Journal of Arid Environments 160 (2019) 25–31

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Spotted skunks (*Spilogale angustifrons*) photo-captured following gray foxes (*Urocyon cinereoargenteus*) in tropical dry forest in central Mexico

Verónica Farías-González*, Cristina N. Vega-Flores

Laboratorio de Recursos Naturales, Unidad de Biología, Tecnología y Prototipos, Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México, Avenida de los Barrios 1, Col. Los Reyes Iztacala, Tlalnepantla de Baz, Estado de México, 54090, Mexico

ARTICLE INFO

Keywords:
Association
Interspecific
Intraguild
Mesocarnivore
Tehuacán-Cuicatlán*Palabras clave:*
Asociación
Interespecífico
Intragremial
Mesocarnívoro
Tehuacán-Cuicatlán

ABSTRACT

During a 4-year monitoring investigation of a mammalian community in a tropical dry forest in central México, we photo-captured southern spotted skunks (*Spilogale angustifrons*) following gray foxes (*Urocyon cinereoargenteus*) in 5 occasions. We were interested in disentangling why spotted skunks moved behind with gray foxes. Our objective was to determine activity patterns and distribution of sympatric gray foxes and southern spotted skunks, explore the frequency and timing of their co-occurrences, and infer about the circumstances of this previously unreported association. Camera trapping took place in Mount Tepetroja, within Tehuacán-Cuicatlán biosphere reserve. From 1 May 2013 thru 30 April 2017, with sampling effort of 18,282 trap-days, we obtained 1089 fox records and 21 skunk records; 5 of these records were of a skunk following a fox. Foxes were crepuscular and nocturnal and skunks nocturnal. Peak activity for foxes was μ = 23:17 h (95% CI = 23:01 to 23:32, r = 0.559), whereas for skunks μ = 1:36 h (95% CI = 00:46 to 02:26, r = 0.876). Our results suggested that skunk activity peak was subordinated to fox activity. We inferred that spotted skunks follow gray foxes maybe as an opportunistic behavior to facilitate mitigation of predation risk and enhance foraging.

RESUMEN

Durante una investigación de monitoreo de una comunidad de mamíferos silvestres en una selva tropical caducifolia en el centro de México que duró 4 años, obtuvimos 5 registros de foto-trampeo de zorrillo manchado (*Spilogale angustifrons*) siguiendo a la zorra gris (*Urocyon cinereoargenteus*). Nuestro interés fue esclarecer por qué los zorrillos manchados siguen e las zorras grises, debido a la falta de estudios sobre interacciones interespecíficas entre estas dos especies. Nuestro objetivo fue determinar los patrones de actividad y distribución de zorras grises y zorrillos machados en simpatría en una reserva natural, explorar la frecuencia y el horario de su co-ocurrencia, e inferir acerca de las circunstancias de esta asociación interespecífica que no ha sido reportada antes. El fototrampeo se llevó a cabo en el Cerro Tepetroja que está localizado dentro de la reserva de la biosfera Tehuacán-Cuicatlán. Del 1 mayo 2013 al 30 abril 2017, con un esfuerzo total de muestreo de 18,282 días-trampa, obtuvimos 1089 registros de zorra gris y 21 de zorrillo manchado, de los cuales en 5 se registraron a las dos especies. Como se esperaba, las zorras grises fueron principalmente crepusculares y nocturnas y los zorrillos fueron principalmente nocturnos. La mayor actividad para las zorras fue μ = 23:17 h (IC 95% = 23:01 a 23:32, r = 0.559), mientras que para los zorrillos μ = 1:36 h (IC 95% = 00:46 a 02:26, r = 0.876). Nuestros resultados sugirieron que la actividad cumbre de los zorrillos estuvo subordinada a la de las zorras. Inferimos que los zorrillos manchados van siguiendo a las zorras grises probablemente como un comportamiento oportunista para facilitar la mitigación del riesgo de depredación y optimizar la provisión de alimento.

1. Introduction

Spotted skunks (*Spilogale spp.*) and gray foxes (*Urocyon cinereoargenteus*) may occur as sympatric species due to morphological attributes and behavioral mechanisms which mitigate the pressures of intraguild competition and predation (Polis et al., 1989, Hunter and Caro, 2008, Di Bitetti et al., 2010). In the mammalian carnivore guild, body size is considered the most influential factor to determine species

* Corresponding author.
E-mail address: v.farias@unam.mx (V. Farías-González).

https://doi.org/10.1016/j.jaridenv.2018.09.010
Received 1 January 2018; Received in revised form 12 September 2018; Accepted 29 September 2018
Available online 11 October 2018

coexistence, and ecological overlap between species is reduced substantially when morphology is related to foraging behavior and prey-handling capabilities (Simberloff and Dayan, 1991). In México, 4 species of spotted skunk are present; the southern spotted skunk (*S. angustifrons*) occurs from central México thru Costa Rica and weights between 0.2 and 0.8 kg, about 6 times less than *U. cinereoargenteus*, which weights between 1.5 and 5 kg (Wozencraft, 2005; Dragoo, 2009; Aranda-Sánchez, 2012; Helgen et al., 2016). Gray foxes and spotted skunks are generalist and opportunistic mesocarnivores that share omnivorousness, predators, locomotion types, and habitat use (Fritzell, 1987; Hunter and Caro, 2008; Dragoo, 2009). Fox and skunk diets vary in relation to seasonality, and a large proportion consist on animal material such as rodents, birds, eggs, lizards, snakes, insects, and small invertebrates (Fritzell and Haroldson, 1982; Cantú-Salazar et al., 2005; Dragoo, 2009). Due to partitioning according to prey mass, the bulk of a fox diet consists mainly of vertebrates, whereas invertebrates constitute the bulk of a skunk diet (Simberloff and Dayan, 1991). Gray foxes are mainly crepuscular and nocturnal and during the day seek resting sites with dense understory (Fritzell and Haroldson, 1982; Fritzell, 1987). In contrast, spotted skunks are nocturnal and during the day rest in underground burrows and dens that may or may not be shared with other conspecifics (Verts et al., 2001; Lesmeister et al., 2008; Dragoo, 2009).

