INSTITUTO POLITÉCNICO NACIONAL

CENTRO INTERDISCIPLINARIO DE INVESTIGACIÓN
PARA EL DESARROLLO INTEGRAL REGIONAL,
UNIDAD OAXACA

"Coexistencia entre especies de zorillos (Carnivora: Mephitidae) en un bosque tropical caducifolio, Oaxaca, México"

TESIS

QUE PARA OBTENER EL GRADO DE:

DOCTORADO EN CIENCIAS EN CONSERVACIÓN Y APROVECHAMIENTO DE RECURSOS NATURALES

PRESENTA:

M. C. ALEJANDRO HERNÁNDEZ SÁNCHEZ

DIRECTOR:

DR. JOSÉ ANTONIO SANTOS MORENO

Santa Cruz Xoxocotlán, Oaxaca, México Junio 2022

SIP-13
REP 2017

INSTITUTO POLITÉCNICO NACIONAL
SECRETARIA DE INVESTIGACIÓN Y POSGRADO

ACTA DE REGISTRO DE TEMA DE TESIS Y DESIGNACIÓN DE DIRECTOR DE TESIS

Ciudad de México, 06 de junio del 2022

El Colegio de Profesores de Posgrado de **CIIDIR UNIDAD OAXACA** en su Sesión
(Unidad Académica)
ordinaria No. 11 celebrada el día 04 del mes noviembre de 2021, conoció la solicitud presentada por el alumno:

Apellido Paterno:	**Hernández**	**Apellido Materno:**	**Sánchez**	**Nombre (s):**	**Alejandro**

Número de registro: A 1 8 0 2 1 4

del Programa Académico de Posgrado: Doctorado en Ciencias en Conservación y Aprovechamiento de Recursos Naturales.

Referente al registro de su tema de tesis; acordando lo siguiente:

1.- Se designa al aspirante el tema de tesis titulado:

"Coexistencia entre especies de zorrillos (Carnivora: Mephitidae) en un bosque tropical caducifolio, Oaxaca, México"

Objetivo general del trabajo de tesis:

Conocer los mecanismos y factores que permiten la coexistencia de especies de zorrillos en un bosque tropical caducifolio en el Parque Nacional Huatulco, Oaxaca, México

2.- Se designa como Directores de Tesis a los profesores:

Director: Dr. José Antonio Santos Moreno

2° Director:

No aplica: ☒

3.- El Trabajo de investigación base para el desarrollo de la tesis será elaborado por el alumno en:

El Área Natural Protegida "Parque Nacional Huatulco", Santa María Huatulco, Oaxaca y en el Laboratorio de Ecología Animal del Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional, Unidad Oaxaca.

que cuenta con los recursos e infraestructura necesarios.

4.- El interesado deberá asistir a los seminarios desarrollados en el área de adscripción del trabajo desde la fecha en que se suscribe la presente, hasta la aprobación de la versión completa de la tesis por parte de la Comisión Revisora correspondiente.

Director de Tesis	2° Director de Tesis (en su caso)
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Aspirante	Presidente del Colegio
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SIP-14
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En la Ciudad de Santa Cruz Xoxocotlán, Oax., siendo las 12:00 horas del día 29 del mes de junio del 2022 se reunieron los miembros de la Comisión Revisora de la Tesis, designada por el Colegio de Profesores de Posgrado Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional, Unidad Oaxaca (CIIDIR UNIDAD OAXACA) para examinar la tesis titulada:

Coexistencia entre especies de zorrillos (Carnivora: Mephitidae) en un bosque tropical caducifolio, Oaxaca, México

del alumno:

Apellido Paterno:	Hernández	**Apellido Materno:**	Sánchez	**Nombre (s):**	Alejandro

Número de registro: A 1 8 0 2 1 4

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Una vez que se realizó un análisis de similitud de texto, utilizando el software antiplagio, se encontró que el trabajo de tesis tiene 15% de similitud. **Se adjunta reporte de software utilizado.**

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El documento reúne las características técnicas esperadas para una tesis de nivel doctorado, con importantes aportaciones sobre la ecología de especies de zorrillos en la costa del estado de Oaxaca.

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CARTA DE AUTORIZACIÓN DE USO DE OBRA PARA DIFUSIÓN

En la Ciudad de México el día 21 del mes de junio del año 2022, el que suscribe **Hernández Sánchez Alejandro** alumno del programa **Doctorado en Ciencias en Conservación y Aprovechamiento de Recursos Naturales** con número de registro **A180214**, adscrito al Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional, Unidad Oaxaca manifiesta que es autor intelectual del presente trabajo de tesis bajo la dirección del **Dr. José Antonio Santos Moreno** y cede los derechos del trabajo intitulado **"Coexistencia entre especies de zorrillos (Carnivora: Mephitidae) en un bosque tropical caducifolio, Oaxaca, México"**, al Instituto Politécnico Nacional, para su difusión con fines académicos y de investigación.

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Hernández Sánchez Alejandro

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CONTENIDO

RESÚMEN GENERAL

Varias especies de zorrillos presentan rasgos morfológicos y ecológicos similares y son simpátricas en porciones significativas de sus áreas de distribución, por lo que se esperaría que presenten mecanismos que promuevan su coexistencia a través del reparto de los recursos críticos y disminuyan el potencial de las interacciones competitivas. No obstante, esta coexistencia también puede ser facilitada por factores ecológicos, ambientales y antropogénicos. Las investigaciones que tratan de comprender cómo las especies de este gremio pueden coexistir aún son escasas. Este estudio se enfocó en conocer los mecanismos y factores que permiten la coexistencia entre dos especies de zorrillos en un bosque tropical caducifolio en el Parque Nacional Huatulco, en la vertiente del Pacífico mexicano. Las especies *Conepatus leuconotus* y *Spilogale pygmaea* se registraron con el método de fototrampeo durante dos años, de noviembre de 2018 a octubre de 2020. Ambas especies se segregan parcialmente en sus patrones de actividad, con máximos de actividad asincrónicos y niveles de actividad mensual diferentes. *Spilogale pygmaea* posiblemente adopta una estrategia de evitación temporal, ya que presentó sus períodos de mayor actividad cuando *C. leuconotus* está menos activo. Los patrones de actividad de estas especies también están determinados por la actividad de sus presas y depredadores, humedad relativa, precipitación, nubosidad y duración de la noche, lo que sugiere que pueden afectar o favorecer la partición del nicho temporal. Por otra parte, la co-ocurrencia espacial de los zorrillos ocurre de manera independiente y el uso de hábitat parece estar explicado por características relacionadas con el hábitat. *Conepatus leuconotus* y *S. pygmaea* usan áreas más alejadas de los cuerpos de agua, sin embargo, la segunda especie también ocupa sitios con mayor humedad del suelo y disponibilidad de presas. Por último, no hubo evidencia de que la abundancia local esté gobernada por el dominio competitivo de la especie más grande, ya que *S. pygmaea* fue más abundante que *C. leuconotus*. Las variables relacionadas con la disponibilidad de recursos y la complejidad del hábitat explican mejor los patrones observados en las abundancias de los zorrillos, aunque el efecto de la disponibilidad de presas sobre la abundancia de las especies fue consistentemente más importante. Los hallazgos de este estudio evidencian que diferentes mecanismos y factores juegan un papel importante en la configuración de los patrones temporales, espaciales y poblacionales de *C. leuconotus* y *S. pygmaea*. Esta información permite mejorar nuestra comprensión sobre los mecanismos que gobiernan la coexistencia de las especies para el manejo y la conservación efectiva de zorrillos amenazados y poco estudiados en ambientes estacionales.

Palabras clave: abundancia, conservación, patrones de actividad, uso de hábitat, segregación.

ABSTRACT

Several species of skunks have similar morphological and ecological traits and are sympatric in significant portions of their ranges, so it would be expected that they present mechanisms that promote their coexistence through the sharing of critical resources and reduce the potential for competitive interactions. However, this coexistence may also be facilitated by ecological, environmental, and anthropogenic factors. Investigations that try to understand how the species of this guild can coexist are still scarce. This study focused on knowing the mechanisms and factors that allow the coexistence between two species of skunks in a deciduous tropical forest at the Huatulco National Park, on the Mexican Pacific slope. The species *Conepatus leuconotus* and *Spilogale pygmaea* were recorded using the camera trap method over two years, from November 2018 to October 2020. Both species partially segregate in their activity patterns, with asynchronous activity peaks and different monthly activity levels. *Spilogale pygmaea* possibly adopts a temporary avoidance strategy, as it exhibited its periods of greatest activity when *C. leuconotus* is less active. Activity patterns of these species are also determined by the activity of prey and predators, relative humidity, precipitation, cloud cover, and night length, suggesting that they may affect or favor the temporal niche partitioning. Furthermore, the spatial co-occurrence of species occurs independently and habitat use appears to be explained by habitat-related characteristics. *Conepatus leuconotus* and *S. pygmaea* use areas further away from water sources, however, the second species also occupies sites with higher prey availability and soil humidity. Lastly, there was no evidence that local abundance is governed by the competitive dominance of the larger species, as *S. pygmaea* was more abundant than *C. leuconotus*. Predictors related to resource availability and habitat complexity better explain the observed patterns in skunk abundances, although the effect of prey availability on this parameter was consistently more important. The findings of our study show that different mechanisms and factors play an important role in shaping the temporal, spatial, and population patterns of *C. leuconotus* and *S. pygmaea*. This information allows us to improve our understanding of the mechanisms that govern the coexistence of species for effective management and conservation of threatened and understudied skunks in seasonal environments.

Keywords: abundance, conservation, activity patterns, habitat use, segregation

ESTRUCTURA DE LA TESIS

El documento consta de seis capítulos. El primer capítulo ***Introducción general*** aborda el marco teórico sobre los mecanismos y factores que pemiten la coexistencia entre especies morfológica y ecológicamente similares, centrándose en la información generada sobre especies de zorrillos simpátricas. En el segundo capítulo ***The Mephitidae in the Americas: a review of the current state of knowledge and future research priorities*** analizamos la literatura científica sobre la familia Mephitidae en el continente Americano publicada de 1900 a 2019 para identificar los patrones y posibles causas de sesgo del estado actual de conocimiento y definir prioridades para orientar los esfuerzos de investigación futuros. En el tercer capítulo ***Drivers of activity patterns of two sympatric skunks (Carnivora: Mephitidae)*** evaluamos la partición del nicho temporal entre *Conepatus leuconotus* y *Spilogale pygmaea* y la influencia de factores bióticos, abióticos y antropogénicos en la configuración de sus patrones de actividad diaria y mensual en un bosque tropical estacional. En el cuarto capítulo ***Dinámica de ocupación y patrones co-ocurrencia de dos especies de zorrillos en un bosque tropical caducifolio en el sureste mexicano*** investigamos el papel de las interacciones interespecíficas y atributos ambientales y antropogénicos a múltiples escalas en el uso de hábitat y su dinámica temporal de *C. leuconotus* y *S. pygmaea,* usando un enfoque basado en el criterio de Máxima Verosímilitud para la estimación de la probabilidad de ocupación y co-ocurrencia de las especies. En el quinto capítulo ***Availability of alternative prey rather than intraguild interactions determines the local abundance of understudied and threatened small carnivores*** evaluamos la variación espacio-temporal en la abundancia relativa de *C. leuconotus* y *S. pygmaea* y el efecto de las interacciones interespecíficas, la disponibilidad de recursos y la complejidad del hábitat sobre la abundancia local de las especies. El sexto capítulo ***Conclusiones generales*** reúne los resultados encontrados en esta investigación sobre la coexistencia entre las especies de zorrillos estudiadas y las implicaciones en la conservación de las mismas en el Parque Nacional Huatulco, Oaxaca, México. El segundo, tercer y quinto capítulo están escritos en inglés, los dos primeros son artículos ya publicados y el último se presenta con las normas editoriales de la revista donde será sometido para su eventual publicación.

CAPÍTULO I.

INTRODUCCIÓN GENERAL

Coexistencia entre especies: mecanismos y factores

Uno de los tópicos de investigación más importantes que ha sido abordado y debatido por varias décadas en ecología es la coexistencia de especies en las comunidades biológicas. Teóricamente, dos o más especies morfológica y ecológicamente similares dentro de un gremio o nivel trófico no pueden coexistir en un mismo espacio indefinidamente por efecto de las interacciones antagónicas entre ellas (Morin, 1999; Jaksic y Marone, 2007). Este argumento se basa en el principio de exclusión competitiva, el cual establece que cuando dos especies compiten por un mismo recurso limitante, un competidor dominará al otro, llevándolo a una modificación evolutiva o conductual, e inclusive a la extinción (Gause, 1934). De acuerdo con este principio, la competencia interespecífica puede excluir a una especie de la comunidad a largo plazo, lo que sugiere un límite superior en el número de especies coexistentes dentro de un espacio y una similitud límite entre dos competidores (Hardin, 1960; MacArthur y Levins, 1967). Sin embargo, éstas pueden coexistir a través de la diferenciación de sus nichos (Schoener, 1974; HilleRisLambers et al., 2012), habiendo una respuesta diferencial de las especies a las condiciones ambientales para que ocurra una coexistencia estable (MacArthur y Levins, 1967; Amarasekare, 2003).

Varias especies similares se encuentran en simpatría en diferentes regiones, con posibilidades de usar los mismos recursos y presentar interacciones interespecíficas negativas. La coexistencia de estas especies se ha explicado a través de mecanismos que permiten disminuir el potencial de las interacciones competitivas y promover el reparto de los recursos, como el desplazamiento de caracteres ecológicos y la diferenciación de nicho. El desplazamiento de caracteres se refiere a la divergencia de rasgos morfológicos, ecológicos o de comportamiento entre especies filogenéticamente relacionadas (Brown y Wilson, 1956; Goldberg y Lande, 2006), como consecuencia de la competencia por el alimento (Dayan y Simberloff, 2005). Esta divergencia de rasgos suele ser más evidente cuando las especies se encuentran en simpatría que cuando están separadas (Goldberg y Lande, 2006). El desplazamiento de caracteres en los linajes simpátricos está ampliamente extendido entre los taxones de animales, siendo el tamaño corporal uno de los rasgos más utilizados para su estudio (Dayan y Simberloff, 1998; 2005).

La diferenciación o partición de nicho, por su parte, supone que las especies pueden coexistir cuando dividen los recursos en al menos una dimensión de nicho o una combinación de ellas (Schoener, 1974; HilleRisLambers et al., 2012). El nicho ecológico está definido como el hipervolumen n-dimensional de factores bióticos y abióticos donde una especie puede reproducirse

y sobrevivir (Hutchinson, 1957). El nicho representa la posición de la especie en un conjunto infinito de dimensiones o ejes en ausencia de competencia y depredación (nicho fundamental) y sólo se puede cuantificar a través de un subconjunto del intervalo potencial dada la presencia de interacciones entre especies (nicho realizado; Krebs 2009). Este subconjunto considera tres dimensiones principales: alimento (espectro de tamaño de presa y frecuencia de consumo), espacio (distribución horizontal y vertical) y tiempo (períodos y horarios de actividad; Schoener, 1974). El uso diferencial de recursos alimenticios, diferente preferencia de hábitat o la segregación de patrones temporales entre especies resulta en una disminución de la competencia interespecífica, lo que facilita la coexistencia de especies (Schoener, 1974; Carothers y Jaksic, 1984; Kronfeld-Schor y Dayan, 2003; HilleRisLambers et al., 2012). Por lo tanto, si hubiese una superposición considerable entre especies en una de las dimensiones, se esperarían diferencias en otras.

Las interacciones interespecíficas y la heterogeneidad espacial son factores que juegan un papel clave en la estructuración de las comunidades biológicas, incluida la forma en que pueden coexistir especies con requerimientos ecológicos similares (Morin, 1999; Chesson, 2000). Las interacciones negativas entre especies, como la competencia y la depredación, pueden promover o limitar la coexistencia de las mismas (Chesson y Kuang, 2008). La competencia interespecífica toma la forma de explotación donde las especies compiten indirectamente por un recurso compartido, o de interferencia donde una especie es directamente antagónica hacia otra y resulta en la muerte o la depredación (depredación intragremio; Polis et al., 1989; Holt y Polis, 1997). Ambas interacciones pueden influir en el uso diferencial del hábitat y en la separación temporal de las especies competidoras, o bien, limitar su coexistencia (Schoener, 1974; Carothers y Jaksic, 1984). No obstante, el resultado final, ya sea la coexistencia o la exclusión, está determinado principalmente por la partición de estas interacciones dominantes (Chesson y Kuang, 2008). Por otra parte, las interacciones positivas como el mutualismo y comensalismo también podrían promover la agregación de especies y conducir a la convergencia de nichos o la facilitación entre especies estrechamente relacionadas (Elias et al., 2008; Crowley y Cox, 2011).

El tipo y el grado de las interacciones interespecíficas dependen de qué especies (mismo grupo taxonómico, gremio o nivel trófico) y en qué cantidad están presentes en la comunidad. El efecto de la competencia y la depredación intragremio se predice de acuerdo con las relaciones del tamaño corporal (Jaksic y Marone, 2007), el cual es considerado el factor principal que determina la dirección y la fuerza de la dinámica intragremial (Polis et al., 1989). La intensidad de la

competencia debería aumentar a medida que las especies presentan mayor similitud morfológica (Morin, 1999; Jaksic y Marone, 2007). Sin embargo, el grado de interacción también depende de la abundancia de los competidores (e.g., la competencia puede ser más pronunciada a mayores densidades de las especies) y de la disponibilidad de recursos (e.g., las interacciones se intensifican cuando los recursos son escasos; Weins, 1993; Gotelli y Graves, 1996).

La heterogeneidad espacial paralelamente promueve la configuración de la coexistencia entre especies pertenecientes al mismo gremio trófico (Levin, 1974; Hastings, 1980; Amarasekare, 2003). Algunos modelos teóricos han demostrado que dos especies que comparten recursos no pueden coexistir en un mismo parche, pero pueden hacerlo en presencia de dos o más parches diferentes (Levin, 1974), o cuando se distribuyen en hábitats de diferente calidad según sus densidades intra e interespecíficas (Pim y Rosenzweig, 1981; Rosenzweig, 1981). Esta selección diferencial del hábitat contribuye a determinar patrones de segregación espacial, permitiendo la coexistencia de las especies (Rosenzweig, 1981; Amarasekare, 2003). La heterogeneidad del hábitat también facilita que las especies con requerimientos ecológicos similares coexistan dada una mayor disponibilidad de recursos, como refugios, alimento y zonas de forrajeo (Tews et al., 2004; D'Amen et al., 2018). Alternativamente, especies con rasgos similares pueden coexistir en hábitats homogéneos a través del filtrado ambiental, es decir, afinidades ambientales y de recursos compartidos (Kraft et al., 2015; Thakur y Wright, 2017).

Coexistencia entre Carnivora: los miembros de la familia Mephitidae como caso de estudio

Los mamíferos del orden Carnivora son un grupo modelo para estudiar los mecanismos de coexistencia, ya que ocupan los niveles tróficos más altos (Ray et al., 2005; Elmhagen y Rushton, 2007) y a menudo exhiben una similitud morfológica y ecológica considerable, principalmente entre especies estrechamente relacionadas (Donadio y Buskirk, 2006; Davies et al., 2007; Davis et al., 2018). Además, diversas especies de carnívoros se encuentran en simpatría a lo largo de su área de distribución (Wilson y Mittermeier, 2009) y por lo tanto, es probable que ejerzan interacciones competitivas entre ellas por el uso de los mismos recursos.

Los mecanismos de coexistencia que se han abordado en este grupo taxonómico son el desplazamiento de caracteres ecológicos y la separación de nichos. El desplazamiento de caracteres entre carnívoros simpátricos ha permitido diferencias en el uso de recursos alimenticios a través de la divergencia de *rasgos* morfológicos, tales como el tamaño corporal, el cráneo y la estructura

dentaria (Van Valkenburgh, 1988; Dayan y Simberloff, 1998, 2005; Donadio y Buskirk, 2006; Davies et al., 2007). Por su parte, la diferenciación de nicho ha sido bien documentada e incluye la segregación de los ejes alimenticio, espacial y temporal. La coexistencia de carnívoros potencialmente competidores se ha atribuido principalmente a la preferencia de presas de distintos tamaños y en diferentes frecuencias de consumo (Wang, 2002; Scognamillo et al., 2003; Gómez-Ortiz et al., 2015). Sin embargo, otras estrategias que facilitan la coexistencia de estas especies son el uso diferencial del hábitat (Davis et al., 2011; Kozlowski et al., 2012; Sollmann et al., 2012; Mueller et al., 2018) y diferencias en los períodos y horarios de actividad diaria y estacional (Di Bitetti et al., 2009, 2010; Oliveira et al., 2010; Oliveira-Santos et al., 2012; Santos et al., 2019), o bien una combinación de ambas (Barrull et al., 2014; Bu et al., 2016).

En ensamblajes de carnívoros (conjunto de especies filogenéticamente relacionados que usan recursos similares dentro de una comunidad; Fauth et al., 1996), los patrones de coexistencia de especies a menudo pueden estar influenciadas simultáneamente por las interacciones interespecíficas y los factores ambientales y antropogénicos. La influencia de las interacciones negativas entre especies (i.e., competencia y depredación intragremio) es ampliamente reconocida dentro de los gremios de carnívoros, ya que determinan su distribución y abundancia y, por lo tanto, estructuran las comunidades y la diversidad local (Rosenzweig, 1966; Palomares y Caro, 1999; Donadio y Buskirk, 2006). Varios rasgos de las especies pueden impulsar la fuerza y la dirección de estas interacciones, entre ellos: tamaño corporal, dieta, hábitos de depredación, estructura social y relación filogenética (Palomares y Caro, 1999; Donadio y Buskirk, 2006; Davies et al., 2007; Hunter y Caro, 2008). Las interacciones competitivas entre carnívoros son más frecuentes y evidentes con diferencias intermedias en el tamaño corporal, hábitos más predatorios o conductas gregarias, y cuando están estrechamente relacionados o pertenecen al mismo gremio trófico (Palomares y Caro, 1999; Donadio y Buskirk, 2006; Hunter y Caro, 2008). No obstante, el tamaño corporal es el rasgo que tiene mayor influencia sobre la competencia interespecífica y la depredación intragremio, cada una de las cuales debería ser más intensa cuando la especie más grande sea menor del doble de tamaño que la más pequeña (Jaksic y Marone, 2007) o fuera de 2-5.4 veces mayor (Donadio y Buskirk, 2006), respectivamente. Ambas interacciones pueden conducir a respuestas en el uso del espacio y el patrón de actividad para que especies similares coexistan (Palomares y Caro, 1999; Kronfeld-Schor y Dayan, 2003; Hunter y Caro, 2008).

Los factores ecológicos también facilitan la coexistencia de carnívoros simpátricos, inclusive, pueden ser más importantes que las interacciones interespecíficas, afectando la presencia y la distribución local de las especies (Gompper et al., 2016; Bender et al., 2017; Rich et al., 2017; Santos et al., 2019). La heterogeneidad ambiental y las características del hábitat podrían considerarse como un factor ecológico determinante en este taxón al promover el uso de diferentes recursos y la selección de hábitat a escala fina (Scognamillo et al., 2003; Gompper et al., 2016). En casos particulares, la disponibilidad y la abundancia adecuada de recursos, como especies presa, agua y refugios, permiten que algunos carnívoros competidores coexistan (Durant, 1998; Scognamillo et al., 2003; Bender et al., 2017; Rich et al., 2017; Santos et al., 2019). Así mismo, las perturbaciones antropogénicas pueden alterar la dinámica de las comunidades de carnívoros e influir en la coexistencia de las especies. La actividad humana contribuye en el incremento o disminución de la segregación de nicho entre competidores, ya sea con cambios en el uso del espacio y en los patrones de actividad o favoreciendo la presencia de especies dominantes o generalistas en áreas con mayor actividad humana (Wang et al., 2015; Moll et al., 2018; Smith et al., 2018). La introducción de especies invasoras también puede alterar las interacciones interespecíficas mediante la exclusión espacial de los competidores más débiles y la depredación de carnívoros nativos (Vanak y Gompper, 2009; Gerber et al., 2012; Kass et al., 2020).

Diversos estudios se han enfocado en conocer los mecanismos y factores que promueven la coexistencia de los Carnivora dentro de las comunidades ecológicas en diferentes regiones. En las Américas, la mayoría de éstos han sido conducidos para identificar los patrones de coexistencia entre depredadores tope y mesodepredadores en ensambles de felinos (e.g., Di Bitetti et al., 2010; Oliveira et al., 2010; Nagy-Reis et al., 2017; Santos et al., 2019), cánidos (e.g., Di Bitetti et al., 2009; Kozlowski et al., 2012; Mueller et al., 2018), o ambos (Lesmeister et al., 2015; Wang et al., 2015; Bender et al., 2017; Lombardi et al., 2020). Este panorama concuerda con la tendencia global de la investigación sobre especies del Orden, donde una alta proporción de carnívoros son poco estudiados, entre ellos los miembros de la familia Mephitidae (Pérez-Irineo y Santos-Moreno, 2013; Brooke et al., 2014).

Las especies pertenecientes a la familia Mephitidae, conocidas comúnmente como zorrillos, se caracterizan por la pérdida de la dentición carnasial y por la presencia de glándulas odoríferas altamente desarrolladas y patrones conspicuos de franjas o manchas de color negro y blanco (Ewer, 1998; Vaughan et al., 2000). Los mefítidos son principalmente insectívoros y consumen en menor

frecuencia vertebrados pequeños, materia vegetal y carroña (Ewer, 1998; Dragoo, 2009) y se encuentran en una diversidad de hábitats, desde bosques tropicales hasta ambientes semiáridos, incluyendo áreas agrícolas y zonas urbanas (Dragoo, 2009; Macdonald et al., 2017). Estas especies son controladores naturales de poblaciones de insectos y roedores, desempeñando un papel ecológico importante en la estructura y dinámica de las comunidades terrestres (Rosatte y Larivière, 2003; Roemer et al., 2009). En general, la familia Mephitidae es un grupo de cuatro géneros (*Conepatus*, *Mephitis*, *Mydaus* y *Spilogale*) y 11 especies actualmente reconocidas, de los cuales tres géneros con nueve especies se distribuyen conjuntamente desde el sur de Canadá hasta Chile (Dragoo, 2009; Macdonald et al., 2017).

Algunos mefítidos presentan rasgos morfológicos y ecológicos similares y se encuentran en simpatría en porciones significativas de sus áreas de distribución (Dragoo, 2009; Macdonald et al., 2017), por lo que se esperaría que presenten mecanismos de coexistencia como ocurre en otros gremios de carnívoros. Las investigaciones que tratan de comprender cómo las especies de este grupo pueden coexistir aún son escasas. El desplazamiento de caracteres entre especies simpátricas solo se ha explorado entre los zorrillos *Mephitis macroura* y *M. mephitis*, con diferencias en la longitud de sus dientes carnasiales (Davies et al., 2007). En contraste, la separación de nichos entre mefítidos ha recibido mayor atención y su estudio se ha enfocado principalmente en el eje espacial en la región suroeste de Estados Unidos. En ensambles de mefítidos se ha documentado que tanto *M. macroura* y *M. mephitis* como *M. mephitis* y *Spilogale gracilis* presentan diferencias en el uso y la selección del espacio para el forrajeo y la ubicación de sus madrigueras, permitiendo que coexistan regionalmente en Arizona (Hass, 2003; Hass y Dragoo, 2017) y Texas (Doty y Dowler, 2006; Neiswenter y Dowler, 2007), respectivamente. Así mismo, *M. macroura* y *M. Mephitis* difieren en sus hábitos alimenticios, la primera consume mayor diversidad de alimentos y muestra una amplitud de nicho más alta que la segunda (Hass, 2003). La coexistencia entre *M. mephitis* y *S. gracilis* también parece ser favorecida por variaciones diarias y estacionales en sus patrones de actividad como respuesta de *S. gracilis* para evitar interacciones directas con la especie dominante y de talla grande, *M. mephitis* (Patton, 1974; Neiswenter et al., 2010).

Sin embargo, otros estudios no sugieren la separación de nicho basada en el espacio, tiempo o alimento como mecanismo para promover la coexistencia entre especies de zorrillos. El modelado de nicho ecológico de *Conepatus leuconotus*, *M. macroura* y *M. mephitis* muestra que estas especies ocupan un espacio ambiental similar en las áreas de contacto, indicando que no hay

evidencia de exclusión competitiva y que existe una posible convergencia de nicho en una escala espacial amplia (Hass y Dragoo, 2017). Las diferencias en el uso del hábitat y los hábitos alimenticios entre las especies parecen ser consecuencia de su adaptación a diferentes ambientes, es decir, *M. macroura* suele ocupar el nicho tropical, *M. mephitis* el templado y *C. leuconotus* ambos, con preferencia del tropical (Hass y Dragoo, 2017). Otras poblaciones simpátricas de *C. leuconotus* y *M. mephitis* tampoco muestran segregación en sus patrones de actividad, ambas especies varían temporalmente pero sin una correlación negativa en sus máximos de actividad (Cochran, 2012).

El mecanismo de coexistencia entre mefítidos puede variar dentro de los ensambles, regiones o ambientes. En ciertos casos hay diferencias marcadas en el uso de hábitat, patrón de actividad o dieta entre las especies; mientras que en otros la separación del nicho es escasa o inexistente. Además, la influencia de las interacciones intespecíficas y los factores ecológicos y antropogénicos no se ha evaluado explicitamente, a pesar de que desempeñan un papel clave en la coexistencia de especies de carnívoros. Es necesario, por lo tanto, profundizar el estudio de estos mecanismos para comprender mejor cómo dos o más especies de zorrillos pueden utilizar los mismos recursos y ocupar los mismos hábitats, así como para conocer qué factores determinan su coexistencia en una escala local.

Mefítidos en México: el bosque tropical caducifolio como área de estudio

La mayor riqueza de especies de mefítidos dentro del continente americano ocurre en México. En el país están presentes ocho especies: *C. leuconotus*, *C. semistriatus*, *M. macroura*, *M. mephitis*, *S. angustifrons*, *S. gracilis*, *S. putorius* y *S. pygmaea* (Dragoo, 2009). Sin embargo, el estado actual de las investigaciones sobre el grupo todavía es insuficiente (Pérez-Irineo y Santos-Moreno, 2011; Servín, 2013), a pesar de su diversidad y distribución en todo el territorio nacional.

Existen pocos estudios orientados a conocer la ecología de los zorrillos, incluida la forma en que pueden coexistir en las regiones donde convergen sus áreas de distribución. La mayoría de los estudios recientes estiman abundancias relativas para algunas especies de mefítidos, principalmente las de talla media como *C. leuconotus*, *C. semistriatus* y *M. macroura* (Hernández-Pérez et al., 2015; Charre-Medellín et al., 2016; Hernández Hernández et al., 2018). Algunos otros muestran datos sobre la densidad poblacional y el patrón de actividad de *C. semistriatus* (Pérez Irineo, 2014; Hernández-Sánchez et al., 2017) y del ámbito hogareño, la dieta y el uso de hábitat

de *S. pygmaea* (Cantú-Salazar et al., 1999, 2005, 2009). En constraste, la coexistencia entre especies zorrillos sólo se ha analizado en poblaciones simpátricas de *M. macroura* y *M. mephitis* en el norte de México por medio de modelos de nicho ecológico (Cruz Torres, 2015). La información obtenida indica que los nichos de ambas especies no comparten similitud ecológica, siendo *M. mephitis* la que utiliza los recursos ambientales disponibles en un intervalo más amplio (Cruz Torres, 2015).

En México, la vertiente del Pacífico ha sido identificada como zona prioritaria para la conservación de especies de mamíferos y en específico, de carnívoros (Valenzuela-Galván et al., 2007). En esta región se distribuye de manera casi continua el bosque tropical caducifolio, notable en un contexto global por su alto grado de endemismo para un número considerable de taxa (Bezaury Creel, 2010). El bosque tropical caducifolio se caracteriza por una estacionalidad climática marcada como resultado de la distribución de la precipitación anual (Murphy y Lugo, 1995; Trejo, 2004). Esta variación estacional genera cambios profundos en la fenología de las plantas y condiciones microclimáticas (Bullock et al., 1995; Trejo, 2010) y en la disponibilidad de recursos alimenticios tales como insectos y frutos (Lister y García, 1992; Valenzuela y Macdonald, 2002; Palacios-Vargas et al., 2007). Por lo tanto, los ensamblajes de mamíferos carnívoros, como los zorrillos, presentan diferentes respuestas conductuales que les permite sobrevivir en este ambiente estacional (Storner y Timm, 2011). Estos mecanismos pueden disminuir el efecto potencial de la competencia interespecífica, la cual suele ser más intensa en estos ambientes cuando los recursos alimenticios son escasos (Palomares y Caro, 1999; Storner y Timm, 2011), y permitir que las especies simpátricas coexistan espacial y temporalmente.

Los bosques tropicales caducifolios del Pacífico mexicano albergan el 52% del total nacional de los Carnivora, incluyendo cuatro especies de zorrillos: *C. leuconotus*, *M. macroura*, *S. angustifrons* y *S. pygmaea* (Ceballos y Martínez, 2010), esta última es endémica de México y está restringida a los bosque secos (Medellín et al., 1998; Cantú-Salazar et al., 2009). Algunos estudios previos presentan las densidades poblacionales y el patrón de uso del hábitat de zorrillos simpátricos en las lagunas inferior y superior del Istmo de Tehuantepec, Oaxaca (Cervantes et al., 2002; Lorenzo et al., 2005). En estos ensambles, *M. macroura* es la especie más abundante, *C. leuconotus* registra una densidad intermedia y *S. angustifrons* presenta la menor densidad poblacional, aunque el patrón de abundancia de las especies de talla similar es inversa entre temporadas y áreas de estudio (Cervantes et al., 2002; Lorenzo et al., 2005). Estos zorrillos

coexisten en diferentes hábitats de selvas secas en esta región, con un uso diferencial del hábitat entre *C. leuconotus* y *M. macroura* dependiendo de la estacionalidad (Cervantes et al., 2002). Otras poblaciones simpátricas de estas tres especies de zorrillos también coexisten en el bosque tropical caducifolio de la Reserva de la Biosfera Tehuacán-Cuicatlán (Pérez-Irineo et al., 2020; Farías-González y Hernández-Mendoza, 2021), las cuales presentan segregación temporal y variaciones estacionales en la abundancia como mecanismos de coexistencia (Farías-González y Hernández-Mendoza, 2021). La especie de mayor talla corporal, *C. leuconotus*, parece determinar la dinámica de las interacciones intragremio en esta área natural protegida (Farías-González y Hernández-Mendoza, 2021).

El Parque Nacional Huatulco, en la porción central de la costa oaxaqueña, presenta elementos naturales que le confieren una importancia relevante para la conservación de los bosques secos y alberga uno de los últimos remanentes del bosque tropical caducifolio en buen estado de conservación (CONANP, 2003). En esta región se encuentran *C. leuconotus* y *S. pygmaea* (Lira-Torres et al., 2008; Briones-Salas et al., 2016) y se presume la posible presencia de *M. macroura*, con su distribución actual en áreas prioritarias adyacentes (Cervantes y Yépez, 1995; Buenrostro-Silva et al., 2012) y potencial a lo largo de la costa de Oaxaca (Dragoo, 2009). Estas especies tienen diferencias en el tamaño corporal, pero se alimentan principalmente de insectos y de algunos vertebrados pequeños (Medellín et al., 1998; Cantú-Salazar et al., 2005; Dragoo y Sheffield, 2009); además de presentar una actividad predominantemente nocturna y crepuscular (Medellín et al., 1998; Farías-González y Hernández-Mendoza, 2021). Por lo tanto, es probable que estos zorrillos estén involucrados en interacciones competitivas. Además, en la zona habitan mesodepredadores nativos como el coyote (*Canis latrans*) y el ocelote (*Leopardus pardalis*; Lira-Torres et al. 2008, Briones-Salas et al. 2016) y exóticos como perros y gatos domésticos (Binnqüist et al., 2017; Nava, 2017), todos con posibilidades de interactuar con los zorrillos. Sin embargo, la información sobre las interacciones ecológicas en este grupo de animales todavía es escasa, lo cual no permite elucidar los mecanismos y factores que facilitan la coexistencia de las especies de zorrillos, mediadas probablemente por la estacionalidad que caracteriza al bosque tropical caducifolio.

Objetivos de investigación

General.

Conocer los mecanismos y factores que permiten la coexistencia entre especies de zorrillos en un bosque tropical caducifolio en el Parque Nacional Huatulco, México.

Específicos.

1. Evaluar el nivel de superposición temporal de los patrones de actividad y su variación estacional entre zorrillos simpátricos, así como la influencia de factores bióticos, abióticos y antropogénicos en la configuración de la actividad de las especies.

2. Evaluar el nivel de co-ocurrencia espacial y su variación estacional entre zorrillos simpátricos, así como el efecto de las interacciones interespecíficas y atributos ambientales y antropogénicos en el uso de hábitat de las especies.

3. Estimar la abundancia y su variación estacional de las especies de zorrillos y analizar la influencia de las interacciones interespecíficas y la disponibilidad de alimento sobre el tamaño poblacional de cada una.

Cada objetivo es abordado en los siguientes capítulos, donde se plantean sus respectivas hipotésis de investigación.

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CAPÍTULO II

THE MEPHITIDAE IN THE AMERICAS: A REVIEW OF THE CURRENT STATE OF KNOWLEDGE AND FUTURE RESEARCH PRIORITIES

_Hernández-Sánchez, A., Santos-Moreno, A., & Pérez-Irineo, G. (2022). The Mephitidae in the Americas: a review of the current state of knowledge and future research priorities. *Mammalian Biology*, 102: 307-320. https://doi.org/10.1007/s42991-022-00249-z

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REVIEW

The Mephitidae in the Americas: a review of the current state of knowledge and future research priorities

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Abstract

The family Mephitidae is almost exclusively restricted to the Americas, 9 of 11 species belonging to 3 genera are distributed from southern Canada to Chile. Despite the high diversity and continental distribution of this taxon, there is no quantitative review that evaluates the state of research to determine current advances and knowledge gaps, as well as the research efforts necessary to develop effective conservation programs and reduce potential threats to species. Our goal was to analyze the scientific literature on the family Mephitidae in the Americas published from 1900 to 2021 to identify the patterns and potential causes of bias based on species, research topics, in addition to regions and countries, and to define research priorities to guide future efforts. We recorded a total of 926 studies related to the American mephitids. The number of publications by species, research topic, and the geographic area was distributed heterogeneously, but we observed significantly marked biases. The most studied species was *Mephitis mephitis*, most of the studies focused on diseases and pathologies, and most of the research was conducted in North America, mainly in the United States. Overall, there was an accumulated and gradual increase in the number of publications over time, with greater scientific production between 2010 and 2021. Our review shows that the research allocation to mephitids, except for *Spilogale putorius*, is driven by economic or human interest rather than conservation reasons. We prioritize future research towards mephitid species, research topics, and geographic areas in the Americas that need it the most to reduce the scientific gap and to increase the availability of relevant information.

