determine the coyote group size in the landfill and outside the landfill, we did not use data from 1996, the dry season of 2000 and the rainy season of 2001 because there were a small number of coyotes with functioning radio-collars. We only found significant positive dynamic interactions on the landfill coyotes (Table 2). We did not find any positive interaction between outside coyote pairs or in landfill coyote pairs with outside coyotes. According to our definition of group, the landfill coyotes were forming a group of three adults – two females (F5 and F6) and one male (M8) – during the rainy season of 2000, and a group of four adults – two females (F5 and F6) and two males (M8 and M9) – during the dry season of 2001. During this last season, the four individuals of the landfill were located together several times in the same area in which we suspected was a common den.

DISCUSSION

Landfill presence and home-range size of coyotes

The results support our prediction that differences in food availability may produce differences in the home-range sizes of coyotes. According to the RDH, territory size may be affected by changes in the spatial distribution of patches of available food (Macdonald, 1983). In this study, coyotes outside the landfill may have access to a greater number of patches compared with landfill coyotes. However, these patches do not have the same amount of food as in the landfill. The greater availability of patches with less food may cause the enlargement of territories, because coyotes in these areas have to use a greater number of patches to attain their energy requirements. Coyotes in the landfill may satisfy their energy requirements in a single patch because of the large quantity of food available, thus

Table 2. Temporal interactions among coyotes *Canis latrans* with overlapping home ranges during the rainy season of 2000 and the dry season of 2001 related to the presence of a landfill in a tropical deciduous forest of Mexico. The value of the Chi-square test (obtained in the 2×2 test)[a] was obtained using the Dynamic Interaction Test proposed by Doncaster (1990) with a critical distance of 500 m. M, male; F, female; *, $P < 0.05$; **, $P < 0.01$; *n, negative interaction $P < 0.05$

	Landfill coyotes			Coyotes outside the landfill			Landfill coyotes and coyotes outside the landfill		
Season	Interaction		Value[a]	Interaction		Value[a]	Interaction		Value[a]
Rain 2000	F5	F6	19.4**	F3	M4	0.7			
		M8	4.1*		M7	0.4			
	F6	M8	5.1*	F3	M6	0.2			
				M2	M5	1.3			
				M4	M6	0.0			
					M7	0.8			
				M6	M7	0.1			
Dry 2001	F5	F6	5.0*	F3	M4	1.5	F4	F5	1.7
		M8	4.1	F4	M5	3.3		M10	0.2
		M9	4.6				M5	F5	0.7
	F6	M8	53.1**					M10	0.2
		M9	36.7**						
	M8	M9	48.8						
	M10	F5	0.01						
		F6	4.4*n						
		M8	1.8						
		M9	0.2						

reducing their home-range size. This probably represents the extreme condition of the territory postulate of the RDH. Under these circumstances, it would be interesting to test the hypothesis that removal of the landfill patch may render the territory untenable for the group of coyotes that depend on it.

Our second prediction, that home-range size of coyotes would increase in response to the seasonality of the area, was rejected. The absence of a seasonal effect on the home-range size of outside coyotes could be explained by the fact that they feed mostly on cotton rats *Sigmodon mascotensis*, which are associated strongly with induced grasslands, and whose greatest densities have been observed in the dry season (A. Miranda, Fundación Ecológica de Cuixmala, pers. comm.), and cultivated fruits, especially papayas which are available throughout the year because of irrigation during the dry season (Hidalgo-Mihart *et al.*, 2001).

Landfill presence and coyote group size

The data obtained during the rainy season of 2000 and the dry season of 2001 suggest that our prediction that group size of landfill coyotes would be larger than group size of outside coyotes is correct. Although there is a possibility that some coyotes outside the landfill were not captured, and therefore that certain coyote pairs were associated with non-captured residents, we assumed from our intensive trapping that most coyotes were caught. Also, during field work we found no evidence of coyote groups outside the landfill, neither visual observations of grouped coyotes nor tracks of more than two individuals walking together.