Several factors relating to the social structure and behavior of gray foxes and spotted skunks remain unclear due to their secretive habits, and scientific information about their interspecific interactions is incomplete (Fritzell and Haroldson, 1982; Dragoo, 2009). Solitary spotted skunks have been photo-captured in other studies but no observations of a spotted skunk following a gray fox have been registered in photo-captures in México (Botello et al., 2013; Hidalgo-Mihart et al., 2014; González et al., 2016) or elsewhere (Helgen et al., 2016). In contrast, interactions between *Urocyon* and *Spilogale* have been studied thoroughly for a diminutive and endangered relative of the gray fox, the island fox (*U. littoralis santacruzae*), and the island spotted skunk (*S. gracilis amphiala*) on the 250 km^2 Santa Cruz Island, in California, U. S. A. (Crooks, 1994; Crooks and Van Vuren, 1995; Roemer et al., 2002; Jones et al., 2008). Skunks (0.50–0.62 kg) and foxes (1.9–2.0 kg) consumed mostly deer mice (*Peromyscus maniculatus*) and insects, but differences in body size suggested that island fox was the dominant competitor (Crooks, 1994; Crooks and Van Vuren, 1995). Also, island skunks were never observed to be active during daylight hours, whereas island foxes were active throughout the diel (Crooks and Van Vuren, 1995). *S. gracilis amphiala* was rare on Santa Cruz Island when *U. littoralis santacruzae* was abundant (Crooks, 1994; Crooks and Van Vuren, 1995), but island skunks suddenly increased from rarity to abundance when the island fox population declined dramatically, suggesting the release of skunks from competition imposed by foxes (Crooks and Soule, 1999; Roemer et al., 2002; Jones et al., 2008). Noteworthy, differences in body size between gray foxes and southern spotted skunks in central México are much larger than those between island foxes and island spotted skunks on Santa Cruz Island.

In the present study, we were interested in disentangling why southern spotted skunks followed gray foxes in central México, a behavior registered with the use of camera traps during the monitoring of a mammalian community in a tropical dry forest within Tehuacán-Cuicatlán biosphere reserve (RBTC, acronym in Spanish). Our goal was to determine activity patterns and distribution of sympatric gray foxes and southern spotted skunks, explore the frequency and timing of their co-occurrences, and understand the circumstances of this interspecific association. We expected that (i) gray foxes would be crepuscular and nocturnal and show a bimodal pattern, (ii) spotted skunks would be nocturnal and show an unimodal pattern, and (iii) synchrony between gray foxes and spotted skunks would occur during the nocturnal period.

2. Materials and methods

2.1. Study area

Our investigation was performed in the locality of Ejido San José Axuxco, Municipality of San José Miahuatlán, southeastern State of Puebla, México. The study area borders south with the State of Oaxaca. Monitoring was participative and the presence of civil authorities from Ejido San José Axuxco and the principal investigator were mandatory to fulfill field work. Sampling took place in Mount Tepetroja, with peak on the geographical coordinates of latitude 18° 13′ 52.2″ N and longitude −97° 12′ 26.3″ W, altitude 1400 m asl, located within Tehuacán-Cuicatlán biosphere reserve, and within protected common lands. Throughout the study, the reserve authorities in Tehuacán, Puebla, were informed about field work, and we followed their guidelines. Vegetation in Mount Tepetroja was tropical dry forest with columnar cacti of genera *Cephalocereus*, *Myrtillocactus*, *Neobuxbaumia* and *Pachycereus* as main physiognomic dominants (Rzedowski, 1978; Valiente Banuet et al., 2000), and trees and bushes mainly of genera *Bursera*, *Castela*, *Ceiba*, *Ficus*, *Fouqueria*, *Parkinsonia* and *Ziziphus* (Rzedowski, 1978; Valiente-Banuet et al., 2000). Mount Tepetroja fosters populations of endangered species of tropical xerophytic plants such as red tetecho (*Neobuxbaumia tetetzo*), Tehuacán ocotillo (*Fouqueria purpusii*), and elephant foot (*Beaucarnea gracilis*; SEMARNAT, 2010). Climate is semiarid with rainy season during summer from May to October, annual precipitation of 300 mm, and annual mean temperature of 22 °C (Dávila et al., 2002). There is no substantial variation in sunset and sunrise timing between the wet and dry seasons in our study area; differences are of approximately 25 min. The sun rises around 6:00 h and sets around 19:20 h.