Keywords Conservation · Knowledge gaps · Research bias · Skunks · Threatened species

Introduction

Mephitidae is a family with 4 genera and 11 currently recognized species (Koepfli et al. 2017). Skunks, the common name of members of this family, are characterized by the loss of carnassial dentition and by presenting highly developed anal scent glands and conspicuous black and white stripe or spot patterns (Ewer 1998; Dragoo 2009). Mephitids are omnivorous species that can have a varied diet, but they feed primarily on invertebrates and less frequently on small vertebrates, carrion, and plant material (Ewer 1998; Dragoo 2009). Therefore, they are important in the structure and dynamics of terrestrial communities (Rosatte and Larivière 2003; Roemer et al. 2009). These species are found in a variety of habitat types, including semi-arid, humid tropical, and temperate environments, and even human-modified environments, and are considered generalists in their resource requirements (Dragoo 2009; Macdonald et al. 2017).

Mephitids are almost exclusively restricted to the Americas. Three genera with nine species of skunks are distributed jointly from Southern Canada to Chile (Table 1), while two species of stink badgers of the genus *Mydaus* are found in Southeast Asia (Dragoo 2009; Macdonald et al. 2017). In particular, the state of knowledge on mephitids has been insufficient globally (Pérez-Irineo and Santos-Moreno 2013) and in specific regions in the Americas, such as

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Table 1 Geographic range and conservation status of the nine species of skunk in the Americas

Scientific name	Common name	Geographic range	Range size (km^2)	Distribution region	Conservation status (IUCN)
Conepatus chinga	Molina's hog-nosed skunk	From southern Peru to southern Bolivia and Brazil to southern Chile and Argentina	5,532,628	South America	Least concern
Conepatus leuconotus	American hog-nosed skunk	From southern United States to northern Nicaragua	2,498,375	North and Central America	Least concern
Conepatus semistriatus	Striped hog-nosed skunk	From southern Mexico to central Panama, along the South American coast from northern Peru to northern Venezuela and eastern Brazil	2,021,496	North, Central, and South America	Least concern
Mephitis macroura	Hooded skunk	From southern United States to the northwest of Costa Rica	1,783,422	North and Central America	Least concern
Mephitis mephitis	Striped skunk	From southern Canada to northern Mexico	12,271,224	North America	Least concern
Spilogale angustifrons	Southern spotted skunk	From central Mexico to central Costa Rica	777,398	North and Central America	Least concern
Spilogale gracilis	Western spotted skunk	From southwestern Canada to western United States to central Mexico	3,825,179	North America	Least concern
Spilogale putorius	Eastern spotted skunk	From the southeast of Manitoba and southwest of Ontario, Canada to eastern United States to the northeast of Mexico	2,979,632	North America	Vulnerable
Spilogale pygmaea	Pygmy spotted skunk	Pacific coast of Mexico	95,505	North America	Vulnerable

Mexico (Pérez-Irineo and Santos-Moreno 2011), Colombia (González- Maya et al. 2011; Andrade-Ponce et al. 2016), and Peru (Cossíos et al. 2012). However, research on the distribution, ecology, conservation status, and other aspects of the natural history of mephitid species has shown significant progress in recent years, with an increasing number of scientific publications (Macdonald et al. 2017; González-Maya 2018).

Previous studies have conducted literature reviews on the most common genera or species of the family Mephitidae, however, these are relatively old (e.g., Van Gelder 1959; Wade-Smith and Verts 1982). Recent reviews have evaluated the state of knowledge of *Mydaus* species (Prolux et al. 2016) while others have only focused on specific research topics for skunk species in the Americas. For example, some authors addressed the conservation status of all American members of this family (Belant et al. 2009) and others also analyzed the conservation status of *Conepatus leuconotus* or the home range and population density of *Mephitis mephitis* in North America (Meaney et al. 2006; Šálek et al. 2015) and the distribution and aspects of the natural history of *C. chinga* and *C. semistriatus* in South America (Kasper et al. 2009). These studies show advances in the knowledge about mephitids in the Americas, but lack information on the current research effort and available data, for example on previously less-studied species such as *Spilogale putorius*, which recently had a notable advancing of its research by the scientific community (Jachowski and Edelman 2021).

To date, there is no quantitative review evaluating the state of research on the family Mephitidae in the Americas despite its high diversity and continental distribution. Therefore, a review of the research on mephitid species is required to document advances in knowledge, identify underrepresented aspects, and if necessary, establish research priorities to direct future efforts (Andrade-Ponce et al. 2016; González-Maya and Ramírez-Chaves 2017). Our goal was to analyze the scientific literature on this taxon published since the previous century, to identify patterns and potential biases in research efforts related to species, topics, and geographic regions. We then suggest future research priorities to fill knowledge gaps for a reliable assessment of the conservation

status of the species and the development of effective conservation strategies.

Materials and methods

Search and selection of literature

We carried out a systematic search of the scientific literature on the family Mephitidae in the Americas published between 1900 and 2021. We set the start date for the literature search based on the start date of the ISI Web of Science to get a complete picture of publication trends on skunk species. We followed the recent taxonomic review (Koepfli et al. 2017), which recognizes that *C. chinga* and *C. humboldtii* belong to the same species (*C. chinga*), a change suggested by Schiaffini et al. (2013). McDonough et al. (2021) recently proposed new taxonomic changes for the genus *Spilogale* and recognized seven species instead of the previous four, with three subspecies rising to the species level: *S. interrupta*, *S. leucoparia*, and *S. yucatanensis*. However, we did not follow this classification because the scientific community has yet to accept these changes in future treatises on mammalian taxonomy. Therefore, our review considered nine species of skunks in the Americas (Table 1).

We carried out the bibliographic searches in three main electronic databases: ISI Web of Knowledge (www.isiwebofknowledge.com), SCOPUS (www.scopus.com), and Google Scholar (https://scholar.google.com), using as keywords the scientific name of the family, subfamily or each species of skunk. We also performed searches using the common names of the skunks in English, Spanish, and Portuguese. We used the same search terms in all three databases, but the search logic differed according to the criteria accepted by each library. To include as many relevant studies as possible, we searched for the literature cited in the obtained publications, mainly from reviews, which were replaced by sources.

We included peer-reviewed articles, book chapters, and technical reports, in which the search terms appeared in the title, abstract, or keywords. We excluded unavailable full texts and undergraduate theses, dissertations, and conference or symposium abstracts, since these types of papers were generally published as scientific articles in later years. The studies were selected in a two-stage process according to the eligibility criteria. Based on the title and abstract, we preliminarily selected the articles if their objective was focused on the investigation of skunk species and the full text, if the studies were carried out specifically in any country or region in the Americas and if this contained information on the research topics considered (see below).

We used standardized data collection and built a comprehensive database (Supplementary data). We recorded the following information of the selected articles: first author, journal or book, year of publication, species or group of species, research topic, and geographic location of the study at the regional (North, Central, or South America) and country level. We defined the location of each study as the area where the fieldwork was carried out or the source of origin of the analyzed specimens. We classified the publications into 15 research topics according to the content of the document following the classification proposed by Guevara-Chumacero et al. (2001) and Pérez-Irineo and Santos-Moreno (2013), with some modifications in the grouping of studies in each research topic to facilitate their analysis (Table 2).

Data analysis

Publications were analyzed by species, research topics, and geographic regions and countries. The total number of publications for each species, research topic, region, and the country was calculated. Studies that addressed multiple species, research topics, regions, or countries were included in the count of each category. Publications that studied taxa at the family, subfamily, or genus level were excluded from the analysis by species, while those that did not focus on a country but a geographic region were not considered in the analysis by country.

The number of articles published by country and region was also expressed as a proportion of skunk species richness. The proportion of publications by region (PPR) and by country (PPC) was equal to the number of publications in each region or country divided by the number of species present in that region or country. We used a map of geopolitical limits of American countries (www.arcgis.com) and the distribution maps of mephitid species from the International Union for Conservation of Nature (IUCN 2020) to quantify the number of species present in each region and country. Likewise, we calculated the size of the geographic range of all species and the area of each region and country to standardize the comparison of the number of publications between species and between regions or countries, respectively. We obtained the square root of both calculations to linearize the relationship.

In addition, we evaluated the patterns in the production of research during the 122 years covered by this study. We pooled the references by decades based on the year of publication, although the last period comprised 12 years (2010–2021). This grouping made it possible to identify the distribution of the number of publications by species and by research topic over time.

We used Chi-square (X^2) tests to evaluate if the number of publications by species, research topic, geographic region, and country varied significantly. We calculated the expected number of studies by species based on the size of their range and the expected number of studies by region and country

Table 2 Research topics considered for the classification of studies on the family Mephitidae in the Americas from 1900 to 2021 and listed in order of decreasing the number of publications

Research topics	Number of publications	Grouping studies
Diseases and pathologies	317	Pathologies, parasitology, hematology, zoonosis, epizootics
Distribution	129	New records, historical and potential distribution, biogeography, zoogeography
Habitat	112	Use and selection of resources, micro and macro habitat, occupancy
Behavior	94	Activity patterns, behavioral habits
Anatomy and morphology	86	Anatomical or morphological descriptions, morphometry, sexual dimorphism
Ecological interactions	79	Competition, coexistence, kleptoparasitism, predation, temporal and spatial interactions
Demography	78	Abundance, density, sex ratio, survival, mortality
Methods/techniques	78	Efficacy, comparison and evaluation, new technique or protocol or methodology
Physiology	61	Metabolism, thermoregulation, hibernation, hormones
Management and conservation	53	Conservation status, anthropogenic threats, programs, plans, strategies, actions
Spatial ecology	47	Home range, core areas, dispersion, movements
Diet	44	Feeding habits, use of resources, trophic analysis
Genetics	34	Karyotype, chromosomes, genetic variation
Reproduction	30	Reproductive status and seasons, litter size
Taxonomy	21	New species or subspecies, classification, phylogeny, systematics

in proportion to their species richness and area size. We expected that the number of articles would be proportional to the range size of each species and the number of species or area size of each region or country, while the frequencies between research topics would be evenly distributed. We used contingency tables to evaluate if the number of publications per research topic varied significantly for each species (contingency table: 9 species × 15 topics). We calculated the expected frequencies following Zar (1999). We also performed a linear regression analysis to evaluate the relationship between the number of publications and the year of publication.

Results

Distribution of research on species

We recorded a total of 926 studies on the mephitids in the Americas published in the last 3 decades (1900–2021, see Supplementary data). Almost 85.5% of all publications focused on a single species, while 13.8% addressed two to six species. Six publications studied the taxon at the family, subfamily, or genus level. The most studied species was *M. mephitis* with 494 publications, followed by *Spilogale putorius* and *S. gracilis* with 143 and 142 each, and finally *C. chinga* with 102. *Mephitis macroura* had 66 publications, *C. leuconotus* 64, and *C. semistriatus* 57. The least studied species were *S. angustifrons* and *S. pygmaea* with 28 and 23 publications, respectively. The number of publications per species was not proportional to the size of its geographic range ($X^2 = 321.38$, d.f. = 8, $P < 0.001$; see Appendix B).

Distribution of studies on research topics

Approximately 74% of all publications addressed one research topic. Number of publications varied between research topics ($X^2 = 844.92$, d.f. = 14, $P < 0.001$). Diseases and pathologies showed the highest number of publications (317 studies, 25.1%), followed by distribution (129, 10.2%), and habitat (112, 8.9%). Behavior, anatomy and morphology, ecological interactions demography, and methods had between 78 and 94 publications each (6.2–7.4%), while physiology, management and conservation, spatial ecology, and diet varied from 44 to 61 each (3.5–4.8%; Table 2). In contrast, research topics with the least number of publications were genetics, reproduction, and taxonomy (> 35 studies each, 1.7–2.7%).

The number of publications by research topic varied significantly for each species ($X^2 = 504.75$, d.f. = 112, $P < 0.001$; Fig. 1). Distribution was the most studied research topic for *C. leuconotus* (18.2%), *C. semistriatus* (28.2%), *M. macroura* (19.8%), *S. angustifrons* (33.3%), and *S. pygmaea* (30.6%), while diseases and pathologies were the most studied for *C. chinga* (14.1%), *M. mephitis* (37.3%), and *S putorius* (20.1%). Topics related to physiology were most frequently addressed in *S. gracilis* (18%). Studies on anatomy and morphology, behavior, distribution, diseases and pathologies, habitat, and taxonomy were conducted in all skunk species, while physiology and reproduction were addressed in 66.7% of them. *Conepatus leuconotus*, *M.*

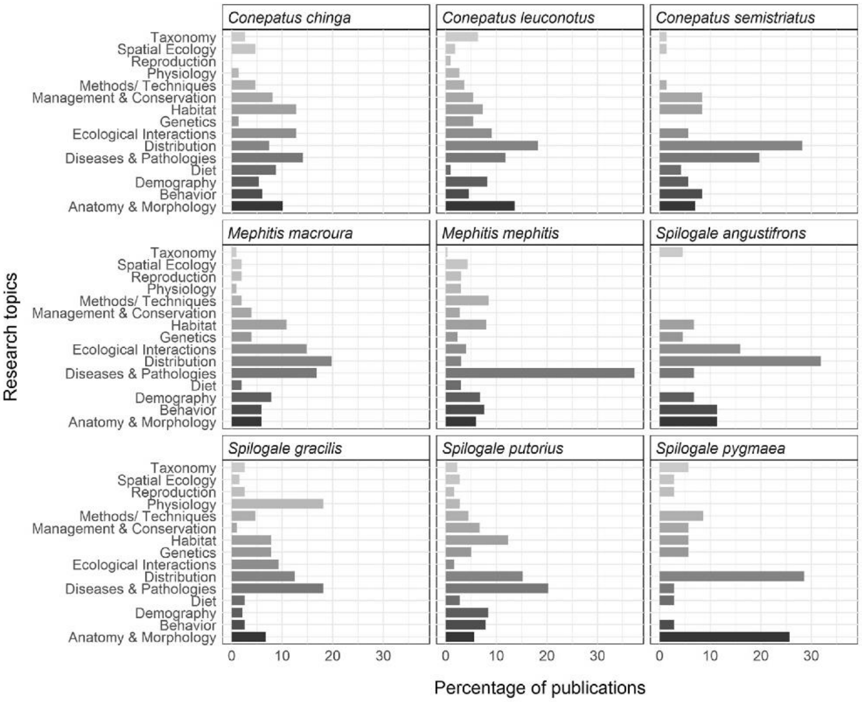

Fig. 1 Percentage of publications on the research topics for each species of skunk in the Americas from 1900 to 2021

macroura, *M. mephitis, S. gracilis*, and *S. putorius* showed at least one publication on all the research topics considered, but *C. semistriatus*, *S. angustifrons*, and *S. pygmaea* had studied from less than 33% of them.

Geographic distribution of research

At the regional level, the highest number of publications was recorded in North America (82.7%), followed by South America (14.7%), and the lowest number was in Central America (2.6%). Number of publications by region was not proportional either to area size ($X^2 = 846.04$, d.f. = 2, $P < 0.001$; Appendix B) or species richness ($X^2 = 328.64$, d.f. = 2, $P < 0.001$). Considering the number of publications in proportion to the number of mephitid species in each region, North and South America showed high and similar values with 774 publications on eight species (PPR = 96.7) and 138 publications on two species (PPR = 69), respectively. Central America showed the lowest value with 25 publications on four species (PPR = 6).

Approximately 95% of the studies were conducted in a single country and only 33% focused on two or more countries. Nineteen countries presented at least one published study, which represents 95% of the countries with the presence of mephitids. The number of publications differed significantly between countries and was not proportional to the area size ($X^2 = 1{,}533.88$, d.f. = 19, $P < 0.001$; see Appendix B) or number of species present ($X^2 = 2{,}656.55$, d.f. = 19, $P < 0.001$). More than 57% of all publications were conducted in the United States (549 publications), while the countries with the lowest number of publications were Guatemala, Honduras, Bolivia, El Salvador, and Paraguay with less than four publications per country (Fig. 2). We did not record studies in Belize, where *C. semistriatus* and *S. angustifrons* are distributed.

The United States and Argentina showed the highest proportion between the number of publications and the number of species in each country (PPC = 109.8 and PPC = 50.0, respectively). In contrast, El Salvador, Guatemala, and Honduras showed low and similar proportion values (PPC < 1.0; Fig. 2). The United States showed the highest number of publications for *C. leuconotus*, *M. mephitis*, *S. gracilis*, and *S. putorius*; Mexico for *M. macroura*, *S. angustifrons*, and *S. pygmaea*; Brazil for *C. semistriatus*; and Argentina for *C. chinga*. *Conepatus chinga*, *C. leuconotus*, *M. mephitis*, *S. gracilis*, *S. putorius*, and *S. pygmaea* were studied in all the countries where they are distributed, while *C. semistriatus* in 83.3%; *M. macroura* in 85.7%; and *S. angustifrons* in 66.7% of the total number of countries where each one is present (Table 3).

Distribution of research over time

The number of publications displayed a gradual increase over time ($r = 0.73$, $P < 0.001$), with greater scientific production between 2010 and 2021 (34.4%, 319

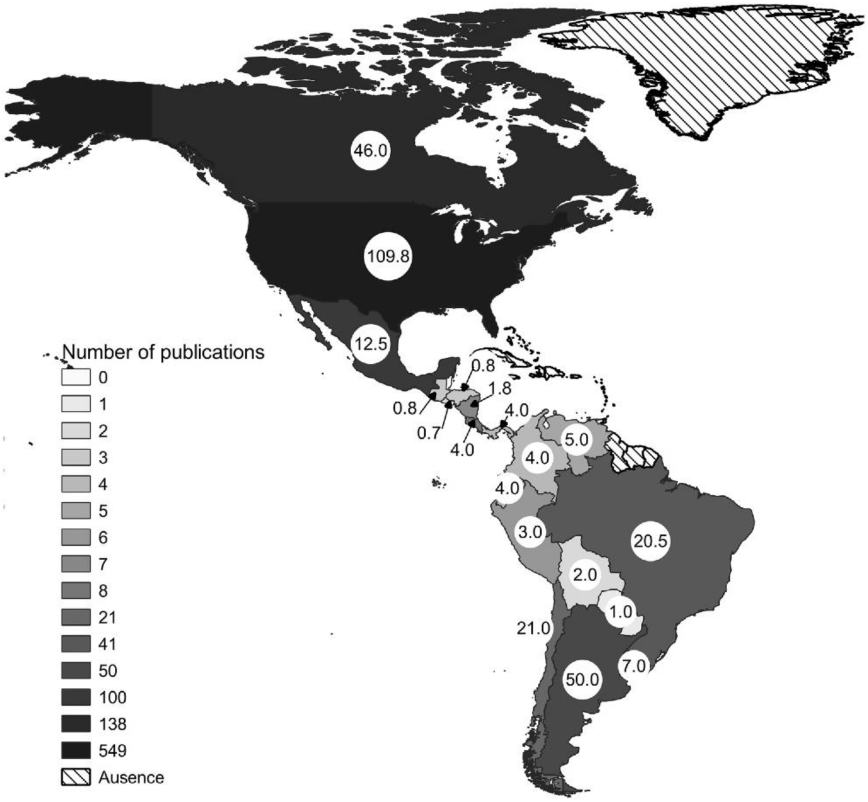

Fig. 2 Map that represents the number of publications of each country within the geographic ranges of skunk species in the Americas. Numbers in the circles indicate the proportion of publications by country (number of publications/richness of skunk species)

Table 3 Number of publications of skunk species by country in the Americas from 1900 to 2021

Country	*Conepatus chinga*	*Conepatus leuconotus*	*Conepatus semistriatus*	*Mephitis macroura*	*Mephitis mephitis*	*Spilogale angustifrons*	*Spilogale gracilis*	*Spilogale putorius*	*Spilogale pygmaea*
Canada	–	–	–	–	137	–	2	1	–
USA	–	35	–	22	350	–	117	135	–
Mexico	–	32	8	37	15	21	26	6	23
Belize	–	–	0	–	–	0	–	–	–
Guatemala	–	1	1	1	–	0	–	–	–
El Salvador	–	1	–	0	–	1	–	–	–
Honduras	–	1	0	1	–	1	–	–	–
Nicaragua	–	2	2	5	–	4	–	–	–
Costa Rica	–	–	4	3	–	–	–	–	–
Panama	–	–	4	–	–	–	–	–	–
Venezuela	–	–	5	–	–	–	–	–	–
Colombia	–	–	4	–	–	–	–	–	–
Ecuador	–	–	4	–	–	–	–	–	–
Peru	5	–	2	–	–	–	–	–	–
Brazil	20	–	23	–	–	–	–	–	–
Bolivia	2	–	–	–	–	–	–	–	–
Paraguay	1	–	–	–	–	–	–	–	–
Uruguay	7	–	–	–	–	–	–	–	–
Argentina	49	–	–	–	–	–	–	–	–
Chile	20	–	–	–	–	–	–	–	–

publications), followed by 2000 to 2009 (15%, 139), and from 1980 to 1989 (14%, 130). The remaining periods showed less than 10% of publications each, with the 1900s and 1910s having the lowest number of published studies (four and two, respectively). The regression model was: Number of publications = 0.199 (years) – 4.660, where both the intercept and the slope were significantly different from zero.

Overall, we recorded a discontinuous increase in the number of publications by species over time (Fig. 3). *Mephitis mephitis* and *S. gracilis* showed a greater increase in the period 1980–1989, *C. leuconotus* and *M. macroura* in 2000–2009, and *C. chinga*, *C. semistriatus*, *S. angustifrons*, *S. putorius*, and *S. pygmaea* had more publications in 2010–2021. However, the gradual increase in the number of publications was low for *S. angustifrons* and *S. pygmaea*. On the other hand, the number of publications on each research topic increased gradually over time, except for physiology and reproduction, which showed a progressive decrease after the 1980s. Research topics such as anatomy and morphology, diseases and pathologies, physiology, and reproduction showed a significant increase in the 1960s and 1970s. However, more than 40% of the articles on behavior, distribution, habitat, ecological interactions, and management and conservation were published in the last decade.

Discussion

This review is the first to assess the state of knowledge of all species of the family Mephitidae present in the Americas. The results obtained indicate that the current research effort and degree of information for each species, research topic, country, and region are heterogeneous, with considerable information gaps. We observed three types of bias in the distribution of the number of publications: (1) taxonomic bias, with *M. mephitis* significantly more studied compared to other species, such as *S. angustifrons* and *S. pygmaea*; (2) a bias in research topics, with most studies focused on diseases and pathologies, and (3) geographic bias at the regional and country levels, with a higher number of studies conducted in North America, mainly in the United States, than in countries of Central and South America.

Taxonomic bias

Research efforts on American mephitids varied strongly among species, however, the number of publications was not directly proportional to the size of their geographic ranges, which is partially consistent with what was observed in canids and felids (Brodie 2009; Tensen 2018). Our review showed that *M. mephitis* was the most studied species in the family Mephitidae. Previous studies have recorded similar observations and have indicated that North American

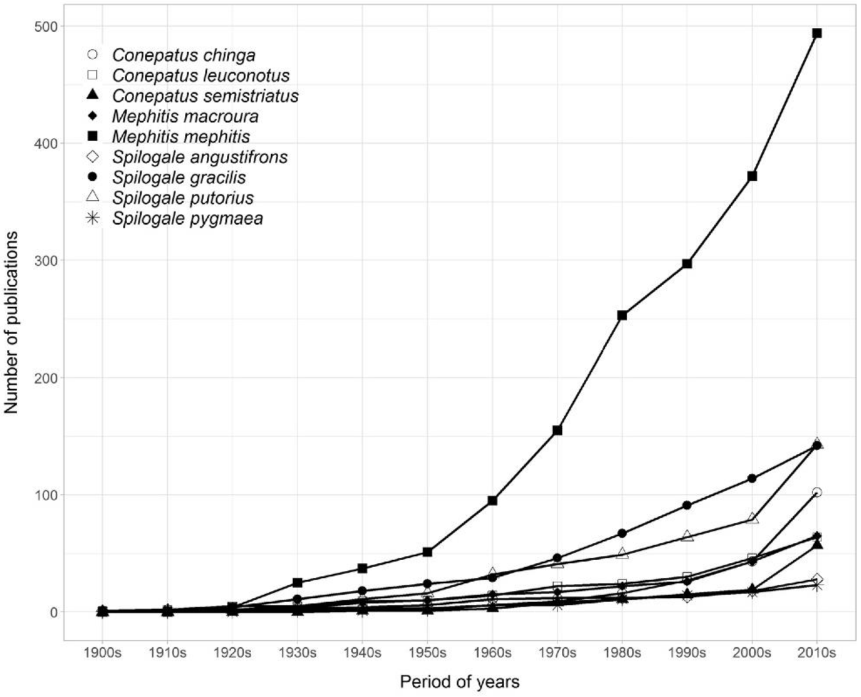

Fig. 3 Accumulated number of publications on skunk species in the Americas from 1900 to 2021

species receive increased research attention (Kasper et al. 2009; Brooke et al. 2014). In contrast, most mephitids did not show sufficient general knowledge available and much of the information remains anecdotal (Rosatte and Larivière 2003; Dragoo 2009; Dragoo and Sheffield 2009). Taxonomic bias towards a few species also exists in well-studied groups; for example, in the families Felidae and Canidae (Brodie 2009; Pérez-Irineo and Santos-Moreno 2013; Tensen 2018).

The interest of the scientific community in the study of mephitid species seems to be influenced by their zoonotic role and presence in urban environments, mainly in North America. *Mephitis mephitis* is a primary terrestrial vector of the rabies virus and is of public health importance (Greenwood et al. 1997; Krebs et al. 2004; Leslie et al. 2006; Oertli et al. 2009; Raghavan et al. 2016; Wohlers et al. 2018), while the other skunk species are not important reservoirs of this virus (Gilbert 2018) and there is a low or absent number of cases that document them (Aranda and López-de Buen 1999; Dragoo et al. 2004; Hass and Dragoo 2006; Oertli et al. 2009). Furthermore, *M. mephitis* adapts successfully to urban environments (Bateman and Fleming 2012; Šálek et al. 2015) and can be perceived as a "nuisance" in the regions where it lives, thus it conflicts with humans over resources (Rosatte and Larivière 2003; Dragoo 2009; Rosatte et al. 2010). The implications of these aspects could contribute significantly to the high percentage of publications recorded for *M. mephitis* (44.1%), as occurs in large-sized carnivore species (Brodie 2009; Brooke et al. 2014; Tensen 2018). Another factor that probably favored greater research on this species is that it is considered common, i.e., abundant, widely distributed, and habitat generalist (Dragoo 2009), thus making it an easy animal to study and observe. Most skunks, on the other hand, are rare, solitary, and elusive (Crooks 1994; Cantú-Salazar et al. 2009; Dragoo 2009; Gompper and Jachowski 2016; Helgen 2016), which simply makes their study difficult and partially explains why information on them is still limited.

Conservation status, restricted distribution, and taxonomic uncertainty possibly also contributed to the disparity in research effort in other skunk species. For example, some subspecies of the spotted skunks *S. putorius* and *S. gracilis* face conservation problems due to a decline in their populations (Crooks 1994; Roemer et al. 2002; Gompper and Hackett 2005), so the emerging concern about their current status surely led to increased research on them. Our analysis revealed that almost 45% of the studies on *S. putorius* were published in the last decade. This probably corresponds to the petition to list the Plains spotted skunk *S. p. interrupta* as Endangered on the Endangered Species Act (ESA, USFWS 2012) and the formation in 2015 of a Cooperative Study Group that has facilitated collaborative research among different institutions throughout its range (Eastern Spotted Skunk Cooperative Study Group 2020; Jachowski and Edelman 2021). Conversely, *S. pygmaea* and *S. angustifrons* were the least studied skunks, with a proportion equal to 5.5% of all publications. *Spilogale pygmaea* is endemic to the Pacific coast of Mexico and is restricted to the deciduous tropical forest (Medellín et al. 1998; Cantú-Salazar et al. 2009) while *S. angustifrons* has presented taxonomic uncertainty since it was first described, being recognized and validated as a distinct species until recently (Wozencraf 2005; Dragoo 2009; McDonough et al. 2021). These factors could have influenced the current state of knowledge of both species and have direct consequences for their conservation.

On the other hand, some authors also have mentioned that South American species of *Conepatus* have received less attention (Kasper et al. 2009). However, *C. chinga* is currently among the top species with the highest number of publications according to our results. We believe that the previous assessment of the state of knowledge on this skunk (Kasper et al. 2009) prompted the development of research for its study. Our review showed that studies on *C. chinga* increased after the publication of this preliminary effort, with 56.9% of the contributions published in the 2010s (Fig. 3). Similarly, *C. semistriatus*, despite being a poorly studied species to date (57 publications), has begun to gain importance in an evident way in the last ten years, with a gradual increase in the number of articles (Fig. 3). This substantial increase perhaps corresponded to the initiative of several researchers who have prioritized the research of this species in different South American countries (Oliveira 2006; González-Maya et al. 2011; Cossíos et al. 2012; Andrade-Ponce et al. 2016).

Bias associated with research topics

Our analysis revealed that research on the family Mephitidae was also biased in terms of the research topics addressed in the published literature. Studies on diseases and pathologies received comparatively more attention than reproductive and taxonomic topics. This result was consistent with that recorded in other reviews on mephitid species (González-Maya et al. 2011; Andrade-Ponce et al. 2016), even at higher taxonomic levels (Pérez-Irineo and Santos-Moreno 2013), which show that taxonomic aspects were rarely addressed in scientific research. Furthermore, the pattern observed in the distribution of publications between topics on mephitids was similar to that on canids, with most studies focused on diseases and other health issues, followed by ecology and behavior related studies, while artificial reproduction and taxonomy were studied the least (Tensen 2018).

Possible factors associated with the thematic bias recorded in our study are the relationship of mephitids with pathogens, technological advances and costs, and specific interests in research and conservation attention. Skunks are hosts of multiple pathogens that cause emerging infectious

diseases (e.g., Aleutian disease virus, Chagas disease, influenza A [H1N1] virus, skunk amdoparvovirus, tularemia), consequently, they may pose a direct risk to humans and domestic and wild species as vectors for disease transmission (Rosatte and Larivière 2003; Rosatte et al. 2010; Newman and Byrne 2017). It was, therefore, to be expected that research on them has focused on diseases and pathologies. For instance, the presence of rabies in populations of skunks, particularly in *M. mephitis*, brought the taxon to the attention of researchers due to the constant outbreaks recorded in its northern range (Greenwood et al. 1997; Guerra et al. 2003; Hass and Dragoo 2006; Oertli et al. 2009; Jimenez et al. 2019). However, although this research topic was the most studied, our review also makes it clear that the knowledge has been significantly higher for species living in urban habitats, such as *M. mephitis* in the United States. This additional bias does not mean that diseases have less influence on the ecology of poorly studied species (Newman and Byrne 2017; Gulas-Wroblewski 2021), but rather reflects existing information gaps despite skunks being important for the public and veterinary health in other regions of their ranges.

Some of the bias in the research effort towards certain topics was probably also due to the technologies used in field samplings, such as camera traps and radiotelemetry. Camera traps allow the study of nocturnal and cryptic species due to their permanent activity and non-invasive nature (Kays and Slauson 2008), and also provide detailed information on small-sized and rare carnivores, such as skunks, in different areas of knowledge (Ramírez-Chaves et al. 2016). Our analysis revealed that the research topics related to distribution, habitat, ecological interactions, and behavior show significant advances in the number of publications since the 2010s, which were largely favored by the development and reduction of costs of camera traps (Rovero et al. 2013). Similarly, radiotelemetry has been used frequently to study demography and spatial ecology of mephitid populations, but publications on these topics have decreased in the last decade, probably due to budgetary and technological limitations associated with this monitoring technique. Estimated costs are often high, including the purchase of radio-tracking equipment, personnel salaries, and fieldwork and transportation expenses (Fuller and Fuller 2012), while the short battery life of the transmitters appears to limit the use of GPS technology for studying species of skunks, particularly the smaller ones (Eastern Spotted Skunk Cooperative Study Group 2020). Thus, recent studies use more cost-effective techniques, such as camera trapping, and focus more on other research topics.

Another factor that may have influenced the heterogeneous distribution of publications between topics is individual interests. We highlighted that habitat and distribution studies became important due to the need to provide information on the basic requirements of all skunks in light of the loss and fragmentation of their habitats and because of the limited availability of valid presence data and the uncertainty in the geographic limits of the known distribution of the species, respectively. Indeed, previous reviews have prioritized these investigations in mephitids at a regional level because of the general scarcity of information (González-Maya et al. 2011; Pérez-Irineo and Santos-Moreno 2011; Cossíos et al. 2012). Likewise, we found that more than 57% of physiology studies were carried out in *S. gracilis* while 22% of articles on management and conservation were published for *C. chinga* and *S. putorius*. The increase in research on these topics reflected both the disproportionate interest in the physiological processes of delayed implantation in *S. gracilis* from the late 1960s to the early 1980s (Mead 1968, 1989) and the current need to implement conservation strategies and plans due to the significant decline in *S. putorius* populations (Gompper and Jachowski 2016; Jachowski and Edelman 2021) and potentially high road mortality rates of *C. chinga* (Serrón et al. 2020; Silva et al. 2021).

Our results, on the contrary, revealed a lack of allocation of research to topics on genetics and taxonomy. In the last decades, the use of genetic and molecular techniques has clarified the phylogeny and systematics of the family Mephitidae (Dragoo et al. 1993; Dragoo and Honeycutt 1997) and of skunks in the genus *Conepatus* (Dragoo et al. 2003; Schiaffini et al. 2013). Recent studies have also provided strong evidence for the recognition of seven distinct *Spilogale* species from modern nuclear and mitochondrial data (McDonough et al. 2021), which has significant implications for the taxonomic status of this genus. However, acceptance or rejection of proposed recommendations always takes time. Even though we followed the group's current taxonomic review (Koepfli et al. 2017), the IUCN (2020) does not recognize that *C. chinga* and *C. humboldtii* are conspecifics while Feijó and Langguth (2013) suggest that *C. amazonicus* is the valid name for the populations of *Conepatus* in eastern Brazil. Other small carnivores, such as procyonids and mustelids, have gone through the same controversies (Pérez-Irineo and Santos-Moreno 2013; Brooke et al. 2014) and the increase in genetic and molecular studies have determined the course of their taxonomic status. Finally, the recorded discrepancies are part of the knowledge on mephitids and more research is urgently needed to shed light on the taxonomically valid list of skunk species.

Geographic bias

Our review indicated a geographic bias in the research effort for mephitids in the Americas, which is consistent with global trends (González-Maya and Ramírez-Chaves 2017) but did not reflect either the species richness or area of each region and country. Some countries showed a high proportion of publications with relatively low or moderate

species richness, such as the United States in North America (PPC = 109.8) and Argentina in South America (PPC = 50). Conversely, Mexico showed a low proportion of publications (PPC = 12.5) even though eight species inhabit the country. Central American countries also showed very low values (PPC ≥ 1.75), since they have a smaller number of publications compared to the number of species present there, a fact that is reflected when compared to previous studies (González-Maya and Ramírez-Chaves 2017; González-Maya 2018).

In addition, we recorded some species of skunks that have not been studied in the countries where they are distributed, which agrees with the results of the review by Pérez-Irineo and Santos-Moreno (2013). For example, *S. angustifrons* does not have any studies in Belize and Guatemala, which represent 33.3% of the countries where it is distributed (Table 3). *Conepatus semistriatus* and *M. macroura* have also not received attention in Central American countries and are represented by few studies in most of them, which is why *C. semistriatus* only has 57 available publications although it occurs in 12 countries from North, Central, and South America (Dragoo 2009). Nevertheless, the fact that some species show a high number of publications does not necessarily mean that they are well-studied since a high proportion of them has been carried out in specific regions and might not represent what occurs in other populations in their ranges, such as *M. mephitis* in the United States and *C. chinga* in Argentina.

The geographic distribution of the published studies can be influenced by various factors, including the availability of economic resources, the charisma of the species, and the accessibility of the area where they are present. The availability of the economic resources for research is heterogeneous among countries. World Bank data indicates that the fund invested in research and development in the United States and Canada was 2.83% and 1.54% of their gross domestic product (GDP) in 2018, respectively; while Central American countries such as El Salvador, Guatemala, Honduras, and Panama invested less than 0.17% (World Bank, 2020). This financial heterogeneity contributed to the geographic bias in research of wildlife in general and mephitids in particular. Likewise, the charisma of a species may have a positive or negative impact on people's attitudes and influences its ability to generate public support or become a conservation icon (Macdonald et al. 2015). Large cats exhibit high charisma unlike species of skunk such as *M. mephitis* (Macdonald et al. 2015) and often receive disproportionate research and conservation attention across much of their range (Brodie 2009; Dickman et al. 2015; Tensen 2018), so it is clear that scientific communities have more pressing priorities and show less interest in skunks in their research. Lastly, accessibility to areas of the Neotropics generates logistical problems to carry out fieldwork, which could explain the absence of studies on mephitids in countries of these latitudes, mainly in Central America. Other authors have observed that research is scarce in remote and difficult-to-access neotropical regions, while most of the studies are conducted in regions where research centers and institutions are concentrated (Andrade-Ponce et al. 2016).

Implications for conservation

Biological and ecological knowledge of a species is essential for a correct evaluation of its conservation status (Mace et al. 2008) and, therefore, the scarcity or absence of this information influences the ability to assess such status (Andrade-Ponce et al. 2016). Nearly 78% of American mephitids are currently listed as Least Concern under the IUCN Red List classification scheme (Table 1; IUCN 2020), while *S. putorius* and *S. pygmaea* are classified as Vulnerable. However, our review revealed that the published literature on ecological and demographic aspects for several of these species is still insufficient, which does not ensure a reliable assessment of their conservation status.

Unfortunately, species that require the most attention do not always receive it. For example, *C. leuconotus* is listed as Least Concern but has experienced an apparent population decline in the northern portion of its range (Meaney et al. 2006); thus, this species could require a reassessment in light of greater availability of information to justify its assignment in some category of risk. Lack of studies on the demography and the threats that affect the populations of *C. semistriatus*, *M. macroura*, and *S. angustifrons*, according to our results, also generates uncertainty in whether they have been indeed correctly classified in the category of Least Concern or if they should be classified as Data Deficient. We considered that there is neither sufficient information nor supported evidence to determine the risk categories of these species. This same situation occurs with *S. pygmaea*, since there is no population data and ecological studies have been lacking for more than a decade, even though its research and conservation have been prioritized in Mexico (Valenzuela and Vázquez 2007; Pérez-Irineo and Santos-Moreno 2011). Overall, many significant changes in the conservation status of small carnivores globally have been due to increased research allocation (González-Maya 2018). Therefore, further research is urgently required to refine the classification of mephitid species.

Although it seems clear that the research effort is not stimulated by the conservation status of carnivore species (Brodie 2009; Brooke et al. 2014; Tensen 2018), the outlook is encouraging for *S. putorius*, one of the two threatened mephitids. Several research groups and centers are currently carrying out projects on this species throughout its range (Eastern Spotted Skunk Cooperative Study Group 2020; Edelman et al. 2021), which may improve our

understanding to identify knowledge gaps, priority research areas, and potential conservation actions. The advancement of knowledge for this skunk has greatly stood out in recent years given the global deterioration of the conservation status of several species of small carnivores (González-Maya 2018). In this regard, our review joins other calls for a focus of research efforts on mephitids, not only to increase the number of research studies, but also to make the available information relevant. We hope that this work contributes to reducing this scientific gap and improves the current state of research on mephitids to allow both a more reliable assessment of the conservation status of these species and the design and development of effective conservation strategies.