We propose two different explanations of group formation in the landfill. First, coyotes are considered to follow an expansionist strategy (Kruuk & Macdonald, 1985), in which benefits obtained by group formation are associated typically with rewards related to cooperative behaviours, such as breeding and food acquisition. Under this strategy, the advantages of the presence of secondary animals are sufficient to compensate the costs of enlarging territories. However, our results suggest that under special circumstances, like abundance of human food waste, the landfill resident pair may have more resources than those needed by them alone and therefore can sustain subordinate coyotes forming a group. This suggests that landfill coyotes in our study area operate as contractors (Kruuk & Macdonald, 1985) and not as expansionists. The contractor strategy explains group formation in animals that maintain a small economically defensible area, which will encompass sufficient resources for a breeding pair and may support additional residents. According to this strategy and the RDH, in these minimum territories the group size is affected primarily by patch richness, indicating that an increase in the amount of food available for each patch, without any concomitant change in patch distribution will affect only group size (Macdonald, 1983). Under these circumstances, it may be possible that a manipulation on amount of trash received by the landfill would produce a parallel change in number of coyotes of the group that depends on it.

A second explanation, alternative to the contractor – expansionist strategy for group formation in the landfill, is the defence of this area from other coyotes or feral dogs. The formation of groups to defend food resources has been previously documented for coyotes (Bekoff & Wells, 1981; Bowen, 1981). In our study area, the landfill represents a continuous food source for coyotes throughout the year, contrasting enormously with the surrounding areas where food resources are limited during the dry season (Valenzuela & Macdonald, 2002). Thus, resident coyotes might need to strongly defend the area from invasions of neighbouring coyotes and the large group of feral dogs that inhabits the landfill. Aggressions of feral dogs to coyotes have been observed in the proximities of the landfill (A. Peña, Fundación Costa Careyes, pers. comm.), thus suggesting that competition for space and food resources between both species could be present. Aggression between canid species are well documented (Palomares & Caro, 1999; Fedriani *et al.*, 2000), and usually explained as a strategy of competitive exclusion. Also, feral dogs are effective scavengers on human food waste and carrion, often displacing native scavengers because of their high plasticity and elevated numbers near human-disturbed areas (Butler & du Toit, 2002).

Coyotes in tropical areas

Human activity has an important effect on the availability and abundance of coyote prey items in our study area (Hidalgo-Mihart *et al.*, 2001). Some authors suggest that food habits of coyotes are influenced strongly by changes in land use associated with agriculture and urbanization (Brillhart & Kaufman, 1994). It also has been documented that coyotes are increasing their range as a consequence of landscape alteration by human activities, creating habitats where coyotes can easily find food (Quinn, 1997). We have little information about the processes involved with the expansion of coyotes in tropical areas. However, deforestation and roadways produced by human activities probably contributed to the establishment of coyote populations in areas like Costa Rica (Vaughan, 1983), the Yucatan Peninsula (Sosa-Escalante *et al.*, 1997) and Belize (Platt, Miller & Miller, 1998) where they were absent only a decade or so ago. The results of this study, where a landfill was strongly beneficial to coyotes, lead us to speculate that populations of this carnivore will tend to increase as a direct consequence of human activities in the tropics.

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CAPÍTULO VI.- DISCUSIÓN GENERAL

VI.- Discusión General

Los coyotes en Chamela, Jalisco

La selección de hábitats abiertos (zonas agrícolas y ganaderas principalmente) por los coyotes en Chamela al nivel de área de actividad (localizaciones dentro del área de actividad), aunado al hecho de que se ven ampliamente beneficiados por la presencia de un basurero, indica que esta especie se ve favorecida por la apertura de nuevas áreas agrícolas y ganaderas, así como por la presencia humana. A pesar de que las razones de esta selección no son claras, muy probablemente se deba a que son el hábitat ideal para una especie cursorial como el coyote, es decir, una especie muy bien adaptada para caminar y cazar áreas abiertas(Kleiman y Eisemberg, 1973), además de que los coyotes han mostrado ser una especie poco adaptada a sobrevivir en bosques densos (Richer et al., 2002). De la misma forma, otros factores que podrían estar influyendo sobre esta selección son el hecho de que es en las zonas abiertas donde se encuentran la mayor parte de sus presas (Hidalgo-Mihart et al., 2001), además de que en la región no existen campañas extensivas para el control de este depredador, lo que probablemente da libertad a los coyotes para moverse en la cercanía de lugares con gran presencia humana. Un factor más que quizá esté favoreciendo el uso de áreas abiertas, es que en el interior del Bosque Tropical Caducifolio (BTC) del área de Chamela, existen altas densidades de otros grandes y medianos carnívoros como el jaguar *Panthera onca*, el puma *Puma concolor,* el ocelote *Leopardus pardalis* y el coatí *Nasua narica* (Fernandez, 2002; Nuñez et al. 2002; Valenzuela, XXXX) los cuales son potenciales depredadores y competidores del coyote, lo que podría estar provocando que esta especie evite entrar al BTC como una estrategia para evadir los peligros de la depredación o la competencia.