2.2. Camera trapping

Our sampling units consisted of stations composed of 1 digital camera trap (LTL Acorn 6210, Little Acorn Outdoors, Green Bay, Wisconsin, U. S. A.), were separated by lineal distances of 500 m between stations, and were placed along the ridgeline of Mount Tepetroja and along a dry creek ravine, in places were the intersection of 2–3 wildlife trails with mammalian scats and footprints were detected. Cameras were tied to columnar cacti or trees at 20–40 cm from the ground. Cameras were activated by a passive detector of infrared light (PIR) sensor when presence of animals was detected. We programmed cameras to operate the 24 h of the day, take a 12 megapixel picture and a 20 s video followed by an inactive delay of 30 s, and print the date and hour of capture according to the natural diel (i.e. not using the daylight savings of the summer schedule). We did not use lures or attractants. Time to first trigger was 0.8 s for the photograph and 3 s for the video. Cameras were visited every 5–8 weeks to replace batteries and 8 MB secure digital high capacity (SDHC) memory cards. Eleventh stations were established in April 2013 (Farías et al., 2015) and another 3 stations were placed during year 2014 and started to operate on March, July, and August, respectively. The last station was placed during June 2015. We analyzed data captured by camera traps from 1 May 2013 to 30 April 2017. During this 4-year period, operating stations at any one time varied from 8 to 15 stations due to battery depletion, camera malfunction, camera destruction by a feral calf (*Bos taurus*), and lost cameras. Sampling effort was estimated by adding the total number of days (1 day = 24 h) that every station worked during the 4-year sampling period, and units were expressed as trap-days, where 1 trap-day was represented by 1 station working during the 24 h of 1 day (Meek et al., 2014).

2.3. Skunk and gray fox records

Mammal species were identified according to Aranda-Sánchez (2012), and for each species we determined the number of photo-captures in each station every day (1 day = 24 h) during the 4-year sampling period. We categorized photo-captures by rainy (May–October) or dry season (November–March). Records of spotted skunks included solitary individuals, or a skunk following a fox. We defined "following" as instances where, at the same camera station, a spotted skunk was recorded in the same picture behind a gray fox, or a spotted skunk was recorded in the video that was captured immediately after a picture of a gray fox was captured. Records of gray foxes included solitary individuals, 2 to 4 foxes, a fox followed by a skunk, or a fox with prey. Except for images in which we could identify 2 or more distinct individuals, we considered images of conspecifics as: (a) 1 record if they were captured within 1 h, or (b) different records if they were captured in periods > 1 h. We used the date and hour of the first image per record.

2.4. *Activity patterns*

Sample size of spotted skunks was insufficient to compare between seasons or among years; therefore, we pooled data for the 4-year period. For each species, we constructed rose diagrams for circular data to illustrate the daily activity patterns using the frequency of independent records for each hour, with the software Oriana 4 (Kovach, 2011). The frequency was represented by the area of the wedge, and we used 24 intervals of 15°, each representing 1 h. We estimated the mean vector (μ), the length of the mean vector (r), and the 95% confidence interval of the mean vector. The mean vector was an indicator of the peak of activity. The length of the mean vector ranged from 0 to 1, and a larger r value indicated that the observations were clustered more closely around the mean than a smaller one (Kovach, 2011).

3. Results

3.1. *Skunk following fox records*

With a total sampling effort of 18,282 trap-days we obtained 1084 records of gray foxes, 16 records of spotted skunks, and 5 records where a skunk followed a gray fox. Therefore, the sum of 16 records of solitary skunks with 5 records of a skunk that followed a gray fox was 21 records, and the sum of 1084 records of gray foxes with 5 records of a skunk that followed a gray fox was 1089 (Table 1, Fig. 1). We were unable to use spotted skunk coat patterns to discriminate between individuals because in every one of the 5 records of a spotted skunk following a gray fox, the skunk was in movement.

The five records in which a southern spotted skunk was photo-captured following a gray fox occurred during dry season, from January to April, on 3 contiguous camera stations (Table 2, Fig. 2). The first record was taken on January 2014 when a gray fox was photo-captured in a picture and 7 s later a spotted skunk was photo-captured in a video running in the same place and direction. In year 2016, a gray fox was photo-captured in a picture and 9 s later a spotted skunk was photo-captured in a video hopping in the same place and direction. The last 3 records occurred on the same camera station. In year 2016, on two different events one month apart, a gray fox was followed by a skunk and both were photo-captured in the same picture. One year later, on March 2017, a gray fox was photo-captured in a picture and 7 s later a spotted skunk was photo-captured in a video hopping in the same place and direction.

Table 1
Record frequency, recording rate (per 100 trap-days), and proportion of stations with detection for gray foxes (*Urocyon cinereoargenteus*) and southern spotted skunks (*Spilogale angustifrons*) in Mount Tepetroja, Tehuacán-Cuicatlán biosphere reserve, México, from 1 May 2013 to 30 April 2017.

	Record frequency	Recording rate	Proportion of stations with detections
Gray fox	1089	5.96	1.00 (n = 15)
Spotted skunk	21	0.12	0.47 (n = 7)
Spotted skunk follows gray fox	5	0.03	0.20 (n = 3)

3.2. *Activity patterns*

Gray foxes were mainly crepuscular and nocturnal, showed a mean vector 43 min before midnight (μ = 23:17 h, 95% CI = 23:01 to 23:32) and a length of mean vector r = 0.559. In contrast, skunks were mainly nocturnal with a mean vector 96 min after midnight (μ = 1:36 h, 95% CI = 00:46 to 02:26) and a length of mean vector r = 0.876 (Fig. 1). Gray foxes and skunks showed unimodal activity patterns and their synchrony occurred during the nocturnal period. The 95% confidence intervals of the main vectors (μ) did not overlap between the activity patterns of the two mesocarnivores. Thus, the active period of spotted skunks showed synchrony with the active period of gray foxes, but the mean activity of skunks occurred after the mean activity of foxes (Fig. 1).

