ORIGINAL RESEARCH

Predation risk in tree squirrels: implications of the presence of free-ranging dogs

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Abstract

Small mammals show variations in activity patterns due to the use of resources and the risk of predation. However, in the case of tree squirrel species, the factors that affect their activity patterns are poorly studied. We used camera trapping to investigate the activity patterns of three different squirrel species of the genus *Sciurus*, two species of squirrel (*Sciurus aureogaster* and *S. oculatus*) from Mexico and one from the Iberian Peninsula (*S. vulgaris*). In addition, we compared their activity patterns with the potential predator community and their most important predators (Mexico: gray fox *Urocyon cinereoargenteus*, ringtail *Bassariscus astutus*, Opossum *Didelphis virginiana*; Spain: red fox *Vulpes vulpes*, pine and stone marten *Martes spp.*), and with feral and free-ranging dogs (*Canis lupus familiaris*). We evaluated the predation risk by the carnivore community on the squirrels when they descend to the ground by studying their temporal overlap and observing if the squirrels have different activity patterns adjusted to the carnivore community in each study area. The results showed that the three species of squirrels consistently descended to the ground during the day, showing a variable maximum peak of activity between 8:00 and 12:00 h. Temporal overlap of activity patterns of the three species with the carnivore community was low ($\Delta = 0.12–0.36$), same as with the main predators (Mexico: gray fox $\Delta = 0.14–0.21$, ringtail $\Delta = 0.08–0.09$, opossum $\Delta = 0.06–0.07$; Spain: red fox $\Delta = 0.39$, martens $\Delta = 0.22$). However, temporal overlap of activity patterns with the domestic dog was moderate-high in the three squirrel species (Mexico $\Delta = 0.55–0.88$, Spain $\Delta = 0.79$). These results show that the species of the genus *Sciurus* have adjusted their activity patterns of ground use to reduce predation risk by wild predators but not with feral and free-ranging dogs, something which can pose a serious conservation problem for these species.

Introduction

Native animal species have been subject to increasing anthropogenic pressure, such as loss and habitat fragmentation, reduction of resources, invasive species, or climate change (Carroll, 2007; Sala et al., 2000; Young et al., 2016). These threats directly affect animal species, reducing their populations and affecting the biodiversity in most ecosystems (Clavel et al., 2011; Dirzo et al., 2014; Nayeri et al., 2021). In addition, they also produce indirect effects on animal species, such as biological, genetic, or behavioral changes that can lead to an increase in intraspecific and interspecific interactions (Gálvez et al., 2021; Henle et al., 2004; Young et al., 2016).

Anthropogenic effects near urban areas are mostly related to habitat loss and fragmentation (Hansen et al., 2005; Henle et al., 2004), hunting by humans (Wood et al., 2000), and disturbances caused by free-ranging or feral dogs and cats (Bryce, 2021; Ritchie et al., 2014).

The domestic dog (*Canis lupus familiaris*) is the world's most abundant carnivore with an estimated population of over 700 million (Hughes & Macdonald, 2013; Sykes et al., 2020), occurring almost worldwide. Although most of these dogs are owned, many live partially or free-ranging (Bryce, 2021; Massei et al., 2010). Domestic dogs can be categorized according to their management and behavior, such as owned dogs, free-ranging dogs, and feral dogs (Hughes & Macdonald, 2013;

Vanak & Gompper, 2009). The free-ranging dogs generally rely on human communities for food and shelter and can be commonly found in farm and rural areas. In contrast, feral dogs are wild and independent of human-derived food sources (Hughes & Macdonald, 2013). Thus, they are more prone to hunting and scavenging (Carrasco-Román et al., 2021; Doherty et al., 2017; Tobajas, Descalzo, Ferreras, et al., 2021).

Feral and free-ranging dogs can have critical ecological impacts on wildlife and receive increasing attention from researchers and conservationists (Bryce, 2021; Doherty et al., 2017; Ritchie et al., 2014; Zapata-Ríos & Branch, 2018). Feral and free-ranging dogs pose a threat to many species of wildlife due to direct predation (Carrasco-Román et al., 2021; Doherty et al., 2017; Nayeri et al., 2021; Young et al., 2011), harass wildlife (Young et al., 2011), disease transmission (Butler et al., 2004; Martínez-Sotelo et al., 2022; Randall et al., 2006), resources competition (Tobajas, Descalzo, Ferreras, et al., 2021; Wierzbowska et al., 2016) or limiting the spatiotemporal use of wildlife (Callan et al., 2020; Carvalho et al., 2019; Lenth et al., 2008). However, effects on the activity patterns of wildlife have not received as much attention in the scientific literature (see Pérez-Irineo et al., 2021; Zapata-Ríos & Branch, 2016), especially on small prey species (see Caravaggi et al., 2018; Mori et al., 2021; Viviano et al., 2021). Furthermore, many prey species are not adapted to the presence of dogs, so they are even less able to reduce the predation risk (Pierce & Sporle, 1997).