Future research priorities

Here, we propose research priorities to focus future efforts on American mephitids to fill knowledge gaps and improve the current state of knowledge for their conservation. We urge the scientific community to direct its research efforts towards mephitid species that are poorly studied, threatened, restricted in range, and lacking in information in much of their range. We believe that research on *S. pygmaea* is necessary to improve the understanding of its ecology and the potential threats it faces due to current anthropogenic changes, such as the loss and fragmentation of its habitat. *Conepatus leuconotus*, *C. semistriatus*, *M. macroura*, and *S. angustifrons* should also receive more attention because they have not been sufficiently studied in the countries where they are distributed, which influences their conservation status.

Future research should focus on poorly studied research topics, as well as those that allow defining the threat status and establishing conservation strategies for mephitid species. Taxonomic studies are required to help to clarify the systematics at the species and subspecies level based on modern genetic and molecular techniques. Likewise, studies on reproduction and genetics are necessary to know the viability and determine the genetic diversity of populations, particularly of threatened species or those in fragmented habitats. Our results also support the prioritization of demographic studies on most species to propose methods for estimating population size, understanding population dynamics, and trends and making long-term assessments. More research efforts should also be directed towards aspects of spatial ecology since these allow the design of standardized monitoring protocols, and towards studies on ecological interactions to understand the mechanisms that structure communities and the effects of anthropogenic threats such as the introduction of exotic and feral species. Finally, diseases and other zoosanitary issues should be addressed in different regions since mephitids have important implications for public health.

We believe that it is necessary to invest more research efforts in Mexico given that it has the highest skunks richness worldwide, including endemic species, which is relevant to identify suitable habitats and to establish priority conservation areas for species. It is also urgent to increase the number of research studies in all the countries of Central America and most of South America (except Brazil and Argentina) since the trends and patterns of skunk populations in each region is important to better understand their conservation status at local and global levels.

Appendix A

See Tables A1, A2, A3.

Table A1 Results for the Chi-squared test comparing the number of publications observed (NPO) with the number of publications expected (NPE) based on the size of the geographic range of each mephitid species

Species	NPO	Range size[a]	NPE	X^2 value
Conepatus chinga	102	2,352.15	174.70	30.26
Conepatus leuconotus	64	1,580.63	117.40	24.29
Conepatus semistriatus	57	1,421.79	105.60	22.37
Mephitis macroura	66	1,335.45	99.19	11.11
Mephitis mephitis	494	3,503.03	260.19	210.12
Spilogale angustifrons	28	881.70	65.49	21.46
Spilogale gracilis	142	1,955.81	145.27	0.07
Spilogale putorius	143	1,726.16	128.21	1.71
Spilogale pygmaea	23	309.04	22.95	0.00
Total		15,065.76		321.38*

*$P < 0.001$

[a] We calculated the square root of the range size to linearize the relationship

Table A2 Results for the Chi-squared test comparing the number of publications observed (NPO) with the number of publications expected in proportion to the area size (NPEas) and the species richness (NPEsr) of each geographic region

Region	NPO	Area size[a]	Species richness	NPEas	X^2 value	NPEsr	X^2 value
North America	774	7,592.96	8	344.8	534.39	534.9	106.92
Central America	24	1,818.27	4	82.6	41.54	267.4	221.58
South America	138	11,202.70	2	508.7	270.11	133.7	0.14
Total		20,613.92	9		846.04*		328.64*

*$P < 0.001$

[a] We calculated the square root of the area size to linearize the relationship

Table A3 Results for the Chi-squared test comparing the number of publications observed (NPO) with the number of publications expected in proportion to the area size (NPEas) and the species richness (NPEsr) of each country in the Americas

Country	NPO	Area size[a]	Species richness	NPEas	X^2 value	NPEsr	X^2 value
Canada	138	3,140.54	3	145.49	0.39	59.69	102.75
United States	549	3,053.02	5	141.44	1,174.39	99.48	2,031.27
Brazil	41	2,912.60	2	134.93	65.39	39.79	0.04
Argentina	50	1,667.36	1	77.25	9.61	19.90	45.55
Mexico	100	1,399.41	8	64.83	19.08	159.17	21.99
Peru	6	1,136.51	2	52.65	41.34	39.79	28.70
Colombia	4	1,066.63	1	49.41	41.74	19.90	12.70
Bolivia	2	1,041.45	1	48.25	44.33	19.90	16.10
Venezuela	5	954.88	1	44.24	34.80	19.90	11.15
Chile	21	863.09	1	39.99	9.01	19.90	0.06
Paraguay	1	632.20	1	29.29	27.32	19.90	17.95
Ecuador	4	505.68	1	23.43	16.11	19.90	12.70
Uruguay	7	422.28	1	19.56	8.07	19.90	8.36
Nicaragua	7	359.14	4	16.64	5.58	79.58	66.20
Honduras	3	336.03	4	15.57	10.15	79.58	73.70
Guatemala	3	330.37	4	15.31	9.89	79.58	73.70
Panamá	4	273.21	1	12.66	5.92	19.90	12.70
Costa Rica	8	226.42	2	10.49	0.59	39.79	25.40
Belize	0	148.39	2	6.87	6.87	39.79	39.79
El Salvador	2	144.71	3	6.70	3.30	59.69	55.75
Total		2,0613.92	9		1,533.88*		2,656.55*

[a] We calculated the square root of the area size to linearize the relationship

*$P < 0.001$

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Declarations

Conflict of interest On behalf of all the authors, the corresponding author states that there is no conflict of interest.

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CAPÍTULO III

DRIVERS OF ACTIVITY PATTERNS OF TWO SYMPATRIC SKUNKS (CARNIVORA: MEPHITIDAE)

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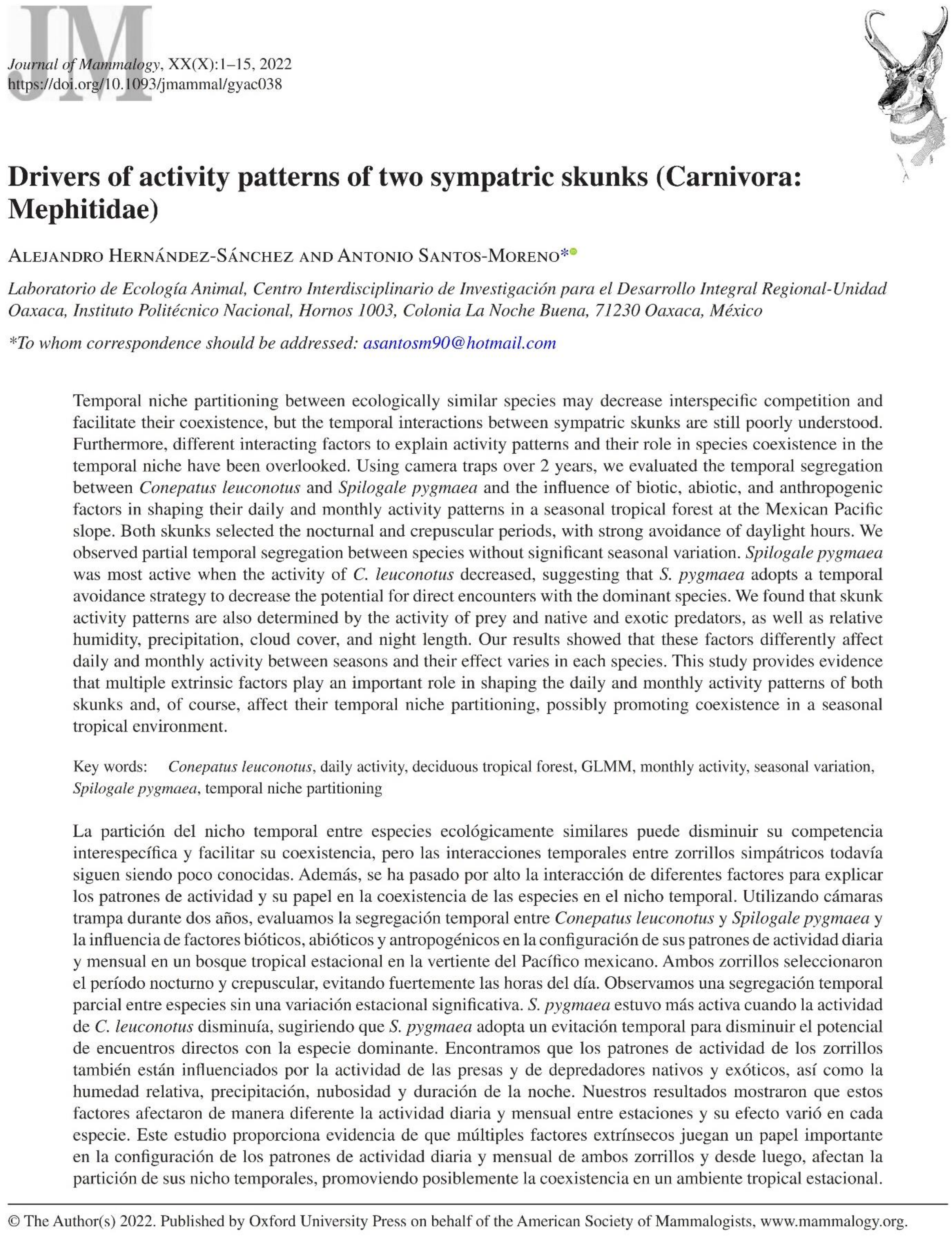

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Drivers of activity patterns of two sympatric skunks (Carnivora: Mephitidae)

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Temporal niche partitioning between ecologically similar species may decrease interspecific competition and facilitate their coexistence, but the temporal interactions between sympatric skunks are still poorly understood. Furthermore, different interacting factors to explain activity patterns and their role in species coexistence in the temporal niche have been overlooked. Using camera traps over 2 years, we evaluated the temporal segregation between *Conepatus leuconotus* and *Spilogale pygmaea* and the influence of biotic, abiotic, and anthropogenic factors in shaping their daily and monthly activity patterns in a seasonal tropical forest at the Mexican Pacific slope. Both skunks selected the nocturnal and crepuscular periods, with strong avoidance of daylight hours. We observed partial temporal segregation between species without significant seasonal variation. *Spilogale pygmaea* was most active when the activity of *C. leuconotus* decreased, suggesting that *S. pygmaea* adopts a temporal avoidance strategy to decrease the potential for direct encounters with the dominant species. We found that skunk activity patterns are also determined by the activity of prey and native and exotic predators, as well as relative humidity, precipitation, cloud cover, and night length. Our results showed that these factors differently affect daily and monthly activity between seasons and their effect varies in each species. This study provides evidence that multiple extrinsic factors play an important role in shaping the daily and monthly activity patterns of both skunks and, of course, affect their temporal niche partitioning, possibly promoting coexistence in a seasonal tropical environment.

Key words: *Conepatus leuconotus*, daily activity, deciduous tropical forest, GLMM, monthly activity, seasonal variation, *Spilogale pygmaea*, temporal niche partitioning

La partición del nicho temporal entre especies ecológicamente similares puede disminuir su competencia interespecífica y facilitar su coexistencia, pero las interacciones temporales entre zorrillos simpátricos todavía siguen siendo poco conocidas. Además, se ha pasado por alto la interacción de diferentes factores para explicar los patrones de actividad y su papel en la coexistencia de las especies en el nicho temporal. Utilizando cámaras trampa durante dos años, evaluamos la segregación temporal entre *Conepatus leuconotus* y *Spilogale pygmaea* y la influencia de factores bióticos, abióticos y antropogénicos en la configuración de sus patrones de actividad diaria y mensual en un bosque tropical estacional en la vertiente del Pacífico mexicano. Ambos zorrillos seleccionaron el período nocturno y crepuscular, evitando fuertemente las horas del día. Observamos una segregación temporal parcial entre especies sin una variación estacional significativa. *S. pygmaea* estuvo más activa cuando la actividad de *C. leuconotus* disminuía, sugiriendo que *S. pygmaea* adopta un evitación temporal para disminuir el potencial de encuentros directos con la especie dominante. Encontramos que los patrones de actividad de los zorrillos también están influenciados por la actividad de las presas y de depredadores nativos y exóticos, así como la humedad relativa, precipitación, nubosidad y duración de la noche. Nuestros resultados mostraron que estos factores afectaron de manera diferente la actividad diaria y mensual entre estaciones y su efecto varió en cada especie. Este estudio proporciona evidencia de que múltiples factores extrínsecos juegan un papel importante en la configuración de los patrones de actividad diaria y mensual de ambos zorrillos y desde luego, afectan la partición de sus nicho temporales, promoviendo posiblemente la coexistencia en un ambiente tropical estacional.

Palabras clave: actividad diaria, actividad mensual, bosque tropical caducifolio, *Conepatus leuconotus*, Modelos Mixtos Lineales Generalizados (MMLG), partición de nicho temporal, *Spilogale pygmaea*, variación estacional

How an animal distributes its activity throughout the daily cycle and uses time as a resource is an important component of animal behavior and ecology, as it provides information on the natural history and ecological niche of a species (Schoener 1974; Kronfeld-Schor and Dayan 2003). For ecologically similar sympatric species, temporal niche partitioning may be a strategy for enabling their coexistence (Schoener 1974; Kronfeld-Schor and Dayan 2003). These species may adjust their activity patterns to reduce the potential for interspecific competition (Carothers and Jaksic 1984; Palomares and Caro 1999), where body size and diet overlap influence the direction and strength of intraguild interactions (Palomares and Caro 1999; Donadio and Buskirk 2006; Hunter and Caro 2008). Nevertheless, shifts in activity patterns of potential competitors may also be determined by behavioral responses to several other biotic and abiotic factors, including anthropogenic pressures (Kronfeld-Schor and Dayan 2003; Shuai et al. 2014; Frey et al. 2017). Investigating temporal activity patterns of sympatric species, especially mammals, can therefore help to identify the responsible drivers and underlying patterns that govern shifts in their activity that could facilitate their coexistence (Pita et al. 2011; Shuai et al. 2014; Bu et al. 2016; Frey et al. 2017).

Activity patterns of skunks are increasingly addressed in research (Benson et al. 2019; Marinho et al. 2020), but temporal interactions between sympatric species of skunks are still poorly understood. Previous studies have documented segregation along the temporal axis among skunks caused by interference competition, which enables them to coexist within diverse assemblages of sympatric species. For example, the striped skunk *Mephitis mephitis* (2–5 kg) and the western spotted skunk *Spilogale gracilis* (0.5–1.8 kg), as well as the American hog-nosed skunk *Conepatus leuconotus* (1.1–4.5 kg), the hooded skunk *M. macroura* (0.6–2.7 kg), and the southern spotted skunk *S. angustifrons* (0.2–0.8 kg) differ in their activity patterns as a response of the smaller-sized species to avoid agonistic encounters with the larger species (Patton 1974; Neiswenter et al. 2010; Farías-González and Hernández-Mendoza 2021). However, other cases show contradictory results and suggest that activity switching is not driven by interspecific competition, for example, between sympatric populations of *C. leuconotus* and *M. mephitis* (Cochran 2012). Although several studies have shown that skunks activity varies according to temperature, moon phase, prey activity, risk of predation, and even human presence (e.g., Cavalcanti et al. 2014; Castillo et al. 2015; Dias 2017; Benson et al. 2019), most have overlooked interacting multiple factors to explain activity patterns and their role for species coexistence in the temporal niche thus far.

Temporal patterns observed in species of skunks within sympatric assemblages remain unclear, particularly in tropical environments. The Mexican Pacific slope has been identified as a priority area for the conservation of carnivore mammals (Valenzuela-Galván et al. 2007). In this region, the deciduous tropical forest predominates (Ceballos and Martínez 2010), an ecosystem with marked climatic seasonality (Trejo 2004, 2010), and temporal variation in resource availability and abundance (Lister and García 1992; Valenzuela and Macdonald 2002). The deciduous tropical forests of the Pacific slope harbor four sympatric skunks: *C. leuconotus*, *M. macroura*, *S. angustifrons*, and the pygmy spotted skunk *S. pygmaea* (Dragoo 2009; Ceballos and Martínez 2010)—this last species is endemic to Mexico and is restricted to these forests (Medellín et al. 1998). *Conepatus leuconotus* is considered the largest body-size skunk in the world while *S. pygmaea* is the smallest (0.1–0.3 kg; Medellín et al. 1998; Dragoo 2009). Both species of skunks are primarily insectivorous but consume small vertebrates as alternative prey when food availability is low (Medellín et al. 1998; Cantú-Salazar et al. 2005; Dragoo and Sheffield 2009). It is therefore likely that these species with differences in body size show high overlap in their feeding habits and are involved in competitive interactions. Competition between species in seasonal environments is frequently more intense when food is scarce (Palomares and Caro 1999; Stoner and Timm 2011) and in response, skunks may show differences in their activity patterns.

Research on activity patterns of *C. leuconotus* and *S. pygmaea* is scarce (Cochran 2012; Buenrostro-Silva et al. 2015; Pérez-Irineo et al. 2020). To date, temporal interaction and factors related to the activity of these species in tropical environments have not been explicitly evaluated. Studies on activity patterns contribute to an understanding of how sympatric species with similar ecological roles segregate time for promoting their coexistence, as well as drivers of shifts in activity rhythms (Kronfeld-Schor and Dayan 2003; Frey et al. 2017). Furthermore, the deciduous tropical forest is a natural system of marked seasonality and fluctuating resources that may provide insight into the degree of plasticity in the activity patterns of species. In this regard, camera traps offer the opportunity to investigate questions about animal behavior and biotic interactions, such as activity patterns and temporal niche partitioning (Burton et al. 2015; Zimmermann et al. 2016; Frey et al. 2017). The fine-scaled time data from camera traps also allow us to explore variation in activity patterns and its effect on the temporal partitioning of sympatric species due to the influence of biotic and abiotic stimuli, as well as the changes driven by anthropogenic factors (Gerber et al. 2012; Bu et al. 2016; Frey et al. 2017).

The goals of the study were: (i) to describe the daily and seasonal activity patterns of *C. leuconotus* and *S. pygmaea* and to analyze their temporal and spatial variation, (ii) to describe and evaluate the temporal segregation between skunks, and (iii) to evaluate the influence of abiotic, biotic, and anthropogenic factors on the activity of skunks in a deciduous tropical forest at the Mexican Pacific slope. Considering the ecological characteristics of the two species studied and the environment they inhabit, we expected that temporal niche partitioning between skunks would be a mechanism to decrease interspecific competition and facilitate species coexistence (Carothers and Jaksic 1984; Kronfeld-Schor and Dayan 2003). Specifically, *S. pygmaea* could present shifts in its activity patterns because, as the smaller-sized species, it might adjust behavior to avoid direct encounters with the dominant competitor (Polis et al. 1989; Palomares and Caro 1999). We also hypothesized that temporal segregation would be greater during the dry season when competition between species tends to be more intense due to the scarcity of food resources (Palomares and Caro 1999; Stoner and Timm 2011). As an alternative hypothesis to niche segregation, species activity patterns were expected to be determined by the activity of potential prey and native and exotic predators or by seasonal variation of different abiotic factors.

MATERIALS AND METHODS

This study was carried out with the permission of the Secretary of the Environment and Natural Resources of Mexico (SEMARNAT, acronym in Spanish) through the licenses of scientific collection for teaching purposes in the field of wildlife (SGPA/DGVS/008795/18 and SGPA/DGSV/11153/19) and followed the American Society of Mammalogists' guidelines for animal research (Sikes et al. 2016).

Study area.—The Huatulco National Park (HNP; 15°39′12″ and 15°47′10″ N, 96°06′30″ and 96°15′00″ W) is in the municipality of Santa Maria Huatulco, on the central portion of the coast of Oaxaca within the Mexican Pacific slope (Fig. 1; CONANP 2003). The region is part of the Priority Terrestrial Region No. 129 Sierra Sur-Costa de Oaxaca (Arriaga et al. 2000). The HNP comprises a land area of 6,374.98 ha (CONANP 2003). Climate is warm subhumid with rains in summer, which is the subtype with the lowest humidity (CONANP 2003; Trejo 2004). This climate is strongly seasonal with a prolonged dry season from November to May and a wet season from June to October (CONANP 2003; Trejo 2004). Average annual temperature ranges between 26 and 28°C and annual precipitation varies between 800 and 1,200 mm (Trejo 2004). The deciduous tropical forest is the dominant plant community (Salas-Morales et al. 2007), characterized by loss of leaves from most of the vegetation during the dry season and a regularly continuous canopy cover in the wet season (Trejo 2004, 2010). The HNP presents natural elements that give it outstanding importance for the conservation of the deciduous tropical forest and harbors one of the last best-conserved remnants of this ecosystem (CONANP 2003).

The HNP is subdivided into five zones according to the conservation state and use of the ecosystems present: protection, restricted use, traditional use, sustainable harvesting of natural resources, and recovery (CONANP 2003). The protection zone is the most conserved and has little human alteration while the others show a higher anthropogenic disturbance degree, mainly the sustainable harvesting and recovery zones (CONANP 2003). At the sustainable harvesting zone, there are dirt roads for access to the study area and the presence of feral dogs *Canis lupus familiaris* has been recorded, due to its proximity to an open-air garbage dump (Binnqüist et al. 2017; Guzmán Pacheco 2019).

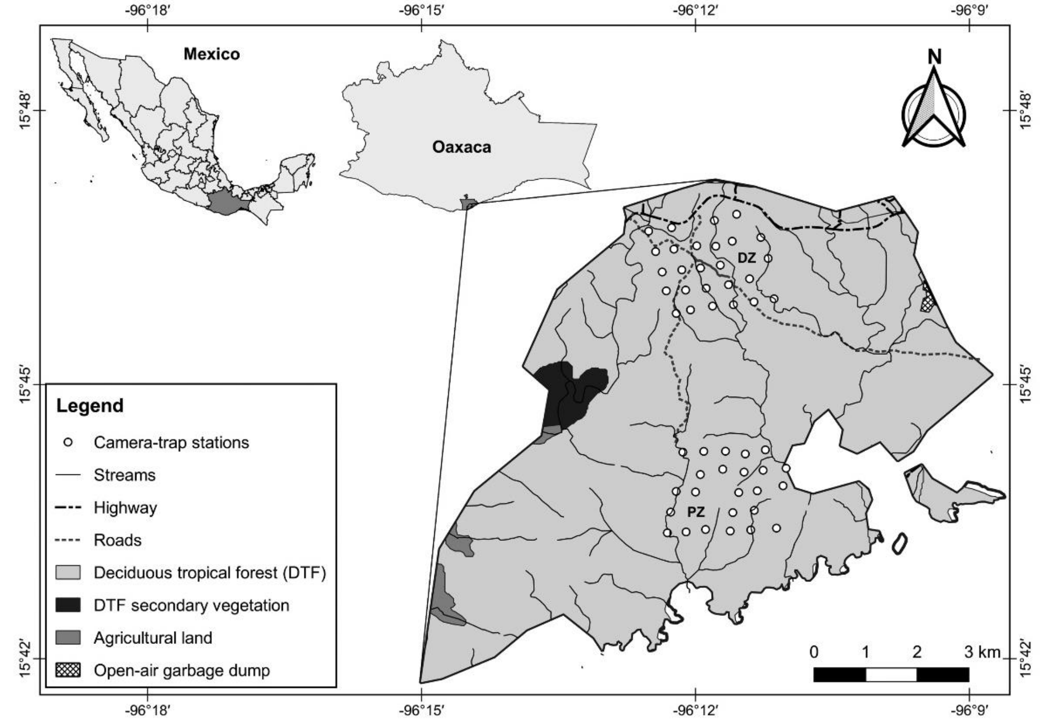

Fig. 1.—Huatulco National Park (HNP) in the state of Oaxaca, Mexico, and distribution of camera-trap stations at protection zone (PZ) and disturbance zone (DZ) inside of the deciduous tropical forest.

The recovery zone is crossed by federal highway 200 with a constant vehicular flow and has some irregularly established human settlements. In addition, hunting and wood extraction is carried out illegally by inhabitants of the communities settled around the study area (personal observation).

Sampling design.—Species activity was recorded through camera trapping and sampling took place from November 2018 to October 2020. We established two study sites based on the HNP zoning, one in the protection zone and the other in the harvesting and recovery zones (hereafter disturbance zone). At each site, we placed 30 single camera-trap stations arranged in a regular grid of 6 × 5 stations and spaced 420 m apart, covering an area of 3.70 km^2 by the location of the outermost stations (Fig. 1). However, only 20–26 stations per site were operating because several traps were stolen. Station spacing and grid size were determined considering the minimum estimate for the home range and the population density of focal species such that there were at least two camera stations in the estimated home range of each species (*C. leuconotus*: 0.64 km^2 and 0.6–1.3 ind/km^2—Cervantes et al. 2002; Brashear et al. 2015; *S. pygmaea*: 0.2 km^2—Cantú-Salazar et al. 1999). Unbaited camera stations were located inside of the forest on animal trails and near streams and were attached to trees about 20–30 cm above the ground. We used Bushnell Trophy Cam and Bushnell Trophy Cam w/Viewscreen (Bushnell Outdoor Products, Overland Park, Kansas), Moultrie 990i Digital Game Camera (Moultrie Products, LLC, Birmingham, Alabama), and ERE-E1 (EREAGLE Technology Co., Ltd, Shenzhen, China). We programmed the camera traps to remain active 24 h every day and often configured them with a high sensitivity level due to the small body size and elusive behavior of *S. pygmaea* (it was effective for capturing small prey mammals as well). Cameras were also set to take three photographs and/or one 10–15 video per trigger event, with a 10-s delay period between consecutive events. The date and time were recorded on all photos and videos. We checked the stations monthly to replace dead batteries and malfunctioning or robbed traps, although we removed the stations located in the protection zone during the second year of sampling due to the constant loss of equipment.

Biotic, abiotic, and anthropogenic variables.—To analyze the biotic variables, we quantified the independent records (see below) of potential prey species, competitors, and native predators detected in the camera traps, which were selected according to published literature. *Conepatus leuconotus* and *S. pygmaea* feed on small mammals when insect prey availability is low; therefore, mice were considered as potential prey (Cantú-Salazar et al. 2005; Dragoo 2009; Dragoo and Sheffield 2009), although it should be noted that these organisms do not represent the full spectrum of prey available to skunks. When competition is asymmetric, the smaller species reduces the interference of the larger or dominant species (Polis et al. 1989; Palomares and Caro 1999), so *C. leuconotus* was a potential competitor for *S. pygmaea*. The coyote *Canis latrans* and the ocelot *Leopardus pardalis* were collectively considered native predators (Dragoo 2009; Dragoo and Sheffield 2009). Similarly, we included independent records of *C. l. familiaris* as an anthropogenic variable, since it is a potential exotic predator of skunks (Dragoo and Sheffield 2009). Although we recorded evidence of human activity during our fieldwork, we did not obtain the exact time or date for most of the information and it, therefore, was not analyzed.

Abiotic variables considered in the analysis were: ambient temperature (°C), relative humidity (%), cloud cover (total number of clouds), precipitation (mm), the illuminated fraction of the moon, and night length (h). Measurements of the four climatic variables were generally recorded every hour during the sampling period and were obtained from the meteorological observatory "Puerto Ángel" (15°40′04″N, 96°29′24″W; id = 76855), administered by the National Water Commission (CONAGUA, acronym in Spanish). We assumed that these variables do not differ between camera-trap locations and the meteorological station, given the little variation in the conditions of the area and the geographical proximity among them (maximum distance of 34.5 km). We obtained the average values of temperature, relative humidity, and cloud cover, and the total value of precipitation per hour and day in both seasons of each year. Data of lunar illumination and night length were obtained for all days of the sampling period with the R package Suncalc (Thieurmel and Elmarhraoui 2019), using the geographical coordinates of HNP (15°46′10″N, 96°11′41″W; GMT-6 h). The illuminated fraction of the moon varies from 0.0 (new moon) to 1.0 (full moon; Thieurmel and Elmarhraoui 2019).

Data analysis.—The activity of focal species was considered as time in which the animals were detected by camera traps. Time and date of the photographic and video records were used to describe activity patterns and levels and temporal segregation of skunk species. We organized information in a database and obtained independent records by time and by date using the R package CamtrapR (Niedballa et al. 2016). We defined an independent record by time and by date as all photographs and videos of the same species taken at each sampling station within 1 h and at least 1 day apart, respectively. When more than one individual was observed in one photograph or video, each was considered as an independent record. We classified records by hour to describe the daily activity and by day to describe monthly activity irrespective of the hour. All records were converted to radians in a range from 0 to 2 * π. The activity was analyzed for species with a minimum of 10 records.

Activity patterns of skunks.—We compared daily and monthly activity distributions of each species between seasons, years, and sampling sites. We pooled data from the two sampling years by season to achieve a sufficient sample size and compared them. When activity did not differ significantly between seasons, we pooled data sets by year and compared them. If no differences were observed between years, we pooled data at each site and tested whether or not they differed to pool them into a set. We used the nonparametric two-sample tests of Mardia–Watson–Wheeler (*W*) and Watson (U^2) in comparisons, but the latter test was only used if the number of records was <10 in one of the data sets (Zar 1999). Then, we tested the uniformity of species activity patterns on the pooled or unpooled activity distributions using Rao's (*U*) spacing test. Statistical analyses

were performed with the R package Circular (Lund et al. 2017) and the significance level of tests was $P \leq 0.05$.

Daily and monthly activity patterns of skunk species were estimated with the nonparametric kernel density method (Ridout and Linkie 2009) using the R package Overlap (Meredith and Ridout 2020). We used this package to investigate the monthly cycle of species as it is not limited to the daily cycle (Meredith and Ridout 2020) as it has normally been used. We categorized the diel cycle into three periods: diurnal, nocturnal, and crepuscular. We defined the diurnal period as the hours from sunrise to sunset, nocturnal as the hours from the end of astronomical twilight to the start of morning astronomical twilight, and crepuscular as the remaining time (Bu et al. 2016). Sunrise and sunset and start and end of astronomical twilight were obtained with the R package Suncalc (Thieurmel and Elmarhraoui 2019). To characterize the daily activity patterns, we tested whether skunks select the periods by comparing use to availability of each period according to Manly et al. (2002): $w_i = o_i/\hat{\pi}_i$; where w_i is the selection ratio for period i, o_i is the proportion of records in period i and $\hat{\pi}_i$ is the proportion of length in period i to the length of all periods. Values $w_i > 1$ indicate that the period is selectively used more than its availability and values $w_i < 1$ indicate that the period is avoided (Gerber et al. 2012; Bu et al. 2016). Raw and standardized selection ratio was calculated with the R package AdehabitatHS using a design I resource selection function (Calenge 2020), where the selection of periods is considered at the population level (Manly et al. 2002). We used log-likelihood chi-square tests to determine if species used the periods nonrandomly (Manly et al. 2002).

We estimated daily and monthly activity levels of skunks, that is, the proportion of time that animals are active to the maximum possible amount of activity if the animals remained continuously active 100% of the time (Rowcliffe et al. 2014). The activity levels and its 95% confidence intervals (*CI*s) obtained from 1,000 bootstrap samples were calculated with the R package Activity (Rowcliffe 2019). We compared the difference in the activity level estimates between seasons, years, and sampling sites for each species using Wald (W) test implemented in the same package. Comparisons were similarly done to the activity pattern.

Temporal segregation between skunks.—To evaluate temporal segregation of daily and monthly activity between skunk species in both seasons, we estimated the overlap coefficient (Δ) through kernel density (Ridout and Linkie 2009; Linkie and Ridout 2011). This coefficient is defined as the area under the curve formed by taking the minimum of the two density functions at each time unit (Linkie and Ridout 2011) and ranges from 0 (no overlap) to 1 (complete overlap; Ridout and Linkie 2009). Overlap coefficient was obtained using Δ_1 estimator and their 95% *CI*s were calculated by bootstrapping 10,000 samples from the estimated probability density functions of each species (Meredith and Ridout 2020). These analyses were performed with the R package Overlap (Meredith and Ridout 2020). Activity overlap degree was defined at three levels: low ($\Delta \leq 0.50$), moderate ($0.50 < \Delta \leq 0.75$), and high ($\Delta > 0.75$; Monterroso et al. 2014). Finally, we compared the differences in patterns and levels of activity between species for each season using the Mardia–Watson–Wheeler and Wald tests, respectively.

Effect of extrinsic factors on the activity of skunks.—To evaluate the influence of biotic, abiotic, and anthropogenic variables on the activity of skunk species in each season, we used a generalized linear mixed model (GLMM) with Poisson error distribution for daily activity and a binomial GLMM for monthly activity. We defined as response variable the number of independent records by an hour of the skunks' activity period for the first model and the absence (0) or presence (1) of activity on each day for the second model. We used these models based on the total number of records and size of each value of the response variable for both species. The activity of the prey, competitor (only for *S. pygamea*), and native and exotic predators, as well as the ambient temperature, relative humidity, cloud cover, and precipitation, were evaluated in both mixed models. In the second model, the effect of illuminated lunar fraction, night length, and interaction between lunar illumination and cloud cover (to identify how different levels of darkness affect monthly activity) were also analyzed. The explanatory variables were included as fixed effects and the 1-h intervals and sampling months were treated as random effects in the first and second models, respectively. We also included as an offset the trapping effort for each day in the latter model. We tested the collinearity of the set of explanatory variables using Spearman's rank correlation and selected the variables with a low correlation coefficient and the most relevant among highly correlated pairs ($\rho > 0.70$).

We ran biologically plausible candidate models with the R package lme4 (Bates et al. 2020) to determine the variables that best explain the daily and monthly activity of species in each season. Comparison between all candidate models was made using the R package AICcmodavg (Mazerolle 2020) and model selection was based on the Akaike Information Criterion corrected for a small sample size (AICc; Burnham and Anderson 2002; Zuur et al. 2009). We considered that models with ΔAICc (relative difference between the AICc of each model with the best model) < 2 had substantial support and that the variables included in these best models were determinant (Burnham and Anderson 2002). Evidence ratios were used to quantify model parsimony, that is, the amount of support in favor of a model in relation to a competing model, and were computed as the ratio of Akaike weights between the best-ranked model (ω_1) and each of the other candidate models in the set (ω_j; Burnham and Anderson 2002). We checked the data for overdispersion in the full models, accepting dispersion parameter levels between 0.5 and 1.5 (Zuur et al. 2009). All analyses were performed in R software (R Core Team 2020).

RESULTS

We obtained 56 independent records of *C. leuconotus* and 902 records of *S. pygmaea* for analysis of daily activity and 55 records of *C. leuconotus* and 683 records of *S. pygmaea* for analysis of monthly activity, with a cumulative sampling effort of

17,150 trap-nights. Almost 45% and 31% of the total records for *C. leuconotus* and *S. pygmaea* occurred during the 2019 wet season in the disturbance zone. Additionally, we obtained 1,571 records of prey species (mice), 521 records of native predators (*C. latrans* and *L. pardalis*), and 92 records of an exotic predator (*C. l. familiaris*; Supplementary Data SD1).

Activity patterns of skunks.—Daily activity patterns of skunks did not differ between seasons and years and only varied between sites in *S. pygmaea* (Table 1A). The overall daily pattern of *C. leuconotus* ($U_1 = 197.89$, $P < 0.001$) and those of *S. pygmaea*, both in the disturbance zone ($U_1 = 212.32$, $P < 0.001$) and in the protection zone ($U_1 = 214.95$, $P < 0.001$), were not uniform. Both species showed a nonrandom use of the periods (Table 2), started and ceased their activity at twilight, and remained active throughout the night, avoiding daylight hours. *Conepatus leuconotus* exhibited a nocturnal–crepuscular activity, using similarly the nighttime ($X^2_1 = 38.71$, $P < 0.001$) and twilight ($X^2_1 = 6.37$, $P < 0.01$) more than expected, with maximum activity from 22:30 to 00:30 and from 02:30 to 04:30 (Fig. 2A). Meanwhile, *S. pygmaea* predominantly selected the nighttime at both sites but also used the crepuscular hours more than expected in the disturbance zone ($X^2_1 = 15.63$, $P < 0.001$) and in proportion to its availability in the protection zone ($X^2_1 = 2.59$, $P = 0.18$). The highest activity levels of *S. pygmaea* occurred between 20:00 and 23:00 and between 03:00 and 05:00 in the disturbance zone, while they were from 19:30 to 20:30, from 21:00 to 23:00, and from 03:30 to 05:30 in the protection zone (Fig. 2B).

Monthly activity patterns of skunk species showed significant differences between seasons (Table 1B) and were not uniform both for *C. leuconotus* ($P < 0.001$) and for *S. pygmaea* ($P < 0.001$). *Conepatus leuconotus* presented its activity peaks at starting and end of the dry season with a notable decrease between February and April, while it was continuously active during the wet season (Fig. 3). On the other hand, *S. pygmaea* exhibited continuous activity in both seasons, but it decreased slightly from March to May during the dry season and showed maximum activity by the end of the wet season (Fig. 3).

Daily and monthly activity levels were variable and differed between seasons, years, or sites, except for the daily level of *C. leuconotus* (0.40, $CI = 0.27–0.45$; Table 1A). Hog-nosed skunks exhibited different monthly activity levels between years ($W_1 = 4.34$, $P = 0.04$; Table 1B), and was more active with 0.55 ($CI = 0.31–0.60$) in 2019 compared to 0.32 ($CI = 0.13–0.45$) in 2020. In contrast, daily activity levels of *S. pygmaea* varied between sites ($W_1 = 6.22$, $P = 0.01$; Table 1A), with greater activity in the disturbance zone with 0.39 ($CI = 0.34–0.42$) than in the protection zone with 0.29 ($CI = 0.23–0.36$). Pygmy skunks also showed differences in monthly activity levels between seasons ($W_1 = 45.65$, $P < 0.001$; Table 1B) and were more active during the dry season with 0.51 ($CI = 0.42–0.54$) than during the wet season with 0.24 ($CI = 0.21–0.28$).

Temporal segregation between skunks.—Daily and monthly activity of *C. leuconotus* and *S. pygmaea* showed a moderate to high overlap and did not differ significantly in either season (Fig. 4). The daily patterns of both skunks overlapped to a high degree in the dry season ($\Delta_1 = 0.78$, $CI = 0.68–0.90$; $W_2 = 3.04$, $P = 0.22$) and in the wet season ($\Delta_1 = 0.81$, $CI = 0.73–0.92$; $W_2 = 2.34$, $P = 0.31$). On the other hand, the overlap of the monthly patterns between these species was moderate during the dry season ($\Delta_1 = 0.71$, $CI = 0.56–0.85$; $W_2 = 3.66$, $P = 0.16$) and it was high during the wet season ($\Delta_1 = 0.77$, $CI = 0.66–0.89$; $W_2 = 0.94$, $P = 0.62$).

Daily activity levels of skunk species were similar in the dry season (0.37, $CI = 0.22–0.44$ for *C. leuconotus*; 0.37, $CI = 0.31–0.41$ for *S. pygmaea*; $W_1 = 0.003$, $P = 0.95$) and in the wet season (0.35, $CI = 0.20–0.42$ for *C. leuconotus*; 0.40, $CI = 0.33–0.42$ for *S. pygmaea*; $W_1 = 0.50$, $P = 0.48$). In contrast, monthly activity levels between skunks were different during the dry season ($W_1 = 8.92$, $P = 0.002$) and wet season ($W_1 = 10.09$, $P = 0.001$). *Conepatus leuconotus* was less active than *S. pygmaea* in the dry season (0.32, $CI = 0.16–0.37$; 0.51, $CI = 0.42–0.54$), but it was more active during the rainy season (0.40, $CI = 0.23–0.40$; 0.24, $CI = 0.21–0.28$; respectively).