4. Discussion and conclusions

4.1. *Skunk following fox records*

Our work is the first published evidence of a short-term association between the southern spotted skunk and the gray fox. The behavior had not been registered in México before, but this fact may be explained because sampling efforts from previous studies were not maintained for long-term monitoring of the same locality for more than two years, thus lowering the chances to register this kind of observation (Botello et al., 2013; Hidalgo-Mihart et al., 2014; González et al., 2016). According to Tobler et al. (2008), length of sampling effort is the factor that best enhances probabilities to detect missing or rare species. Also, previous to camera-trap instrumentation in research protocols, ecological studies on mephitids would not commonly obtain information about associations with gray foxes or other mammals present in the study area (Cervantes et al., 2002; Neiswenter and Dowler, 2007), or information about interspecific interactions different to predation (Lesmeister et al., 2010).

Possibly, at least 4 individual skunks were photo-captured performing the behavior during the 4-year of our monitoring. The first record was taken on January 2014, and we assumed this was the first individual skunk exhibiting the fox following behavior. The second record was taken almost two years after the first record, on February 2016, and we inferred as unlikely that we had photo-captured the same individual of 2014, so we assumed this case as the second individual skunk which followed a fox. The third and fourth of our records might have higher chances to belong to the same individual because these two records were taken 30 days apart, on March and April 2016, and in the same camera station (AX08, Table 2); therefore, we assumed this two records belonged to the third individual skunk detected following a fox. The fifth record was taken eleven months after the fourth record, on March 2017, and we assumed this was the fourth individual skunk performing the behavior. Lesmeister et al. (2010) reported low survival rates for a population of *S. putorius* in which 58% of study animals died over the course of the study mainly due to predation; mean annual survival for 33 radio-tracked individuals was 0.354 and mean survival after capture was 169 days (range 5–496 days). Lesmeister et al. (2010) study offers insight into the low probability of an individual skunk surviving for more than 6 months in the wild.

Although we found the 5 records of skunk following fox within 3 adjacent stations, we deny the possibility that this behavior belonged to just one or two rare acting spotted skunks and that the interesting behavior should not be attributed to the *S. angustifrons* population in our study area. The camera stations setup of our study was based on the average home range size of mesocarnivore species. We assumed that the