La transformación de alrededor del 25% de los bosques tropicales originales en la costa de Jalisco a zonas agrícolas y ganaderas en los últimos 25 años (Miranda, 2002), posiblemente ha beneficiado a los coyotes en el área, ampliando las zonas donde pueden vivir y potencialmente aumentar el tamaño de sus poblaciones. La tendencia actual de deforestación en la región (alrededor del 2.2% anual; Miranda, 1998), muy probablemente tenga como consecuencia un continuo aumento de las poblaciones de coyote. Ante este escenario, es de esperarse que los conflictos entre humanos y coyotes en el área se incrementen (sobre todo la depredación de aves de corral y el daño cultivos comerciales; Hidalgo-Mihart, 2001). De la misma forma, debido a que los coyotes en el área probablemente son los depredadores dominantes de los ambientes deforestados (Cantú-Salazar et al., 1998), es de esperarse que la dinámica de la comunidad de depredadores medianos y presas se vea afectada por el aumento de las poblaciones de coyote, pues se ha documentado que variaciones positivas o negativas en el tamaño de las poblaciones de esta especie tienen efectos en cascada en aquellos lugares donde los coyotes son los depredadores principales (Crooks y Soulé, 1999; Henke y Bryant, 1999). Debido a esta situación, es necesario el desarrollo de programas de manejo y control para los coyotes adecuadas a la estructura natural y económico-social de la región que permitan disminuir el daño económico, así como reducir el impacto ecológico de la especie.

En la actualidad el control de coyotes y otros depredadores como mapaches (*Procyon lotor*), tejones (*Nasua narica*) y zorras grises (*Urocyon cinereoargenteus*) en el área de Chamela, se basa principalmente en la colocación de cebos envenenados y se realiza por esfuerzos individuales de productores de cultivos comerciales como papaya y sandía, así como en los casos de depredación de aves de corral. Estos esfuerzos a pesar de que dan como resultado la eliminación indiscriminada de una gran cantidad de animales (depredadores y no depredadores), tienen un efecto temporal en la disminución de los daños. La causa más probable de esta situación puede ser similar a la que se presenta en otras área a lo largo de la distribución del coyote, donde en poco tiempo individuos transeúntes sustituyen a los individuos eliminados. Para evitar este tipo de situaciones, se ha recomendado que los esfuerzos de control deben coordinarse entre una gran cantidad de productores, de modo que las áreas sujetas a control se incrementen y se evite la rápida reinvasión por coyotes transeúntes (Knowlton et al., 1999). Sin embargo, debido a que bajo condiciones normales los coyotes en la región ocupan áreas de actividad de entre 15 y 36 km^2, un esfuerzo de control adecuado requiere de grandes superficies, lo que bajo el modelo actual de tenencia de la tierra implica la coordinación de ejidatarios y pequeños propietarios, los cuales en muchos casos tienen visiones encontradas sobre la necesidad de invertir tiempo y recursos para controlar coyotes, sobre todo porque estos aparentemente no tienen efecto alguno sobre muchas de las actividades económicas de la región (e. g., producción de mango o chile, o actividad turística).

Debido a estas visiones encontradas y a que en un futuro es de esperarse un aumento en las poblaciones de coyotes en el área, es necesario que en la región se lleve a cabo una estimación periódica de los daños económicos producidos por los coyotes de tal forma que se pueda establecer si la relación del beneficio del programa de control y manejo contra su costo es positiva o negativa (Bodenchuck et al., 2002). En caso de que la relación fuera positiva se debe concertar qué programa preventivo de control es el más adecuado (e.g., trampeos extensivos o uso de pistolas de cianuro M44), los cuales deben ser pagados por aquellos beneficiarios del control. En caso de que la relación fuera negativa se deben de recomendar programas de manejo únicamente en aquellos lugares y momentos donde se producen los daños, incluyendo además del control la utilización de métodos no letales como el uso perros guardianes y cercas para el caso de los cultivos, y gallineros para las aves de corral (Knowlton et al., 1999).