Additionally, we evaluated whether the daily and monthly activity of *S. pygmaea* differed between the disturbance zone

Table 1.—Comparisons between two skunk species of differences in the daily (A) and monthly (B) activity patterns and levels between seasons, years, and study sites in the deciduous tropical forest at Huatulco National Park (HNP), Oaxaca, Mexico. Statistic values of the Mardia–Watson–Wheeler (*W*) or Watson (U^2) tests and the Wald test with their significance levels (*P*) are shown.

Comparisons	*Conepatus leuconotus*				*Spilogale pygmaea*			
	$W/U^2_{\text{d.f.}}$	*P*	$\text{Wald}_{\text{d.f.}}$	*P*	$W_{\text{d.f.}}$	*P*	$\text{Wald}_{\text{d.f.}}$	*P*
A. Daily activity								
Seasons								
Dry vs. wet	5.53_2	0.06	0.05_1	0.82	0.30_2	0.86	0.70_1	0.40
Years								
2019 vs. 2020	3.20_2	0.20	0.74_1	0.39	2.30_2	0.31	0.55_1	0.46
Sites[a]								
PZ vs. DZ	0.18_2	>0.05	1.64_1	0.20	7.17_2	0.03	6.22_1	0.01
B. Monthly activity								
Seasons								
Dry vs. wet	39.96_2	<0.001	1.34_1	0.25	284.60_2	<0.001	45.65_1	<0.001
Years								
2019–2020	—	—	4.34_1	0.04	—	—	—	—

[a] Comparison between protection zone (PZ) and disturbance zone (DZ).

Table 2.—Raw and standardized selection ratios and tests of random use of the time periods given their availability by skunk species within the deciduous tropical forest at Huatulco National Park (HNP), Oaxaca, Mexico.

Species[a,b]	Periods[c,d]			Random use test[e]	*P*
Conepatus leuconotus	Crepuscular –	Nocturnal >>	Diurnal	79.49	<0.001
Use (%)	25.0	75.0	0.0		
Availability (%)	10.4	39.0	50.6		
Selection ratio	2.40	1.92	0.0		
Standard selection ratio	0.56	0.44	0.0		
Spilogale pygmaea (PZ)	Nocturnal >>	Crepuscular >>	Diurnal	302.53	<0.001
Use (%)	85.7	14.3	0.0		
Availability (%)	39.0	10.4	50.6		
Selection ratio	2.20	1.37*	0.0		
Standard selection ratio	0.62	0.38	0.0		
Spilogale pygmaea (DZ)	Nocturnal >>	Crepuscular >>	Diurnal	987.86	<0.001
Use (%)	84.1	15.9	0.0		
Availability (%)	39.0	10.4	50.6		
Selection ratio	2.16	1.53	0.0		
Standard selection ratio	0.59	0.41	0.0		

[a] Protection zone (PZ) and disturbance zone (DZ).

[b] Standardized selection ratio is the probability that an animal selects one time period over the others, assuming that all periods are equally available (Manly et al. 2002).

[c] Periods ranked from most to least preferred, a dash (–) indicates a nonsignificant difference between two periods and >> indicates a significant difference ($P \leq 0.05$).

[d] An asterisk (*) indicates when the selection ratio is not statistically different than 1, that is, use is proportional to their availability.

[e] Log-likelihood chi-square test of random use of periods, where a significant *P*-value indicates nonrandom use of time.

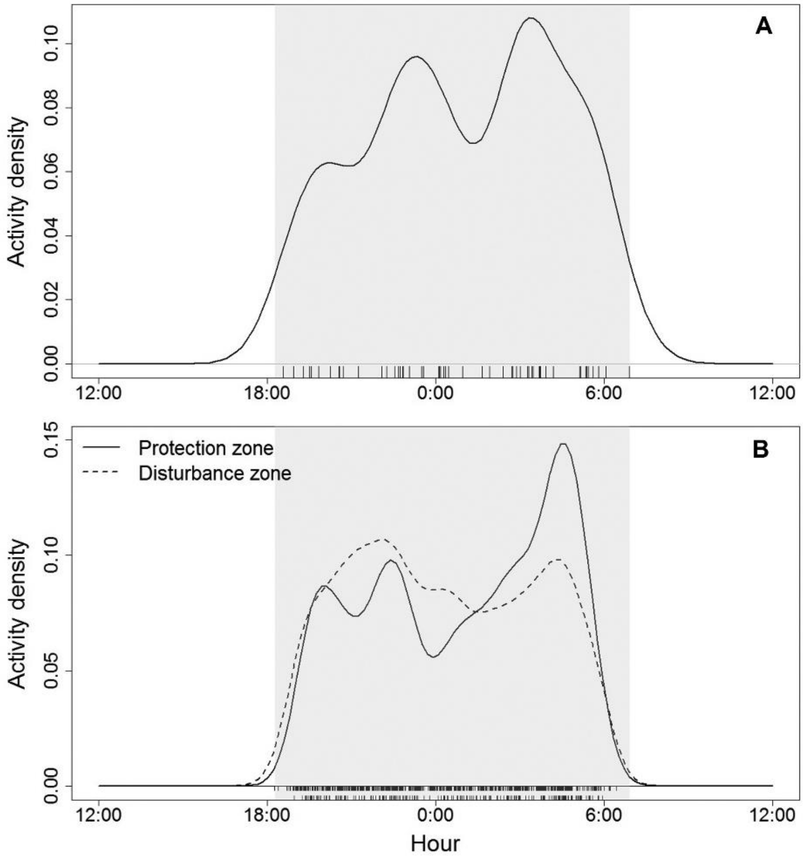

Fig. 2.—Daily activity patterns of *Conepatus leuconotus* (A) and *Spilogale pygmaea* (B) in the deciduous tropical forest at Huatulco National Park (HNP), Oaxaca, Mexico, from November 2018 to October 2020. The shaded area indicates the period of time between sunset and sunrise. The time of the activity records is shown as ticks on the x-axis.

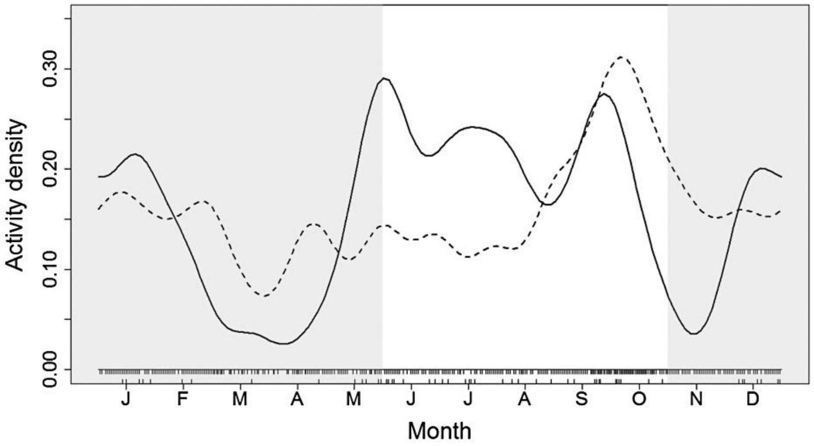

Fig. 3.—Monthly activity patterns of *Conepatus leuconotus* (solid line) and *Spilogale pygmaea* (dashed line) in the deciduous tropical forest at Huatulco National Park (HNP), Oaxaca, Mexico, from November 2018 to October 2020. The shaded area indicates the dry season. The date of the activity records is shown as ticks on the x-axis.

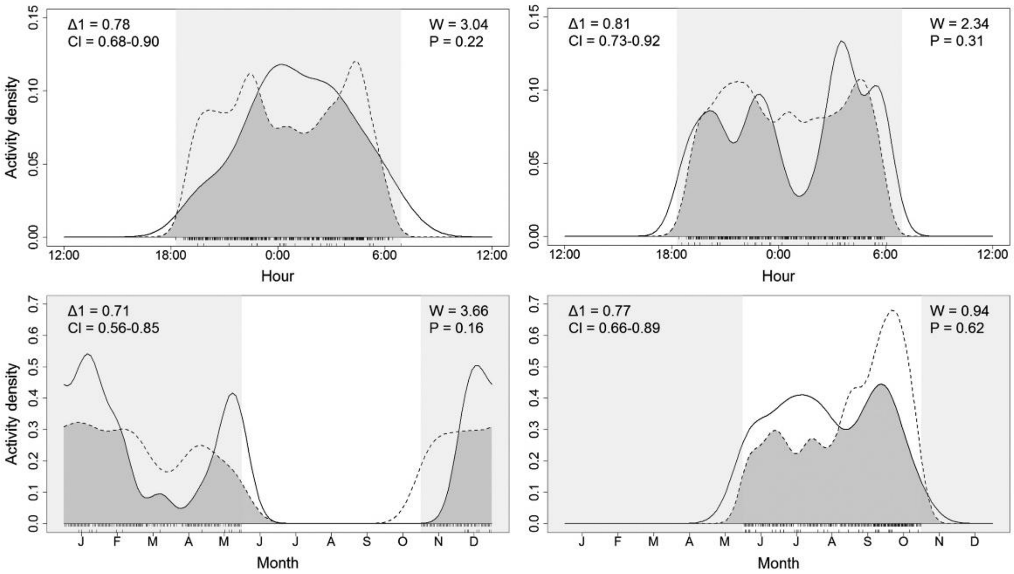

Fig. 4.—Overlap of daily (top) and monthly (bottom) activity patterns between *Conepatus leuconotus* (solid line) and *Spilogale pygmaea* (dashed line) during the dry and wet seasons in the deciduous tropical forest at Huatulco National Park (HNP), Oaxaca, Mexico. The overlap is represented by the gray shaded area. The period of time between sunset and sunrise and the dry season is represented by the light-gray shaded area as appropriate.

where there were more records of *C. leuconotus* and the protection zone where *C. leuconotus* was uncommon. *Spilogale pygmaea* showed differences in daily (W_2 = 6.22, P = 0.01) and monthly (W_2 = 14.42, P < 0.001) patterns between sampling sites. Daily and monthly activity patterns of the pygmy skunks observed at protection zone were more similar to that of the hog-nosed skunks (W_2 = 0.35, P = 0.84; W_2 = 1.32, P = 0.52) than at the disturbance zone (W_2 = 3.24, P = 0.20; W_2 = 3.37, P = 0.18, respectively), where they occur in sympatry (Supplementary Data SD2).

Effect of extrinsic factors on the activity of skunks.—In seven of the eight sets of GLMMs evaluated to explain the daily and monthly activity of skunk species in each season, only the top model showed a ΔAICc < 2 with weight from 0.70 to 1.0 (Table 3). Among the GLMMs that explained the daily activity of *C. leuconotus* in the dry season, the null model (including only the random effect) was the second best-supported model but the top model was significantly better (likelihood ratio test—LRT χ^2 = 6.03, P = 0.049). All the best models included at least one fixed effect (Table 3).

Table 3.—Candidate mixed models evaluated to determine the variables that best explained the daily (A) and monthly (B) activity of skunk species for each season within the deciduous tropical forest at Huatulco National Park (HNP), Oaxaca, Mexico.

Species	Dry season						Wet season					
	Candidate models	*K*	AICc	ΔAICc	ω	Evidence ratio	Candidate models	*K*	AICc	ΔAICc	ω	Evidence ratio
A. Daily activity												
Conepatus leuconotus	Humidity + Native predators	4	69.28	0.00	0.5562	1.00	Precipitation + Prey	4	81.27	0.00	0.8981	1.00
	Null	2	69.94	0.65	0.4015	1.39	Prey + Native predators + Exotic predator	5	85.98	4.71	0.0852	10.54
	Prey + Native predators + Exotic predator	5	75.36	6.08	0.0266	20.91	Null	2	89.65	8.37	0.0136	66.04
	Temperature + Humidity + Precipitation	5	76.68	7.39	0.0138	40.30	Humidity + Precipitation + Cloud cover	5	93.15	11.88	0.0024	374.21
	Full	8	80.72	11.44	1.83E−03	303.93	Full	8	95.66	14.39	6.74E−04	1332.49
Spilogale pygmaea	Competitor + Prey + Native predators	5	185.65	0.00	0.8431	1.00	Precipitation + Cloud cover + Prey + Exotic predator	6	159.67	0.00	0.9943	1.00
	Competitor + Prey + Native predators + Exotic predator	6	189.02	3.37	0.1564	5.39	Full	9	170.00	10.33	5.68E−03	175.05
	Full	9	201.27	15.62	3.42E−04	2465.20	Competitor + Prey + Native predators + Exotic predator	6	191.71	32.04	1.10E−07	9.04E+06
	Temperature + Humidity + Precipitation	5	202.99	17.33	1.45E−04	5814.48	Humidity + Precipitation + Cloud cover	5	237.49	77.82	1.26E−17	7.90E+16
	Null	2	288.91	103.25	3.20E−23	2.64E+22	Null	2	418.68	259.01	5.67E−57	1.75E+56
B. Monthly activity												
Conepatus leuconotus	Cloud cover	3	166.41	0.00	0.7667	1.00	Cloud cover + Precipitation	4	175.67	0.00	0.7671	1.00
	Null	2	168.93	2.52	0.2172	3.53	Null	2	178.57	2.90	0.1802	4.26
	Prey + Native predators + Exotic predator	5	174.83	8.42	0.0114	67.25	Humidity + Precipitation + Night length + Cloud cover * Lunar illumination	8	181.91	6.24	0.0338	22.69
	Temperature + Humidity + Precipitation + Night length + Cloud cover * Lunar illumination	9	176.66	10.26	0.0045	170.37	Prey + Native predator + Exotic predator	5	183.37	7.70	0.0163	47.06
	Full	12	182.65	16.24	2.28E−04	3362.72	Full	11	187.08	11.41	2.56E−03	299.65
Spilogale pygmaea	Prey + Exotic predator	4	516.15	0.00	0.7001	1.00	Night length + Cloud cover + Prey	5	248.19	0.00	0.9963	1.00
	Null	2	519.03	2.88	0.1660	4.22	Full	12	259.43	11.25	0.0036	276.75
	Competitor + Prey + Native predators + Exotic predator	6	519.52	3.37	0.1298	5.39	Competitor + Prey + Native predators + Exotic predator	6	266.78	18.59	9.14E−05	1.09E+04
	Temperature + Humidity + Precipitation + Night length + Cloud cover * Lunar illumination	9	527.10	10.95	0.0029	241.41	Humidity + Precipitation + Night length + Cloud cover * Lunar illumination	8	268.26	20.07	4.36E−05	2.28E+04
	Full	13	528.87	12.72	1.21E−03	578.59	Null	2	280.00	31.82	1.23E−07	8.10E+06

K = number of parameters; AICc = Akaike Information Criterion corrected for small samples; ΔAICc = relative difference between the AICc of each model with the best model; ω = model weight. Interactions between variables are represented by *.

According to the parameters estimates in the best-fitting mixed models for daily activity, the records number of *C. leuconotus* was positively associated with relative humidity ($\beta = 0.81$, $P = 0.05$) and native predators ($\beta = 0.59$, $P = 0.03$) in the dry season and with precipitation ($\beta = 0.34$, $P = 0.04$) and prey ($\beta = 0.67$, $P = 0.002$) in the wet season (Table 4A). Meanwhile, the best-fitting models for *S. pygmaea* activity showed that the dominant competitor ($\beta = 0.17$, $P = 0.02$), prey ($\beta = 0.56$, $P < 0.001$), and native predators ($\beta = 0.18$, $P = 0.005$) in the dry season and precipitation ($\beta = 0.42$, $P < 0.001$) and prey ($\beta = 0.92$, $P < 0.001$) in the wet season were positively associated with the records of this species (Table 4A). Cloud cover ($\beta = -0.40$, $P < 0.001$) and exotic predator ($\beta = -0.19$, $P = 0.001$) also had a significant but negative effect on daily activity of *S. pygmaea* in the wet season.

The best-fitting mixed models for the monthly activity of species indicated that the presence of *C. leuconotus* activity was positively associated with cloud cover in the dry ($\beta = 0.41$, $P = 0.02$) and wet season ($\beta = 0.43$, $P = 0.05$; Table 4B). The presence of *S. pygmaea* activity was positively associated with prey ($\beta = 0.20$, $P = 0.06$) and negatively with the exotic predator ($\beta = -0.21$, $P = 0.11$) in the dry season, although the relationship was not significant. The best-fitting model for *S. pygmaea* activity in the wet season revealed that night length ($\beta = 0.51$, $P < 0.001$) and prey ($\beta = 0.65$, $P < 0.001$) had a positive effect, while cloud cover ($\beta = -0.51$, $P < 0.001$) had a negative effect on activity presence of this species (Table 4B).

DISCUSSION

Activity patterns of skunks.—Information on the activity of *C. leuconotus* and *S. pygmaea* is scarce compared to other species of the same genera, which have received greater attention in North and South America (Neiswenter et al. 2010; Cavalcanti et al. 2014; Castillo et al. 2015; Dias 2017; Benson et al. 2019). Our findings present the first detailed description of the *S. pygmaea* daily and seasonal patterns, with a large sample size that allowed inference about temporal and spatial variation. Both species of skunks predominantly selected the nocturnal and crepuscular period ($w_i > 1$), with strong avoidance of daytime. This overall pattern is consistent with that recorded for these species (Buenrostro-Silva et al. 2015; Pérez-Irineo et al. 2020; Farías-González and Hernández-Mendoza 2021) and other skunks in dry forests regions, including *S. angustifrons* in Mexico (Farías-González and Vega-Flores 2019; Pérez-Irineo et al. 2020) and the striped hog-nosed skunk *C. semistriatus* in Brazil (Cavalcanti et al. 2014; Dias 2017; Marinho et al. 2020). However, unlike the daily activity patterns and levels observed in previous research (Cochran 2012; Buenrostro-Silva et al. 2015), *C. leuconotus* and *S. pygmaea* remained continuously active during the night and exhibited uni-, bi-, or multimodal patterns depending on the season, year, or study site. These results suggest that both species exhibited behavioral plasticity that allowed them to shift their activity within the preferred period, probably in response to changing environmental and ecological stimuli (Halle 2000; Pita et al. 2011; Monterroso et al. 2014; Gaston 2019).

Our study revealed important seasonal differences in the monthly activity patterns of both species, with more continuous and greater activity in the wet season in the deciduous tropical forest at the PNH. This variation in activity may indicate that skunks exhibit behavioral adaptations similar to those of other mammals to deal with environments of marked seasonality (Pita et al. 2011; Stoner and Timm 2011; Quaglietta et al. 2018). Behavioral adjustments due to seasonal changes are facilitated by the photoperiod (Halle 2000; Kronfeld-Schor and Dayan 2003), which could allow these species their correct synchronization with this tropical environment. Although monthly activity has generally not been addressed in seasonal patterns, some studies also document activity switching between seasons for skunk species in semiarid and temperate regions, observing greater activity during the warm or spring–summer months (Lariviere and Messier 1997; Neiswenter et al. al. 2010; Castillo et al. 2015). However, this variation

Table 4.—Parameter estimates for the best-fitting mixed-effects models for the daily (A) and monthly (B) activity of skunk species in each season within the deciduous tropical forest at Huatulco National Park (HNP), Oaxaca, Mexico.

Species	Dry season					Wet season				
	Variable	β	*SE*	*Z*-value	*P*-value	Variable	β	*SE*	*Z*-value	*P*-value
A. Daily activity										
Conepatus leuconotus	Intercept	-0.39	0.32	-1.22	0.22	Intercept	-0.12	0.27	-0.43	0.66
	Relative humidity	0.81	0.42	1.95	0.05	Precipitation	0.35	0.17	2.04	0.04
	Native predators	0.59	0.28	2.13	0.03	Prey	0.67	0.21	3.18	0.002
Spilogale pygmaea	Intercept	2.57	0.09	29.89	<0.001	Intercept	2.42	0.08	30.36	<0.001
	Competitor	0.17	0.07	2.39	0.02	Precipitation	0.42	0.05	8.31	<0.001
	Prey	0.56	0.08	7.21	<0.001	Cloud cover	-0.40	0.09	-4.54	<0.001
	Native predators	0.18	0.06	2.80	0.005	Prey	0.92	0.06	14.32	<0.001
						Exotic predator	-0.19	0.06	-3.27	0.001
B. Monthly activity										
Conepatus leuconotus	Intercept	-6.32	0.36	-17.71	<0.001	Intercept	-5.54	0.30	-18.29	<0.001
	Cloud cover	0.41	0.18	2.24	0.03	Cloud cover	0.43	0.22	1.97	0.05
						Precipitation	-1.36	0.98	-1.39	0.17
Spilogale pygmaea	Intercept	-2.94	0.12	-24.45	<0.001	Intercept	-2.66	0.15	-17.59	<0.001
	Prey	0.20	0.11	1.84	0.07	Night length	0.51	0.14	3.55	<0.001
	Exotic predator	-0.21	0.13	-1.60	0.11	Cloud cover	-0.51	0.15	-3.33	<0.001
						Prey	0.65	0.19	3.41	<0.001

has been attributed to the mating season of species (Lariviere and Messier 1997; Castillo et al. 2015). Our data showed that *C. leuconotus* was less active from mid-February through mid-May and *S. pygmaea* from late March to July, periods when both species are breeding and birthing (Medellín et al. 1998; Dragoo and Sheffield 2009). These results, therefore, suggest that for both species the mating season does not significantly affect the monthly patterns and levels of activity in the study area, as has also been observed for *C. leuconotus* in Texas (Cochran 2012).

Furthermore, the daily and monthly activity levels of the two skunks were heterogeneous and differed either between seasons, years, or sites. Consistent with our findings, *S. pygmaea* showed a seasonal variation in its monthly activity levels, remaining active longer in the drought months in the study area. This result could be explained by temporal and spatial variation in resource availability. During the dry season, litter arthropods are two to three times less abundant and 30% more dispersed (Valenzuela and Macdonald 2002), in addition to the fact that water becomes restricted to a small waterhole within the protected area (personal observation), so presumably, these species require longer foraging times to obtain sufficient resources. Similar patterns also occur in other mammals in dry forest areas (Stoner and Timm 2011). On the other hand, although the activity levels between years and between sites may have been altered by an uneven sampling effort as a consequence of restricted access to the HNP due to the health emergency in 2020 and the theft and removal of camera traps at the protection zone, respectively, we consider that it did not influence the overall pattern of the data since the sample size of each analyzed data set was not directly proportional to the displayed sampling effort.

Temporal partitioning between skunks.—Shifts in activity patterns of ecologically similar species may be driven by interspecific competition and temporal niche partitioning can decrease this competition and facilitate the coexistence among potential competitors (Carothers and Jaksic 1984; Kronfeld-Schor and Dayan 2003). Following our predictions, we observed partial segregation of activity patterns between *C. leuconotus* and *S. pygmaea* in the deciduous tropical forest at HNP. Both species showed similar activity patterns with moderate to high overlap but exhibited asynchronous peaks of activity and different monthly activity levels that consistently alternated between coexisting skunks across the seasons. In particular, *S. pygmaea* showed its periods of greatest activity or was more seasonally active when the activity of *C. leuconotus* decreased. In cases when competition is asymmetric, the subordinate or smaller-sized species adjusts its behavior to avoid agonistic interactions with the dominant or larger-sized competitor (Polis et al. 1989; Palomares and Caro 1999). Our results, thus, suggest that *S. pygmaea* adopts temporal avoidance to reduce the potential for direct encounters with *C. leuconotus* at the study area. Other studies have also recorded temporal segregation between sympatric skunks (Neiswenter et al. 2010; Farías-González and Hernández-Mendoza 2021) and between small-to-medium mammal species (e.g., Pita et al. 2011; Monterroso et al. 2014), showing that shifts in the activity of subordinate species facilitate their coexistence with the dominant competitor. Additionally, the activity pattern of *S. pygmaea* at the protection zone, where *C. leuconotus* was rarely recorded, was different from that observed at the disturbance zone but was more similar to the pattern of *C. leuconotus*, which was recorded more frequently in the latter zone. This adds support for the hypothesis that pygmy skunks adjust their temporal niche when in sympatry with American hog-nosed skunks.

Most agonistic encounters between potential competitors in seasonal environments occur when food is scarce (Palomares and Caro 1999; Stoner and Timm 2011); consequently, we predicted that temporal segregation among skunks would be greater in the dry season at HNP. Overall, there was a more marked differentiation of activity peaks and relatively less activity overlap during the dry season than wet season, where the daily and monthly patterns of species overlapped slightly more (Fig. 4). In contrast to what might be expected, we did not find significant variations in niche segregation between seasons. This could be largely explained by the possible dietary flexibility of these skunks and the high availability of food resources. Both species adjust food resource use in response to seasonal fluctuations in prey abundance and may consume small mammals as alternative prey when insect availability is low (Cantú-Salazar et al. 2005; Dragoo and Sheffield 2009). Rodents, such as the spiny pocket mouse *Heteromys pictus*, are nocturnal and abundant in both seasons at the study area (unpublished data), so skunks were able to incorporate this prey item into their diet. The daily and monthly activity, mainly of *S. pygmaea*, was influenced by that of mice (Table 4). Most likely, these factors minimized competition and allowed the skunks to maintain a constant overlap of activity. Other species such as *M. mephitis* and *S. gracilis* also exhibit similar activity during the summer, when resources are most abundant in Texas (Neiswenter et al. 2010). Our study provides evidence that coexistence between *C. leuconotus* and *S. pygmaea* may occur through a trade-off between maximizing foraging efficiency and reducing the chances of negative encounters in both seasons.

Effect of extrinsic factors on the activity of skunks.—Although we observed temporal niche segregation among skunks, our alternative hypothesis was also true. The activity patterns of species were determined by extrinsic factors such as the activity of native and exotic predators and some abiotic stimuli, all with a relatively high weight of evidence. However, these factors differently affected the daily and monthly activity of skunks and its effect varied between seasons, indicating some behavioral plasticity of species in response to changing ecological and environmental stimuli.

The Mephitidae co-occur with more potential predators than members of other families (Hunter and Caro 2008) and the predators may be more active during the nighttime and twilight in warm environments to avoid severe weather conditions (Monterroso et al. 2014; Marinho et al. 2020). Skunks, therefore, have a potentially high predation risk but may avoid it by using noxious anal secretions (Hunter and Caro 2008; Allen

et al. 2016). The effectiveness of this antipredator defense mechanism would allow both skunks to be active at the same hours as *L. pardalis* and *C. latrans* during the drought months in the deciduous tropical forest at the study area. In contrast, the daily activity of *C. l. familiaris* had a negative effect on that of *S. pygmaea* in the wet season. Feral dogs are crepuscular–diurnal at HNP (Guzmán Pacheco 2019) and our data confirmed high activity at dawn during this season. This could indicate that pygmy skunks shift their activity in this period since they are susceptible to predation by *C. familiaris* as has been observed with other skunks in recent studies (Carrasco-Román et al. 2021). The presence and activity of exotic species affect the dynamics of intraguild interactions (Gerber et al. 2012; Frey et al. 2017), resulting in shifts in the activity of native species such as skunks and that in turn could alter temporal niche partitioning, with negative effects on their coexistence in the study area.

Our study also revealed that humidity and precipitation, factors associated with the typical climatic seasonality of dry forests, contributed to explaining the daily and monthly activity of skunks. *Conepatus leuconotus* exhibited seasonal changes in their daily activity related to the variation in relative humidity. Their unimodal pattern at the hours of the night with higher humidity during the dry season possibly reflected a behavioral thermoregulation strategy to minimize physiologically stressful conditions, such as water loss. Some authors have also suggested that the activity pattern of *C. semistriatus* is associated with thermoregulatory restrictions in semiarid ecosystems (Cavalcanti et al. 2014; Dias 2017). Data show that relative humidity has a direct influence on the temporal patterns of these animals in warm subhumid climates such as that of the study area since it is dealing with the lowest humidity subtype. Precipitation varies strongly between seasons, which generates profound changes in the phenology of plants and food resource availability (Lister and García 1992; Valenzuela and Macdonald 2002; Trejo 2010). Most likely, the skunks adjusted their daily activity to the high abundance of insects during the wet season, and this resulted in a positive and significant association. Both species showed a bimodal pattern this season, with an activity maximum after dusk and another before dawn, possibly reflecting bouts of bulk feeding of insects, similar to some small mammals (Diete et al. 2017). We speculated that the monthly activity of both skunks could also be explained by precipitation—peaking sharply in June and September, months when the highest rainfall and abundance of insects occur in seasonally dry forest regions (Lister and García 1992; CONANP 2003).

Other abiotic factors that explained skunk activity patterns were cloud cover and night length. Cloud cover had an opposite effect on activity, either daily or monthly, of each species—positive for *C. leuconotus* and negative for *S. pygmaea*. We attributed this effect to a response of skunks to the risk of predation and competition. The contrasting aposematic coloration of skunks stands out when viewed in low-light conditions (Hunter and Caro 2008). Therefore, cloudier nights may help maximize the effectiveness of this warning signal in *C. leuconotus*, as it is more detectable by predators due to its larger body size. Increased activity during those nights has been predicted to potentially lower the risk of predation (Stokes et al. 2001). In addition, the effect of cloud cover was more significant in the dry season (Table 4B), which is reasonable because the fall of leaves in most of the dry forest vegetation generates an inherent increase in visibility due to the lack of shade (personal observation). Conversely, *S. pygmaea* was less likely to be active in cloudy hours and nights during the wet season at HNP, which was probably due to pygmy skunks adopting a temporal avoidance strategy to decrease the interference of the dominant competitor in cloudy conditions. Activity during suboptimal times such as those with the highest predation risk may incur physical fitness costs (Frey et al. 2017), as could occur in *S. pygmaea*, since it becomes risk-prone by being active in periods of less cloudiness. Behavioral risk-taking decisions vary in response to the perceived threat levels by each species (Halle 2000; Kronfeld-Schor and Dayan 2003), and possibly these decisions allowed both skunks to coexist along the time niche axis. Finally, *S. pygmaea* was also more active on long nights in September and October, suggesting that the species was able to adjust its activity to maximize food acquisition in the wet season. Consequently, nighttime length is of general importance in this species (Gaston 2019).

This camera-trap study is one of the few investigations that has evaluated the temporal patterns in sympatric skunks (Neiswenter et al. 2010; Cochran 2012; Farías-González and Hernández-Mendoza 2021) and the effects of interspecific competition and other biotic, abiotic, and anthropogenic factors on species activity. We showed that multiple extrinsic factors play an important role in shaping activity patterns of both skunks and affect their temporal niches partitioning, possibly promoting coexistence in a seasonal tropical forest. In addition, the analysis of monthly activity with a seasonal approach allowed us to understand even more the time niche axis segregation and the factors that explain temporal patterns at this level since although skunks can be active in the same hours within the preferred period, it does not necessarily mean that they maintain the same activity timing and level every day. This approach has been considered an alternative for niche partitioning based on lability of the temporal activity of species, but it remains little explored for most animals and its role in enhancing species coexistence is unknown (Pita et al. 2011; Gaston 2019). Therefore, future studies on temporal niche partitioning should consider several factors simultaneously with a seasonal perspective to identify the responsible drivers that govern both daily and monthly activity patterns and improve understanding of the coexistence of sympatric species.

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Number of independent records per hour (daily activity) and per day (monthly activity) of skunk species and their prey and predators during the dry and wet seasons in the protection (PZ) and disturbance (DZ) zones within the deciduous tropical forest at Huatulco National Park (HNP), Oaxaca, Mexico, from November 2018 to October 2020.

Supplementary Data SD2.—Daily (A) and monthly (B) activity patterns of *Spilogale pygmaea* at the site without (protection zone) and with (disturbance zone) *Conepatus leuconotus* in the deciduous tropical forest at Huatulco National Park (HNP), Oaxaca, Mexico. The time between sunset and sunrise and the dry season is represented by the shaded area as appropriate. The time or date of the activity records is shown as ticks on the x-axis as appropriate.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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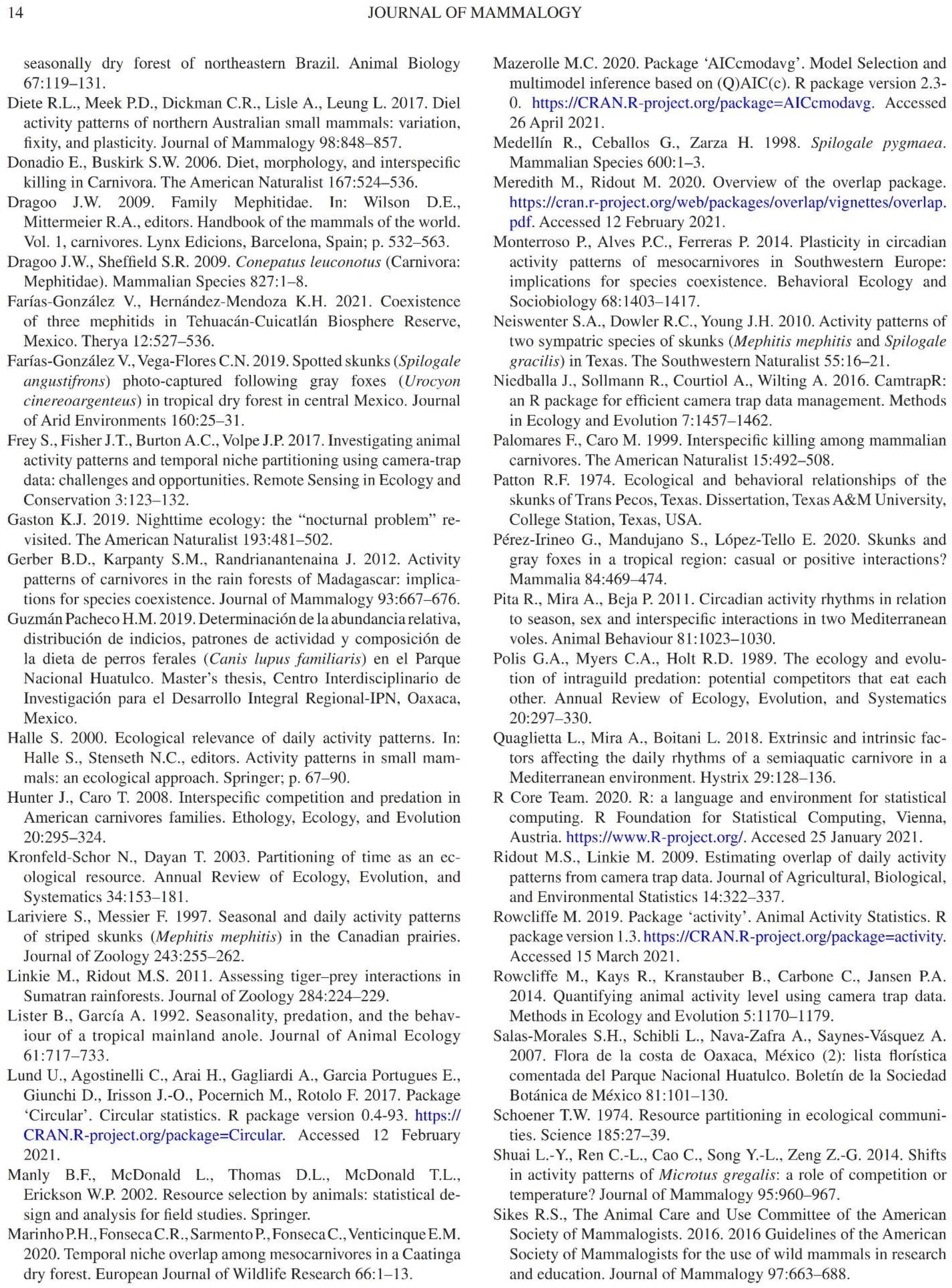

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CAPÍTULO IV

DINÁMICA DE OCUPACIÓN Y PATRONES DE CO-OCURRENCIA DE DOS ESPECIES DE ZORRILLOS EN UN BOSQUE TROPICAL CADUCIFOLIO EN EL SURESTE MEXICANO

Resúmen

La competencia interespecífica puede conducir a la segregación espacial entre varios pares de carnívoros coexistentes. Sin embargo, generalemente es difícil distinguir la diferencia entre las preferencias de hábitat y las exclusiones competitivas cuando se estudian los patrones de co-ocurrencia de especies. Hasta la fecha se ha prestado poca atención a la co-ocurrencia espacial de zorrillos simpátricos en regiones tropicales, donde a menudo co-ocurren más de dos especies. En este estudio evaluamos el papel de las interacciones entre especies junto con características del hábitat y factores antropogénicos en el uso del hábitat de *Conepatus leuconotus* y *Spilogale pygmaea* en un bosque tropical caducifolio en buen estado de conservación en el sureste de México. Estimamos las probabilidades de ocupación y de co-ocurrencia de las especies a lo largo del tiempo utilizando un enfoque basado en la Máxima Verosímilitud, mientras se consideraba explícitamente la detectabilidad imperfecta. Nuestros resultados mostraron que la distancia a la fuente de agua más cercana, la disponibilidad de mamíferos pequeños y la humedad del suelo fueron las variables más importantes que influyeron en el uso de hábitat de las especies de zorrillos. La cobertura arbustiva y el número de madrigueras también explicaron la probabilidad de extinción al menos para *S. pygmaea*. La probabilidad de ocupación de ambas especies aumentó durante las temporadas muestreadas, pero fue mayor en *S. pygmaea*. No hubo evidencia de que *C. leuconotus* afectara las probabilidades de ocupación y de detección de *S. pygmaea*, ambas especies co-ocurren y se detectan de manera independiente durante el período de estudio. Este estudio revela que los factores relacionados principalmente con la disponibilidad de recursos determinan los patrones de uso de hábitat de *C. leuconotus* y *S. pygmaea* en lugar de la competencia intragremio en el bosque tropical caducifolio del Parque Nacional Huatulco, en el sureste mexicano.

Palabras clave: *Conepatus leuconotus*, disponibilidad de recursos, modelos dinámicos, Parque Nacional Huatulco, *Spilogale pygmaea*.

Introducción

Comprender cómo coexisten especies con requerimientos ecológicos similares y qué factores influencian su distribución son intereses centrales en la ecología de comunidades (Morin 1999; Guisan y Thuiller 2005). Las interacciones interespecíficas, como la competencia, tienen el potencial de dar forma a los nichos ecológicos de las especies, lo que puede afectar su ocurrencia y distribución y, por lo tanto, limitar o promover la coexistencia entre ellas (Schoener 1982; Morin 1999; Chesson y Kuang 2008). Las especies competidoras pueden dividir los recursos en uno o más ejes principales de nicho (espacio, alimento y tiempo) para reducir el riesgo de encuentros directos y de este modo, coexistir a través de la diferenciación de nicho (Schoener 1974; HilleRisLambers et al. 2012). Las interacciones de las especies a menudo son difíciles de observar directamente en la naturaleza, pero se pueden inferir de los patrones de co-ocurrencia, i.e. presencia conjunta de especies (Hastings 1987; Morales-Castilla et al. 2015; MacKenzie et al. 2018). El estudio de estos patrones generalmente ayuda a conocer los mecanismos subyacentes por los cuales las especies pueden o no coexistir, incluida la partición de nicho (MacKenzie et al. 2018).