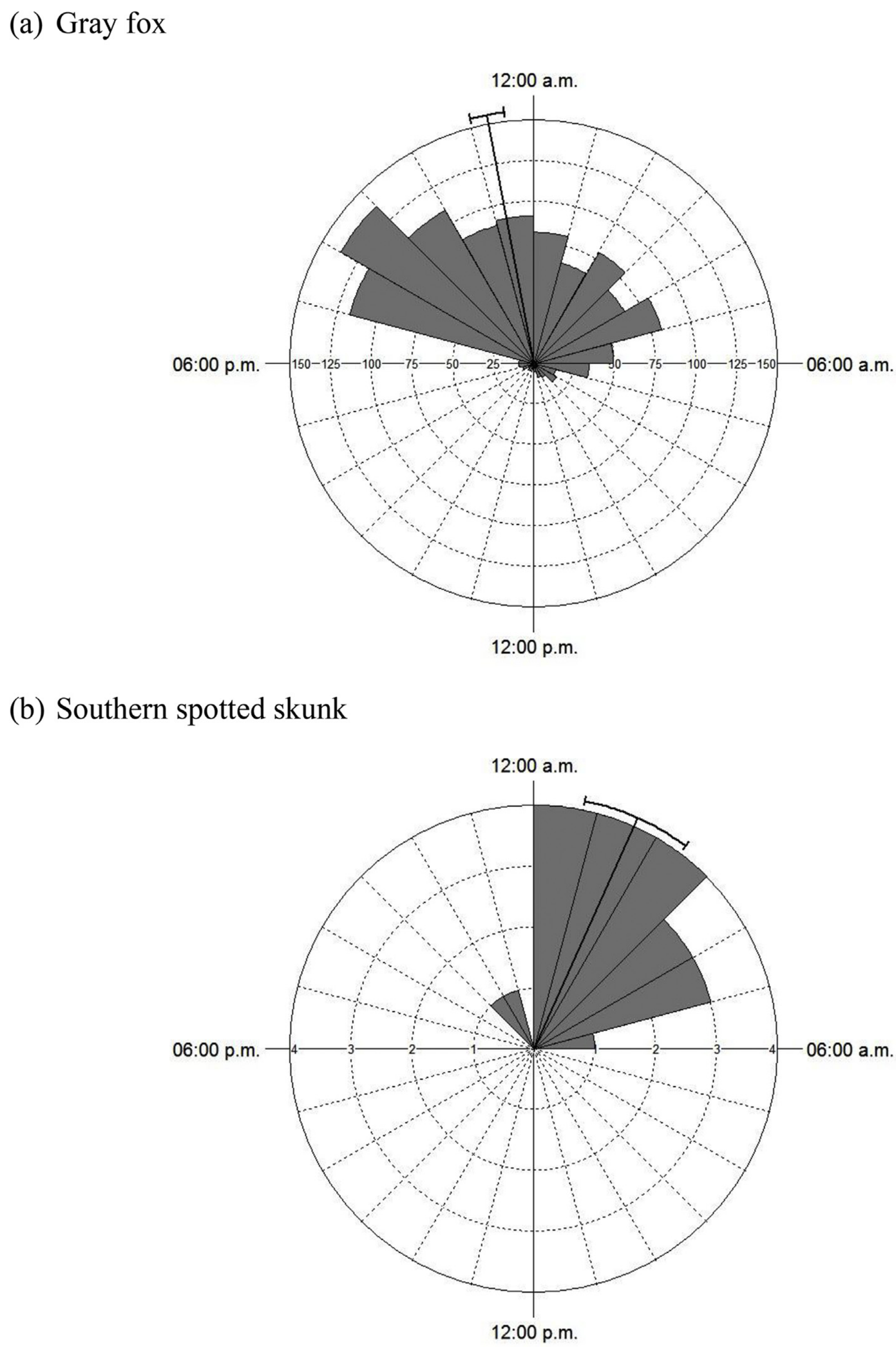

Fig. 1. Activity patterns of (a) gray foxes (*Urocyon cinereoargenteus*, n = 1089) and (b) southern spotted skunks (*Spilogale angustifrons*, n = 21) in Mount Tepetroja, Tehuacán-Cuicatlán biosphere reserve, México, from May 2013 to April 2017. The direction of the mean vectors and the 95% confidence intervals are indicated. The sun rises around 6:00 a.m. and sets around 7:20 p.m.

lineal distance of 500 m between stations would allow the inclusion of one camera station in one home range, in the best scenario. *U. cinereoargenteus* is a monogamous species, individuals remain solitary for the majority of the year, have an average home range size of 2.1 km^2, and use only small portions of this range each day (Fritzell and Haroldson, 1982). Home range size for *Spilogale spp*. is smaller than for *U. cinereoargenteus*. In a population of *S. putorius*, home range was dependent on gender and season, and was bigger for males during the breeding season in spring (Lesmeister et al., 2009). For autumn, winter, spring, and summer, females of *S. putorius* maintained average home ranges of 65 ha, 71 ha, 135 ha, and 54 ha, respectively, in contrast with 76 ha, 175 ha, 866 ha, and 142 ha for males (Lesmeister et al., 2009).

4.2. Activity patterns and distribution

As expected, gray foxes were mainly crepuscular and nocturnal, spotted skunks were mainly nocturnal, and synchrony between them occurred during the nocturnal period, in Mount Tepetroja, central México (Fig. 1). The peaks of activity of skunks and foxes were 139 min apart; gray fox peak of activity occurred before midnight and skunk peak occurred after midnight. Probably, activity peaks did not overlap because skunks might be subordinated to gray foxes. In addition to this argument, skunk records were not as widely distributed in the study area compared to gray fox records (Fig. 2). Other studies indicated that occurrence of spotted skunks was noticeably higher in vegetation types