Los coyotes en las zonas tropicales de México y Centroamérica

El resultado del modelo de nicho indicó que en el sur de México y Centroamérica los coyotes no se encuentran potencialmente distribuidos en las áreas donde se conservan aún grandes áreas de bosque tropical húmedo, lo que puede considerarse como un indicador de la importancia de estas áreas para detener la expansión de esta especie. Sin embargo, la tendencia actual de deforestación, en la cual entre 324,000 y 431,000 ha de bosque son deforestados cada año en Centroamérica (Kaimowitz, 1996) y para 1990 sólo el 10% de las selvas altas perennifolias y el 45% de las subcaducifolias mantenían un buen estado de conservación en México (Challenger, 1998), implica que muy probablemente en el futuro continuará la expansión del área de distribución de esta especie.

Áreas como la Lacandona y el sur de Yucatán en México, el Petén y Selva Maya en Guatemala, la península de Osa en Costa Rica o el centro y sur de Panamá pueden ser potencialmente invadidas en un futuro por los coyotes, debido a que en ellas existen intensas presiones por ampliar la frontera agrícola y ganadera como resultado de la apertura de caminos y la llegada de nuevos pobladores (Kaimowitz, 1996; Cuarón, 2000; Hayes et al., 2002; Rosero-Bixby, 2002).

Un caso especial es el Darién al sur de Panamá, en donde a pesar de que los coyotes aún no han invadido, el modelo de distribución mostró que al menos en su parte norte es un hábitat potencialmente favorable para los coyotes. Esta región ha funcionado para evitar la llegada de una gran cantidad de especies de hábitats abiertos a Sudamérica (Webb, 1985), pues ha conservado su estatus de bosque tropical húmedo desde el Pleistoceno (Colinvaux, 1997). Se cree que el macizo de bosque de esta región (alrededor de 150 km lineales) pueden evitar la invasión del coyote a Sudamérica. Sin embargo nuevos proyectos de desarrollo como la carretera que comunicaría Panamá con Colombia (temporalmente detenida por los altos costos y conflictos ambientales; Webster et al., 1996) pueden favorecer la deforestación en el área y la potencial migración de los coyotes hacia el sur (Monge-Nájera y Morera-Brenes, 1986; De La Rosa y Nocke, 2000). Los efectos de esta invasión son impredecibles pues la llegada de un nuevo y adaptable depredador al área puede alterar tanto los ciclos económicos como los ecológicos. Desde el punto de vista económico existe el peligro de depredación de ganado (principalmente ovino y caprino) y daños a productos agrícolas. Desde el punto de vista ecológico la llegada de los coyotes a un área de alto endemismo de cánidos (Ginsberg y Macdonald, 1990), puede provocar la declinación de las canidos de pequeño tamaño como se ha visto en otras áreas de su distribución (Cohn, 1998).

En la actualidad no se han desarrollado métodos específicos de control de coyotes para áreas tropicales. Comúnmente se utilizan procedimientos letales a baja escala como el envenenamiento indiscriminado o la cacería con rifle, pero no existen datos sobre la efectividad de éstos para reducir los daños. Tampoco existe información sobre el efecto de la aplicación de medidas no letales como el uso de perros guardianes o de cercas. Otras alternativas tales como la restauración de depredadores naturales del coyote, han demostrado tienen efectos importantes sobre los las poblaciones de esta especie en el norte de su distribución (Crabtree y Sheldon, 1999), pero tienen poca aplicación para áreas tropicales, pues los potenciales depredadores como el jaguar o el puma, son comúnmente especialistas del interior de bosque y debido a la selección de los coyotes por hábitats abiertos y deforestados, es poco probable que tengan un efecto sobre las poblaciones de este cánido. Es así que quizá la única opción viable en este momento para evitar la expansión del coyote sea la conservación y restauración de bosques naturales, los cuales la especie parece no seleccionar; sin embargo, es una opción poco realista al observar las elevadas tasas de pérdida de hábitat naturales en el sur de México y Centroamérica.

LÍNEAS DE INVESTIGACIÓN FUTURAS

La expansión del área de distribución y tamaño de las poblaciones de coyote en México y Centroamérica podría ser el detonador de nuevos y complejos conflictos entre humanos y fauna silvestre. Sin embargo, al mismo tiempo esto representa una oportunidad para el desarrollo de proyectos de investigación que formulen planes de manejo de la especie, en los cuales se aplique el conocimiento científico a la resolución de conflictos económicos.

Las líneas de investigación que en un futuro ayudarán entender mejor la forma en la que los coyotes responden a las zonas tropicales y por lo tanto a desarrollar mejores planes de manejo para la especie en estas áreas pueden dividirse en dos tipos: biológicas y económicas.