Los mamíferos del orden Carnivora son un grupo ideal para evaluar el grado en que las especies simpátricas co-ocurren en el espacio, ya que exhiben una similitud morfológica y ecológica alta (Gompper et al. 2016; Nagy-Reis et al. 2017). La competencia interespecífica puede conducir al uso diferencial del espacio en varios pares de especies de carnívoros coexistentes (Palomares y Caro 1999; Donadio y Buskirk 2006). Esta interacción es más evidente entre especies con diferencias en el tamaño corporal, donde el miembro de mayor talla a menudo determina la dinámica intragremial (Palomares y Caro 1999; Donadio y Buskirk 2006; Hunter y Caro 2008). Sin embargo, aunque las interacciones interespecíficas tienen el potencial de estructurar los ensamblajes de carnívoros, las características del hábitat y los factores antropogénicos también pueden ser impulsores fuertes de los patrones de co-ocurrencia de especies competidoras (Lesmeister et al. 2015; Gompper et al. 2016; Nagy-Reis et al. 2017; Easter et al. 2021). Por lo tanto, es necesario evaluar simultáneamente las interacciones de las especies con las asociaciones del hábitat y las presiones antropogénicas para comprender cómo los carnívoros coexisten espacialmente y determinar sí un competidor dominante excluye o limita el uso de hábitat del competidor subordinado (Gompper et al. 2016; Nagy-Reis et al. 2017; Easter et al. 2021).

A pesar de que hay evidencia suficiente que las interacciones entre especies están muy extendidas en el orden Carnivora, la dinámica intragremio no ha sido clara en carnívoros de talla pequeña y media (Nagy-Reis et al. 2017; Easter et al. 2021; Vitekere et al. 2020). Varias especies de zorrillos simpátricos presentan rasgos morfológicos y ecológicos similares (Dragoo 2009; Macdonald et al. 2017), por lo que probablemente presenten algún mecanismo que permita su coexistencia disminuyendo los efectos de la competencia interespecífica. Los escasos estudios sobre la coexistencia entre especies de zorrillos se han enfocado en la segregación espacial en la región suroeste de Estados Unidos. Investigaciones previas han documentado que el zorrillo rayado *Mephitis mephitis* presenta diferencias en el uso y la selección de hábitat a escala local con el zorrillo manchado occidental *Spilogale gracilis* y el zorrillo encapuchado *M. macroura*, lo que permite que coexistan en regiones de Arizona (Hass 2003; Hass y Dragoo 2017) y Texas (Doty y Dowler 2006; Neiswenter y Dowler 2007). No obstante, la coexistencia de estas especies parece estar explicada por sus asociaciones con el hábitat. Por ejemplo, *S. gracilis* forrajea y prefiere sitios de madriguera en áreas con cobertura densa, mientras que *M. mephitis* utiliza una mayor diversidad de hábitats (Doty y Dowler 2006; Neiswenter y Dowler 2007). Otros estudios también sugieren que los zorrillos usan el hábitat según las características estructurales de la vegetación y la disponibilidad de recursos (Crooks 1994; Lesmeister et al. 2008, 2009; Sprayberry y Edelman 2018), o incluso seleccionan estructuras de asentamientos humanos (Larivière et al. 1999).

Hasta el momento se ha prestado poca atención a la coexistencia de especies de zorrillos en México, y sus patrones de co-ocurrencia espacial siguen siendo poco conocidos en las regiones tropicales, donde a menudo co-ocurren más de dos especies (Cervantes et al. 2002; Lorenzo et al. 2005; Farías-González y Hernández-Mendoza 2021). La vertiente del Pacífico mexicano es una área prioritaria para la conservación de mamíferos carnívoros tropicales (Valenzuela-Galván et al. 2007): esta región alberga el 52% de las especies del orden Carnivora de México, incluyendo cuatro especies de zorrillos: *M. macroura*, el zorrillo de nariz de cerdo Americano *C. leuconotus*, el zorrillo manchado sureño *S. angustifrons* y el endémico zorrillo manchado pigmeo *S. pygmaea* (Dragoo 2009; Ceballos y Martínez 2010). Además, gran parte de esta región está cubierta con bosque tropical caducifolio (Ceballos y Martínez 2010), el cual se caracteriza por una estacionalidad climática marcada (Trejo, 2004, 2010). Esta variación estacional genera cambios temporales en la complejidad estructural de la vegetación y condiciones del microhábitat (Bullock et al. 1995; Trejo 2010) así como en la disponibilidad de recursos (Lister y García 1992; Valenzuela y Macdonald 2002), lo que influencia que el uso de hábitat animal varíe espacial y temporalmente a escala local. Algunas investigaciones indican que poblaciones simpátricas de *C. leuconotus*, *M.*

macroura y *S. angustifrons* coexisten en hábitats de bosques secos dentro de esta región prioritaria (Cervantes et al. 2002; Lorenzo et al. 2005), con un uso diferencial del hábitat entre *C. leuconotus* y *M. macroura* dependiendo de la temporada (Cervantes et al. 2002).

Los patrones de co-ocurrencia entre *C. leuconotus* y *S. pygmaea* particularmente no han sido estudiados a lo largo de la vertiente del Pacífico mexicano, donde se encuentran en simpatría. Estas especies tienen diferencias en el tamaño corporal (1.1-4.5 kg y 0.1-0.3 kg, respectivamente —Medellín et al. 1998; Dragoo y Sheffield 2009) pero explotan la misma base de recursos: se alimentan de insectos y algunos vertebrados pequeños (Cantú-Salazar et al. 2005; Dragoo y Sheffield 2009) y presentan actividad nocturna y crepuscular (Medellín et al. 1998; Pérez-Irineo et al. 2020). Por lo tanto, la competencia entre ellas es probablemente alta y se cree que *C. leuconotus* es el competidor dominante en este sistema biológico, en función de su mayor tamaño y uso más amplio de hábitats (Hass 2003; Dragoo y Sheffield 2009). Las interacciones competitivas, además, pueden ser más intensas en ambientes estacionales cuando el alimento es escaso (Palomares y Caro 1999; Storner y Timm 2011), como en el bosque tropical caducifolio durante la temporada de sequía. Sin embargo, la influencia tanto de la competencia interespecífica como de las características del hábitat y los factores antropogénicos sobre la co-ocurrencia de estas especies aún no se ha evaluado. El estudio de los patrones de co-ocurrencia permitirá comprender mejor cómo los zorrillos estudiados coexisten en el espacio e identificar los factores que determinan su ocurrencia a escala local, lo cual puede proporcionar información ecológica básica para enfocar los esfuerzos futuros de conservación y manejo de estas especies.

Una consideración adicional al analizar la co-ocurrencia de especies es tener en cuenta la detección imperfecta, lo cual permite evitar errores de omisión (ausencias falsas) y de predicción (MacKenzie et al. 2004a; Beissinger et al. 2016). Estos errores pueden generar interpretaciones incorrectas sobre los patrones de co-ocurrencia (MacKenzie et al. 2004a; MacKenzie et al. 2018). El modelado de ocupación resuelve estos problemas al incorporar la probabilidad de detección y al modelar simultáneamente las interacciones de especies y covariables asociadas con el hábitat (MacKenzie et al. 2004a; Richmond et al. 2010; Rota et al. 2016). Además, estos modelos son adecuados para especies nocturnas o de hábitos crípticos que presentan baja detectabilidad, como los zorrillos (MacKenzie et al. 2004b; Nagy-Reis et al. 2017; Eng y Jachowski 2019). No obstante, a pesar de que su uso se ha extendido, pocos estudios han modelado los cambios en la co-ocurrencia de especies a lo largo del tiempo (Lombardi et al. 2020; Vitekere et al. 2020). Estos modelos

dinámicos son útiles para identificar los procesos que subyacen a los cambios en la ocupación y estudiar la dinámica de las interacciones de especies (Haynes et al. 2014; MacKenzie et al. 2018).

En el presente estudio evaluamos el papel de las interacciones competitivas y los factores ambientales y antropogénicos en el uso del hábitat de dos zorrillos simpátricos en un bosque tropical caducifolio en buen estado de conservación en el sureste de México. Usando un enfoque basado en el criterio de Máxima Verosímilitud, estimamos las probabilidades de ocupación y de co-ocurrencia a lo largo del tiempo mientras se consideraba explícitamente la imperfección de la detectabilidad. Evaluamos dos hipótesis, la primera es que estas especies se segregarían en el espacio basándose en gran medida en la complejidad del paisaje y las perturbaciones antropogénicas. Estudios previos indican que *S. pygmaea* es especialista en el hábitat y prefiere áreas conservadas con cobertura vegetal densa (Cantú-Salazar et al. 2009; Helgen et al. 2016), mientras que *C. leuconotus* es generalista y tolera áreas perturbadas o con la presencia de humanos (Helgen, 2016). Nuestra segunda hipótesis es que *S. pygmaea*, el zorrillo de talla más pequeña, evitará a *C. leuconotus*, el zorrillo más grande, en el espacio a lo largo de las temporadas, debido a que se encuentra en desventaja competitiva por los recursos. El tamaño corporal puede influir en las interacciones competitivas entre especies y las especies más grandes pueden superar a las más pequeñas (Palomares y Caro 1999; Donadio y Buskirk 2006).

Materiales y métodos

Área de estudio. El estudio fue conducido en el Parque Nacional Huatulco (PNH; 15°39'12" y 15°47'10" N, 96°06'30" y 96°15'00" O), ubicado en el municipio de Santa María Huatulco en la porción central de la costa del estado de Oaxaca, México (Fig. 1; CONANP 2003). El PNH es un área natural protegida de carácter federal y comprende una superficie terrestre de 6,374.98 ha (CONANP 2003). La región forma parte de la Región Terrestre Prioritaria No. 129, Sierra Sur y Costa de Oaxaca (Arriaga et al. 2000). La topografía de la zona se caracteriza por lomeríos suaves, con elevaciones que van desde el nivel del mar hasta poco más de los 200 m s.n.m. (CONANP 2003). Existen corrientes y cuerpos de agua intermitentes como los arroyos Xúchilt-Arenal, Chachacual y El Faisán-Cacaluta y las lagunas Culebra, La Poza y Zanate, que en ocasiones llegan a permanecer todo el año (CONANP 2003; INEGI 2008). También hay dos lagunas salobres y una poza de agua pequeña alimentada por los escurrimientos en la temporada de lluvias (CONANP 2003). Estas fuentes de agua son importantes para la fauna silvestre durante la sequía, ya que la

disponibilidad de este recurso es limitada en el área de estudio. El clima es cálido subhúmedo con lluvias en verano, que es el subtipo de menor humedad (Trejo 2004). Este clima es estacional, con lluvias concentradas de junio a octubre y un período prolongado de sequía de noviembre a mayo (CONANP 2003; Trejo 2004). La temperatura media anual fluctúa de 26 a 28°C y la precipitación anual varía de 800 a 1,200 mm (Trejo 2004).

La vegetación dominante es el bosque tropical caducifolio (Salas-Morales et al. 2007), que se caracteriza por una estacionalidad fenológica marcada (Trejo 2010). Fisionómicamente, el estrato arbóreo oscila de 6 a 16 m y presenta copas extendidas y poco densas, mientras que los estratos arbustivo y herbáceo son abundantes en la temporada de lluvias y constituyen una proporción significativa de la estructura de la comunidad (Castillo-Campos et al. 1997; Salas-Morales et al. 2007; Trejo 2010). El PNH presenta elementos naturales que le confieren una importancia sobresaliente para la conservación del bosque tropical caducifolio y alberga uno de los últimos remanentes de esta vegetación en buen estado de conservación (CONANP 2003). El área protegida también alberga una diversidad alta de mesocarnívoros, que incluye dos especies de zorrillos, *C. leuconotus* y *S. pygmaea*, y algunos mesodepredadores nativos como el coyote *Canis latrans* y el ocelote *Leopardus pardalis* (Lira et al. 2008; Briones-Salas et al. 2016). Estas especies juegan un papel importante en el ecosistema porque no se conoce la presencia de depredadores de talla mayor.

El PNH está dividido en cinco zonas de acuerdo con el estado de conservación y el aprovechamiento de los ecosistemas presentes (CONANP 2003). La zona de protección es la más conservada y las actividades permitidas son la investigación y la educación, mientras que las demás muestran cierto grado de perturbación humana, principalmente las zonas de aprovechamiento y de recuperación (CONANP 2003). Existen asentamientos humanos ubicados a lo largo de los límites del área natural protegida, lo que ha dado como resultado un paisaje fragmentado con vegetación nativa y de crecimiento secundario, tierras agrícolas, vías de comunicación (carreteras y caminos de terracería) y áreas sin vegetación (e.g. basurero a cielo abierto), así como la introducción de poblaciones ferales de perros domésticos *C. lupus familiaris* (Binnqüist et al. 2017; Guzmán Pacheco 2019).

Colecta de datos. Entre noviembre 2018 y octubre 2020, colectamos datos de presencia-ausencia de las dos especies de zorrillos y tres mesodepredadores potenciales (*L. pardalis*, *C. latrans* y *C. l. familiaris*) a través de tres temporadas de muestreo con cámaras trampa en dos sitios

de estudio, seleccionados con base en la zonificación del PNH (Cuadro 1). Colocamos 30 estaciones simples de cámaras trampa en cada sitio, las cuales se distribuyeron en una cuadrilla regular de 6 x 5 estaciones en el interior del bosque y se espaciaron a 420 m entre sí, lo que correspondió a un área de muestreo de 3.7 km^2. Sin embargo, varias cámaras trampa fueron robadas y únicamente estuvieron operando de 22-26 estaciones por sitio (Fig. 1). El espaciado de las estaciones y el tamaño de la cuadrilla se definieron con base en la estimación mínima del ámbito hogareño y la densidad poblacional para las especies focales, de modo que hubiera al menos dos estaciones de cámaras en el ámbito hogareño estimado de cada especie (*C. leuconotus*: 0.64 km^2 y 0.6-1.3 ind/km^2 — Cervantes et al. 2002; Brashear et al. 2015; *S. pygmaea*: 0.20 km^2 — Cantú-Salazar et al. 1999). Las estaciones de fototrampeo se instalaron sin cebo sobre senderos de animales y en sitios cercanos a arroyos y se fijaron en los troncos de los árboles a unos 20-30 cm por encima del suelo. Ninguna estación de muestreo se ubicó cerca de senderos de humanos o caminos de terracería transitados. Usamos cuatro modelos de cámara trampa (Bushnell Trophy Cam®, Bushnell Trophy Cam w/Viewscreen®, ERE-E1 y Moultrie Digital Game 990i), las cuales fueron programadas para operar las 24 h del día. Las cámaras se configuraron para tomar tres fotografías y/o grabar un video de 10-15 s por cada evento de activación, con un tiempo de retraso de 10 s entre eventos consecutivos. Revisamos las cámaras mensualmente para reemplazar las baterías, así como las cámaras en mal funcionamiento o robadas.

Basados en los datos de las cámaras trampa, creamos historias de detección de las especies para cada estación de muestreo, donde registramos si la especie fue detectada (1) o no detectada (0) en cada noche trampa. Para este estudio, definimos tres períodos primarios (temporadas climáticas) con 10 ocasiones de muestreo secundarias cada uno. Las ocasiones de muestreo fueron igual a 12 noches-trampa consecutivas, de modo que cada período primario consistió en 120 noches-trampa. Colapsamos las historias de detección en este período de tiempo para evitar la violación del supuesto de detección independiente para los conjuntos de datos de ambos zorrillos y mejorar la convergencia de los modelos en los análisis de ocupación y co-ocurrencia. Una especie se consideró detectada durante una ocasión de muestreo si fue fotografiada al menos una vez durante ese período (Lombardi et al. 2020). El período de tiempo entre períodos primarios se consideró suficiente para detectar cambios en los estados de ocupación de las especies.

Covariables explicativas. Identificamos las covariables biológicamente más importantes que pudieran influir en el uso y selección de recursos de las especies de zorrillo de acuerdo con la

literatura publicada (Crooks 1994; Doty y Dowler 2006; Cantú-Salazar et al. 2009; Eng y Jachowski 2019). Las covariables seleccionadas se clasificaron en cuatro grupos: complejidad del hábitat, disponibilidad de recursos, presencia de especies interactuantes y perturbación antropogénica (Cuadro 2). Estas covariables se registraron para cada estación de cámara trampa y sus mediciones se obtuvieron utilizando métodos de campo y de detección remota a partir de capas de sistemas de información geográfica existentes. Las mediciones de la vegetación se tomaron en cuadrantes de muestreo de 20 x 20 m centrados en la ubicación de las cámaras trampa y en subcuadrantes de 4 x 4 m localizados en las esquinas y en el centro de cada cuadrante (Higgins et al. 1996; Mostacedo y Fredericksen 2000). En general, las covariables asociadas con el hábitat, la disponibilidad de recursos y la presencia de otros carnívoros se midieron en cada temporada de muestreo (i.e. covariables de tiempo, factores que varían entre temporadas), mientras que las de perturbación antropogénica se estimaron sólo una vez para todas las temporadas (i.e. covariables de sitio, factores que varían entre sitios, pero son constantes entre temporadas).

La complejidad del hábitat incluyó la cobertura arbustiva, visibilidad horizontal, cobertura del dosel, Índice de Vegetación de Diferencia Normalizada (NDVI, por sus siglas en inglés) y pendiente. La cobertura arbustiva se obtuvo a partir de la longitud máxima (d_1) y perpendicular (d_2) de las copas de todos los arbustos en los cinco subcuadrantes de muestreo, utilizando la fórmula: $CA = \Sigma (\pi * (1/4 (d_1 + d_2))^2)$. La visibilidad a nivel del suelo se estimó con ayuda de un tablero de ajedrez de 48 x 48 cm pintado alternativamente con cuadrados blancos y negros de 8 x 8 cm (Cantú-Salazar et al. 2009). Con un observador en posición de gateo ubicado en el centro del cuadrante, colocamos el tablero a nivel del suelo y se alejó hasta que ningún cuadrado blanco fuera visible en las cuatro direcciones cardinales, luego medimos estas distancias lineales y obtuvimos un valor promedio. La cobertura del dosel se midió en el centro y a 5 y 10 m del cuadrante en las cuatro direcciones cardinales utilizando un densiómetro esférico cóncavo (Forestry Suppliers Modelo-C). Todas las mediciones de la cobertura se promediaron en cada estación de muestreo. Por otra parte, el NDVI se derivó de imágenes satelitales Landsat 8 tomadas en abril y agosto de 2019 y marzo de 2020 con una cobertura de nubes inferior al 10%, las cuales se descargaron del Servicio Geológico de Estados Unidos (http://earthexplorer.usgs.gov/). Las imágenes satelitales fueron corregidas atmosféricamente y calculamos el NDVI promedio en un búfer de 200 m de radio alrededor de cada estación de muestreo. Los valores de pendiente se obtuvieron utilizando imágenes en formato raster del modelo digital de elevación tipo superficie con una resolución

espacial de 5 m a escala 1:10 000 (cartas D14B19E3 y D14B29B1), generados por el Instituto Nacional de Estadística, Geografía e Informática (INEGI 2016). Los cálculos del NDVI y pendiente se realizaron utilizando el software QGIS 3.4.6 (QGIS Development Team 2020).

Las variables de disponibilidad de recursos fueron el número de madrigueras potenciales, humedad del suelo, distancia a la fuente de agua más cercana y disponibilidad de presas. El número de madrigueras se estimó a partir del conteo de cavidades en el suelo y oquedades en troncos caídos y en la base de árboles en pie dentro de cada cuadrante de muestreo. Las cavidades u oquedades con una entrada ≥ 5 cm y ≥ 15 cm de diámetro se consideraron madrigueras potenciales para *S. pygmaea* y *C. leuconotus*, respectivamente (obs. pers.; Cantú-Salazar et al. 2009; Reid 2016). La humedad del suelo se obtuvo a partir del Índice de Agua de Diferencia Normalizada Modificado (MNDWI, por sus siglas en inglés) y su cálculo se utilizó como un sustituto de la disponibilidad de insectos de hojarasca, ya que la diversidad y abundancia de éstos se relaciona directamente con la humedad del suelo (Palacios-Vargas et al. 2007). El MNDWI también se generó con las imágenes satelitales Landsat 8 corregidas y obtuvimos un valor promedio en un búfer de 200 m de radio para cada estación de muestreo. Además, este índice permite mapear los cuerpos de agua (Xu 2006) y se utilizó para medir la distancia de las cámaras trampa a la fuente de agua (arroyo, laguna o pozo de agua) más cercana presente en el área de estudio. La disponibilidad de presas se estimó utilizando los registros de las cámaras trampa de mamíferos terrestres de tamaño pequeño (< 1 kg; principalmente roedores y marsupiales pequeños), considerados como especies presa potenciales (Cantú-Salazar et al. 2005; Dragoo y Sheffield 2009). Esta covariable se calculó como la relación entre el número total de registros independientes de presas y el esfuerzo de muestreo para cada estación de cámara trampa en cada período de muestreo multiplicado por 100 (Rovero y Spitale 2016). Un registro independiente consideró todas las fotografías de mamíferos pequeños tomadas por cada estación de muestreo en un lapso de 1 hora. Por otra parte, la presencia de especies interactuantes incluyó las estimaciones de la probabilidad de ocupación de cada una de las tres especies de mesodepredadores potenciales (*L. pardalis*, *C. latrans* y *C. l. familiaris*), modeladas a partir de los datos de las cámaras trampa con los modelos de ocupación de una sola especie en una temporada, en lugar de utilizar el número de registros de cada especie.

Las distancias de las cámaras trampa a los poblados, carreteras, áreas de cultivo, basurero municipal y áreas de vegetación nativa > 0.5 km^2 fuera del área protegida más cercanas se incluyeron como una estimación del grado de perturbación antropogénica (e.g., presencia humana, ruido, tráfico, fuente de alimento antropogénica y fragmentación), que podrían influir en la presencia de ambas especies de zorrillos. También consideramos la covariable distancia ponderada al borde del área protegida como propone Nagy-Reis et al. (2017). Primero, medimos la distancia lineal desde cada estación de cámara trampa hasta el límite más cercano del PNH. Luego, multiplicamos las distancias por el peso del estado de protección de la subárea en la que se encontraba cada estación de muestreo (zona de aprovechamiento y recuperación =1; zona de uso restringido 2; zona de protección = 3). Las distancias se calcularon utilizando mapas de la red nacional de caminos a escala 1:50 000 (INEGI 2019), del uso de suelo y vegetación de México serie VI a escala 1:250 000 (INEGI 2017) y de la zonificación del PNH (http://sig.conanp.gob.mx) con el software QGIS 3.4.6 (QGIS Development Team 2020).

Finalmente, seleccionamos variables ambientales como temperatura, precipitación e iluminación lunar para evaluar su influencia en la detección de las especies de zorrillos. Estas variables pueden afectar ya sea la capacidad de las cámaras trampa para detectar a los animales o el comportamiento y la actividad de carnívoros nocturnos (Kays et al. 2017; Lesmeister et al. 2015; Zapata-Ríos y Branch 2018), y por lo tanto, la detectabilidad de la especie también es afectada. La temperatura y la precipitación diaria de cada periodo de muestreo se obtuvieron del observatorio meteorológico de Puerto Ángel (15°40'04" N, 96°29'24" O; id = 76855), administrada por la Comisión Nacional del Agua (CONAGUA). La iluminación lunar se estimó a partir de las fechas de cuando se realizó el muestreo utilizando el paquete Suncalc (Thieurmel y Elmarhraoui 2019). Los valores promedio de las tres variables se calcularon para cada ocasión de muestreo (i.e. variables de observación que cambian en cada ocasión de muestreo).

Todas las covariables continuas se estandarizaron para que tuvieran una media de cero y una unidad de desviación estándar antes del análisis para facilitar la convergencia de los modelos. Probamos la colinealidad de las covariables utilizando el coeficiente de correlación de rango de Spearman (Zuur et al. 2009); usamos un valor de $\rho > 0.70$ para indicar una alta colinealidad y excluimos las variables altamente correlacionadas de los mismos modelos.

Modelos de ocupación de una sola especie multi-temporada o dinámico. Usamos modelos de ocupación de una sola especie para varias temporadas con un enfoque basado en Máxima Verosimilitud para estimar la probabilidad de ocupación de cada especie de zorrillo (MacKenzie et al. 2003; MacKenzie et al. 2006). Nos referimos a temporada o período primario como las

temporadas climáticas de seca y de lluvia en las que se realizaron los períodos de muestreo (Cuadro 1). Los modelos dinámicos estiman cuatro parámetros: probabilidad de detección (p, probabilidad de que una especie sea detectada en un sitio dado que está presente), ocupación inicial (ψ, probabilidad de que una especie esté presente en un sitio en la primera temporada), colonización (γ, probabilidad de que un sitio esté desocupado por la especie en una temporada y luego sea ocupado en la siguiente) y extinción (ε, probabilidad de que un sitio esté ocupado por una especie en una temporada y luego sea desocupado en la siguiente; MacKenzie et al. 2003; MacKenzie et al. 2006). Estos modelos utilizan un diseño robusto, lo que significa que los parámetros están demográficamente cerrados (no hay entradas ni salidas de individuos a la población) durante las ocasiones de muestreo en cada temporada, pero pueden estar demográficamente abiertos entre temporadas (hay entradas y salidas de individuos; MacKenzie et al. 2006). Las tasas de colonización y de extinción representan los cambios en la probabilidad de ocupación del sitio entre los períodos primarios (Schuette et al. 2013). Debido a que el ámbito hogareño de los zorrillos es mayor en comparación con el área muestreada por las estaciones de cámaras trampa, interpretamos la probabilidad de ocupación como una medida del uso de hábitat en lugar de la ocupación real (MacKenzie et al. 2006, 2018).

Evaluamos la influencia potencial de covariables relacionadas con la complejidad del hábitat, disponibilidad de recursos, presencia de especies o perturbación antropogénica en cada parámetro del modelo dinámico para evitar estimaciones sesgadas (Tabla 2; MacKenzie et al. 2003; MacKenzie et al. 2006) e identificar los factores que afectan el uso de hábitat de los zorrillos a escala local. En lugar de ajustar un conjunto de modelos candidatos extremadamente grande por todas las combinaciones plausibles de covariables analizadas, adoptamos un enfoque de modelado de etapas para reducir el número de modelos e identificar el mejor modelo. Primero, construimos un conjunto de modelos para seleccionar las covariables de observación que influían en la probabilidad de detección (p) para cada especie mientras manteníamos constante los demás parámetros. Aunque las fuentes de variación en la probabilidad de detección no eran de interés ecológico primario, el modelado de este parámetro fue importante para la estimación de la probabilidad de ocupación de los zorrillos. En una segunda etapa, mantuvimos las covariables mejor soportadas para la probabilidad de detección y a continuación, construimos un conjunto de modelos de una o varias covariables de efectos de sitio y de tiempo (estacionales) que podrían afectar la probabilidad de ocupación inicial (ψ). Por último, construimos otro conjunto de modelos

que incluían covariables de tiempo para explicar la probabilidad de colonización (γ) y de extinción (ε), reteniendo las covariables del modelo mejor ajustado para la probabilidad de ocupación y de detección. El conjunto de modelos para cada especie se construyó evitando modelos que incluyeran más de una variable relacionada con un efecto dado (Schuette et al. 2013). Este conjunto no fue exhaustivo, pero tenía como objetivo evaluar la influencia de varias combinaciones de variables para evaluar nuestras hipótesis.

Ejecutamos y evaluamos los modelos de ocupación candidatos utilizando el paquete Unmarked (Chandler et al. 2022) en el software R (R Development Core Team 2020). Usamos el Criterio de Información de Akaike corregido para un tamaño de muestra pequeño (AICc) para la selección del modelo final (Burnham y Anderson 2002). La comparación entre todos los modelos evaluados se realizó utilizando el paquete AICcmodavg (Mazerolle 2020). Consideramos que las covariables de los modelos mejor clasificados (ΔAICc < 2, diferencia relativa entre el AICc de cada modelo con el mejor modelo) tenían una influencia fuerte en los parámetros estimados (ψ, γ, ε, p) si los intervalos de confianza (IC) al 95% de sus coeficientes beta no incluían cero y una influencia moderada si los IC al 80% de sus coeficientes no incluían cero (Anderson 2008). Evaluamos los ajustes del modelo con el parámetro de sobredispersión ($\hat{c}$) en el modelo más parsimonioso utilizando la prueba de bondad de ajuste de MacKenzie-Bailey con un bootstrap de 1,000 repeticiones (MacKenzie y Bailey 2004). También proporcionamos las tendencias en la probabilidad de ocupación de las especies a través de las predicciones medias de ocupación suavizada (Chandler et al. 2022).

Modelos de co-ocurrencia de una sola temporada. Para evaluar la co-ocurrencia entre los zorrillos, utilizamos modelos de ocupación de dos especies para cada temporada (MacKnezie et al. 2004a, 2006) en el paquete Wiqid (Meredith et al. 2020). Usamos la parametrización condicionada ψBa/rBa propuesta por Richmond et al. (2010), la cual asume que hay una especie dominante o de mayor talla y otra subordinada o de talla más pequeña. En nuestro sistema biológico, esta suposición fue válida dada la diferencia en tamaño corporal de los zorrillos (Dragoo 2009) y designamos a *C. leuconotus* como dominante y a *S. pygmaea* como subordinada. Los parámetros de la ocupación y detección de la segunda especie se estimaron como probabilidades condicionadas a la presencia o ausencia de la primera (Apéndice I; MacKenzie et al. 2018).

Modelamos los parámetros estimados incorporando las covariables cuyos IC al 95 % no incluían cero en el modelo final dinámico de una sola especie mejor clasificado para cada zorrillo,

teniendo en cuenta las posibles diferencias en las preferencias de hábitat. De acuerdo con Nagy-Reis et al. (2017), construimos modelos que asumieron que la ocupación de la especie subordinada estaba influenciada por la especie dominante ($\psi^{SC} \neq \psi^{Sc}$) o fuera independiente ($\psi^{SC} = \psi^{Sc}$). También construimos modelos donde la probabilidad de detección de la especie subordinada estaba influenciada por la presencia ($p^{S} \neq r^{Sc}$; $p^{S} \neq r^{SC}$) o detección ($r^{Sc} \neq r^{SC}$) de la especie dominante o fuera independiente de la misma ($p^{S} = r^{Sc} = r^{SC}$), así como modelos que asumían que la detección de la especie dominante estaba influenciada por la presencia de la especie subordinada ($r^{C} \neq p^{C}$) o independiente ($r^{C} = p^{C}$). Seguimos el mismo enfoque de selección de modelos candidatos que en el análisis de modelos dinámicos de una sola especie.

También calculamos el factor de interacción de especies (FIE) para la probabilidad de ocupación ($\varphi = \psi^{C}\psi^{SC} / \psi^{C} [\psi^{C}\psi^{SC} + [1- \psi^{C}]\ \psi^{Sc}]$) y la probabilidad de detección ($\delta = r^{C}r^{SC} / r^{C} [r^{C}r^{SC} + [1- r^{C}]\ r^{Sc}]$; Richmond et al. 2010). El FIE indica si la ocupación o la probabilidad de detección de la especie subordinada es afectada por la de la especie dominante (Richmond et al. 2010). Si FIE = 1, las especies co-ocurren o se detectan de forma independiente. Si FIE < 1, las especies co-ocurren o se detectan con menos frecuencia de lo esperado por el azar (i.e. evasión, la especie dominante desplaza a la subordinada), mientras que si FIE > 1, las especies co-ocurren o se detectan con más frecuencia de lo esperado por el azar (i.e. agregación; MacKenzie et al. 2004a; Richmond et al. 2010). Consideramos los parámetros estimados, los modelos mejor clasificados (ΔAICc <2) y el FIE calculado para inferir sobre los patrones de co-ocurrencia de las especies de zorrillos en las tres temporadas analizadas.

Resultados

Obtuvimos 44 detecciones de *C. leuconotus* y 381 de *S. pygmaea* durante las tres temporadas de muestreo, con un esfuerzo de muestreo de 10,697 noches-trampa (Cuadro 1). El 61% del total de detecciones de *C. leuconotus* y el 48% de *S. pygmaea* se registraron en la temporada de lluvia 2019. *Conepatus leuconotus* fue detectado en 23 estaciones de cámaras trampa mientras que *S. pygmaea* en 39 de ellas, lo que resultó una estimación de ocupación naïve de 0.48 y 0.81, respectivamente. También obtuvimos 86 detecciones de *C. latrans*, 42 de *C. l. familiaris* y 171 de *L. pardalis* (Cuadro 1).

Ocupación dinámica de una sola especie. Ajustamos 27 modelos de ocupación para *C. leuconotus* y 29 modelos de ocupación para *S. pygmaea* (Apéndice II). El modelo mejor clasificado

mostró un ajuste adecuado tanto en *C. leuconotus* ($\chi^2 = 886.09$, $P = 0.928$) como en *S. pygmaea* ($\chi^2 = 10543.12$, $P = 0.35$). De acuerdo con el modelo final $\psi_{(\text{Vishor+Humsue+Disagua})}\ \gamma_{(\text{Madri+Disagua})}\ \varepsilon_{(.)}\ p_{(.)}$, la probabilidad de ocupación inicial de *C. leuconotus* se relacionó positivamente con la distancia a la fuente de agua más cercana y negativamente con la humedad del suelo. Ambas covariables mostraron un efecto moderado sobre este parámetro (Cuadro 3). Todas las covariables tuvieron una influencia baja sobre los demás parámetros, con sus intervalos de confianza superponiéndose con cero.

El modelo final para *S. pygmaea* fue $\psi_{(\text{Humsue+Disagua+Dispre})}\ \gamma_{(\text{Ocuper+Ocucoy})}\ \varepsilon_{(\text{Cobarb+Madri})}\ p_{(\text{Ilun})}$. La probabilidad de ocupación inicial de *S. pygmaea* se relacionó positiva y fuertemente con la distancia a la fuente de agua más cercana y moderadamente con la disponibilidad de presas y la humedad del suelo (Cuadro 3). La probabilidad de extinción se relacionó positivamente con la cobertura arbustiva pero negativamente con el número de madrigueras, ambas covariables tuvieron un efecto moderado. La iluminación lunar mostró un fuerte efecto negativo sobre la probabilidad de detección de esta especie. Ninguna covariable se relacionó con la probabilidad de colonización (Cuadro 3).

La probabilidad de ocupación de ambas especies aumentó durante las tres temporadas muestreadas (Fig. 2). El aumento en la ocupación de *C. leuconotus* fue gradual, de 0.39 en la temporada de seca 2019 a 0.49 en la temporada de seca 2020. Mientras tanto, el aumento en la ocupación de *S. pygmaea* fue más notoria en la segunda temporada, pasando de 0.58 en la temporada de seca 2019 a 0.78 en la temporada de lluvia 2019 (Fig. 2).

Patrones de co-ocurrencia de especies. No hubo evidencia de que *C. leuconotus* afecte las probabilidades de ocupación y de detección de *S. pygmaea*. El modelo mejor clasificado de cada temporada mostró que la probabilidad de ocupación de *S. pygmaea* es independiente de la de *C. leuconotus* ($\psi^{SC} = \psi^{Sc} = 0.52\text{-}0.88$), contrario a lo esperado bajo la hipótesis de segregación espacial (Cuadro 4; Fig. 3). Similarmente, la probabilidad de detección de *S. pygmaea* es independiente de la presencia o detección de *C. leuconotus* ($p^S = r^{Sc} = r^{SC} = 0.29\text{-}0.43$), dependiendo de la temporada (Cuadro 4; Fig. 3). Los modelos mejor clasificados también indicaron que la probabilidad de detección de *C. leuconotus* fue mayor en presencia de *S. pygmaea* ($p^C = 0.01\text{-}0.06 < r^C = 0.05\text{-}0.08$) en las temporadas de seca y de lluvia 2019, mientras que fue igual en presencia de *S. pygmaea* ($p^C = r^C = 0.05$) en la temporada de seca 2020. El FIE para las probabilidades de ocupación y de

detección fue igual a 1 en las tres temporadas, excepto para la probabilidad de detección durante la temporada de lluvia 2019 (δ = 1.78).

Discusión

Este estudio evaluó explícitamente la importancia relativa de características relacionadas con el hábitat y factores antropogénicos en modelos de ocupación dinámicos y el papel de las interacciones interespecíficas en modelos de co-ocurrencia para investigar el uso de hábitat y los patrones de co-ocurrencia de *C. leuconotus* y *S. pygmaea* en el Parque Nacional Huatulco, dentro de la vertiente del Pacífico mexicano. Nuestros hallazgos mostraron que la distancia a la fuente de agua más cercana, la disponibilidad de mamíferos pequeños y la humedad del suelo (como un sustituto de la disponibilidad y abundancia de insectos) fueron los predictores más importantes que influyeron en el uso de hábitat de las especies de zorrillos en un ambiente fuertemente estacional. Mientras tanto, las interacciones interespecíficas tuvieron un efecto bajo sobre la ocurrencia y el uso de hábitat de las especies a escala local. Estos resultados son consistentes con lo observado en otros ensambles de zorrillos simpátricos en la región suroeste de Estados Unidos, donde el uso del hábitat de las especies está determinado principalmente por las características de la vegetación (Doty y Dowler 2006; Neiswenter y Dowler 2007) y otras formas de complejidad estructural del hábitat (Hass 2003; Hass y Dragoo 2017).

La distancia a la fuente de agua más cercana, dados los intervalos de confianza de sus estimaciones beta, tuvo un efecto positivo fuerte en la ocupación de *S. pygmaea* y moderado en *C. leuconotus*. Ambas especies usaron sitios más alejados de los cuerpos de agua en nuestra área de estudio, lo cual podría deberse a que en áreas cercanas a este recurso aumenta la probabilidad de interacciones negativas como la depredación intragremio (Rosenstock et al. 2004; Perera-Romero et al. 2021), principalmente durante los períodos de escasez de agua. Estudios previos han documentado que la depredación tiene un efecto negativo importante en los zorrillos pigmeos en los bosques caducifolios de Chamela, México (Cantú-Salazar 2002). Es probable que esta especie use áreas más distantes de las fuentes de agua para disminuir el potencial de eventos de depredación por parte de coyotes y ocelotes. Estos depredadores presentaron mayor número de detecciones en sitios dentro de la zona de protección del área protegida (Cuadro 1), que están más cercanos a los cuerpos de agua durante la temporada de sequía.

Otros factores también relacionados con la disponibilidad de recursos, como el alimento, tuvieron un efecto moderado sobre la probabilidad de ocupación de los zorrillos. Específicamente, observamos que en sitios con mayor humedad del suelo hubo mayor probabilidad de ocupación de *S. pygmaea*, pero menor de *C. leuconotus*. La relación que fue negativa es contraria a lo esperado, ya que la humedad del suelo se relaciona directamente con la diversidad y abundancia de insectos de hojarasca (Palacios-Vargas et al. 2007) y *C. leuconotus* es considerada la especie más insectívora (Dragoo 2009; Dragoo y Sheffield 2009). Sin embargo, ésta debería interpretarse con cautela por el número relativamente bajo de detecciones de esta especie y los intervalos de confianza amplios en nuestras estimaciones. También encontramos que la disponibilidad de mamíferos pequeños tuvo un efecto positivo en la probabilidad de ocupación de *S. pygmaea*, lo cual puede explicarse por la flexibilidad dietética de esta especie. Los zorrillos pigmeos son capaces de ajustar su uso de los recursos alimenticios en respuesta a las variaciones en la abundancia de presas y de consumir mamíferos pequeños como presa alternativa cuando la disponibilidad de insectos es baja (Medellín et al. 1998; Cantú-Salazar et al. 2005). Por lo tanto, *S. pygmaea* pudo ocupar más sitios donde este tipo de presas estuviera más disponible. Este factor a menudo influye en la ocupación y uso de hábitat de carnívoros simpátricos (Rich et al. 2017; Santos et al. 2019), incluyendo especies de zorrillos (Lorenzo et al. 2005; Meaney et al. 2006).