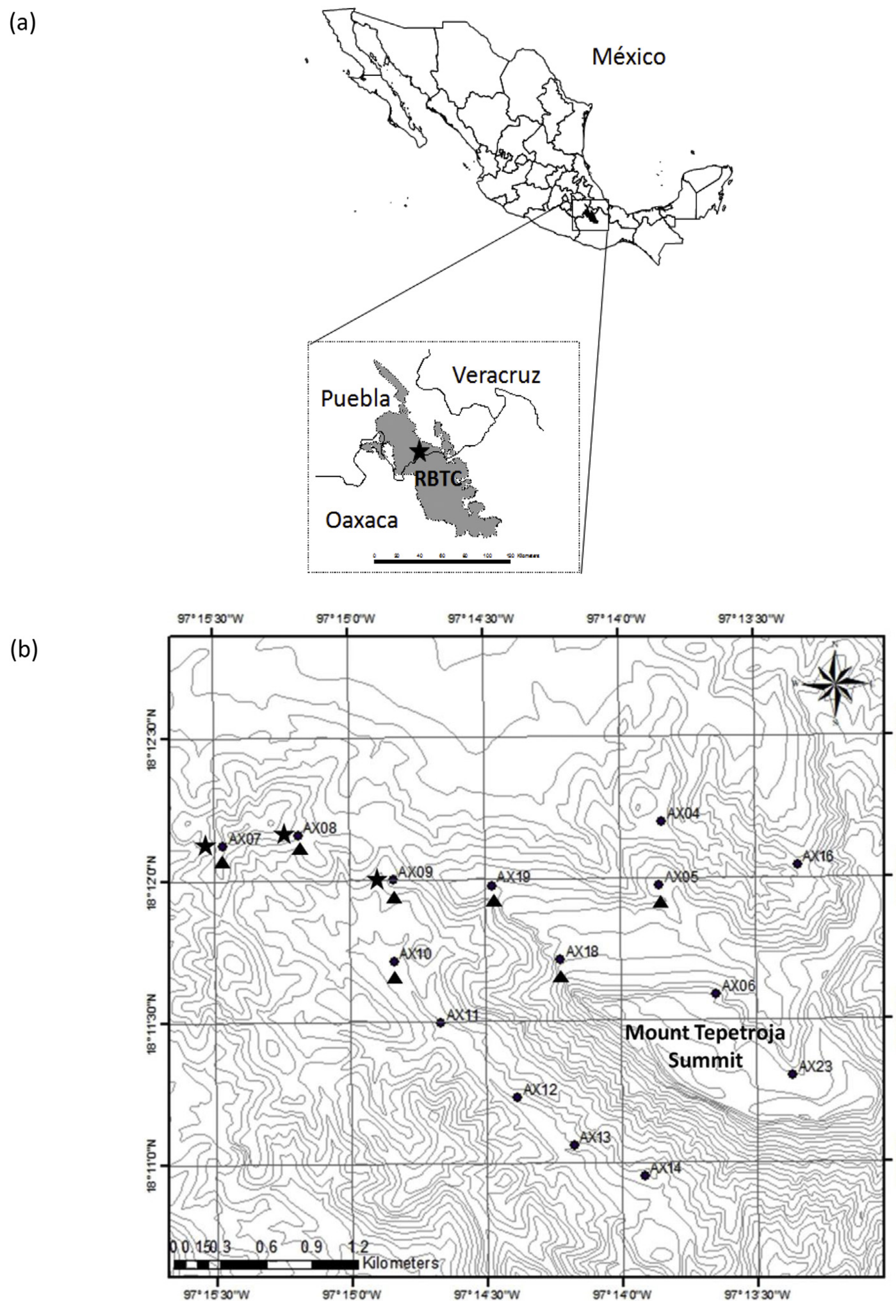

Fig. 2. (a) Location of Mount Tepetroja (black star) in relation to the limits of the Tehuacán-Cuicatlán biospehere reserve (RBTC), and the states of Puebla and Oaxaca in México. (b) Location of 15 camera-trap stations (AX) in Mount Tepetroja. Records of presence of gray foxes (circles), spotted skunks (triangles), and a spotted skunk following a gray fox (stars) are indicated for each camera-trap station.

that provide cover, structural characteristics, and complexity that reduce risk of predation (Cervantes et al., 2002; Lesmeister et al., 2009). However, camera-trap stations in our study area were placed within the same vegetation type, tropical dry forest. As well, other factors such as presence of potential competitors and/or predators might be considered to explain spatio-temporal segregation of spotted skunks in Mount Tepetroja (Di Bitetti et al., 2010). Thus, provided that in future studies we analyze specific attributes of vegetation understory in the study area, we would only be able to infer that temporal and spatial segregation between skunks and foxes were behaviors that added up to allow species coexistence (Hunter and Caro, 2008; Di Bitetti et al., 2010).

4.3. Insights on coexistence

We propose that spotted skunks follow gray foxes because this behavior may be an interspecific association between the two mesocarnivores that benefits skunks, the subordinate species (Stensland et al., 2003, Mattisson et al., 2011). In our study area, the differences in body size between gray foxes and spotted skunks may permit not only their coexistence, but also short-term and opportunistic interactions during the active periods of both species (Simberloff and Dayan, 1991; Stensland et al., 2003). Due to the six-fold differences in their body sizes, similarities in locomotion and activity patterns may not imply strong competition; instead, terrestrial and arboreal capabilities may allow spotted skunks to move along in close proximity to gray foxes. According to Simberloff and Dayan (1991), differences in foraging

Table 2
Date and timing (hour:minute:second) of photo-detection and geographical location (decimal degrees) of the 5 records in which a southern spotted skunk (*Spilogale angustifrons*) followed a gray fox (*Urocyon cinereoargenteus*) in Mount Tepetroja, Tehuacán-Cuicatlán biosphere reserve, México, from 1 May 2013 to 30 April 2017.

Date of photo-detection	Timing of gray fox detection	Timing of skunk detection	Camera-trap station	Location of camera-trap station
30 Jan 2014	21:22:03	21:22:10	AX07	18.20208 N −97.25773 W
13 Feb 2016	04:47:44	04:47:53	AX09	18.20001 N −97.24737 W
14 Mar 2016	02:02:41	02:02:41	AX08	18.20269 N −97.25322 W
13 Apr 2016	00:29:38	00:29:38	AX08	
28 Mar 2017	01:30:00	01:30:07	AX08	

behavior between Mephitidae and Canidae likely reduce the potential for interference or exploitative competition. Possibly, spotted skunks in our study area accompany gray foxes to facilitate mitigation of predatory risk and therefore enhance foraging (Stensland et al., 2003; Hunter and Caro, 2008). Spotted skunks might benefit from the association by reducing their vulnerability to common predators when in close proximity with gray foxes (Stensland et al., 2003; Mattisson et al., 2011). Within mammalian carnivores, coyotes (*Canis latrans*) and badgers (*Taxidea taxus*) have been observed to form interspecific hunting-associations to enhance predatory effectiveness on a common prey (Minta et al., 1992), and wolverines (*Gulo gulo*) appear to benefit from coexistence with lynx (*Lynx rufus*) through increased scavenging opportunities (Mattisson et al., 2011; Khalil et al., 2014).

In contrast with interactions between island foxes and island spotted skunks where the skunk is limited by the fox, our results may be interpreted as an association where gray foxes tolerate the close proximity of southern spotted skunks, although gray foxes receive no benefit (Stensland et al., 2003). Temporary tolerance has been documented between conspecifics of solitary and territorial felids (Elbroch and Quigley, 2017), as well as between competing heterospecifics (Stensland et al., 2003; López-Bao et al., 2016). But the temporal association between gray foxes and skunks is different from tolerance because apparently skunks do not benefit as scavengers or co-feeders, no agonistic encounters between gray foxes and spotted skunks have been documented, and the big differences in body size between them suggest competition attenuation (Stensland et al., 2003). Co-occurrence of gray foxes and spotted skunks does not seem to be a hunting-association where both species are benefited through partnerships of complex and coordinated predatory tasks (Minta et al., 1992). Thus, the short-term association of a dyad consisting of a gray fox and a spotted skunk may be a non-agonistic mechanism of competition and coexistence, where the skunk appears to be benefited but the gray fox might not.