Biológicas.- Es importante determinar si los coyotes responden a grandes áreas agrícolas y ganaderas de la misma forma como lo hicieron en este trabajo, en el que se determinó el uso de hábitat de esta especie en un región donde se combinaban zonas abiertas con zonas de bosque tropical conservado. Esto debe hacerse debido a que las condiciones existentes en una extensa zona donde no existen áreas sin influencia humana, pueden reducir por ejemplo la disponibilidad de sitios de refugio y crianza o cambiar la dinámica de las presas potenciales, lo que tendría consecuencias sobre las poblaciones de coyotes, de tal forma que las recomendaciones de manejo pueden ser diferentes.

Se debe de trabajar en la implementación y mejoramiento de técnicas que permitan conocer cambios en la abundancia de coyotes en grandes áreas geográficas (nivel estado o provincia). Una de las posibles soluciones a esto es la utilización de estaciones olfativas. Sin embargo, debido a que éste método no ha sido adaptado a zonas tropicales, es necesario determinar las mejores técnicas de muestreo (e. g., densidad de transectos, longitud de transectos, tipo de atrayente, etc.) así como desarrollar las técnicas de análisis estadístico que disminuyan sesgos y mejoren la calidad de los resultados.

Es imprescindible una revisión del estatus taxonómico de los coyotes en toda su área de distribución y en particular para el sur de México y Centroamérica, pues muchos de las subespecies han sido descritas con base en unos pocos ejemplares. Un análisis filogeográfico permitiría conocer si los coyotes en el sur de México y Centroamérica son inmigrantes de las poblaciones del centro de México o son restos de las poblaciones que vivieron en el Pleistoceno en el área. Estos resultados ayudarían a establecer la historia de los coyotes en el área así como estipular qué factores geológicos e históricos han determinado la distribución pasada y presente de los coyotes en la región.

Económicas.- Es necesario establecer la magnitud de los daños a cultivos y ganado producidos por los coyotes en zonas tropicales. Para esto es preciso determinar las mejores estrategias que permitan cuantificar los daños de forma más adecuada dependiendo de la escala a la que se trabaje (local o regional). En el caso de una escala local, se deben precisar los costos y posibles sesgos de técnicas como las entrevistas o la inspección visual de daños, de tal forma que se establezcan métodos estandarizados que permitan implantar las mejores formas de manejo y control, así como realizar comparaciones entre áreas. A nivel regional se deben determinar las formas de cuantificar los daños basados en reportes de asociaciones de productores de tal forma que se puedan establecer mejores programas gubernamentales para el manejo de esta especie.

Se debe trabajar en el desarrollo de protocolos de control que sustituyan al envenenamiento indiscriminado. Algunas soluciones posibles son por ejemplo el uso de pistolas de cianuro (M44), las cuales se han desarrollado específicamente para cánidos y se usan ampliamente en otras áreas de la distribución del coyote. De la misma forma se deben establecer protocolos de monitoreo que permitan determinar el efecto de los programas de control tanto en las poblaciones de coyotes así como en los daños pensando siempre en el mejoramiento de la relación costo-beneficio

Es necesario finalmente determinar la mejor forma de incluir el costo ambiental asociado al programa de control dentro de la relación del beneficio del programa de control contra su costo económico.

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VI.- APÉNDICE. TAMAÑO DEL ÁREA DE ACTIVIDAD ESTACIONAL DE LOS CO YOTES ESTUDIADOS EN CHAMELA, JALISCO CONTRA NÚMERO DE LOCALIZACIONES