La ocupación de las especies puede variar a lo largo del tiempo y los modelos dinámicos son útiles para identificar los procesos que subyacen a los cambios en la ocupación (MacKenzie et al. 2003; MacKenzie et al. 2018). Nuestros modelos indicaron que la cobertura arbustiva y el número de madrigueras explicaron la probabilidad de extinción al menos para *S. pygmaea*. Las asociaciones positiva y negativa con estos factores están respaldadas por observaciones previas de otros autores. Los zorrillos pigmeos usan frecuentemente cavidades en el suelo como madrigueras en claros de bosque sin protección vegetal asociada (Cantú-Salazar et al. 2009), por lo que existe una menor probabilidad de que un sitio se desocupe en la siguiente temporada a menor cobertura arbustiva y mayor número de madrigueras en el sitio. Esto significa que las madrigueras son un recurso importante para la especie, ya que pueden proporcionan refugio contra las temperaturas altas del día y protección contra los depredadores terrestres y aéreos en el bosque tropical caducifolio de nuestra área de estudio. Otras investigaciones también han sugerido que la disponibilidad de sitios de madriguera adecuados puede limitar la presencia de las especies de zorrillos manchados *S. gracilis amphiala* y *S. putorius* en regiones de Estados Unidos (Crooks

1994; Lesmeister et al. 2008). Además, estas especies dependen de una variedad de estructuras que incluyen cavidades en el suelo y asociadas con rocas, troncos huecos, sistemas de raíces y oquedades en árboles (Doty y Dowler 2006; Lesmeister et al. 2008; Sprayberry y Edelman 2018; Eng y Jachowski 2019), tal como pudimos observar eventualmente para *S. pygmaea* durante el trabajo de campo.

Diferentes factores antropogénicos también pueden alterar los patrones de ocupación y co-ocurrencia de carnívoros (Schuette et al. 2013; Easter et al. 2021). Sin embargo, no encontramos evidencia de que la probabilidad de ocupación de ambos zorrillos estuviera afectada por estos factores, a pesar de ser consideradas especies sensibles al cambio de uso de suelo y a otras actividades humanas (Meaney et al. 2006; Helgen 2016; Helgen et al. 2016). Si bien el Parque Nacional Huatulco es un área relativamente conservada y protegida, existen poblaciones de perros ferales que han sido favorecidas por la cercanía del basurero municipal a cielo abierto (Binnqüist et al. 2017; Guzmán Pacheco 2019) y el hábitat circundante está seriamente amenazado con la conversión de áreas de vegetación natural de bosque caducifolio a zonas de cultivo, pastoreo y asentamientos humanos. Por lo tanto, aún no podemos descartar un posible efecto de algún factor antropogénico sobre el uso del hábitat de estos zorrillos amenazados.

La competencia intragremio tiene el potencial de afectar la ocurrencia y distribución de los carnívoros, ya que puede conducir a la segregación espacial entre pares de especies competidoras (Palomares y Caro 1999; Donadio y Buskirk 2006). Los zorrillos estudiados no se segregaron espacialmente en el área de estudio, ya que ambas co-ocurren y se detectan de manera independiente. Este resultado contradice la hipótesis de que la presencia de *C. leuconotus* podría limitar el uso de hábitat de la especie más pequeña, *S. pygmaea*, al menos dentro de la escala analizada. En general, *S. pygmaea* se registró en 39 estaciones de cámaras trampa mientras que *C. leuconotus* se registró en 22 de ellas y únicamente en una cámara trampa se detectó en forma exclusiva. La falta de la partición espacial del nicho impulsada por las interacciones interespecíficas tambén se ha observado en otros ensamblajes de carnívoros, sugiriendo que las preferencias de hábitat estructuran la comunidad (Lesmeister et al. 2015; Gompper et al. 2016; Nagy-Reis et al. 2017; Rich et al. 2017).

En conclusión, nuestros hallazgos revelaron que los factores relacionados principalmente con la disponibilidad de recursos, entre ellos agua, presas y madrigueras, determinan los patrones de uso de hábitat de *C. leuconotus* y *S. pygmaea* en lugar de las interacciones intragremio en el bosque tropical caducifolio del Parque Nacional Huatulco, Oaxaca, México. No obstante, alentamos a realizar más investigaciones para evaluar simultáneamente los efectos de características asociadas al hábitat y las relaciones ecológicas interespecíficas sobre la distribución, el uso de hábitat y la co-ocurrencia de estos carnívoros pequeños.

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Cuadros

Cuadro 1. Datos de las tres temporadas de muestreo con cámaras trampa y número de detecciones de las especies de zorrillos y de mesodepredadores en la zona de aprovechamiento (ZA) y de protección (ZP) en el Parque Nacional Huatulco, Oaxaca, México, de 2018-2020.

Temporada de muestreo	Zona de muestreo	Período	Número de cámaras	Noches-trampa	Número de detecciones				
					Conepatus leuconotus	*Spilogale pygmaea*	*Leopardus pardalis*	*Canis latrans*	*Canis lupus familiaris*
Seca 2019	ZA	1 Dic. 2018-30 Marzo 2019	26	2,585	10	106	19	15	15
	ZP	13 Dic. 2018-11 Abril 2019	22	1,613	0	30	29	26	3
Lluvia 2019	ZA	1 Junio 2019-28 Sep. 2019	26	2,836	24	121	54	19	13
	ZP	13 Junio 2019 -10 Oct. 2019	22	1,868	3	62	42	15	4
Seca 2020	ZA	19 Nov. 2019 -17 Marzo 2020	24	1,795	7	62	27	11	7

Cuadro 2. Covariables seleccionadas para los modelos dinámicos de ocupación de *Conepatus leuconotus* y *Spilogale pygmaea* durante tres periodos de muestreo con cámaras trampa en el bosque tropical caducifolio en el Parque Nacional Huatulco, Oaxaca, México, de noviembre 2018 a octubre 2020. El tipo de covariable corresponde a: estacional, covariables de tiempo que varían entre temporadas; específico del sitio, covariables que varían entre sitios pero son constantes entre temporadas; observación, covariables que cambian en cada ocasión de muestreo. La escala de la covariable corresponde a: S, sitio (cuadrante de muestreo de 400m^2 centrado en la ubicación de cada cámara trampa); AH, ámbito hogareño (distancia radial de 200 m); P, paisaje (área de estudio de 63.75 km^2).

Covariable	Acrónimo	Tipo[1]	Intervalo	Escala[2]	Fuente de datos
Complejidad del hábitat					
Cobertura arbustiva	Cobarb	Estacional	0.44-99.94 m^2	S	Muestreo en campo
Visibilidad horizontal	Vishor	Estacional	7.00-27.75 m	S	Muestreo en campo
Cobertura del dosel	Cobdos	Estacional	65.45-97.34 %	S	Muestreo en campo
Índice de Vegetación de Diferencia Normalizada	NDVI	Estacional	0.38-0.88	AH	Imagen satelital LANDSAT 8
Pendiente	Pend	Específico del sitio	3.00-57.32 %	S	Modelo digital de elevación
Disponibilidad de recursos					
Número de madrigueras	Madri	Estacional	3-45 0-22	S	Muestreo en campo
Humedad del suelo	Humsue	Estacional	-0.61-0.51	AH	Imagen satelital LANDSAT 8
Distancia a la fuente de agua más cercana	Disagua	Estacional	0.10-7.53 km	P	Imagen satelital LANDSAT 8
Disponibilidad de presas	Dispre	Estacional	0-31.67	S	Datos de cámaras trampa
Presencia de especies					
Tasas de ocupación de *Leopardus pardalis*	Ocuoce	Estacional	0.09-1.00	S	Datos de cámaras trampa
Tasas de ocupación de *Canis latrans*	Ocucoy	Estacional	0.12-1.00	S	Datos de cámaras trampa
Tasas de ocupación de *Canis lupus familiaris*	Ocuper	Estacional	0.13-1.00	S	Datos de cámaras trampa
Perturbación antropogénica					

Distancia al poblado más cercano	Dispob	Específico del sitio	0.78-6.64 km	P	Mapa de red de caminos
Distancia a la carretera más cercana	Discar	Específico del sitio	0.10-4.80 km	P	Mapa de red de caminos
Distancia al cultivo más cercano	Discul	Específico del sitio	1.00-4.63 km	P	Mapa de vegetación
Distancia al basurero más cercano	Disbas	Específico del sitio	2.87-6.68 km	P	Mapa de vegetación
Distancia al área de vegetación nativa > 0.5 km^2 más cercano	Disavn	Específico del sitio	0.66-4.74 km	P	Mapa de vegetación
Distancia ponderada al borde del área protegida	Dispanp	Específico del sitio	0.05-7.66 km	P	Mapa de zonificación del área protegida
Ambientales					
Temperatura	Temp	Observación	25.10-30.81 °C	S	Observatorio meteorológico
Precipitación	Prec	Observación	0-136.08 ml	S	Observatorio meteorológico
Iluminación lunar	Ilun	Observación	0-1	S	Paquete R Suncalc

Cuadro 3. Parámetros estimados del modelo de ocupación de una sola especie dinámico y sus intervalos de confianza (IC) al 95% y al 80% para *Conepatus leuconotus* y *Spilogale pygmaea* en el bosque tropical caducifolio en el Parque Nacional Huatulco, Oaxaca, México.

Covariable	β	Error estándar	IC al 95%		IC al 80%		Covariable	β	Error estándar	IC al 95%		IC al 80%	
			0.025	0.975	0.1	0.9				0.025	0.975	0.1	0.9
			Conepatus leuconotus							*Spilogale pygmaea*			
Ocupación (ψ)													
Intercepto	-4.95	3.09	-11.00	1.10	-8.91	-0.99	Intercepto	9.81	6.23	-2.40	22.02	1.84	17.78
Visibilidad horizonal	-2.06	1.81	-5.61	1.50	-4.38	0.27	Humedad del suelo	2.28	1.19	-0.05	4.61	0.76	3.80
Humedad del suelo	-9.26	6.54	-22.08	3.55	-17.65	-0.88	Distancia a fuente de agua	2.10	1.05	0.04	4.16	0.76	3.44
Distancia a fuente de agua	9.84	6.84	-3.58	23.25	1.07	18.61	Disponibilidad de presas	21.40	12.05	-2.22	45.02	5.98	36.82
Colonización (γ)													
Intercepto	-32.54	38.30	-107.62	42.53	-81.64	16.55	Intercepto	7.11	6.75	-6.12	20.34	-1.53	15.75
Madrigueras	4.79	10.70	-16.14	25.73	-8.90	18.48	Ocupación de perros	-21.43	19.19	-59.04	16.18	-45.99	3.13
Distancia a fuente de agua	26.46	31.20	-34.70	87.63	-13.53	66.46	Ocupación de coyotes	21.60	19.43	-16.48	59.68	-3.27	46.47
Extinction (ε)													
Intercepto	-13.10	193.00	-391.31	365.21	-260.38	234.28	Intercepto	-2.24	0.90	-4.01	-0.47	-3.40	-1.09
							Cobertura arbustiva	0.55	0.42	-0.27	1.38	0.02	1.09
							Madrigueras	-1.27	0.94	-3.12	0.58	-2.48	-0.06
Detection (p)													
Intercepto	-2.33	0.19	-2.70	-1.97	-2.57	-2.09	Intercepto	-0.52	0.09	-0.71	-0.34	-0.64	-0.40
							Iluminación lunar	-0.23	0.09	-0.41	-0.04	-0.35	-0.11

Cuadro 4. Modelos de co-ocurrencia de dos especies de zorrillos en cada temporada utilizados para evaluar el papel de las interacciones interespecíficas en el uso del hábitat de *Conepatus leuconotus* y *Spilogale pygmaea* en el Parque Nacional Huatulco, Oaxaca, México. K = Número de parámetros; AICc = Criterio de Información de Akaike ajustado para muestras pequeñas; ΔAICc = diferencia del AICc de cada modelo con el mejor modelo; ω = peso del modelo.

Modelo candidato[1]	K	AICc	ΔAICc	ω
Temporada seca 2019				
$\psi^{C},\psi^{SC},p^{C},r^{C},p^{S},r^{Sc}$	8	388.59	0.00	0.66
$\psi^{C},\psi^{SC},p^{C},r^{C},p^{S},r^{Sc},r^{SC}$	9	391.24	2.65	0.17
$\psi^{C},\psi^{SC},\psi^{Sc},p^{C},p^{S},r^{Sc},r^{SC}$	9	391.30	2.71	0.17
$\psi^{C},\psi^{SC},\psi^{Sc},p^{C},p^{S}$	7	403.33	14.74	0.00
$\psi^{C},\psi^{SC},\psi^{Sc},p^{C},r^{C},p^{S}$	8	405.88	17.29	0.00
$\psi^{C},\psi^{SC},p^{C},p^{S}$	6	405.95	17.35	0.00
Temporada lluvia 2019				
$\psi^{C},\psi^{SC},p^{C},r^{C},p^{S},r^{Sc}$	8	598.78	0.00	0.43
$\psi^{C},\psi^{SC},p^{C},r^{C},p^{S},r^{Sc},r^{SC}$	9	599.31	0.53	0.33
$\psi^{C},\psi^{SC},\psi^{Sc},p^{C},p^{S},r^{Sc},r^{SC}$	9	600.93	2.15	0.15
$\psi^{C},\psi^{SC},\psi^{Sc},p^{C},r^{C},p^{S},r^{Sc},r^{SC}$	10	602.17	3.39	0.08
$\psi^{C},\psi^{SC},p^{C},p^{S}$	6	606.02	7.24	0.01
$\psi^{C},\psi^{SC},\psi^{Sc},p^{C},p^{S}$	7	607.43	8.65	0.01
Temporada seca 2020				
$\psi^{C},\psi^{SC},p^{C},p^{S}$	6	222.39	0.00	0.66
$\psi^{C},\psi^{SC},\psi^{Sc},p^{C},p^{S}$	7	224.35	1.96	0.25
$\psi^{C},\psi^{SC},p^{C},r^{C},p^{S},r^{Sc}$	8	227.19	4.80	0.06
$\psi^{C},\psi^{SC},p^{C},r^{C},p^{S},r^{Sc},r^{SC}$	9	229.73	7.34	0.02
$\psi^{C},\psi^{SC},\psi^{Sc},p^{C},p^{S},r^{Sc},r^{SC}$	9	230.13	7.74	0.01
$\psi^{C},\psi^{SC},\psi^{Sc},p^{C},p^{S},r^{Sc},r^{SC}$	9	231.19	8.80	0.01

[1] Los nombres de los parámetros se muestran en el Apéndice I.

Figuras

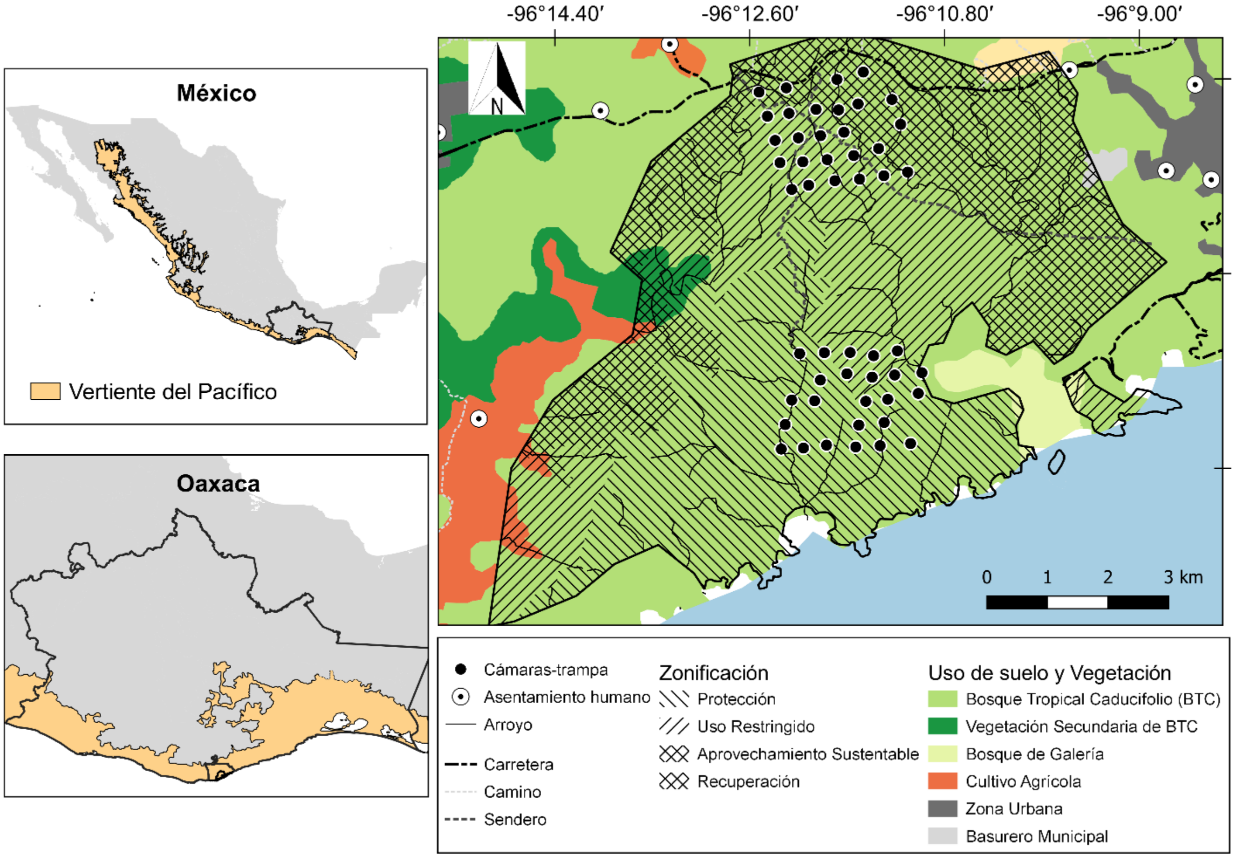

Figura 1. Localización del Parque Nacional Huatulco en la porción central de la costa del estado de Oaxaca, en el sureste de México y disposición de las estaciones de cámaras-trampa en el bosque tropical caducifolio del área natural protegida.

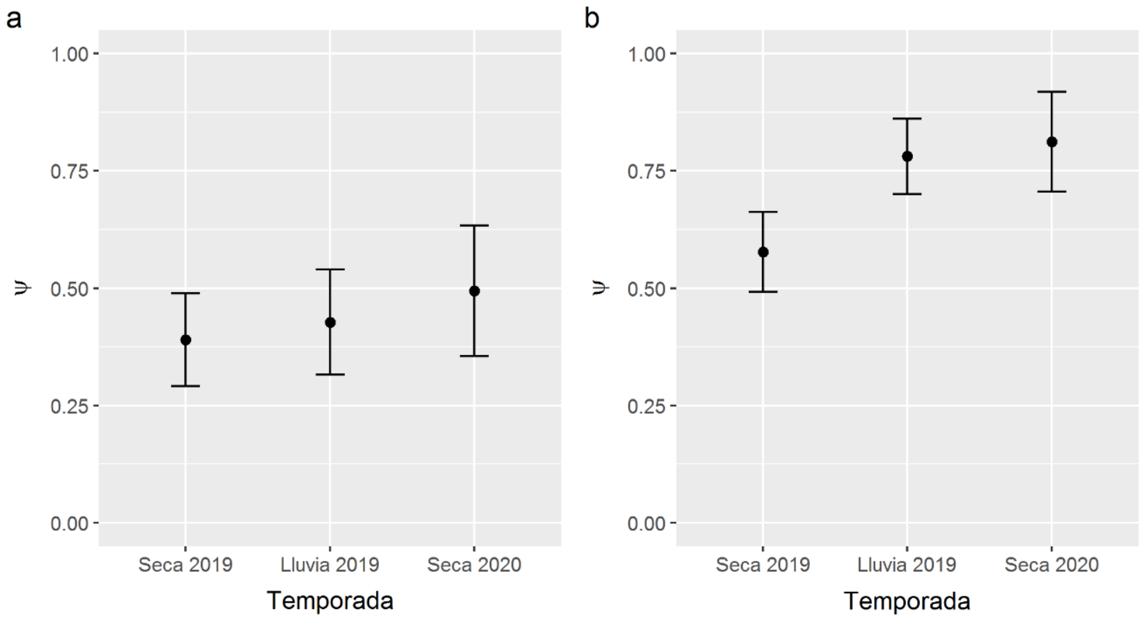

Figura 2. Tendencia de la probabilidad de ocupación estimada para *Conepatus leuconotus* (a) y *Spilogale pygmaea* (b) durante tres temporadas muestreadas en el Parque Nacional Huatulco, Oaxaca, México, de 2018 a 2020.

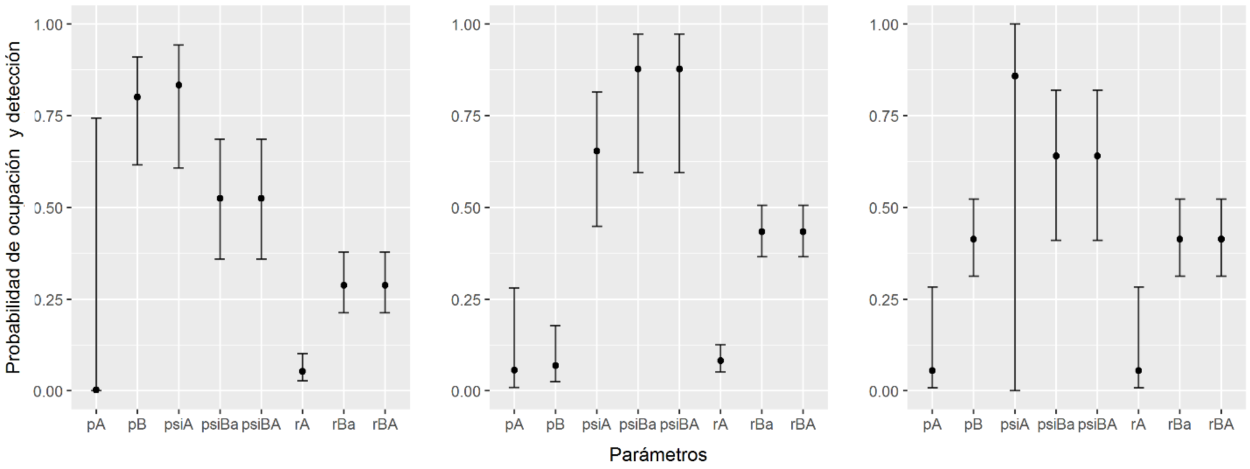

Figura 3. Probabilidad de ocupación (ψ) y de detección (p, r) estimados a partir de los modelos de co-ocurrencia de *Conepatus leuconotus* y *Spilogale pygmaea* en el Parque Nacional Huatulco, Oaxaca, México. Los nombres de los parámetros se muestran en el Apéndice I.

Apéndice I. Parámetros estimados para el modelo de ocupación de dos especies para una sola temporada entre *Conepatus leuconotus* y *Spilogale pygmaea*. Modificado de Richmond et al. (2010).

Parámetro	Descripción
ψ^{C}	Probabilidad de ocupación de *C. leuconotus*
ψ^{SC}	Probabilidad de ocupación de *S. pygmaea* cuando *C. leuconotus* esté presente
ψ^{Sc}	Probabilidad de ocupación de *S. pygmaea* cuando *C. leuconotus* esté ausente
p^{C}	Probabilidad de detección de *C. leuconotus* cuando *S. pygmaea* esté ausente
p^{S}	Probabilidad de detección de *S. pygmaea* cuando *C. leuconotus* esté ausente
r^{C}	Probabilidad de detección de *C. leuconotus* cuando *S. pygmaea* esté presente
r^{SC}	Probabilidad de detección de *S. pygmaea* cuando *C. leuconotus* esté presente y sea detectado
r^{Sc}	Probabilidad de detección de *S. pygmaea* cuando *C. leuconotus* esté presente y no sea detectado

Apéndice II. Modelos candidatos ajustados para determinar las covariables que mejor explican la probabilidad de detección, ocupación, colonización y extinción de *Conepatus leuconotus* y *Spilogale pygmaea* en el bosque tropical caducifolio del Parque Nacional Huatulco, Oaxaca, México.

Apéndice 2A. Modelos candidatos ajustados para determinar las covariables que explican mejor la probabilidad de detección de *Conepatus leuconotus* y *Spilogale pygmaea*. K = Número de parámetros; AICc = Criterio de Información de Akaike ajustado para muestras pequeñas; ΔAICc = diferencia del AICc de cada modelo con el mejor modelo; ω = peso del modelo.

Modelos candidatos	K	AICc	ΔAICc	ω	Modelos candidatos	K	AICc	ΔAICc	ω
Conepatus leuconotus					*Spilogale pygmaea*				
$p_{(.)}$	4	285.22	0.00	0.33	$p_{(\text{Ilun})}$	5	790.72	0.00	0.46
$p_{(\text{Ilun})}$	5	286.51	1.29	0.17	$p_{(\text{Temp+Ilun})}$	6	792.66	1.95	0.17
$p_{(\text{Prec})}$	5	287.09	1.87	0.13	$p_{(\text{Prec+Ilun})}$	6	792.71	2.00	0.17
$p_{(\text{Temp})}$	5	287.09	1.88	0.13	$p_{(.)}$	4	794.55	3.83	0.07
$p_{(\text{Prec+Ilun})}$	6	288.20	2.98	0.08	$p_{(\text{Temp+Prec+Ilum})}$	7	794.66	3.95	0.06
$p_{(\text{Temp+Ilun})}$	6	288.21	2.99	0.07	$p_{(\text{Prec})}$	5	796.12	5.40	0.03
$p_{(\text{Temp+Prec})}$	6	289.04	3.83	0.05	$p_{(\text{Temp})}$	5	796.43	5.71	0.03
$p_{(\text{Temp+Prec+Ilum})}$	7	290.09	4.87	0.03	$p_{(\text{Temp+Prec})}$	6	798.12	7.40	0.01

Apéndice 2B. Modelos candidatos ajustados para determinar las covariables que explican mejor la probabilidad de ocupación de *Conepatus leuconotus* y *Spilogale pygmaea*. K = Número de parámetros; AICc = Criterio de Información de Akaike ajustado para muestras pequeñas; ΔAICc = diferencia del AICc de cada modelo con el mejor modelo; ω = peso del modelo.

Modelos candidatos	K	AICc	ΔAICc	ω	Modelos candidatos	K	AICc	ΔAICc	ω
Conepatus leuconotus					*Spilogale pygmaea*				
$\psi_{(\text{Vishor+Humsue+Disagua})}$	7	265.83	0.00	0.81	$\psi_{(\text{Humsue+Disagua+Dispre})}$	8	768.62	0.00	0.69
$\psi_{(\text{Humsue+Disagua})}$	6	269.18	3.36	0.15	$\psi_{(\text{Madri+Humsue+Disagua+Dispre})}$	9	770.20	1.58	0.31
$\psi_{(\text{Madri+MNDWI+Disagua+Dispre})}$	8	272.09	6.26	0.04	$\psi_{(\text{Disagua+Dispre+Ocuoce+Disbas})}$	9	781.13	12.52	0.00

ψ(Vishor+Pend)	6	278.30	12.47	0.00	ψ(Disbas)	6	785.30	16.68	0.00
ψ(Dispob+Discar+Discul+Disbas+Disavn+Dispanp)	10	278.58	12.75	0.00	ψ(Ocuoce+Ocuper)	7	787.12	18.50	0.00
ψ(Cobarb+Vishor+Cobdos+NDVI+Pend)	9	281.44	15.62	0.00	ψ(Ocuoce+Ocucoy+Ocuper)	8	788.60	19.98	0.00
ψ(Ocuper)	5	285.10	19.27	0.00	ψ(Vishor+Cobarb)	7	789.78	21.16	0.00
ψ(.)	4	285.22	19.39	0.00	ψ(Dispob+Discar+Discul+Disbas+Disavn+Dispanp)	11	789.98	21.37	0.00
ψ(Ocuoce+Ocucoy+Ocuper)	7	287.93	22.11	0.00	ψ(.)	5	790.72	22.10	0.00
					ψ(Cobarb+Vishor+Cobdos+NDVI+Pend)	10	795.63	27.02	0.00

Apéndice 2C. Modelos candidatos ajustados para determinar las covariables que explican mejor la probabilidad de colonización y extinción de *Conepatus leuconotus* y *Spilogale pygmaea*. K = Número de parámetros; AICc = Criterio de Información de Akaike ajustado para muestras pequeñas; ΔAICc = diferencia del AICc de cada modelo con el mejor modelo; ω = peso del modelo.

Modelos candidatos	K	AICc	ΔAICc	ω	Modelos candidatos	K	AICc	ΔAICc	ω
Conepatus leuconotus					*Spilogale pygmaea*				
γ(Madri+Disagua) ε(.)	9	262.85	0.00	0.44	γ(Ocuper+Ocucoy) ε(Cobarb+Madri)	12	761.62	0.00	0.60
γ(Disagua+Cobarb) ε(.)	9	265.64	2.79	0.11	γ(Ocuoce+Ocucoy+Ocuper) ε(.)	11	764.38	2.76	0.15
γ(Disagua) ε(Madri)	9	265.64	2.79	0.11	γ(Ocuper+Ocucoy) ε(Ocuoce)	11	764.56	2.94	0.14
γ(.) ε(.)	7	265.83	2.97	0.10	γ(.) ε(Madri+Cobarb)	10	767.00	5.37	0.04
γ(Cobarb+Vishor) ε(NDVI)	10	265.86	3.00	0.10	γ(.) ε(Madri)	9	767.79	6.16	0.03
γ(Ocuoce+Ocucoy+Ocuper) ε(.)	10	266.36	3.50	0.08	γ(Disagua) ε(Madri)	10	768.61	6.99	0.02
γ(.) ε(Ocuoce+Ocucoy+Ocuper)	10	269.12	6.27	0.02	γ(.) ε(.)	8	768.62	7.00	0.02
γ(Ocucoy) ε(Ocucoy)	9	269.41	6.56	0.02	γ(Cobarb+Vishor) ε(Cobarb+Cobdos)	12	771.26	9.64	0.00
γ(.) ε(Madri+Humsue+Disagua+Dispre)	11	270.43	7.58	0.01	γ(.) ε(Cobarb+Vishor+Cobdos+NDVI)	12	772.24	10.62	0.00
γ(.) ε(Cobarb+Vishor+Cobdos+NDVI)	11	271.69	8.84	0.01	γ(.) ε(Ocuoce+Ocucoy+Ocuper)	11	772.38	10.76	0.00
γ(Cobarb+Vishor+Cobdos+NDVI) ε(.)	11	271.75	8.90	0.01	γ(Cobarb+Vishor+Cobdos+NDVI) ε(.)	12	773.04	11.42	0.00
γ(Madri+Dispre) ε(Disagua+Humsue)	11	275.62	12.76	0.00	γ(.) ε(Madri+Humsue+Disagua+Dispre)	12	773.72	12.10	0.00
					γ(Madri+Humsue+Disagua+Dispre) ε(.)	12	774.62	13.00	0.00

CAPÍTULO V

AVAILABILITY OF ALTERNATIVE PREY RATHER THAN INTRAGUILD INTERACTIONS DETERMINE LOCAL ABUNDANCE OF UNDERSTUDIED AND THREATENED SMALL CARNIVORES

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Availability of alternative prey rather than intraguild interactions determines the local abundance of understudied and threatened small carnivores

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Abstract

Intraguild interactions, including competition and predation, influence the structure and local dynamics of carnivore mammals' assemblages. The potential effects of these interactions are primarily determined by the body size of carnivores and may result in inverse relationships in abundance between competing members and, ultimately, lead to the exclusion or coexistence of species. The relative importance of interspecific interactions along with landscape characteristics in determining population patterns of currently declining sympatric small carnivores, such as skunks, remains poorly documented. Therefore, we assessed the spatio-temporal variation in the relative abundance of American hog-nosed skunks *Conepatus leuconotus* and pygmy spotted skunks *Spilogale pygmaea* and the effect of interspecific interactions, resource availability, and habitat complexity on their local abundance in areas with the deciduous tropical forest at Huatulco National Park, south of the Mexican Pacific slope. We used presence-absence data for skunk species from three camera-trapping surveys at two study sites from 2018 to 2020 in combination with Royle-Nichols occupancy models fitted in a Bayesian framework to estimate abundance, incorporating the effects of covariates related to the factors evaluated. We analyzed the relationship between the abundance of skunks with Generalized Linear Models. Both species showed significant differences in their abundances between seasons and between study sites. Overall, pygmy skunks were more abundant than hog-nosed skunks. We found negative relationships among the relative abundances of skunks during the dry seasons, but no evidence that local abundance is governed by the competitive dominance of the larger species. Patterns of skunk abundance were better explained by prey availability and other predictors related to habitat complexity rather than interspecific interactions, with the highest predictive accuracies of the models and strong positive and negative relationships. Our study highlights the underlying factors that determine the local abundance of these understudied and threatened small carnivores, allowing us to better understand the conditions necessary to maintain and recover their populations and the mechanisms that govern their coexistence for effective management and conservation of species in seasonal tropical environments.

Keywords: American hog-nosed skunks, conservation, deciduous tropical forest, Huatulco National Park, pygmy spotted skunks, Royle-Nichols model.

Introduction

Mammalian carnivores play a key role in structuring and local dynamics of ecological communities in terrestrial systems, since these species not only regulate prey populations but may also affect other members of the group through the top-down effects (Linnell and Strand, 2000; Ritchie and Johnson, 2009). Therefore, carnivores may act as competitors and predators of one another at the same trophic level (Holt and Polis, 1997; Fedriani et al., 2000), meaning that intraguild interactions have the potential to shape carnivore assemblages (Palomares and Caro, 1999; Donadio and Buskirk, 2006; Oliveira and Pereira, 2014).

Intraguild interactions can result in exploitative competition when species compete indirectly for shared resources or interference competition in which one species is directly agonistic towards another through aggressive behaviors (Linnell and Strand, 2000), or the death (intraguild predation; Polis et al., 1989; Holt and Polis, 1997). These competitive interactions often occur between species with high diet overlap during periods of food scarcity (Wiens, 1993; Palomares and Caro, 1999; Donadio and Buskirk, 2006) and can lead to either the exclusion of one species or the coexistence of both competitors (Holt and Polis, 1997; Linnell and Strand, 2000). The outcomes of the interference competition are strongly determined by the body size of the carnivores (Donadio and Buskirk, 2006), with generally asymmetrical interactions where the smaller member almost invariably occupies the subordinate position (Palomares and Caro, 1999; Linnell and Strand, 2000). Additionally, the strength of competition is more intense between same-family species pairs at intermediate and large differences in body size (Donadio and Buskirk, 2006).

Large carnivores can suppress populations of mesocarnivores and mesocarnivores in turn suppress smaller carnivores through resource competition, intraguild predation or killing, and fear-driven spillovers (Palomares and Caro, 1999; Ritchie and Johnson, 2009; Oliveira and Pereira, 2014; Prugh and Sivy, 2020). The effects of these interactions result in inverse relationships between the abundances of competing carnivores (Mac Nally, 1983; Linnell and Strand, 2000; Prugh and Sivy 2020), with reduced densities of subordinate species (Fedriani et al., 2000; Roemer et al., 2002; Oliveira et al., 2010; Wikenros et al., 2017; Fowler et al., 2021) and, ultimately, may lead to their local extinction (Crooks and Soulé, 1999; Ritchie and Johnson, 2009). For example, some canids show a clear negative relationship in their relative abundances in regions of North America (Fedriani et al., 2000; Levi and Wilmers, 2012; Fowler et al., 2021). Densities observed in small neotropical felids are also lower in areas of South America where the largest member of the guild, ocelot *Leopardus pardalis*, is abundant (Di Bitetti et al., 2010; Oliveira et al., 2010). The effects of interference competition, however, decrease when the dominant competitor is absent or in low numbers, and consequently, subordinate carnivores may reach high densities (Roemer et al. 2002; Jones et al., 2008; Oliveira et al., 2010; Jensen and Humphries, 2019). Nevertheless, the abundance of potential competitors could also reflect associations with food availability or differences in habitat preference and, thus, show weak evidence for competitive interactions (Glen and Dickman, 2008; Kalle et al., 2014; Wikenros et al., 2017).

Although agonistic encounters between small carnivores have been considered relatively insignificant (Hunter and Caro, 2008), some studies have documented interspecific interactions involving members of the family Mephitidae (Patton, 1974; Hass and Dragoo, 2018; Pérez-Irineo et al., 2020). In addition, skunks are under particularly high potential predation pressure (Hunter and Caro, 2008; Oliveira and Pereira, 2014). The American hog-nosed skunk *Conepatus leuconotus* (1.1-4.5 kg; hereafter hog-nosed skunks) and the pygmy spotted skunk *Spilogale pygmaea* (0.1-0.3 kg; hereafter pygmy skunks) overlap widely in their ranges within the Mexican Pacific slope (Dragoo, 2009; Ceballos and Martinez, 2010). Both species feed mainly on insects and some small vertebrates when insect availability is low (Cantú-Salazar et al., 2005; Dragoo and Sheffield, 2009), and are found in habitats with vegetation cover but can use open areas (Medellín et al., 1998; Cervantes et al., 2002; Dragoo and Sheffield, 2009). Specifically, they inhabit the deciduous tropical forest in this region (Cantú-Salazar et al., 2009; Pérez-Irineo et al., 2020), an ecosystem with marked environmental seasonality and temporal changes in resource availability and vegetation structure (Valenzuela and Macdonald, 2002; Palacios-Vargas et al., 2007; Trejo, 2010). In this regard, hog-nosed skunks and pygmy skunks share similar ecological attributes that may predispose them to intraguild interactions in a seasonal environment with periods of resources scarcity, so this natural system provides the opportunity to investigate the possible effects of interspecific competition on the abundance of sympatric species. Likely, intraguild dynamics are also influenced by the presence of mesocarnivores (e.g., ocelots, coyotes *Canis latrans*), which may act as top predators in some areas where large carnivores are absent (Briones-Salas et al., 2016), affecting negatively to populations of skunks through intraguild predation.

To date, scarce data are available on the abundance of these skunk species in Mexico, despite their populations being in decline (Helgen, 2016; Helgen et al., 2016). Some research has recorded inverse temporal variations between densities of hog-nosed skunks and hooded skunks

Mephitis macroura in seasonal tropical habitats (Cervantes et al., 2002; Lorenzo et al., 2005; Farías-González and Hernández-Mendoza, 2021), and others suggests that the large-sized species determines the dynamics of the interactions between skunks when presenting a high relative abundance (Farías-González and Hernández-Mendoza, 2021). In other assemblages, however, there is also evidence that the subordinate skunk could have some competitive dominance by being in higher numbers (Hass and Dragoo, 2018). Despite the above, the relative importance of interspecific interactions along with landscape characteristics in determining abundance patterns of skunks remains poorly documented. Data provided by camera traps in combination with novel hierarchical modeling approaches allow to estimate the abundance of species and increase the ecological information of unmarked animal populations (Kalle et al., 2014; Burton et al., 2015; Gilbert et al., 2021). The Royle-Nichols models are a suitable alternative for estimating population size from detection-non-detection data, accounting for imperfect detection and incorporating covariate effects to avoid biased estimates (Royle and Nichols, 2003; MacKenzie et al., 2018).