Interspecific relationships and niche partitioning between predators and prey species modulate the spatial and temporal patterns (Viviano et al., 2021; Zapata-Ríos & Branch, 2016). In constant coevolution, predators and prey have developed tactics to maximize the probability of hunting the prey and, conversely, the prey to reduce the risk of predation (Futuyma & Moreno, 1988; Tobajas, Rouco, Fernandez-de-Simon, et al., 2021). In the case of prey, modifying the activity patterns is one of the primary adaptations to reduce the risk of predation (Descalzo et al., 2021; Viviano et al., 2021; Zapata-Ríos & Branch, 2016). Although the activity patterns may depend on predation risk, other factors such as the available resources, habitat characteristics, seasonality, or intraspecific relationships affect these patterns (Díaz-Ruiz et al., 2016; Gálvez et al., 2021; Villafuerte et al., 1993). Nevertheless, some studies have shown adaptations in prey activity patterns to reduce the likelihood of encountering predators (Descalzo et al., 2021; Harrington et al., 2009; Monterroso et al., 2013). However, the possible adaptations of tree squirrel species to reduce predation risk have been consistently overlooked (see Caravaggi et al., 2018; Pérez-Irineo et al., 2021).

Tree squirrels are common prey for mesocarnivores and raptors (Azevedo et al., 2006; Gómez-Ortiz et al., 2015; Selonen et al., 2010), as well as for domestic dogs (Carrasco-Román et al., 2021; Sheehy & Lawton, 2015; Vanak & Gompper, 2009). In the case of terrestrial predators, arboreal squirrels' hunting occurs when they are on the ground searching for resources to feed themselves (Ditgen et al., 2007; Moller, 1983). The endogenous patterns of diurnal squirrels have temperature-dependent seasonal variations with a general biphasic pattern in summer (resting during the warmest hours) and a short and uninterrupted phase of activity in winter, variations modulated by the habitat

and resource availability (Thomas et al., 2018; Tonkin, 1983; Váczi et al., 2006). However, predators' effects on variations in their activity patterns are not well known (Blake et al., 2012; Caravaggi et al., 2018).

We describe the temporal activity patterns of two species of Mexican tree squirrels (Mexican red-bellied squirrel *Sciurus aureogaster* and Peter's squirrel *S. oculatus*) and one from the Iberian Peninsula (red squirrel *S. vulgaris*) during their use of the ground. On the ground, the tree squirrel is most vulnerable to predation. In addition, we investigate interspecific relationships between squirrels and their predators by comparing the squirrels' activity patterns with the potential predator community and their most important predators (Mexico: gray fox (*Urocyon cinereoargenteus*), ringtail (*Bassariscus astutus*), opossum (*Didelphis virginiana*); Spain: red fox (*Vulpes vulpes*), pine and stone marten (*Martes spp.*), and with free-ranging dogs (*Canis lupus familiaris*)). Finally, we evaluate the risk of predation by the carnivore community on the squirrels when they descend to the ground by studying their temporal overlap in activity patterns and observing if the squirrels have different activity patterns adjusted to the carnivore community in each study area.

We hypothesized that predator–prey temporal overlaps would be minimized by a squirrel's specific use of the ground to reduce exposure to predators. Furthermore, the temporal overlap in activity patterns with domestic dogs would be higher than with the native predator community probably due to the lack of life-history adaptation by the squirrels to this invasive species.

Materials and methods

Study areas and squirrel species

The study was carried out in three different areas (two in Mexico and one in Spain) containing populations of one of the tree squirrel species studied (Fig. 1). However, the species were not in sympatry with other squirrels. All areas were inside a human-modified landscape with the presence of human settlements surrounding or inside the study areas.

S. aureogaster is an arboreal medium-sized diurnal squirrel native from Mexico and southwestern Guatemala, inhabiting a wide variety of forest habitats ranging from tropical scrub and broadleaf formations to cold and wet temperate cloud forests in the highlands (Ramos-Lara & Cervantes, 2011). The population of *S. aureogaster* studied was in San Bartolo Tutotepec municipality in central Mexico's eastern part of Hidalgo State (20°44′ N, 98°28′ W, Fig. 1). The study was conducted between 1600 and 2000 m asl, in an area dominated by a templated forest, with remnants of cloud forests in the highlands, represented mainly through species such as conifers (*Pinus spp.*), oaks (*Quercus spp.*), liquidambar (*Liquidambar styraciflua*), and mixed sub-humid vegetation. In the lower areas, there was a predominance of sub-evergreen tropical forests, secondary vegetation, and grasslands. The climate is hot and humid, with rains in summer.