Conflicts of interest

None.

Competing interests

The authors declare no competing financial, general and institutional interests.

Contributors

Both authors materially participated in the research and article preparation and have approved the final manuscript submitted. Verónica Farías-González participated in designing the study based on previous research, obtaining the funding, collection of field data, analysis and interpretation of data, writing of the report, and in the decision to submit the article for publication. Cristina N. Vega-Flores participated in the analysis and interpretation of the data, the elaboration of the map and figures, and in the decision to submit the article for publication.

Acknowledgments

We thank and acknowledge the collaboration with Ejido San José Axuxco, Municipality of San José Miahuatlán, State of Puebla, México. The National Commission of Protected Natural Areas (CONANP, acronym in Spanish) through the Tehuacán-Cuicatlán biosphere reserve (RBTC) authorities facilitated permits to fulfill fieldwork. The National Forest Commission (CONAFOR) gave support to civil authorities in Ejido San José Axuxco. VF was supported by Program PAPIIT, projects UNAM-DGAPA-PAPIIT IN221814 and UNAM-DGAPA-PAPIIT IA200812. We acknowledge the comments and suggestions kindly provided by two anonymous reviewers, which improved substantially the document.

Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.jaridenv.2018.09.010.

References

Aranda-Sánchez, M.J., 2012. Manual para el rastreo de mamíferos silvestres de México. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad e Instituto de Ecología, A. C. Ciudad de México, México, pp. 255.

Botello, F., Villaseñor, E., Guevara, L., Méndez, A., Cortés, A., Iglesias, J., Izúcar, M., Luna, M., Martínez, A., Salazar, J.M., 2013. Registros notables del zorrillo manchado (*Spilogale angustifrons*) y del jaguarundi (*Puma yagouaroundi*) en la Reserva de la Biosfera de Tehuacán-Cuicatlán, Oaxaca, México. Rev. Mex. Biodivers. 84, 713–717. https://doi.org/10.7550/rmb.28873.

Cantú-Salazar, L., Hidalgo-Mihart, M.G., López-González, C., González-Romero, A., 2005. Diet and food resource use by the pygmy skunk (*Spilogale pygmaea*) in the tropical dry forest of Chamela, Mexico. J. Zool. 267, 283–289. https://doi.org/10.1017/S0952836905007417.

Cervantes, F.A., Loredo, J., Vargas, J., 2002. Abundance of sympatric skunks (Mustelidae: Carnivora) in Oaxaca, Mexico. J. Trop. Ecol. 18, 463–469. https://doi.org/10.1017/S0266467402002328.

Crooks, K.R., 1994. Demograhpy and status of the island fox and the island spotted skunk on Santa Cruz Island, California. SW. Nat. 39, 354–357.

Crooks, K.R., Soule, M.E., 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400, 563–566.

Crooks, K.R., Van Vuren, D., 1995. Resource utilization by two insular endemic mammalian carnivores, the island fox and island spotted skunk. Oecologia (Berl.) 104, 301–307.

Dávila, P., Arizmendi, M.C., Valiente-Banuet, A., Villaseñor, J.L., Casas, A., Lira, R., 2002. Biological diversity in the Tehuacán-Cuicatlán valley, Mexico. Biodivers. Conserv. 11, 421–442.

Di Bitetti, M.S., De Angelo, C.D., Di Blanco, Y.E., Paviolo, A., 2010. Niche partitioning and species coexistence in a Neotropical felid assemblage. Acta Oecol. 36, 403–412. https://doi.org/10.1016/j.actao.2010.04.001.

Dragoo, J.W., 2009. Family Mephitidae (skunks). In: Wilson, D.E., Mittermeier, R.A. (Eds.), Handbook of the Mammals of the World. vol. 1. Lynx Editions, Barcelona, pp. 532–562 Carnivores.

Elbroch, L.M., Quigley, H., 2017. Social interactions in a solitary carnivore. Current Zoology 63 (4), 357–362. https://doi.org/10.1093/cz/zow080.

Farías, V., Téllez, O., Botello, F., Hernández, O., Berruecos, J., Olivares, S.J., Hernández, J.C., 2015. Primeros registros de 4 especies de felinos en el sur de Puebla, México. Rev. Mex. Biodivers. 86, 1065–1071. https://doi.org/10.1016/j.rmb.2015.06.014.

Fritzell, E.K., 1987. Gray fox and island fox. In: Novak, M., Baker, J.A., Obbard, M.E., Malloch, B. (Eds.), Wild Furbearer Management and Conservation in North America. Ontario Ministry of Natural Resources, Toronto. Canada, pp. 408–420.

Fritzell, E.K., Haroldson, K.J., 1982. Urocyon cinereoargenteus. Mamm. Species 189, 1–8.

González, C.A., Guzmán-Guzmán, S., Alarcón-Villegas, L., 2016. Nuevas localidades del zorrillo manchado del sur *Spilogale angustifrons* (Carnivora, Mephitidae) en Veracruz, México. Acta Zool. Mexic. 32 (3), 387–389.

Helgen, K., Reid, F., Timm, R., 2016. *Spilogale angustifrons*. The IUCN Red List of Threatened Species 2016. eT136636A45221538.