Knowledge of the underlying ecological factors that affect the abundance of small carnivores will allow us to understand the mechanisms that govern the coexistence of species for effective management and conservation of understudied and threatened skunks in seasonal environments. The goals of our study were to assess the abundance and spatio-temporal variation of hog-nosed skunks and pygmy skunks and to assess the effect of interspecific interactions, resources availability, and habitat complexity on their local abundance in areas with deciduous tropical forest within the southern region of the Mexican Pacific slope. Based on the effect of body size and taxonomic relationship on competitive interactions in carnivores (Palomares and Caro, 1999; Donadio and Burskik, 2006) and the intraguild dynamics between skunks in similar habitats (Farías-González and Hernández-Mendoza, 2021), we hypothesized that hog-nosed skunks (large-sized species) would be more abundant than pygmy skunks (smaller species) and we predicted negative relationship in abundance among skunks, which may vary with population changes in the dominant competitor. We also expected that intraguild predation would have a negative effect on the local abundance of skunks due to the potentially high predation risk of these species (Hunter and Caro, 2008). The effects of these interactions could be more evident during the dry season, when they are more likely to occur by resource scarcity (Palomares and Caro, 1999; Donadio and Buskirk, 2006). Alternatively, we hypothesized that resource availability and habitat structure would be more influential than intraguild interactions on the abundance of skunks.

Materials and Methods

Study area. The study was carried out in the Huatulco National Park (15°39'12"-15°47'10" N, 96°06'30"-96°15'00" W), located within the municipality of Santa María Huatulco on the coast of the state of Oaxaca, south of the Mexican Pacific slope (Fig. 1; CONANP, 2003). The Huatulco National Park has 6,374.98 ha of land area (CONANP, 2003), and is part of Priority Terrestrial Region No. 129 Sierra Sur and Costa de Oaxaca (Arriaga et al., 2000). Climate is warm subhumid with rains in summer, characterized by lower humidity and strong seasonality (Trejo, 2004). The average annual temperature fluctuates between 26-28°C and annual precipitation varies between 800-1,200 mm, with the rainy season occurring from June to October and the dry season from November to May (CONANP, 2003; Trejo, 2004). The predominant type of vegetation is the deciduous tropical forest (Salas-Morales et al., 2007), which presents natural elements that stand out nationally and internationally for their conservation (CONANP, 2003). This protected area harbor to one of the last well-conserved fragments of this vegetation (CONANP, 2003). It is also harbors native and exotic mesopredators such as coyotes and ocelots (Lira et al. 2008; Briones-Salas et al., 2016) and feral dogs *C. lupus familiaris* (Guzmán Pacheco, 2019), respectively; but it is virtually free of top predators, as the cougar *Puma concolor* has not been recorded for more than 10 years (Lira et al., 2008).

Definition of sampling sites. We defined two sampling sites based on the zoning of the Protected Natural Area, one in the protection zone and the other between the sustainable harvesting and recovery zones (hereafter disturbed zone). A detailed description of the zones is shown in Hernández-Sánchez and Santos-Moreno (2022). The sampling sites have a similar deciduous tropical forest floristic composition and are separated by a linear distance of 3 km (distance between the closest sampling stations of both sites). We considered the sampling sites to be independent based on published home range data for hog-nosed skunks (0.64-1.94 km^2; Brashear et al., 2015) and pygmy skunks (0.20 km^2; Cantú-Salazar et al., 1999).

Camera trap survey. We carried out a systematic survey with camera traps from November 2018 to October 2020 to record the presence-absence of skunk species in the two study areas. We installed 30 camera trap stations in each area following a grid sampling design of 6 x 5 stations, with a regular spacing of 420 m apart. However, several camera traps were stolen and only 48 stations in total operated (Fig. 1). The sampling design was defined based on estimates of the home range of pygmy skunks (Cantú-Salazar et al., 1999) and population densities of hog-nosed skunks in similar environments (0.5-1.3 ind/km^2; Cervantes et al., 2002; Lorenzo et al., 2005). All sampling stations consisted of a camera trap unbaited, which was placed on the trees approximately 20-30 cm above the ground in the inside of the forest. We used four camera trap models: Bushnell Trophy Cam® and Bushnell Trophy Cam w/Viewscreen® (Bushnell Outdoor Products, Overland Park, Kansas), ERE-E1 (EREAGLE Technology Co., Ltd, Shenzhen, China), and Moultrie 990i Digital Game Camera (Moultrie Products, LLC, Birmingham, Alabama). Camera traps were configured to take a three-photo burst and/or record one 10-15 s video for each trigger event (with a 10-s delay between consecutive events), to remain active 24 h every day, and to record the date and time on all photos and videos. Data processing and creation of detection histories for both species of skunks were performed with the R package *CamtrapR* (Niedballa et al., 2016).

Predictive covariates. Based on previous research on the ecology of the focal and similar species (Cervantes et al., 2002; Brashear et al., 2015; Hass and Dragoo, 2018; Farías-González and Hernández-Mendoza, 2021), we compiled information on covariates that could influence their abundances in the study area. We selected a set of biologically important predictor variables to model the abundance of each skunk, including four variables related to interspecific interactions, four to resource availability, and two to habitat complexity (details on covariate calculations in Table 1). Covariate values were recorded at each camera trap station and obtained using field and remote sensing methods from geographic information systems. Vegetation structure measurements were taken in 20 x 20 m sampling quadrants centered on the location of each camera trap and in 4 x 4 m sub-quadrants located at the corners and center of each quadrant (Higgins et al., 1996; Mostacedo and Fredericksen, 2000). Additionally, we selected three covariates for modeling the probability of detection of the species of skunks (Table 1).

All continuous covariates were standardized (mean = 0; standard deviation = 1) before analysis to facilitate the comparison of model estimates and allow improved parameter estimation and interpretation of relative effect sizes (Kéry and Royle, 2016). We tested multicollinearity between predictor variables using the variance inflation factor (VIF) in the R package *HH* (Heiberger, 2022). We considered evidence of collinearity between covariates with VIF values > 5 (Zuur et al., 2010; Heiberger and Holland, 2015), and in this case, we excluded highly collinear predictors from the same models.

Modeling framework. We used the Royle-Nichols model (hereafter R-N model) to estimate the abundance of skunk species from detection-non-detection data (Royle and Nichols, 2003). The

R-N model considers the heterogeneity in site-specific detectability to be derived from variation in local abundance, i.e., it is an occupancy model of abundance-induced heterogeneity (Royle and Nichols, 2003; Kéry and Royle, 2016; MacKenzie et al., 2018). The relationship between heterogeneous detection probability and abundance is $P_{ij}=1-(1-r_j)^{N_i}$, where p_{ij} is the probability of detecting the species at site i, r_j is the probability of detecting an individual, and N_i is the number of individuals at site i (Royle and Nichols, 2003; MacKenzie et al., 2018). In this way, the R-N model provides estimators of the parameters λ and r, which are defined as the average abundance per site and the detection probability, respectively (Royle and Nichols, 2003).

The R-N model assumes that the population is demographically closed (the population size must not change during the study period), the detection of an animal at a site is independent of the detection of any other animal, and the detection probability is equal for all individuals (Royle and Nichols, 2003; MacKenzie et al., 2018). Due to the fact that the sampling was carried out over two years, we considered three surveys of 120 consecutive trap-nights each to take into account the populations closure in the analysis, which corresponded to three climatic seasons studied: dry season 2019, rainy season 2019 and dry season 2020 (Table 2). We pooled the data into 12 trap-night intervals with a total of 10 sampling occasions per survey. The R-N model requires spatial independence of the sampling stations, meaning that the camera traps must be far enough apart that they do not detect the same individuals (Gilbert et al., 2021). Given that the distance between camera trap stations was less than the home range diameter of hog-nosed skunks, we suspected a violation of the assumption of independent detections for this species. Therefore, we interpreted abundance in relative rather than absolute terms, as suggested by other authors when model assumptions are not met (Stanley and Royle, 2005; Thorn et al., 2011; Gilbert et al., 2021). However, even as relative abundance, this model explains the observation process by adjusting for detection probability (Dénes et al., 2015; Kéry and Royle, 2016) and provides reliable estimates with sample sizes ≤ 100 sites and > 5 sampling occasions (Royle and Nichols, 2003; MacKenzie et al., 2018).

We followed a two-stage modeling approach for building the candidate models of each skunk species. We first identified the best model for the detection probability while holding the average abundance per site constant. We modeled detection probability without covariates (null model) and as a function of sampling effort and lunar illumination, one model with each individually and another with both covariates. In the second stage, we built the models for the average abundance, fixing the best-supported detection model. By our hypotheses, we designed three subsets of models to explain the abundance of species by variables related to: (a) interspecific interactions, (b) resource availability and habitat complexity, or (c) a combination of both. We fit biologically plausible models on each subset, including the individual and combined effects of the covariates shown in Table 1. The structure of the models was similar for both species to facilitate their comparison.

We run all models with the R package *Ubms* version 1.1.0 (Kellner, 2021), in which R-N models are fitted in a Bayesian framework using the programming language Stan (Carpenter et al. 2017). Fitting models in a Bayesian framework is recommended when datasets have small sample sizes, few detections, and low detection probabilities (Kéry and Schaub, 2012; Kéry and Royle, 2016), as is the case for hog-nosed skunks. We used the default "uninformative" priors for the abundance parameters (intercept and regression coefficients) of the R-N model (Kellner, 2021; Kellner et al. 2022). Bayesian models were run using three Markov Chain Monte Carlo chains of 2,000 iterations each, with a burn-in of 1,000 iterations per chain. Since Ubms uses Stan's modeling language, a low number of iterations are required to reach model convergence and obtain stable parameter estimates (Hoffman and Gelman, 2014; Carpenter et al., 2017). Model convergence was assessed by verifying that the Gelman-Rubin (R-hat) diagnostic statistic was equal to 1 for each parameter and by visually examining the model traceplots (Gelman et al., 2014; Kellner et al., 2022). We estimated 95% Bayesian credible intervals (BCIs) of the posterior distribution to determine the significance of covariate effects. We considered a covariate to have strong support if the 95% BCIs of its coefficient did not overlap with zero (Kéry and Royle, 2016).

We performed the selection of candidate models within and between subsets of each species using leave-one-out cross-validation for pairwise model comparisons (LOO-CV; Vehtari et al., 2017) in the package Ubms (Kellner, 2021). Candidate models were ranked in descending order of their expected log pointwise predictive density (elpd), which estimates the predictive accuracy of the models (Vehtari et al., 2017). We calculated the differences in elpd between each model and the superior model (Δelpd), the standard errors of these differences (SE [Δelpd]), and the model weights, analogous to the Akaike Information Criterion weights (Vehtari et al., 2017). We interpreted that the model with the largest elpd performed better, and we considered the top model to have more support than another model if the absolute difference in elpd was greater than the standard error of that difference (Vehtari et al., 2017; Kellner, 2021). We tested the fit of the top-ranked model with the MacKenzie-Bailey X^2 goodness-of-fit test for occupancy models (MacKenzie and Bailey, 2004), using posterior predictive checks (Kellner, 2021; Kellner et al., 2022). Bayesian P-values close to 0.5 indicated that the model fits well (Kéry and Royle, 2016; Kellner, 2021). Finally, we generated response curves for the covariates included in the top-ranked models (marginal effects plots) for both skunks.

Abundance analysis. We estimated the mean abundance of hog-nosed skunks and pygmy skunks for the three surveyed seasons and two study areas from the predicted parameter values in the best-fit R-N models. Before statistical comparison of species abundance, we performed exploratory analyzes of the data and removed outlier observations. We compared the differences in abundances of both skunks between seasons in each study area and between study areas. We used the non-parametric Mann-Whitney-Wilcoxon (W) and Kruskal-Wallis (H) tests when two or more unpaired groups were compared (Zar, 1999), respectively. If significance was found in the Kruskal-Wallis test, we used the Mann-Whitney test post-hoc for pairwise group comparisons with a significance level correction. Additionally, we considered that the R-N model fitted in a Bayesian framework may provide reasonable estimates of the absolute abundance of pygmy skunks, so we estimated the population density of the species with the formula λ*R/Effective area of sampling, where λ is the average number of individuals per site and R is the number of sites sampled (Royle and Nichols, 2003).

We analyzed the relationship in abundances among skunks with a Generalized Linear Model with gamma error distribution and an inverse link function (Bolker, 2008; Korner-Nievergelt et al., 2015). This model is suitable for continuous variables with positive values (from zero to infinity) and right-skewed kurtosis (Bolker, 2008), as is the case of population abundance. We fitted the gamma regression models using the glm function. All data analyzes were performed with the statistical software R (Development Core Team, 2020).

Results

Abundance of skunks. Average abundance per site of hog-nosed skunks showed statistical differences between seasons in both, the disturbed zone (H = 18.52, d.f. = 2, $P < 0.001$) and the protection zone (W = 421, $P < 0.001$), being significantly higher during the dry season 2019 in both areas (Fig. 2). In contrast, the average abundance per site of pygmy skunks did not vary between seasons in the disturbed zone (H = 4.47, d.f. = 2, P = 0.11), but showed differences in the protection zone (W = 0, P < 0.001), with high abundance during the rainy season 2019 (Fig. 2). Between study areas, average abundance per site differed significantly for hog-nosed skunks (W = 2841, P < 0.001) and pygmy skunks (W = 1865, P = 0.004). Both species showed higher abundance in the disturbance zone (Fig. 2). The population density of pygmy skunks ranged from 1.31 ind/km^2 during the dry season 2019 in the protection zone to 10.62 ind/km^2 during the rainy season 2019 in the disturbed zone.

The relationship between the abundance of pygmy skunks and hog-nosed skunks was negative but not significant (P > 0.63) during the 2019 and 2020 dry seasons in the disturbed zone (Fig. 3). In contrast, the relationship in abundance between skunks was positive and significant during the rainy season 2019 both in the disturbed zone (β = -0.05, P = 0.004) and in the protection zone (β = -0.27, P < 0.001; Fig. 3). Skunk abundances showed a positive but not significant relationship during the dry season 2019 in the protection zone (β = -5.03, P = 0.14; Fig. 3).

Factors affecting the detection and abundance of skunks. The null models had the highest predictive accuracy and were the best-supported models for the detection probability of hog-nosed skunks in the 2019 and 2020 dry seasons, while the model that included the sampling effort had the highest predictive accuracy in the rainy season 2019 (Table S1). The full model had similar predictive accuracy to the top model in the rainy season (pairwise Δelpd was smaller than its SE[Δelpd]), but its weight was low (ω = 0.37). Models that included lunar illumination and sampling effort showed the highest predictive accuracy and were the best-supported models for the detection probability of pygmy skunks in the rainy season 2019 and dry season 2020, respectively (Table S1). Meanwhile, all candidate models had similar predictive accuracy in the dry season 2019 and, therefore, the null model was considered our better explanation of the detectability of the species (Table S1).

Overall, the models that only included covariates related to resource availability and habitat complexity and the models that combined the above covariates with those of interspecific interactions showed the highest predictive accuracies and were the best supported in explaining the average abundance per site of both skunks (Table S2). The subset of models that only included interspecific interaction covariates showed the lowest predictive accuracy (Table S2). The top-ranked model that explained hog-nosed skunk abundance during the dry season 2019 and the rainy season 2019 had larger pairwise Δelpd than its SE[Δelpd], with a model weight equal to 1 (Table 3). All candidate models were similar in predictive accuracy during the 2020 dry season, but the top-ranked model had a much higher model weight than the others (ω = 0.72). The top-ranked model explaining pygmy skunk abundance during the dry season 2020 had larger pairwise Δelpd than its SE[Δelpd] and a model weight equal to 1, while the two best-supported models during the dry season 2019 and the rainy season 2019 showed similar predictive accuracy, although the top model had a much higher model weight in both cases (ω > 0.65; Table 3). All of the top-ranked models showed acceptable fit based on posterior predictive checks, with Bayesian p-values of 0.53-0.67 for hog-nosed skunks and 0.25-0.42 for pygmy skunks.

Distance to the nearest water source (β = 1.23, BIC = 0.28–2.42) in the dry season 2019 and the availability of small mammals (β = 0.88, BIC = 0.29–1.49) in the rainy season 2019 had a strong positive effect, while soil humidity (β = -1.29, BIC = -2.64–-0.25) and canopy cover (β = -1.04, BIC = -1.74–-0.43) in the rainy season 2019 showed a strong negative effect on the abundance of hog-nosed skunks (Fig. 4 and Fig. 5). Shrub cover (β = -1.36, BIC = -3.55–0.29) and coyote presence (β = -1.11, BIC = -2.71–0.04) had a negative effect but without strong support (their 95% BICs were overlapped with zero) to explain the abundance of this species in the dry season 2020 (Fig. 4). On the other hand, the availability of small mammals had a strong positive effect on the abundance of pygmy skunks in the dry season 2019 (β = 0.63, BIC = 0.36–0.89), rainy season 2019 (β = 0.65, BIC = 0.48–0.83), and in the dry season 2020 (β = 0.56, BIC = 0.10–0.99). The abundance of this species was also positively related to the distance to the nearest water source in the dry season 2019 (β = 0.75, BIC = 0.27–1.29) but negatively related to the shrub cover in the dry season 2020 (β = -1.65, BIC = -2.86–-0.50), both relationships showed strong support (Fig. 4 and Fig. 5). Distance to the nearest water source (β = -0.24, BIC = -0.51–0.04) and presence of coyotes (β = -0.33, BIC = -0.72–0.00) had a negative effect but without strong support for explain the abundance of pygmy skunks in the rainy season 2019 (Fig. 4).

Detectability of hog-nosed skunks was positively related to sampling effort in the rainy season 2019 (β = 1.32, BIC = -0.06–2.81), although the relationship did not show strong support (Fig. 4). Meanwhile, detectability of pygmy skunks strongly decreased with lunar illumination in the rainy season 2019 (β = -0.23, BIC = -0.46–-0.01) and with sampling effort in the dry season 2020 (β = -0.69, BIC = -1.30–-0.12, Fig. 4). The detection probability of hog-nosed skunks and pygmy skunks ranged from 0.02–0.09 and 0.11–0.20, respectively.

Discussion

There is a paucity of published information documenting the abundance and variation over space and time of American hog-nosed skunks and pygmy spotted skunks throughout their range, as well as possible ecological factors that may affect them (Meaney et al., 2006; Dragoo, 2009). In this regard, our research contributes to the knowledge of population ecology and provides data on the relative importance of underlying factors that determine the abundance patterns of both skunks, which coexist sympatrically in a seasonal tropical forest at Huatulco National Park within the Mexican Pacific slope.

The estimated abundance of skunk species showed spatio-temporal variations in our study area. The population dynamics of hog-nosed skunks was similar compared to what was recorded in the Superior Lagoon of the Isthmus of Tehuantepec, Mexico (Cervantes et al., 2002) with a significantly higher abundance during the dry season, but it differed from that of the Tehuacán-Cuicatlán Biosphere Reserve, Mexico, where this species was more abundant during the rainy season (Farías-González and Hernández-Mendoza, 2021). Similarly, the dynamics of pygmy skunk abundance appears to be consistent with results found in populations of southern spotted skunks *S. angustifrons* in the Inferior Lagoon of the Isthmus of Tehuantepec, Mexico (Lorenzo et al., 2005) with higher abundance during the rainy season, although it contrasts with some observations for this similar species in other seasonal tropical forest regions (Cervantes et al., 2002; Farías-González and Hernández-Mendoza, 2021). However, unlike previous studies of spotted skunks (Cervantes et al., 2002; Lorenzo et al., 2005; Farías-González and Hernández-Mendoza, 2021; Harris et al., 2021), we recorded significant seasonal differences in the abundance of pygmy skunks, at least in the protection zone.

While the disparity in the abundance estimates for both skunks could be due to methodological and data analysis aspects, the R-N models adjusted in a Bayesian framework allowed us to reliably estimate this population parameter when taking into account the sample size, the number of detections, and the detection probability of the species (Royle and Nichols, 2003; Kéry and Royle, 2016). Although we interpreted our results as relative abundance for hog-nosed skunks, this species likely has relatively low abundance because its detection rates were low (r = 0.02–0.09) during the seasons surveyed at the Huatulco National Park, even though the bias can be 10-15% for detectability less than 0.1 (Royle and Nichols, 2003; MacKenzie et al., 2018). In contrast, estimates of abundance expressed as population density for pygmy skunks were higher than those for southern skunks in the Isthmus of Tehuantepec (< 0.6 ind/km^2, Cervantes et al., 2002; Lorenzo et al., 2005), but are within the range of recorded densities for other spotted skunks in regions of the United States, such as the island skunks *S. gracilis amphiala* (9.0-19.0 ind/km^2, Jones et al., 2008) and eastern skunks *S. putorius* (5.02 ind/km^2─Crabb 1948; 6.52-23.29 ind/km^2─Harris et al., 2021). This finding suggests that pygmy skunks may be locally abundant in conserved and low-disturbance areas, although further abundance estimates are unfortunately not available and are therefore required elsewhere in the species' range.

Several authors have speculated that interspecific interactions are a potential factor that may determine changes in abundance of sympatric skunks (Patton, 1974; Meaney et al., 2006; Farías-González and Hernández-Mendoza, 2021; Harris et al., 2021). Nevertheless, the relative importance of its effects has not been explicitly evaluated, with some exceptions (Roemer et al., 2002; Hass and Dragoo, 2018). Previous studies have recognized an apparent inverse relationship in abundances between skunk species (Patton, 1974; Farías-González and Hernández-Mendoza, 2021) and between skunks and other small carnivores (Roemer et al., 2002; Jones et al., 2008) as a possible result of interference competition in seasonal environments. Our results partially supported the predicted hypotheses since, as expected, we observed negative but not significant relationships between the relative abundances of the studied species during the dry seasons 2019 and 2020 in the disturbance zone at Huatulco National Park. Hog-nosed skunks, however, were similar to or slightly more abundant than pygmy skunks in this season, so we found weak evidence that local abundance is governed by competitive dominance by larger-sized species. In other mephitid assemblages, larger species such as hog-nosed skunks or striped skunks *M. mephitis* are present in higher numbers and determine the dynamics of intraguild interactions with smaller members (Patton, 1974; Farías-González and Hernández-Mendoza, 2021), which contrasts with what was recorded in the study area.

Our models, on the other hand, also revealed that the relative abundances of both skunks were positively and significantly related during the rainy season in both the disturbance and protection zones, with a higher abundance of pygmy skunks. This relationship possibly reflected reduced interference competition, where the subordinate species could be the dominant member of the guild by being more abundant as has been suggested for island spotted skunks and hooded skunks in regions of the United States (Jones et al., 2008; Hass and Dragoo, 2018). Despite there being changes in population demographics, we did not find evidence that one species limited the populations of the other and, in fact, the R-N models that only included covariates of interspecific interactions, such as the presence of the competing skunk, showed the lowest predictive accuracies. We also did not observe or record direct encounters between skunk species during fieldwork or in camera traps in the deciduous tropical forest of our study area and, therefore, inconsistency or rarity of interference may prevent the occurrence of a true competition (Mac Nally, 1983). In addition, other research has documented that hog-nosed skunks, hooded skunks, and southern spotted skunks may roam or feed nearby without physical interactions (Cervantes et al., 2002).

The abundance of potential competitors could also reflect associations with food availability or differences in habitat preference (Glen and Dickman, 2008; Kalle et al., 2014; Winkeros et al., 2017), as suggested in sympatric skunks (Cervantes et al., 2002; Lorenzo et al., 2005; Farías-González and Hernández-Mendoza, 2021). The availability of small mammals (mice and small marsupials) had a strong positive effect on the relative abundance of skunk species during the seasons surveyed at Huatulco National Park. Small mammals are considered alternative prey for hog-nosed skunks and pygmy skunks in periods of insect scarcity (Cantú-Salazar et al., 2005; Dragoo and Sheffield, 2009), and the consistently high importance of its effects indicates a continued availability of this type of prey. The spiny pocket mouse *Heteromys pictus* was the predominant rodent in the deciduous tropical forest of the study area, with higher densities during the rainy season (unpublished data), which is consistent with population studies of this species in areas surrounding the coast of Oaxaca, Mexico (Briones-Salas and González, 2016). Although both skunks can switch food sources in response to fluctuations in prey abundance, pygmy skunks have morphological adaptations that allow them to more efficiently exploit small mammalian prey (Medellín et al., 1998; Dragoo, 2009). They are likely to have gained a competitive advantage, similar to other small carnivores (Jones et al., 2008; Jensen and Humphries, 2019), at least to acquire this prey and play a role as a superior exploitative competitor on the shared resource in an environment seasonal (Holt and Polis, 1997). This possibly explain why the availability of small mammals was the most important driver of abundance for this species according to the best-ranked models. Overall, our findings support that food availability leads to spatio-temporal variations in the abundance of skunk species (Lorenzo et al., 2005; Jones et al., 2008; Harris et al., 2021), and if so, it may decrease the potential for competitive interactions (Petersen et al., 2019; Dick et al., 2021).

Other bottom-up predictors also contributed to the observed patterns to explain the abundance of species, including strong associations both positive with distance to the nearest water source in both skunks and negative with NDVI in hog-nosed skunks and with shrub cover in pygmy skunks. The higher abundance of the species in the sites furthest from the water bodies in our study area may be due to the increased probability of negative interactions between species in areas close to them during periods of water scarcity (Rosenstock et al., 2004; Perera-Romero et al., 2021). Intraguild predation particularly has a negative impact on small carnivore populations (Palomares and Caro, 1999; Oliveira and Pereira, 2014; Prugh and Sivy, 2020), so the abundance of skunks may represent a trade-off between the need to satisfy their requirements of water and avoid lethal encounters with potential predators. Furthermore, both species are likely able to obtain water from their food in arid and seasonal tropical regions (Cantú-Salazar et al., 2005; Meaney et al., 2006; Dragoo, 2009).

The R-N models with better predictive accuracy also indicated that hog-nosed skunks and pygmy skunks were more abundant in areas with less tree cover in the rainy season and less shrub cover in the dry season, respectively. These relationships could be largely explained by the fact that skunks have anal scent glands and contrasting aposematic coloration that act as antipredator defense mechanisms (Hunter and Caro, 2008; Dragoo, 2009), which more successfully deter terrestrial predators such as coyotes in open areas where skunks are more susceptible to ambush attacks (Stankowich et al., 2014; Fisher and Stankowich, 2018). While nocturnal avian predators such as owls are another important source of mortality for skunks (Lesmeister et al., 2010; Fisher and Stankowich, 2018). The species we studied were more active on cloudier nights (Hernández-Sánchez and Santos-Moreno, 2022) or showed greater detectability when there was less lunar illumination, conditions that presumably offer some protection against these predators. Therefore, it is likely that skunk predation by terrestrial and aerial predators is not frequent enough and that skunk abundance is higher in areas with less vegetation cover, either tree or shrub, depending on seasonality.

Conservation implications

Populations of the hog-nosed skunks and pygmy skunks are currently experiencing a decline, attributed primarily to habitat loss and interspecific interactions (Helgen, 2016; Helgen et al., 2016). Our data corroborate this population trend for hog-nosed skunks while showing a high density for threatened and endemic species such as pygmy skunks. Nevertheless, this study also provides information on the underlying factors that determine the local abundance of these species, which allows us to improve our understanding of the conditions necessary to maintain or recover their populations and the mechanisms that govern their coexistence in the deciduous tropical forest at the Huatulco National Park. Direct or indirect human-induced changes may also have cascading effects on skunk populations in this seasonal environment and, thus, management and conservation programs require the inclusion of both ecological and anthropogenic factors that affect the abundance of these threatened and understudied carnivores in this protected natural area (e.g. presence of feral dogs). Further studies are needed to assess how temporal changes in resource availability, habitat complexity, and communities of competitors and predators (native and exotic) might influence this parameter in other regions where both species are sympatric, and to assess the long-term population dynamics and trends of species.

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Tables

Table 1. Biologically important selected covariates and their predicted effects on modeling the abundance and detection probability of skunk species.

Covariates	Abbrev	Description	Range	Prediction
Abundance				
Interspecific interactions				
Presence of competitors	competitor	Number of independent records (>1 h apart) of American hog-nosed skunks (*Conepatus leuconotus*) or pygmy spotted skunks (*Spilogale pygmaea*)	0-2 0-58	Abundance of the subordinate competitor will decrease with the presence of the dominant competitor
Presence of coyotes	coyotes	Number of independent records (>1 h apart) of coyotes (*Canis latrans*) per site	0-17	Abundance will decrease with the presence of coyotes, a potential predator of skunks
Presence of dogs	dogs	Number of independent records (>1 h apart) of dogs (*Canis lupus familiaris*) per site	0-12	Abundance will decrease with the presence of dogs, a potential exotic predator of skunks
Presence of ocelots	ocelots	Number of independent records (>1 h apart) of ocelots (*Leopardus pardalis*) per site	0-76	Abundance will decrease with the presence of ocelots, a potential predator of skunks
Resource availability/ Habitat complexity				
Potential burrows	burrows	Number of potential burrows within each sampling quadrant with an entrance ≥ 5 cm in diameter for pygmy skunks and ≥ 15 cm for hog-nosed skunks (obs. pers.; Reid 2016)	3-45 0-22	Abundance will be greater in sites with a greater number of potential burrows.
Availability of small mammals	avasmam	Relationship between the number of independent records (> 1 h of difference) of small mammals (rodents and marsupials < 1 kg in weight) and the sampling effort for each camera trap station multiplied by 100	0-31.67	Abundance will increase with higher availability of small mammals, considered as potential prey (Cantú-Salazar et al., 2005; Dragoo and Sheffield, 2009).

Soil humidity (as proxy for litter arthropod availability)	soilhum	Mean Modified Normalized Difference Water Index (MNDWI) values in a 200 m radius circular buffer around each sampling station, estimated from Landsat 8 satellite images atmospherically corrected with QGIS 3.4.6 software (QGIS Development Team, 2020). Satellite images were downloaded from the United States Geological Survey	-0.61-0.51	Abundance will be greater in sites with higher soil humidity, due to its direct relationship with the diversity and abundance of insects (Palacios-Vargas et al., 2007)
Distance to the nearest water source	diswater	Euclidean distance from the camera trap stations to the nearest water source (stream, pond, or waterhole) in the study area. The distances were estimated based on the MNDVI, which also allows mapping of water bodies (Xu, 2006)	0.10-7.53 km	Abundance will be higher closer to water sources
Shrub cover	shrcover	Estimation of the shrub cover from the maximum (d1) and perpendicular (d2) lengths of the shrub crowns using the formula: $CA = \Sigma (\pi * (1/4 [d1 + d2])^2)$. Measurements were taken in the five sampling sub-quadrants	0.44-99.94 m^2	Abundance will be higher in sites with higher shrub cover.
Canopy cover	cancover	Average Normalized Difference Vegetation Index (NDVI) values calculated in a 200 m radius circular buffer around each sampling station from corrected Landsat 8 satellite images	0.38-0.88	Abundance will be higher at sites with higher canopy cover
Detection				
Sampling effort	effort	Number of nights each camera trap station was active	27-120	Higher sampling effort values will increase the detection rate of skunks
Lunar illumination	lunillu	Average values of lunar illumination for each sampling occasion estimated with the R package *suncalc* (Thieurmel and Elmarhraoui, 2019)	0-1	Brighter nights should increase the detection rate of hog-nosed skunks or decrease that of pygmy skunks, consistent with reports from similar species (Zapata-Ríos and Branch 2018; Benson et al. 2019)

Table 2. Details of the three surveys considered and number of detections of skunk species during each surveyed season in the study areas at Huatulco National Park within the Mexican Pacific slope.

Study areas	Survey	Surveyed period	Number of camera trap stations	Trap-nights	Number of detections	
					American hog-nosed skunk	Pygmy spotted skunk
Disturbed zone	Dry season 2019	Dec 1, 2018-Mar 30, 2019	26	2,585	10	106
	Rainy season 2019	Jun 1, 2019-Sep 28, 2019	26	2,836	24	121
	Dry season 2020	Nov 19, 2019-Mar 17, 2020	24	1,795	7	62
Protection zone	Dry season 2019	Dec 13, 2018-Apr 11, 2019	21	1,613	0	30
	Rainy season 2019	Jun 13, 2019-Oct 10, 2019	22	1,868	3	62

Table 3. Selection of best-supported candidate models from model subsets explaining the abundance of skunk species in each surveyed season using leave-one-out cross-validation for pairwise model comparisons. elpd = expected log pointwise predictive density; Δelpd = pairwise differences in elpd (relative to the top model); SE[Δelpd] = standard error of Δelpd; ω = model weight. Letters in the "subset" column denote the set of covariates of the model evaluated for abundance: interspecific interactions (a), resource availability and habitat complexity (b), and a combination of both subsets (c).

Survey	Subset	Model*	elpd	Δelpd	SE [Δelpd]	ω
American hog-nosed skunk						
Dry season 2019	b	$r_{(.)}\lambda_{(\text{diswater})}$	-41.220	0.000	0.000	1.000
	c	$r_{(.)}\lambda_{(\text{diswater + coyotes + ocelots})}$	-42.011	-0.791	0.330	0.000
	Null	$r_{(.)}\lambda_{(.)}$	-43.878	-2.658	1.457	0.000
	a	$r_{(.)}\lambda_{(\text{coyotes})}$	-44.533	-3.312	1.610	0.000
Rainy season 2019	c	$r_{(\text{effort})}\lambda_{(\text{cancover + avamam + soilhum + ocelots})}$	-72.760	0.000	0.000	1.000
	b	$r_{(\text{effort})}\lambda_{(\text{cancover + avamam + soilhum})}$	-73.593	-0.833	0.664	0.000
	Null	$r_{(\text{effort})}\lambda_{(.)}$	-80.118	-7.358	2.138	0.000
	a	$r_{(\text{effort})}\lambda_{(\text{ocelots})}$	-80.569	-7.809	2.181	0.000
Dry season 2020	c	$r_{(.)}\lambda_{(\text{shrcover + coyotes})}$	-29.581	0.000	0.000	0.715
	a	$r_{(.)}\lambda_{(\text{coyotes})}$	-30.002	-0.421	1.053	0.000
	Null	$r_{(.)}\lambda_{(.)}$	-30.120	-0.539	1.706	0.285
	b	$r_{(.)}\lambda_{(\text{shrcover})}$	-30.229	-0.649	1.612	0.000
Pygmy spotted skunk						
Dry season 2019	b	$r_{(.)}\lambda_{(\text{avamam + diswater})}$	-143.540	0.000	0.000	0.648
	c	$r_{(.)}\lambda_{(\text{avamam + diswater + ocelots})}$	-143.865	-0.325	1.737	0.243
	a	$r_{(.)}\lambda_{(\text{ocelots})}$	-151.631	-8.091	5.096	0.109
	Null	$r_{(.)}\lambda_{(.)}$	-152.581	-9.041	4.839	0.000
Rainy season 2019	c	$r_{(\text{lunillu})}\lambda_{(\text{avamam + diswater + coyotes})}$	-193.257	0.000	0.000	0.702
	b	$r_{(\text{lunillu})}\lambda_{(\text{avamam + diswater})}$	-193.933	-0.676	2.118	0.298
	Null	$r_{(\text{lunillu})}\lambda_{(.)}$	-211.041	-17.784	5.896	0.000
	a	$r_{(\text{lunillu})}\lambda_{(\text{coyotes})}$	-211.149	-17.892	6.009	0.000
Dry season 2020	b	$r_{(\text{effort})}\lambda_{(\text{shrcover + avamam})}$	-72.616	0.000	0.000	1.000
	c	$r_{(\text{effort})}\lambda_{(\text{shrcover + avamam + coyotes})}$	-73.298	-0.682	0.591	0.000
	a	$r_{(\text{effort})}\lambda_{(\text{coyotes})}$	-77.968	-5.352	2.683	0.000
	Null	$r_{(\text{effort})}\lambda_{(.)}$	-79.545	-6.929	2.247	0.000

* The abbreviations of the covariates in the candidate models are shown in Table 1.

Figures

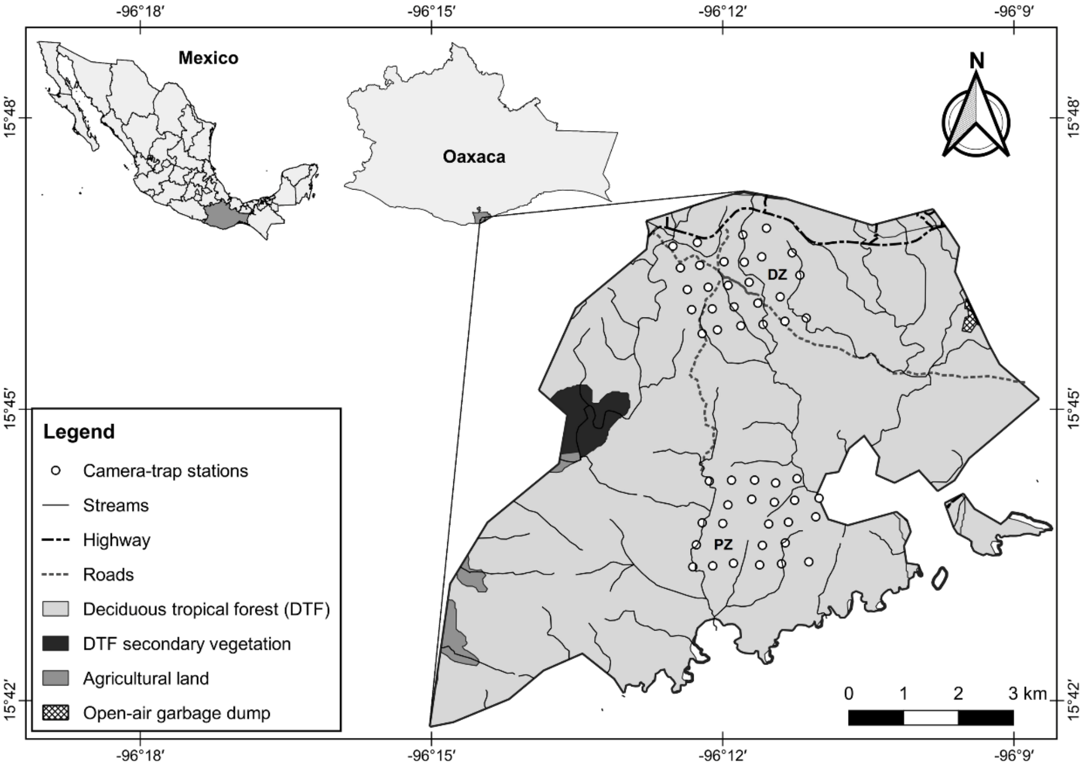

Figure 1. Location of the camera trap stations inside the tropical deciduous forest in the disturbed zone (DZ) and protection zone (PZ) at the Huatulco National Park, Oaxaca, Mexico.