The endemic *S. oculatus* is a Mexican tree medium-large sized diurnal squirrel found in habitats consisting of

Figure 1 Locations of the three study areas corresponding to the tree squirrel studied. *Sciurus aureogaster* in San Bartolo Tutotepec, Hidalgo State, Mexico; *Sciurus oculatus* in Huasca de Ocampo, Hidalgo State, Mexico; *Sciurus vulgaris* in Virós forest, Lérida Province, Spain.

coniferous-oak forest, between 1500 and 3600 m asl, located along the Trans-Mexican Neovolcanic belt and in areas of the Sierra Madre Oriental (Best, 1995; Monterrubio-Rico et al., 2013; Valdez-Alarcón & Téllez-Girón, 2005). The population studied was from a management unit for wildlife conservation located in Rancho Santa Elena (Huasca de Ocampo) in the southern part of Hidalgo State (20°08′ N, 98°31′ W, Fig. 1). The study area is populated by a homogeneous pine forest (*Pinus spp.*) with dispersed oaks (*Quercus spp.*) and open areas with dry scrublands between 2300 and 2900 m asl. The climate is temperate and semi-cold, with rains in summer.

Sciurus vulgaris is a small tree diurnal squirrel that inhabits mainly coniferous forests, although it can also be found in deciduous forests. Its distribution extends between sea level and 2000 m asl throughout Europe and North Asia. The population of *S. vulgaris* studied was from Virós forest in Alt Pirineu Natural Park on the southern slope of the Catalan Pyrenees, Northeastern Spain (42°52′ N, 1°29′ W, Fig. 1). The area studied have a sub-Mediterranean mountain climate with habitats dominated by Scots Pine (*Pinus sylvestris*) with scattered deciduous species and a shrub understory of mainly boxwood (*Buxus sempervirens*) and common juniper (*Juniperus communis*) between 1200 and 1900 m asl.

Camera trap surveys

The activity patterns of *S. aureogaster* were studied with 17 camera traps (Bushnell Trophy Cam HD, Bushnell Outdoor Products, Kansas, USA) placed in the study area. The cameras were uniformly distributed throughout the study area at a distance of 451 ± 89 m (mean ± SE) between cameras. Cameras were installed on trees at approximately 30–50 cm height and were programmed to take consecutive photos with a minimum time

delay (0 s). We did not use attractants for squirrels. Cameras were maintained at the site for approximately 6 months and revisited every 2 weeks from November 2013 to June 2014.

In the *S. oculatus* study area, 20 camera traps (12 Cuddeback® Attack series, Non-Typical, Inc., Green Bay, Wisconsin, USA, and 8 Wildview® Xtreme series, Grand Prairie, Texas, USA) were uniformly spaced throughout the area, following a grid-sampling that averaged 694 ± 74 m (mean ± SE) between cameras. Cameras were installed on trees at approximately 30–50 cm height, without any rodent-specific bait. We programmed the cameras to a minimum time delay (0 s) between consecutive photos to maximize the number of photos taken per captured individual. Cameras were maintained at the site for 50 days and revisited every 9–10 days from October to December 2014.

Sciurus vulgaris activity patterns were studied using 25 camera traps (Moultrie M-990i Gen 2 and M-999i, Moultrie Feeders, Birmingham, AL, USA) uniformly distributed throughout the study area at a distance of 847 ± 115 m (mean ± SE) between cameras. Cameras were installed on trees at approximately 30–50 cm height without attractant for the squirrel. We programmed the cameras to a minimum time delay (0 s) between consecutive photos. Cameras were installed independently in time and space, maintained at the site for 15–45 days, and revisited every 1 or 2 weeks from March to December 2015.

During the camera trap surveys, the presence of squirrels and all the potential predator species of squirrels were recorded 24 h a day (Table 1). A relative abundance index (RAI) of squirrels and predators was calculated for the whole study period by dividing the total number of independent capture events of each species on each camera-trap site by the sampling effort (trap nights) on that site and expressed as integer records per

Table 1 Coefficients of overlapping of activity patterns between squirrel species and predators (Δ_1), overlap degree, 95% confidence intervals (CI 95%), values of relative abundance index (RAI), and Mardia–Watson–Wheeler test (W)