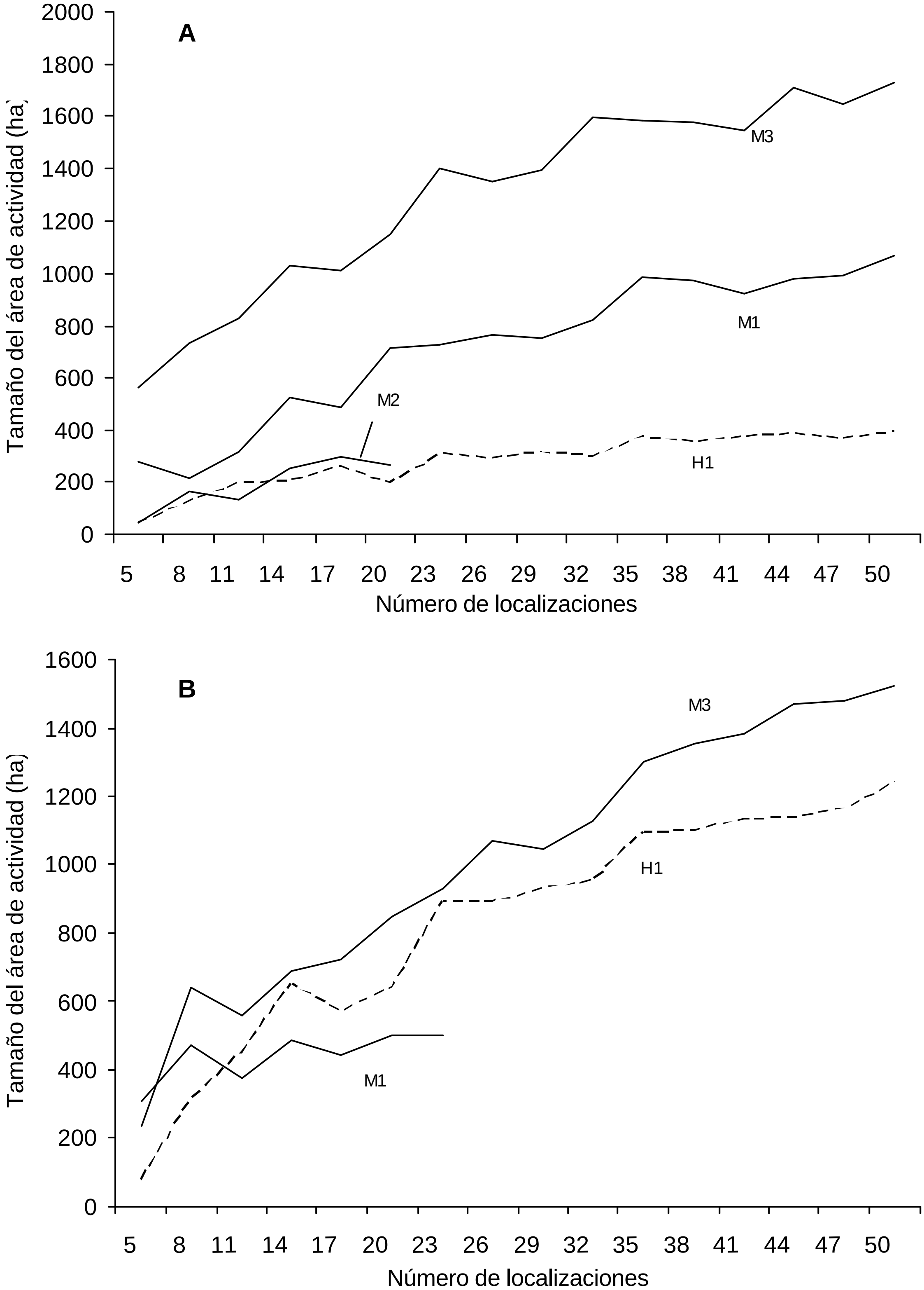
2000
1800
1600
1400
1200
1000
800
600
400
200
0
A
M3
M1
M2
H1
Tamaño del área de actividad (ha)
5 8 11 14 17 20 23 26 29 32 35 38 41 44 47 50
Número de localizaciones
1600
1400
1200
1000
800
600
400
200
0
B
M3
H1
M1
Tamaño del área de actividad (ha)
5 8 11 14 17 20 23 26 29 32 35 38 41 44 47 50
Número de localizaciones