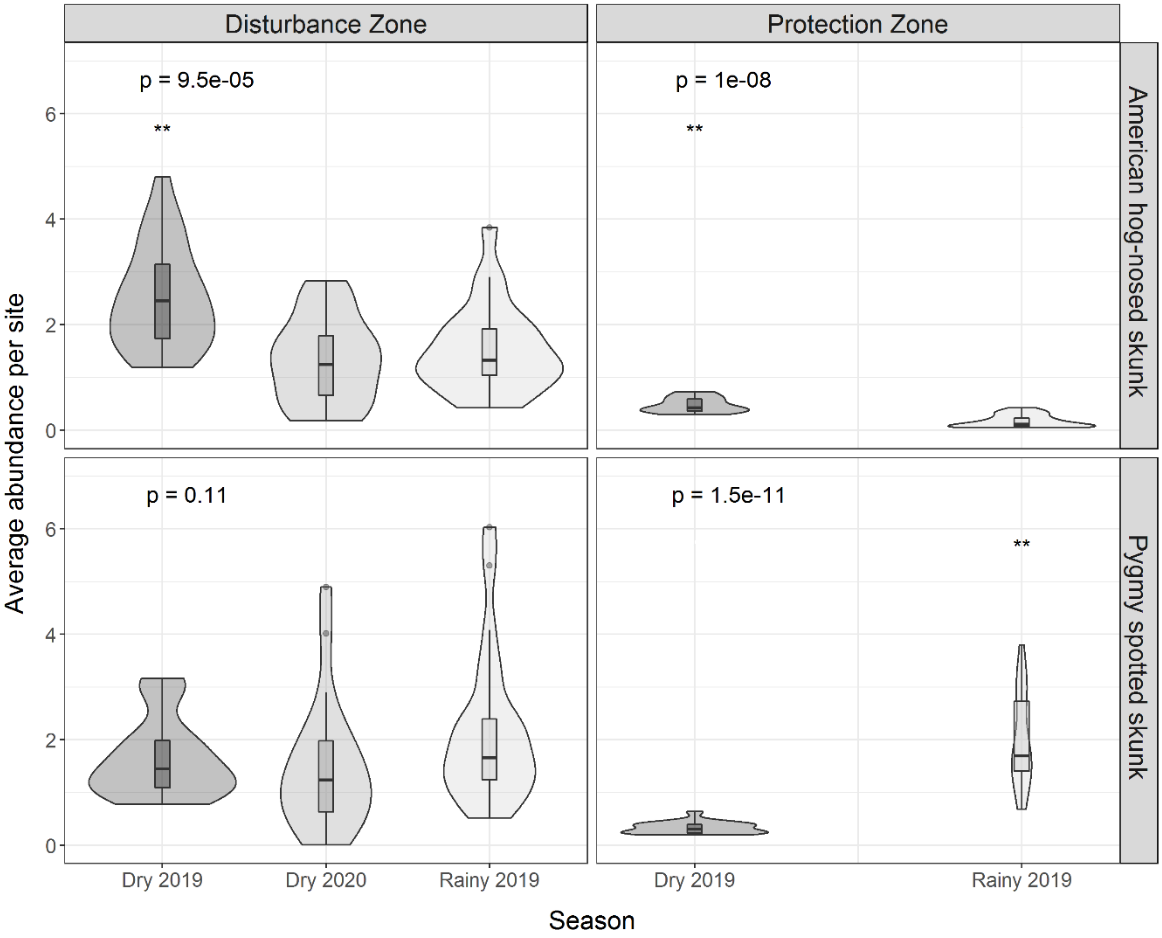

Figure 2. Predicted average abundances per site for skunk species during the surveyed seasons in each study area using the Royle-Nichols model fitted in a Bayesian framework at Huatulco National Park on the Mexican Pacific slope. The significance level of the differences in abundance is shown in each panel; asterisks indicate statistically different estimates.

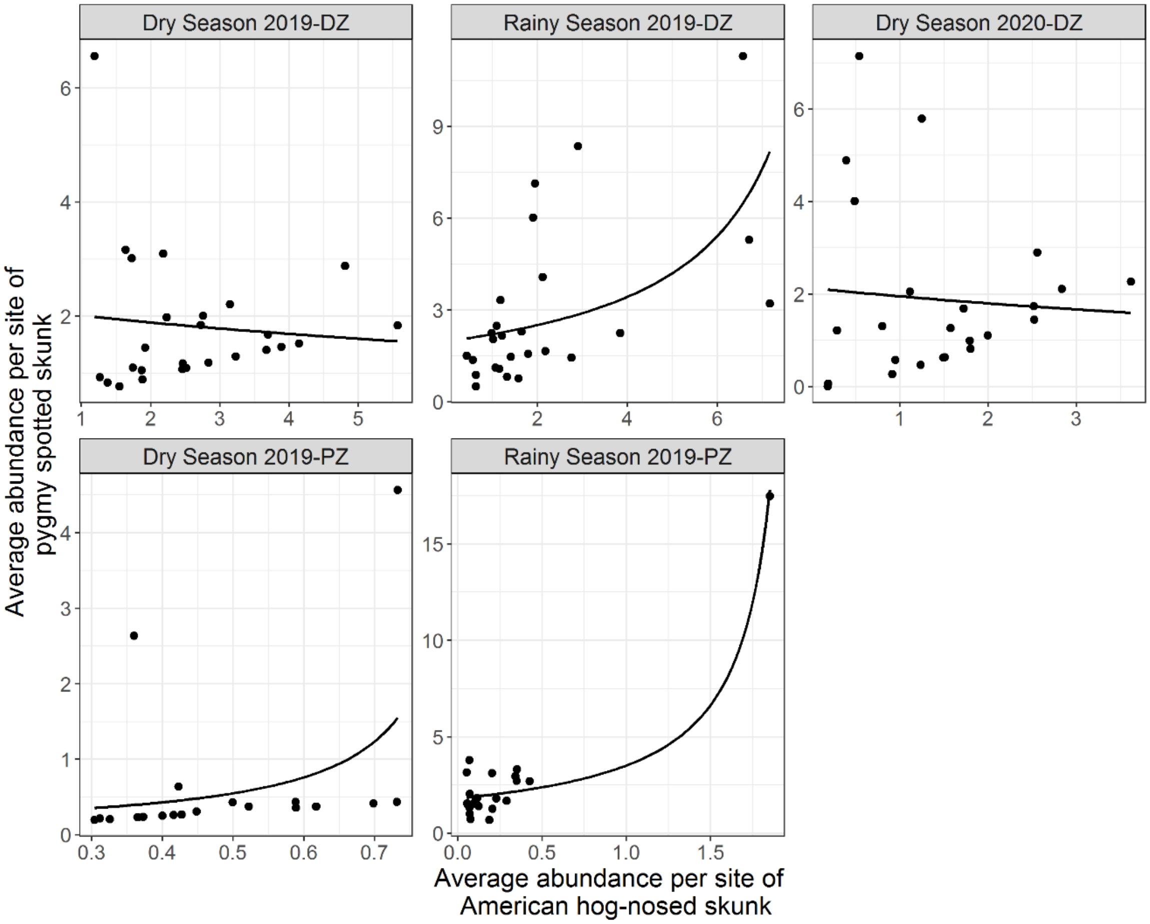

Figure 3. Relationships in average abundance per site between pygmy skunks and hog-nosed skunks during the surveyed seasons in the disturbed (DZ) and protected (PZ) zones at Huatulco National Park on the Mexican Pacific slope.

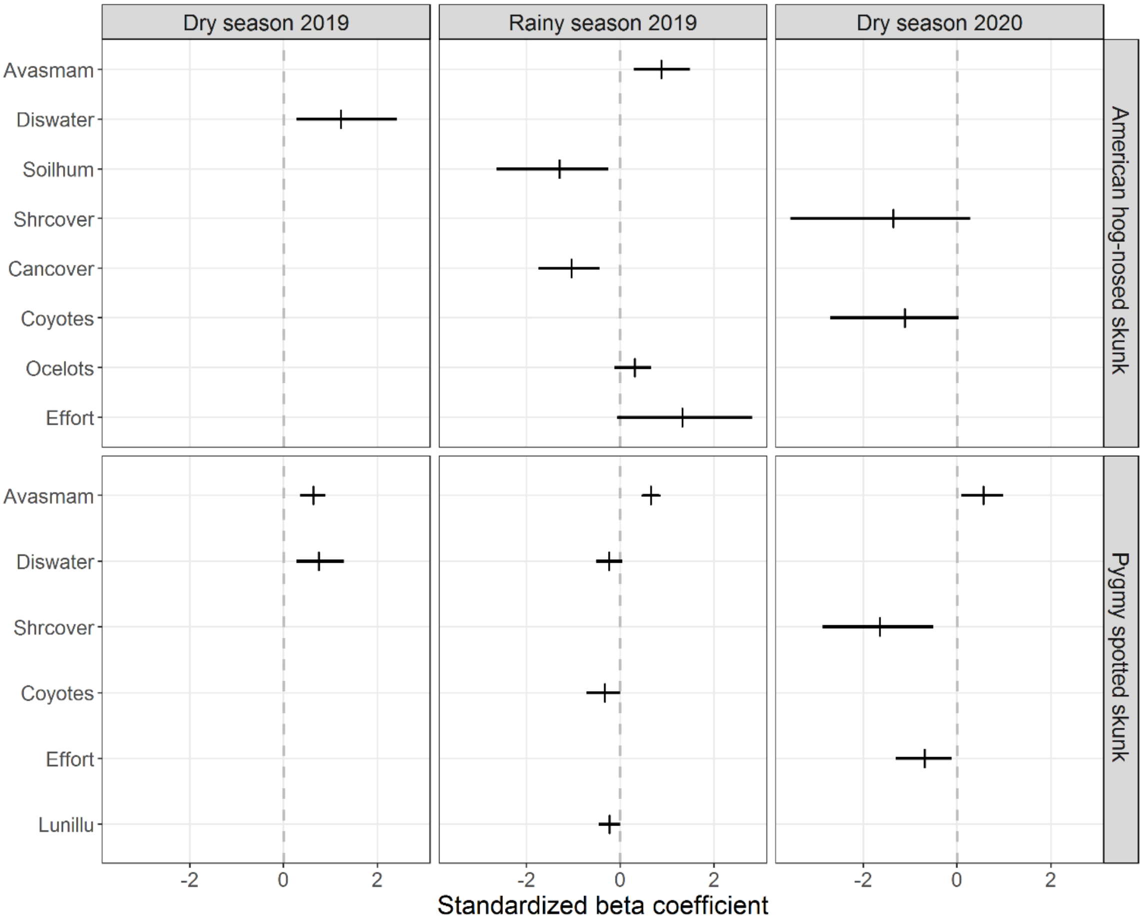

Figure 4. Standardized beta coefficients showing the covariates effect from best-ranked models on the abundance of skunk species in the seasons surveyed. Covariates had a strong effect on abundance if the 95% Bayesian credible interval (BCI) of its coefficients did not overlap with zero. The vertical lines indicate the means and the horizontal lines are 95% BCIs of the beta coefficients.

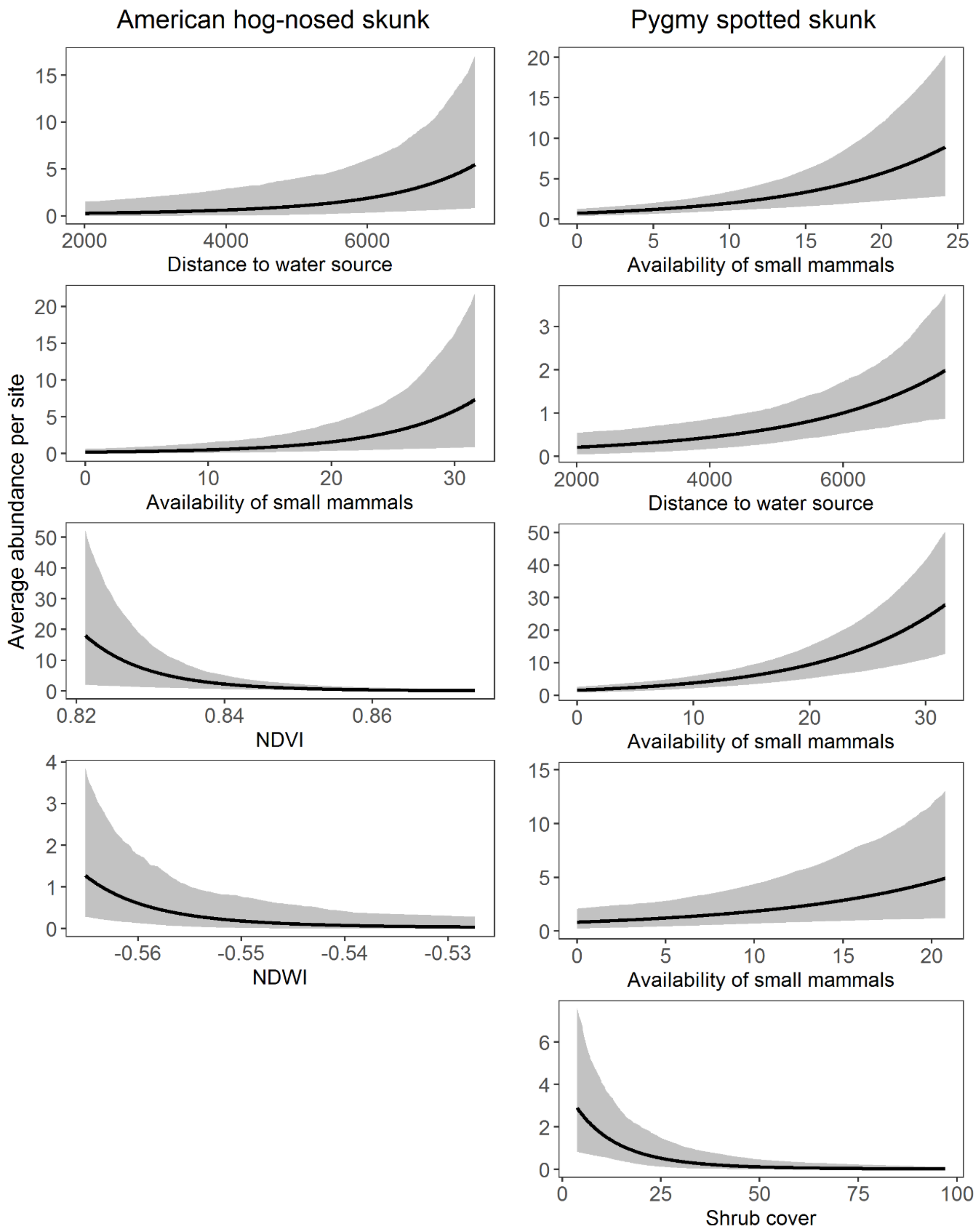

Figure 5. Marginal effects plots of strongly supported covariates (95% credible intervals do not include 0) generated from top-ranked models on the abundance of skunk species in the seasons surveyed. For each plot, the focal covariate varies across its range of original values. The bold lines indicate posterior means and the ribbons are 95% credible intervals.

Supplementary Data

Table S1. Selection of candidate models explaining detection probability of skunk species in each surveyed season using leave-one-out cross-validation for pairwise model comparisons. elpd = expected log pointwise predictive density; Δelpd = pairwise differences in elpd (relative to the top model); SE[Δelpd] = standard error of Δelpd; ω = model weight.

Survey	American hog-nosed skunk					Pygmy spotted skunk				
	Model*	elpd	Δelpd	SE [Δelpd]	ω	Model*	elpd	Δelpd	SE [Δelpd]	ω
Dry season 2019	$r_{(.)}$	-43.833	0.000	0.000	1.000	$r_{(\text{effort + lunillu})}$	-152.012	0.000	0.000	0.528
	$r_{(\text{effort})}$	-44.624	-0.791	0.275	0.000	$r_{(\text{effort})}$	-152.119	-0.107	1.120	0.074
	$r_{(\text{lunillu})}$	-44.907	-1.074	0.650	0.000	$r_{(\text{lunillu})}$	-152.158	-0.145	2.620	0.135
	$r_{(\text{effort + lunillu})}$	-45.830	-1.997	0.803	0.000	$r_{(.)}$	-152.581	-0.569	2.996	0.263
Rainy season 2019	$r_{(\text{effort})}$	-79.999	0.000	0.000	0.633	$r_{(\text{lunillu})}$	-211.041	0.000	0.000	0.942
	$r_{(\text{effort + lunillu})}$	-80.320	-0.321	1.473	0.367	$r_{(\text{effort + lunillu})}$	-211.494	-0.453	1.029	0.058
	$r_{(.)}$	-81.597	-1.598	1.115	0.000	$r_{(.)}$	-212.604	-1.563	1.437	0.000
	$r_{(\text{lunillu})}$	-82.116	-2.117	1.228	0.000	$r_{(\text{effort})}$	-212.732	-1.690	1.633	0.000
Dry season 2020	$r_{(.)}$	-30.030	0.000	0.000	1.000	$r_{(\text{effort})}$	-79.492	0.000	0.000	0.939
	$r_{(\text{lunillu})}$	-30.695	-0.666	0.290	0.000	$r_{(\text{effort + lunillu})}$	-80.462	-0.971	0.347	0.000
	$r_{(\text{effort})}$	-30.945	-0.916	0.393	0.000	$r_{(.)}$	-80.760	-1.269	1.772	0.061
	$r_{(\text{effort + lunillu})}$	-31.558	-1.528	0.539	0.000	$r_{(\text{lunillu})}$	-81.485	-1.993	1.791	0.000

[*] The abbreviations of the covariates in the candidate models are shown in Table 1.

Table S2. Selection of candidate models of a priori hypotheses explaining abundance of skunk species by covariates related to interspecific interactions, resource availability and habitat complexity, and a combination of both subsets in each surveyed season using leave-one-out cross-validation for pairwise model comparisons. elpd = expected log pointwise predictive density; Δelpd = pairwise differences in elpd (relative to the top model); SE[Δelpd] = standard error of Δelpd; ω = model weight.

	American hog-nosed skunk					Pygmy spotted skunk				
Survey	Model*	elpd	Δelpd	SE [Δelpd]	ω	Model*	elpd	Δelpd	SE [Δelpd]	ω
Dry season 2019	*Interespecific interactions*									
	$\lambda_{\text{(coyotes)}}$	-44.533	0.000	0.000	0.555	$\lambda_{\text{(ocelots)}}$	-151.631	0.000	0.000	0.534
	$\lambda_{\text{(competitor)}}$	-44.657	-0.124	1.139	0.445	$\lambda_{\text{(competitor)}}$	-151.894	-0.264	3.205	0.465
	$\lambda_{\text{(ocelots)}}$	-44.869	-0.336	0.714	0.000	$\lambda_{\text{(coyotes + ocelots)}}$	-152.651	-1.020	0.319	0.000
	$\lambda_{\text{(dogs)}}$	-44.956	-0.424	0.793	0.000	$\lambda_{\text{(dogs)}}$	-152.852	-1.221	2.716	0.000
	$\lambda_{\text{(coyotes + ocelots)}}$	-45.215	-0.682	0.617	0.000	$\lambda_{\text{(coyotes + ocelots + dogs)}}$	-152.903	-1.272	0.764	0.000
	$\lambda_{\text{(coyotes + ocelots + dogs)}}$	-46.380	-1.848	0.983	0.000	$\lambda_{\text{(coyotes)}}$	-153.460	-1.830	2.341	0.000
	$\lambda_{\text{(competitor + coyotes + ocelots + dogs)}}$	-46.830	-2.298	1.426	0.000	$\lambda_{\text{(competitor + coyotes + ocelots + dogs)}}$	-153.785	-2.154	2.773	0.000
	Resource availability and habitat complexity									
	$\lambda_{\text{(diswater)}}$	-41.220	0.000	0.000	1.000	$\lambda_{\text{(avasmam + diswater)}}$	-143.540	0.000	0.000	0.680
	$\lambda_{\text{(shrcover + cancover + burrows + avasmam + soilhum + diswater)}}$	-43.366	-2.146	1.804	0.000	$\lambda_{\text{(burrows + avasmam + soilhum + diswater)}}$	-146.205	-2.665	2.002	0.000
	$\lambda_{\text{(burrows + avasmam + soilhum + diswater)}}$	-43.375	-2.155	1.032	0.000	$\lambda_{\text{(avasmam + soilhum)}}$	-148.184	-4.644	4.200	0.154
	$\lambda_{\text{(shrcover + cancover)}}$	-44.104	-2.884	1.732	0.000	$\lambda_{\text{(shrcover + cancover + burrows + avasmam + soilhum + diswater)}}$	-148.454	-4.914	3.315	0.000
	$\lambda_{\text{(shrcover + cancover + burrows)}}$	-45.334	-4.114	2.169	0.000	$\lambda_{\text{(diswater)}}$	-149.997	-6.457	5.447	0.166
	$\lambda_{\text{(avasmam + soilhum)}}$	-45.532	-4.312	2.019	0.000	$\lambda_{\text{(shrcover + cancover + burrows)}}$	-154.176	-10.636	5.663	0.000
						$\lambda_{\text{(shrcover + cancover)}}$	-154.402	-10.862	4.915	0.000
	Combination									
	$\lambda_{\text{(diswater + coyotes)}}$	-41.944	0.000	0.000	0.766	$\lambda_{\text{(avasmam + diswater + ocelots)}}$	-143.865	0.000	0.000	0.644

	$\lambda_{\text{(shrcover + cancover + avasmam + diswater + coyotes + ocelots)}}$	-42.611	-0.667	1.562	0.234	$\lambda_{\text{(burrows + avasmam + competitor)}}$	-147.853	-3.988	4.670	0.226
	$\lambda_{\text{(shrcover + cancover + competitor)}}$	-45.026	-3.083	2.230	0.000	$\lambda_{\text{(avasmam + coyotes + ocelots)}}$	-147.985	-4.120	3.839	0.033
	$\lambda_{\text{(avasmam + coyotes + ocelots)}}$	-45.982	-4.039	2.081	0.000	$\lambda_{\text{(shrcover + cancover + avasmam + diswater + coyotes + ocelots)}}$	-148.560	-4.695	3.001	0.000
	$\lambda_{\text{(shrcover + cancover + coyotes + ocelots)}}$	-46.068	-4.124	2.031	0.000	$\lambda_{\text{(shrcover + cancover + avasmam + burrows + competitor)}}$	-148.964	-5.099	4.784	0.000
	$\lambda_{\text{(burrows + avasmam + competitor)}}$	-46.700	-4.756	2.150	0.000	$\lambda_{\text{(shrcover + cancover + competitor)}}$	-153.658	-9.793	5.692	0.096
	$\lambda_{\text{(shrcover + cancover + avasmam + burrows + competitor)}}$	-47.234	-5.290	2.586	0.000	$\lambda_{\text{(shrcover + cancover + coyotes + ocelots)}}$	-154.774	-10.909	4.666	0.000
Wet season 2019	*Interespecific interactions*									
	$\lambda_{\text{(ocelots)}}$	-80.569	0.000	0.000	0.924	$\lambda_{\text{(coyotes)}}$	-211.216	0.000	0.000	0.611
	$\lambda_{\text{(dogs)}}$	-81.001	-0.432	0.594	0.076	$\lambda_{\text{(ocelots)}}$	-211.682	-0.466	1.873	0.265
	$\lambda_{\text{(coyotes)}}$	-81.160	-0.591	0.458	0.000	$\lambda_{\text{(dogs)}}$	-211.955	-0.739	1.921	0.001
	$\lambda_{\text{(coyotes + ocelots)}}$	-81.521	-0.952	1.017	0.000	$\lambda_{\text{(coyotes + ocelots)}}$	-212.068	-0.852	1.226	0.000
	$\lambda_{\text{(competitor)}}$	-81.547	-0.978	0.978	0.000	$\lambda_{\text{(competitor)}}$	-212.172	-0.956	2.139	0.122
	$\lambda_{\text{(coyotes + ocelots + dogs)}}$	-82.501	-1.932	1.107	0.000	$\lambda_{\text{(coyotes + ocelots + dogs)}}$	-212.279	-1.063	1.384	0.000
	$\lambda_{\text{(competitor + coyotes + ocelots + dogs)}}$	-84.288	-3.719	1.615	0.000	$\lambda_{\text{(competitor + coyotes + ocelots + dogs)}}$	-213.446	-2.231	1.707	0.000
	Resource availability and habitat complexity									
	$\lambda_{\text{(cancover + avasmam + soilhum)}}$	-73.593	0.000	0.000	1.000	$\lambda_{\text{(avasmam + diswater)}}$	-193.749	0.000	0.000	0.926
	$\lambda_{\text{(shrcover + cancover + burrows + avasmam + soilhum + diswater)}}$	-75.545	-1.952	1.235	0.000	$\lambda_{\text{(avasmam)}}$	-194.454	-0.704	1.279	0.074
	$\lambda_{\text{(shrcover + cancover + burrows)}}$	-77.248	-3.655	2.357	0.000	$\lambda_{\text{(burrows + avasmam + soilhum + diswater)}}$	-195.024	-1.275	0.700	0.000
	$\lambda_{\text{(shrcover + cancover)}}$	-77.317	-3.724	2.466	0.000	$\lambda_{\text{(shrcover + cancover + burrows + avasmam + soilhum + diswater)}}$	-196.494	-2.745	1.284	0.000
	$\lambda_{\text{(avasmam + soilhum)}}$	-78.609	-5.016	2.811	0.000	$\lambda_{\text{(shrcover + cancover)}}$	-212.836	-19.087	6.134	0.000
	$\lambda_{\text{(burrows + avasmam + soilhum + diswater)}}$	-79.069	-5.476	2.189	0.000	$\lambda_{\text{(shrcover + cancover + burrows)}}$	-214.223	-20.473	6.318	0.000
	Combination									

Dry season 2020	$\lambda_{(\text{cancover + avasmam + soilhum + ocelots})}$	-72.760	0.000	0.000	1.000	$\lambda_{(\text{avasmam + diswater + coyotes})}$	-193.177	0.000	0.000	0.823
	$\lambda_{(\text{shrcover + cancover + competitor})}$	-78.131	-5.371	2.110	0.000	$\lambda_{(\text{avasmam + coyotes})}$	-193.901	-0.723	1.363	0.001
	$\lambda_{(\text{shrcover + cancover + burrows + avasmam + competitor})}$	-78.639	-5.879	2.797	0.000	$\lambda_{(\text{avasmam + coyotes + ocelots})}$	-194.187	-1.010	1.737	0.154
	$\lambda_{(\text{shrcover + cancover + coyotes + ocelots})}$	-79.198	-6.438	2.501	0.000	$\lambda_{(\text{avasmam + burrows + competitor})}$	-196.495	-3.317	2.534	0.022
	$\lambda_{(\text{avasmam + burrows + competitor})}$	-80.428	-7.668	3.050	0.000	$\lambda_{(\text{shrcover + cancover + burrows + avasmam + competitor})}$	-197.942	-4.765	2.883	0.000
	$\lambda_{(\text{avasmam + coyotes + ocelots})}$	-82.655	-9.895	2.876	0.000	$\lambda_{(\text{shrcover + cancover + coyotes + ocelots})}$	-212.512	-19.335	6.535	0.000
	$\lambda_{(\text{diswater + coyotes + ocelots})}$	-82.755	-9.995	2.807	0.000	$\lambda_{(\text{shrcover + cancover + competitor})}$	-213.796	-20.619	6.462	0.000
	Interespecific interactions									
	$\lambda_{(\text{coyotes})}$	-30.002	0.000	0.000	0.716	$\lambda_{(\text{coyotes})}$	-77.968	0.000	0.000	1.000
	$\lambda_{(\text{competitor})}$	-30.947	-0.945	0.729	0.000	$\lambda_{(\text{coyotes + ocelots})}$	-79.333	-1.365	0.626	0.000
	$\lambda_{(\text{ocelots})}$	-31.182	-1.180	2.175	0.000	$\lambda_{(\text{competitor})}$	-80.261	-2.292	2.012	0.000
	$\lambda_{(\text{dogs})}$	-31.256	-1.254	2.606	0.284	$\lambda_{(\text{competitor + coyotes + ocelots + dogs})}$	-80.547	-2.579	1.651	0.000
	$\lambda_{(\text{coyotes + ocelots})}$	-31.619	-1.617	1.251	0.000	$\lambda_{(\text{ocelots})}$	-80.565	-2.597	1.691	0.000
	$\lambda_{(\text{coyotes + ocelots + dogs})}$	-32.989	-2.987	2.478	0.000	$\lambda_{(\text{dogs})}$	-80.641	-2.673	1.552	0.000
	$\lambda_{(\text{competitor + coyotes + ocelots + dogs})}$	-34.322	-4.320	2.755	0.000	$\lambda_{(\text{coyotes + ocelots + dogs})}$	-80.858	-2.890	0.828	0.000
	Resource availability and habitat complexity									
	$\lambda_{(\text{shrcover})}$	-30.229	0.000	0.000	1.000	$\lambda_{(\text{shrcover + avasmam})}$	-72.616	0.000	0.000	1.000
	$\lambda_{(\text{shrcover + cancover})}$	-31.173	-0.943	0.390	0.000	$\lambda_{(\text{shrcover + cancover + burrows})}$	-75.110	-2.494	1.769	0.000
	$\lambda_{(\text{shrcover + cancover + burrows})}$	-32.230	-2.000	0.631	0.000	$\lambda_{(\text{shrcover + cancover + burrows + avasmam + soilhum + diswater})}$	-75.623	-3.007	1.787	0.000
	$\lambda_{(\text{avasmam + soilhum})}$	-32.763	-2.534	1.223	0.000	$\lambda_{(\text{shrcover + cancover})}$	-75.965	-3.349	2.028	0.000
	$\lambda_{(\text{burrows + avasmam + soilhum + diswater})}$	-34.035	-3.805	2.008	0.000	$\lambda_{(\text{avasmam + diswater})}$	-76.562	-3.946	2.099	0.000

$\lambda_{(\text{shrcover + cancover + burrows + avasmam + soilhum + diswater})}$	-35.521	-5.292	3.444	0.000	$\lambda_{(\text{burrows + avasmam + soilhum + diswater})}$	-77.914	-5.298	2.147	0.000
Combination									
$\lambda_{(\text{shrcover + coyotes})}$	-29.581	0.000	0.000	1.000	$\lambda_{(\text{shrcover + avasmam + coyotes})}$	-73.298	0.000	0.000	1.000
$\lambda_{(\text{shrcover + cancover + competitor + coyotes})}$	-31.248	-1.667	1.201	0.000	$\lambda_{(\text{shrcover + cancover + coyotes + ocelots})}$	-75.397	-2.099	1.490	0.000
$\lambda_{(\text{shrcover + cancover + competitor})}$	-31.302	-1.722	1.055	0.000	$\lambda_{(\text{shrcover + cancover + avasmam + coyotes + ocelots})}$	-75.594	-2.296	0.605	0.000
$\lambda_{(\text{shrcover + cancover + coyotes + ocelots})}$	-31.776	-2.195	1.197	0.000	$\lambda_{(\text{avasmam + diswater + competitor})}$	-76.929	-3.631	2.633	0.000
$\lambda_{(\text{avasmam + coyotes + ocelots})}$	-32.716	-3.135	1.894	0.000	$\lambda_{(\text{shrcover + cancover + burrows + competitor})}$	-76.954	-3.656	1.942	0.000
$\lambda_{(\text{burrows + avasmam + competitor})}$	-33.452	-3.872	1.506	0.000	$\lambda_{(\text{shrcover + cancover + competitor})}$	-77.041	-3.743	2.185	0.000
					$\lambda_{(\text{avasmam + coyotes + ocelots})}$	-77.906	-4.608	2.044	0.000

* The abbreviations of the covariates in the candidate models are shown in Table 1.

CAPÍTULO VI

CONCLUSIONES GENERALES

Coexistencia entre especies de zorrillos en un bosque tropical caducifolio

De acuerdo con nuestros resultados, las especies de zorrillos estudiadas *Conepatus leuconotus* y *Spilogale pygmaea* coexisten simpátricamente en el nicho temporal y espacial en uno de los últimos fragmentos mejor conservados del bosque tropical caducifolio en el Parque Nacional Huatulco, dentro de la vertiente del Pacífico mexicano. Esta coexistencia de especies es facilitada por diferentes mecanismos, estrategias y factores que promueven el uso de los mismos recursos y disminuyen el potencial de las interacciones competitivas.

En pimer lugar, proporcionamos evidencia de una segregación parcial de los patrones de actividad entre *C. leuconotus* y *S. pygmaea*, con una asincronía en sus máximos de actividad y niveles de actividad mensual diferentes, que se alternaron de manera consistente durante las tres temporadas muestreadas. Nuestros resultados también sugieren que *S. pygmaea* adopta una estrategia de evitación temporal en simpatría con *C. leuconotus*, ya que esta especie de menor talla corporal presentó sus periodos de mayor actividad cuando el miembro de talla más grande era menos activo. El ajuste en el nicho temporal de los zorrillos pigmeos posiblemente facilita su coexistencia con el competidor dominante en el área de estudio. Sin embargo, la segregación temporal entre las especies no muestra variaciones significativas entre temporadas, observándose una superposición moderada y constante de sus actividades. Los patrones de actividad de estas especies también están determinados por factores extrínsecos relacionados con la actividad de sus presas (mamíferos pequeños) y depredadores nativos (coyote y ocelote) y exóticos (perro), así como por predictores asociados con la estacionalidad climática (humedad relativa y precipitación) y el ambiente (nubosidad y duración de la noche). Estos múltiples factores influyen distintamente en la actividad diaria y mensual de los zorrillos con efectos positivos o negativos, dependiendo de la estacionalidad, lo que indica cierto grado de plasticidad conductual de las especies dentro del periodo de actividad preferido en respuesta a estímulos ecológicos y ambientales cambiantes.

En segundo lugar, ambos zorrillos co-ocurren y se detectan de forma independiente, es decir, las probabilidades de ocupación y de detección de *S. pygmaea* no son afectadas por las de *C. leuconotus*. La co-ocurrencia espacial de estas especies, más bien, parece estar explicada por sus asociaciones con el hábitat. Por ejemplo, *C. leuconotus* y *S. pygmaea* ocupan sitios más alejados de los cuerpos de agua, aunque la especie de manor talla además usa áreas con mayor humedad del suelo (un sustituto de disponibilidad y abundancia de insectos) y disponibilidad de mamíferos pequeños. Nuestros resultados también indicaron que existe una menor probabilidad de que *S.*

pygmaea desocupe un sitio en la siguiente temporada a menor cobertura arbustiva y mayor número de madrigueras en el sitio. En general, la probabilidad de ocupación de las dos especies de zorrillos aumentó durante las temporadas muestreadas, siendo más notorio en *S. pygmaea* durante la temporada de lluvia.

Por último, observamos relaciones inversas pero no significativas en las abundancias relativas entre las especies de zorrillos durante las temporadas de sequía en la zona de perturbación en el Parque Nacional Huatulco. Sin embargo, no encontramos evidencia de que la abundancia local esté gobernada por el dominio competitivo de la especie más grande, ya que *C. leuconotus* fue similar o ligeramente más abundante que *S. pygmaea* en esta temporada. Nuestros modelos, además, revelan que las abundancias relativas de ambos zorrillos se relacionan positiva y significativamente durante la temporada de lluvia, periodo en que los zorrillos pigmeos fueron más abundantes. Esto podría reflejar una competencia de interferencia baja, donde inclusive la especie subordinada puede ser el miembro dominante y tener cierta ventaja competitiva dentro de este gremio de carnívoros. No obstante, predictores relacionados con la disponbilidad de recursos y con la complejidad del hábitat explican mejor los patrones observados en las abundancias de las especies. Los modelos de abundancia con la precisión predictiva más alta mostraron asociaciones fuertes, tanto positivas con la disponibilidad de mamíferos pequeños y la distancia a la fuente de agua más cercana en ambos zorrillos como negativas con la cobertura arbórea en *C. leuconotus* y la cobertura arbustiva en *S. pygmaea*, aunque el efecto de la disponibilidad de presas fue consistentemente más importante.

Los hallazgos de este estudio evidencian que diferentes mecanismos y factores juegan un papel importante en la configuración de los patrones temporales y espaciales de *C. leuconotus* y *S. pygmaea*. Esta información permite mejorar nuestra comprensión sobre los mecanismos que gobiernan la coexistencia de estas especies en un ambiente tropical estacional en el Parque Nacional Huatulco, Oaxaca, México.

Importancia del conocimiento generado

El esfuerzo de investigación actual y el grado de información disponible para los zorrillos son heterogéneos y especialmente las especies *C. leuconotus* y *S. pygmaea* han recibido poca atención de la comunidad científica, con base en nuestra revisión de literatura de la familia Mephitidae. En este sentido, nuestro estudio muestra un avance significativo en el conocimiento de ambas especies

congruente con prioridades de investigación y contribuye a reducir la brecha científica y mejorar el estado actual de las investigaciones sobre ellas. Destacamos la importancia de los resultados obtenidos debido a que brindan información ecológica de las especies sobre: 1) patrones detallados de la actividad diaria y estacional, 2) uso del hábitat a escala local, y 3) estimaciones de su abundancia, mostrando patrones espacio-temporales. Estos datos son importantes para conocer los requerimientos ecológicos necesarios, proponer métodos de estimación y hacer evaluaciones a largo plazo para identificar los cambios en estos aspectos. Además, toda esta información es un componente clave para definir estrategias de conservación efectivas para estas especies.

Los conocimientos generados no solo son valiosos desde una perspectiva ecológica básica, sino que también ayudan a comprender el papel de las interacciones interespecíficas en la ocurrencia, distribución y abundancia de las especies. De esta manera, los patrones de actividad, la co-ocurrencia espacial y la abundancia poblacional permiten entender las respuestas de los zorrillos a los cambios antropogénicos actuales y su capacidad de segregación en el espacio o tiempo, lo cual es importante en la toma decisiones para enfocar esfuerzos futuros de investigación.

Implicaciones para la conservación de zorrillos amenazados

Ambas especies de zorrillos presentan problemas de conservación a nivel regional o nacional y las causas principales de esta situación actual posiblemente son los cambios en la composición de las comunidades animales y la pérdida de hábitat. En el área de estudio, existen poblaciones de perros ferales que han sido favorecidas por la cercanía del basurero municipal a cielo abierto y la falta de continuidad de programas de control y erradicación de fauna nociva. Asimismo, la zona de influencia presenta la pérdida y fragmentación del bosque tropical caducifolio por la conversión de áreas de vegetación natural a zonas de cultivo, pastoreo y asentamientos humanos, que reflejan diferentes grados de perturbación del ecosistema. Los efectos de estas presiones antropogénicas fuertes, en sinergia con eventos globales como el cambio climático, podrían aumentar el colapso de hábitats y alterar las interacciones interespecíficas existentes, con el desplazamiento de los competidores más débiles y la depredación de especies nativas. Esta investigación por lo tanto, sugiere que la coexistencia entre zorrillos podría verse afectada a corto o mediano plazo como consecuencia de los impactos potenciales. Sin embargo, la información proporcionada en conjunto con los programas subsidiados por la Comisión Nacional de Áreas Naturales Protegidas pueden permitir a los administradores del Parque Nacional Huatulco, la comunidad científica, el sector

gubernamental y otras partes interesadas la priorización de acciones y estrategias de conservación necesarias para estas especies amenazadas y poco estudiadas, frenando en última instancia la pérdida de biodiversidad en esta región prioritaria.