Species	RAI	Δ_1	Overlap	CI 95%	W	*P* value
Mexican red-bellied squirrel (*Sciurus aureogaster*)	8.27					
Predator community	15.20	0.162	Low	0.12–0.20	362.43	<0.01
Felids community	0.91	0.209	Low	0.08–0.34	40.41	<0.01
Coyote (*Canis latrans*)	1.28	0.199	Low	0.09–0.29	71.85	<0.01
Dog (*Canis familiaris*)	8.85	0.588	Moderate	0.49–0.64	80.76	<0.01
Gray fox (*Urocyon cinereoargenteus*)	6.59	0.21	Low	0.15–0.27	234.35	<0.01
Cacomistle (*Bassariscus sumichrasti*)	0.87	0.086	Low	0.05–0.13	298.85	<0.01
Raccoon (*Procyon lotor*)	1.78	0.077	Low	0.02–0.14	108.14	<0.01
Opossum (*Didelphis virginiana*)	3.03	0.063	Low	0.02–0.11	185.52	<0.01
Coati (*Nasua narica*)	1.24	0.578	Moderate	0.44–0.71	20.86	<0.01
Peter's squirrel (*Sciurus oculatus*)	4.31					
Predator community	12.53	0.122	Low	0.05–0.21	89.24	<0.01
Dog (*Canis familiaris*)	3.11	0.882	High	0.75–0.99	0.84	0.66
Gray fox (*Urocyon cinereoargenteus*)	3.21	0.143	Low	0.03–0.26	52.90	<0.01
Ringtail (*Bassariscus astutus*)	3.31	0.081	Low	0.01–0.17	59.29	<0.01
Opossum (*Didelphis virginiana*)	3.01	0.069	Low	0.01–0.15	55.71	<0.01
Red squirrel (*Sciurus vulgaris*)	3.38					
Predator community	65.96	0.362	Low	0.23–0.51	34.67	<0.01
Dog (*Canis familiaris*)	4.12	0.788	High	0.60–0.92	1.25	0.54
Red fox (*Vulpes vulpes*)	52.33	0.396	Low	0.25–0.53	33.47	<0.01
Martes sp. (*Martes foina* and *Martes martes*)	13.64	0.225	Low	0.09–0.36	38.72	<0.01

100 trap nights (O'Brien et al., 2003). Consecutive records of the same species were considered for the analyses as independent events when at least 30 min elapsed between them (Tobajas, Descalzo, Villafuerte, et al., 2021).

Statistical analyses

The activity patterns of squirrels and predators were estimated through the R package overlap (Meredith & Ridout, 2017; Ridout & Linkie, 2009) within R 4.0.0 (R Core Team, 2020) using the times of day of the independent events recorded of each species. Activity patterns were estimated for each species when the sample size was at least 25 independent detections ($N \geq 25$), less in the case of felid species in the *S. aureogaster* study area where all felid records were pooled for the analyses. In addition, the activity patterns of all squirrels' predators pooled were calculated, including all potential wild predator events (without domestic dogs). In the study area of *S. vulgaris*, the records of the two sympatric species of mustelids, pine marten (*Martes martes*) and stone marten (*Martes foina*), were pooled due to the difficulty in identifying each species in the pictures (Tobajas, Oliva-Vidal, Piqué, et al., 2021). The coefficient of activity pattern overlap (Δ) between the squirrels and all the potential predators of each area was calculated using the Δ_1 estimator recommended for small sample sizes (Ridout & Linkie, 2009).

We considered the values of overlap values as low when Δ was <0.50, moderate when $0.50 \leq \Delta < 0.75$, and high when $\Delta \geq 0.75$ (Monterroso et al., 2014). We calculated the 95% confidence intervals for the overlap (Δ_1) using the bootstrap sampling from 1000 replicates (Monterroso et al., 2014). To compare if the distribution of the detection across the diel

activity between sampling pairs was significant, we used the Mardia–Watson–Wheeler test (W) with the same data of the time of day used in the activity pattern overlap analyses (Gerber et al., 2012).

Results

Camera-trapping and species detected

The total sampling effort was 2973 camera-trap-days in the study area of *S. aureogaster*, which was detected in 246 independent events. Fifteen potential predator species were detected, but only seven species reached the minimum number of 25 independent events (Table 1). The highest RAI was for the domestic dog, followed by a gray fox (*Urocyon cinereoargenteus*), opossum (*Didelphis virginiana*), raccoon (*Procyon lotor*), coyote (*Canis latrans*), coati (*Nasua narica*), and ringtail (*Bassariscus astutus*), respectively (Table 1). The felid community was composed mainly of margay (*Leopardus wiedii*), followed by ocelot (*Leopardus pardalis*) and jaguarundi (*Herpailurus yagouaroundi*). Several predator species were detected but with insufficient data for estimating their activity patterns: hooded skunk (*Mephitis macroura*), long-tailed weasel (*Mustela frenata*), white-backed hog-nosed skunk (*Conepatus leuconotus*), kinkajou (*Potos Flavus*), and domestic cat (*Felis catus*).