Figura 1

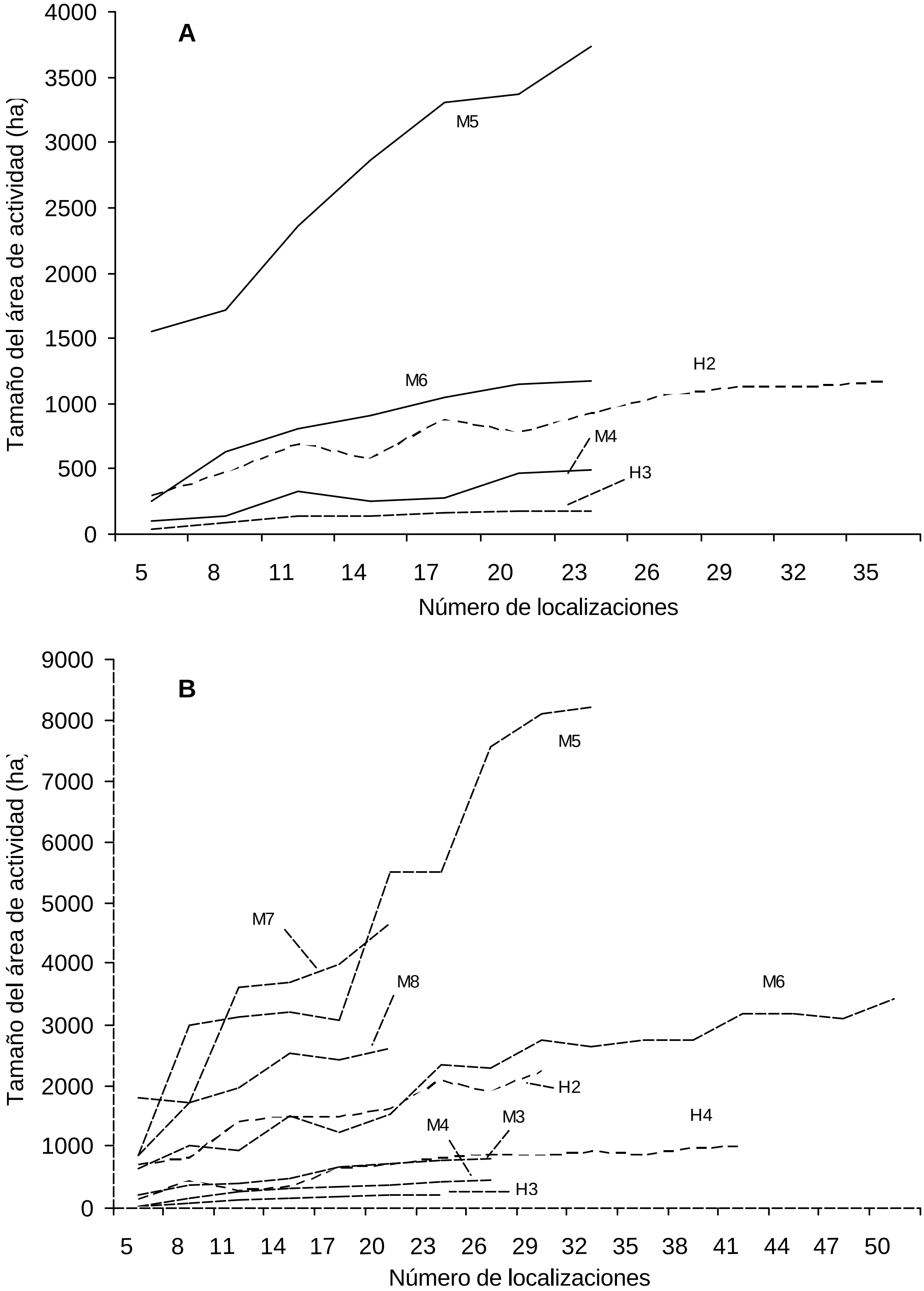
A
M5
M6
H2
M4
H3
Tamaño del área de actividad (ha)
Número de localizaciones
B
M5
M7
M8
M6
H2
M4
M3
H4
H3
Tamaño del área de actividad (ha)
Número de localizaciones