Hidalgo-Mihart, M.G., Pérez-Solano, L.A., Contreras-Moreno, F.M., de la Cruz, A.J., 2014. Ampliación del área de distribución del zorrillo manchado del sur *Spilogale angustifrons* Howell 1902 en el Estado de Campeche, México. Acta Zool. Mexic. 30 (1), 232–236.

Hunter, J., Caro, T., 2008. Interspecific competition and predation in American carnivore families. Ethol. Ecol. Evol. 20 (4), 295–324. https://doi.org/10.1080/08927014.2008.9522514.

Jones, K.L., Van Vuren, D.H., Crooks, K.R., 2008. Sudden increase in a rare endemic carnivore: ecology of the island spotted skunk. J. Mammal. 89 (1), 75–86.

Khalil, H., Pasanen-Mortensen, M., Elmhagen, B., 2014. The relationship between wolverine and larger predators, lynx and wolf, in a historical ecosystem context. Oecologia 175, 625–637. https://doi.org/10.1007/s00442-014-2918-6.

Kovach, W.L., 2011. Oriana – Circular Statistics for Windows, Ver. 4. Kovach Computing Services, Pentraeth, Wales, U.K.

Lesmeister, D.B., Gompper, M.E., Millspaugh, J.J., 2008. Summer resting and den site selection by eastern spotted skunks (*Spilogale putorius*) in Arkansas. J. Mammal. 89 (6), 1512–1520.

Lesmeister, D.B., Gompper, M.E., Millspaugh, J.J., 2009. Habitat selection and home range dynamics of eastern spotted skunks in the Ouachita Mountains, Arkansas, USA. J. Wildl. Manag. 73 (1), 18–25. https://doi.org/10.2193/2007-447.

Lesmeister, D.B., Millspaugh, J.J., Gompper, M.E., Wong, T.W., 2010. Eastern spotted skunk (*Spilogale putorius*) survival and cause specific mortality in the Ouachita Mountains, Arkansas. Am. Midl. Nat. 164, 52–60.

López-Bao, J.V., Mattisson, J., Persson, J., Aronsson, M., Andrén, H., 2016. Tracking neighbours promotes the coexistence of large carnivores. Sci. Rep. 6, 23198. https://doi.org/10.1038/srep23198.

Mattisson, J., Persson, J., Andrén, H., Segerström, P., 2011. Temporal and spatial interactions between an obligate predator, the Eurasian lynx (*Lynx lynx*), and a facultative scavenger, the wolverine (*Gulo gulo*). Can. J. Zool. 89 (2), 79–89. https://doi.org/10.1139/Z10-097.

Meek, P.D., Ballard, G., Claridge, A., Kays, R., Moseby, K., O'Brien, T., O'Connell, A., Sanderson, J., Swann, D.E., Tobler, M., Townsend, S., 2014. Recommended guiding principles for reporting on camera trapping research. Biodivers. Conserv. 23, 2321–2343. https://doi.org/10.1007/s10531-014-0712-8.

Minta, S.C., Minta, K.A., Lott, D.F., 1992. Hunting associations between badgers (*Taxidea taxus*) and coyotes (*Canis latrans*). J. Mammal. 73 (4), 814–820. https://doi.org/10.2307/1382201.

Neiswenter, S.A., Dowler, R.C., 2007. Habitat use of western spotted skunks and striped skunks in Texas. J. Wildl. Manag. 71 (2), 583–586. https://doi.org/10.2193/2005-623.

Polis, G.A., Myers, C.A., Holt, R.D., 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Annu. Rev. Ecol. Systemat. 20, 297–330.

Roemer, G.W., Donlan, C.J., Courchamp, F., 2002. Golden eagles, feral pigs, and insular carnivores: how exotic species turn native predators into prey. Proc. Natl. Acad. Sci. Unit. States Am. 99, 791–796.

Rzedowski, J., 1978. Vegetación de México. Limusa. Distrito Federal. México.

SEMARNAT, 2010. Norma Oficial Mexicana NOM-059-SEMARNAT-2010, Protección ambiental - Especies nativas de México de flora y fauna silvestres - Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio - Lista de especies en riesgo. Diario Oficial de la Federación. 30 de diciembre de 2010, Segunda Sección, México.

Simberloff, D., Dayan, T., 1991. The guild concept and the structure of ecological communities. Annu. Rev. Ecol. Systemat. 22, 115–143.

Stensland, E., Angerbjörn, A., Berggren, P., 2003. Mixed species groups in mammals. Mamm Rev. 33 (3), 205–223.

Tobler, M.W., Carrillo-Percastegui, S.E., Leite-Pitman, R., Mares, R., Powell, G., 2008. An evaluation of camera traps for inventorying large and medium sized terrestrial rainforest mammals. Anim. Conserv. 11, 169–178.

Valiente-Banuet, A., Casas, A., Alcántara, A., Dávila, P., Flores-Hernández, N., Arizmendi, M.C., et al., 2000. La vegetación del valle de Tehuacán-Cuicatlán. Bol. Soc. Bot. México 67, 27–74.

Verts, B.J., Carraway, L.N., Kinlaw, A., 2001. Spilogale gracilis. Mamm. Species 674, 1–10.

Wozencraft, W.C., 2005. Order carnivora. In: Wilson, D.E., Reeder, D.M. (Eds.), Mammal Species of the World: a Taxonomic and Geographic Reference, pp. 532–628.