We obtained 43 independent records for the *S. oculatus* in a total sampling effort of 998 camera-trap days. We detected four species of predators in the study area with more than 25 independent records (domestic dog, gray fox, opossum, and ringtail) with similar RAI values (Table 1). In addition, six species of predators that did not reach the minimum number to

estimate the activity patterns were detected: the bobcat (*Lynx rufus*), coyote, domestic cat, hooded skunk, white-backed hognosed skunk, and western spotted skunk (*Spilogale gracilis*).

In the *S. vulgaris* study area, the squirrel was detected on 32 independent occasions in 946 camera-trap-days. We detected seven predator species, but it only was possible to estimate the activity pattern in the red fox (*Vulpes vulpes*), the domestic dog, and the marten species (*Martes* spp.). The RAI of foxes was the highest, followed by marten species and domestic dogs (Table 1). Other detected species of predators with few events were the European badger (*Meles meles*), least weasel (*Mustela nivalis*), and common genet (*Genetta genetta*).

Squirrel-specific activity patterns

The three species of squirrels studied show diurnal activity patterns when descending to the ground, with a variable peak of activity between 8:00 and 12:00 h (Fig. 2). Despite existing variability according to seasonality and day length of each study area, squirrels use the ground briefly, showing a peak activity in the morning. *S. aureogaster* is the species that shows the earliest and shortest peak of activity, around 7:00 and 10:00 h (Fig. 2). In the case of *S. oculatus*, the activity peak was broader between 8:00 and 12:00 h (Fig. 2). Finally, *S. vulgaris* shows the latest activity peak of the three species between 9:00 and 13:00 h (Fig. 2). All three species show a slight peak of activity in the afternoon, being more marked in *S. aureogaster* (Fig. 2).

Predator–prey relationships

Temporal overlap in activity patterns between the three squirrel species with their respective wild predator community was low (*S. aureogaster*: $\Delta_1 = 0.16$, CI 0.12–0.20; *S. oculatus*: $\Delta_1 = 0.12$, CI 0.05–0.21; *S. vulgaris*: $\Delta_1 = 0.36$, CI 0.23–0.51, Table 1, Fig. 3). In the intraspecific pairwise comparison in each study area, *S. aureogaster* showed a low temporal overlap in activity patterns with almost all wild predator species (range Δ_1: 0.06–0.21), except with the coati ($\Delta_1 = 0.58$, CI 0.44–0.27) and

dogs ($\Delta_1 = 0.59$, CI 0.49–0.64) that showed a moderate overlap (Table 1, Figs 3 and 4). Likewise, pairwise comparison between *S. oculatus* and the different predator species showed low overlap (range Δ_1: 0.07–0.14), except for the dog, which was high ($\Delta_1 = 0.88$, CI 0.75–0.99, Table 1, Figs 3 and 4). Similarly, the values of temporal overlap in the pairwise comparison between *S. vulgaris* and predators showed a low overlap with all species (range Δ_1: 0.23–0.40), except for the dog, which was high ($\Delta_1 = 0.79$, CI 0.60–0.92, Table 1, Figs 3 and 4). Accordingly, the coefficient of overlap results, the Mardia–Watson–Wheeler test revealed significantly different activity patterns between squirrels and almost all predator species, less with dogs for *S. oculatus* and *S. vulgaris* (Table 1).

Discussion

Predator species play an essential role in maintaining ecosystem functions (Atkins et al., 2019; Estes et al., 2011; Jiménez et al., 2019) and shape the ecology of prey species, such as spatiotemporal activity patterns (McNicol et al., 2020; Monterroso et al., 2013). The landscape of fear or predation risk is one of the modeling forces that predators compel on prey species (Creel & Christianson, 2008; Preisser et al., 2005). This adaptation by prey species has been developed during coevolutionary history with their predators, seeking optimization in using available resources while reducing predation risk (Descalzo et al., 2021; Gerber et al., 2012). Our results show that squirrels avoid predators using the ground when the risk of predation by wild predator species is lower. The tree squirrel species studied show activity patterns of descent to the ground concentrated for a short period when their overlap with the wild carnivore community is low (Table 1; Figs 2 and 3). The squirrels show a diurnal ground activity with a peak of activity between 8:00 and 12:00 h (Fig. 2), similar to other studies (Caravaggi et al., 2018; Pérez-Irineo et al., 2021; Ramos-Lara & López-González, 2017).