Figura 2

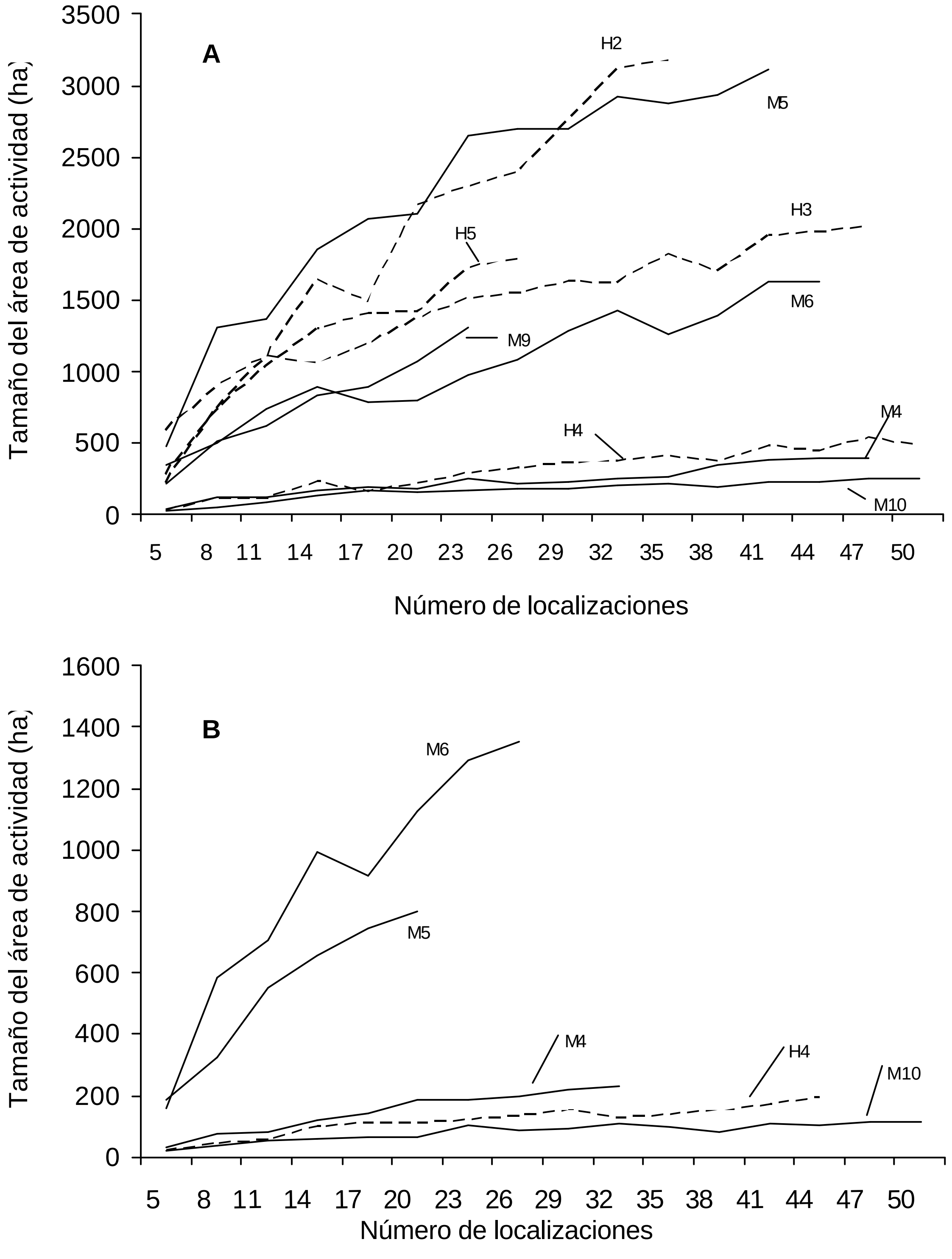
A
3500
3000
2500
2000
1500
1000
500
0
Tamaño del área de actividad (ha)
H2
M5
H3
H5
M6
M9
M4
H4
M10
5
8
11
14
17
20
23
26
29
32
35
38
41
44
47
50
Número de localizaciones
B
1600
1400
1200
1000
800
600
400
200
0
Tamaño del área de actividad (ha)
M6
M5
M4
H4
M10
Número de localizaciones

Figura 3

Figura 1.- Tamaño del área de actividad estacional de los coyotes estudiados en Chamela, Jalisco durante 1996 contra el número de localizaciones. A) Temporada seca B) Temporada de lluvias. El área de actividad se obtuvo por medio del método del Polígono Mínimo Convexo. Las líneas continuas representan a los machos y las discontinuas a las hembras. Los símbolos representan el número de identificación de cada uno de los coyotes estudiados.

Figura 2.- Tamaño del área de actividad estacional de los coyotes estudiados en Chamela, Jalisco durante 2000 contra el número de localizaciones. A) Temporada seca B) Temporada de lluvias. El área de actividad se obtuvo por medio del método del Polígono Mínimo Convexo. Las líneas continuas representan a los machos y las discontinuas a las hembras. Los símbolos representan el número de identificación de cada uno de los coyotes estudiados.

Figura 3.- Tamaño del área de actividad estacional de los coyotes estudiados en Chamela, Jalisco durante 2001 contra el número de localizaciones. A) Temporada seca B) Temporada de lluvias. El área de actividad se obtuvo por medio del método del Polígono Mínimo Convexo. Las líneas continuas representan a los machos y las discontinuas a las hembras. Los símbolos representan el número de identificación de cada uno de los coyotes estudiados.