Our results support the hypothesis that predator–prey overlaps would be minimized by specific use of the ground by squirrels to reduce the exposure to predators, descending to the
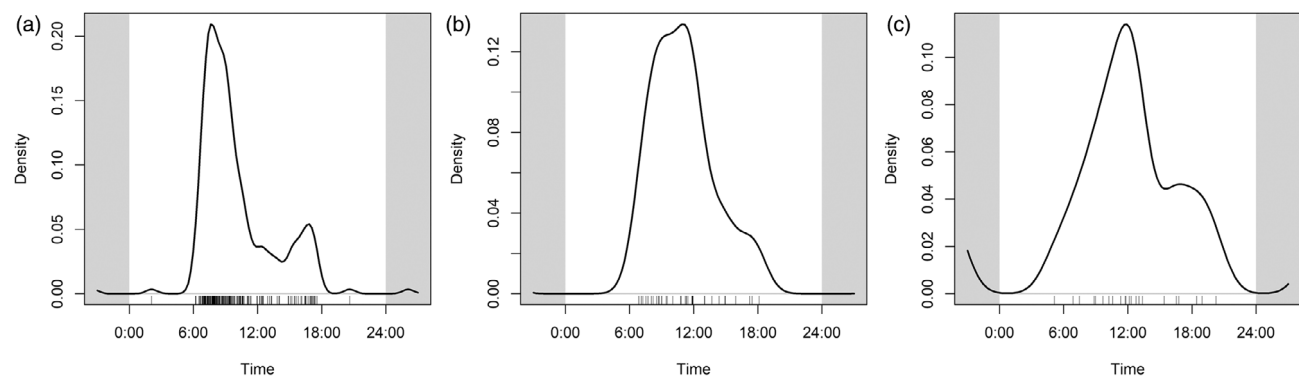

Figure 2 Circadian activity patterns of the three squirrel species studied using camera traps. (a) *Sciurus aureogaster* (Mexico), (b) *Sciurus oculatus* (Mexico), (c) *Sciurus vulgaris* (Spain).
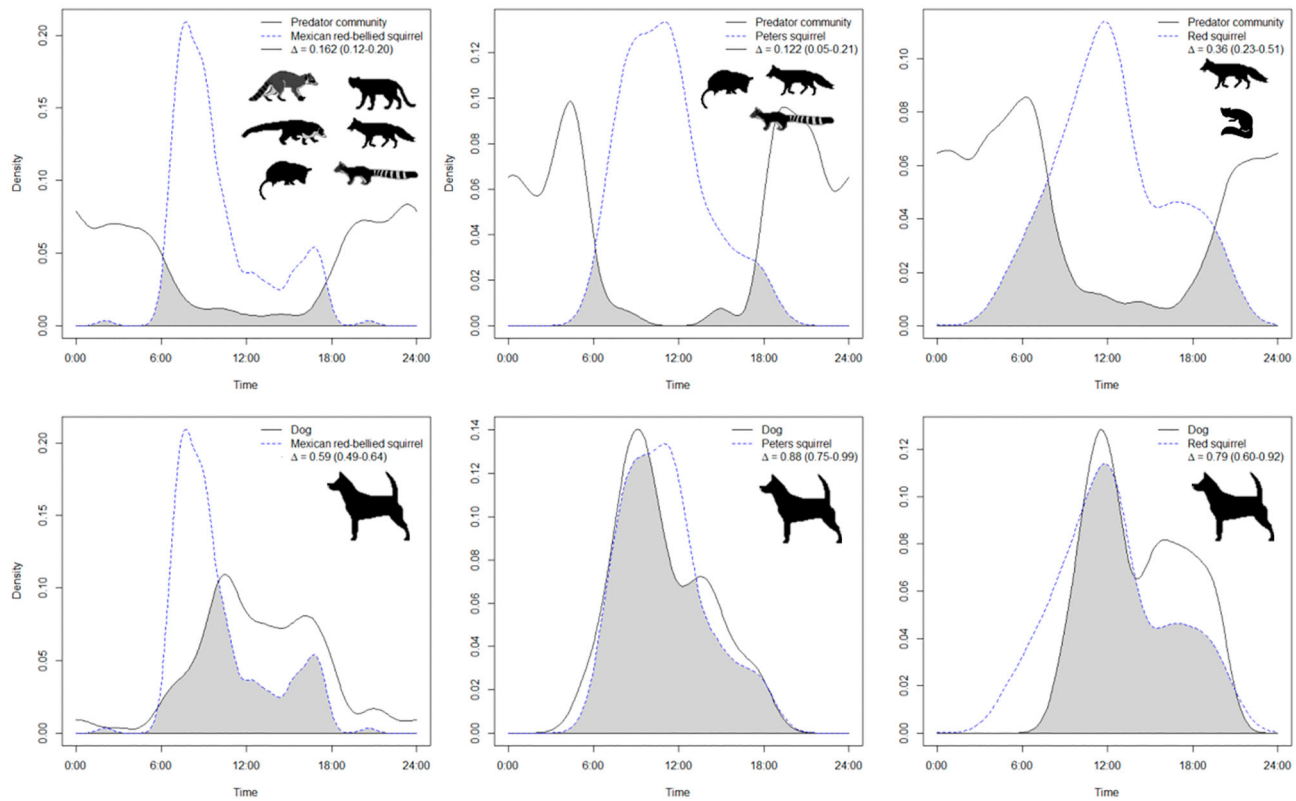
Figure 3 Temporal overlap (Δ_1) between the activity patterns of wild predator community and domestic dogs (solid line) with squirrel species (dashed line) in the three study areas (Figure 1). The overlap coefficient is represented by the shaded area.

ground in a shorter period and not overlapping with predators. The overlap between squirrel species and wild predators has been low (Fig. 4), except for the coati for *S. aureogaster*, primarily a diurnal species (Bianchi et al., 2020; Pérez-Irineo et al., 2021). These results are similar to other recent studies on *S. aureogaster* and *S. vulgaris* (Caravaggi et al., 2018; Pérez-Irineo et al., 2021). In contrast, our data are the first published on the temporal relationships between *S. oculatus* and its predator community. The results show that squirrels have adjusted their activity on the ground to reduce predation risk by the predator's community that each species has in its area (Fig. 3). However, the data show that squirrel species have a moderate-high overlap with feral and free-ranging dogs (Table 1, Fig. 3). This overlap with dogs may be due to a lack of antipredator strategies to the presence of free-ranging dogs due to the short time coexisting, the lack of ability to change the endogenous diurnal activity rhythm, or perhaps because squirrels do not consider them as much of a threat compared to wild predators (Bianchi et al., 2020; Kronfeld-Schor & Dayan, 2003; Zapata-Ríos & Branch, 2016).

Squirrels are species with the ability to escape to the trees quickly to minimize predation by dogs. However, squirrels have been part of free-ranging dogs' diets and other terrestrial predators (Carrasco-Román et al., 2021; Gómez-Ortiz et al., 2015; Sheehy & Lawton, 2015; Turkia et al., 2020). If we look at the overlap data at the species level (Table 1,

Fig. 4), it is observed that the overlap between the squirrels and predators with arboreal habits (i.e., ringtail, raccoon, opossum, or marten) is generally lower than with the mostly terrestrial predators (i.e., red fox, coyote, gray fox, felid species). We suggest that the squirrels may prioritize the temporal avoidance of predators with arboreal habits. In this sense, squirrels have low visual acuity in low light conditions (Jacobs et al., 1982), so using the ground during a short period of the day may be an adaptation to reduce the risk of predation while optimizing their antipredator abilities (Caravaggi et al., 2018). In the case of coati, the squirrels may not see it as a threat as it is a primarily omnivorous species and not an active predator (Valenzuela, 1998).

Human settlements in natural areas produce habitat fragmentation and land-use intensification (Hansen et al., 2005; Henle et al., 2004), as well as the increase in the abundance of free-ranging dogs (Bryce, 2021). Anthropogenic disturbances can change the activity patterns of wild animals, probably by modifying the interactions between species and affecting their abundance (Ngoprasert et al., 2007; Norris et al., 2010; Tobajas et al., 2020; Zapata-Ríos & Branch, 2016). These effects can produce changes in the activity patterns of wild species, increasing competition between wild predators (mainly nocturnal) while reducing temporal overlap in activity patterns with domestic predators (mainly diurnal) (Gálvez et al., 2021). In our study areas, this may cause a reduction in temporal overlap
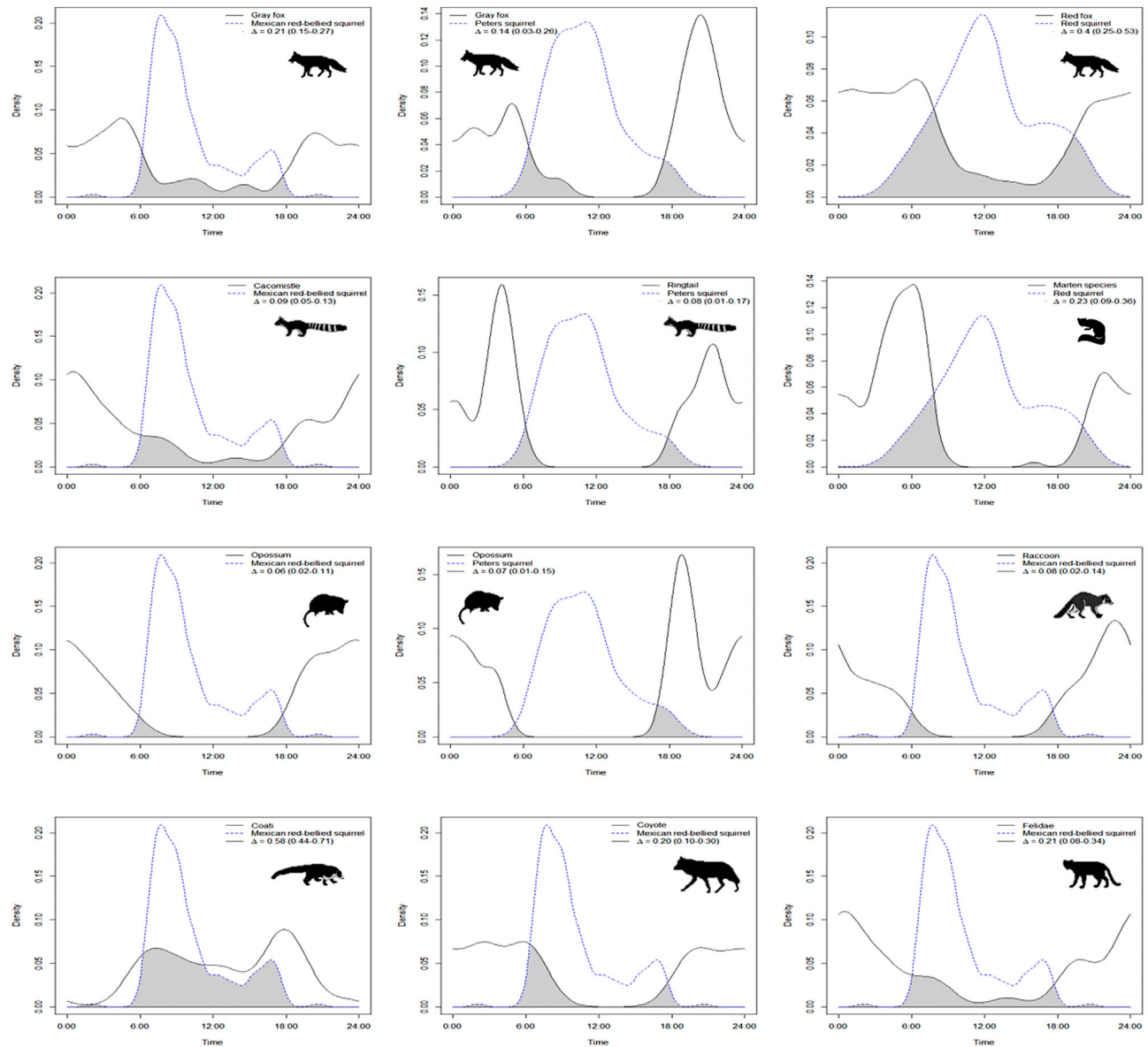
Figure 4 Temporal overlap (Δ_1) between the activity patterns of wild predator species (solid line) and squirrel species (dashed line) in the three study areas (Figure 1). The overlap coefficient is represented by the shaded area.

with wild crepuscular and cathemeral predator species as these species become more nocturnal due to the presence of free-ranging dogs (Gálvez et al., 2021; Zapata-Ríos & Branch, 2016).

However, this effect of dogs on wild predator patterns remains unclear (Bianchi et al., 2020), as dog activity patterns may depend on various factors such as human food provisioning (Silva-Rodríguez & Sieving, 2011). In the case of dogs that depend primarily on food offered by humans (i.e., free-ranging dogs), it has been described as more diurnal (Farris et al., 2015; Silva et al., 2018), while feral dogs are generally more nocturnal (Zapata-Ríos & Branch, 2016). Our data show

that dogs in the *S. oculatus* and *S. vulgaris* areas are primarily diurnal, while those in the *S. aureogaster* area had more crepuscular activity (Fig. 3). This behavior explains the lower temporal overlap between the dog and the squirrels in *S. aureogaster* area compared to the other study areas (Table 1, Fig. 3). It is also worth mentioning that many of the dogs observed in this area had thinner and malnourished bodies, suggesting that they probably were feral dogs. However, this reduction in the temporal overlap between *S. aureogaster* and dogs could also be due to the greater abundance of dogs in this area, the most abundant predator species. This high abundance may have caused a rapid adaptation of the squirrels in

this area to use the ground in a short period to reduce the risk of predation by dogs (Descalzo et al., 2021; Viviano et al., 2021; Zapata-Ríos & Branch, 2016). However, the lack of spatial replicas in areas with less abundance of dogs does not allow us to test this hypothesis.

Feral and free-ranging dogs pose a severe threat to wildlife, especially carnivore species that may share diseases or prey species (Butler et al., 2004; Martínez-Sotelo et al., 2022; Nayeri et al., 2021; Randall et al., 2006; Young et al., 2011). Here, we show a high risk of predation by feral and free-ranging dogs on the three squirrels species studied in different ecosystems, so this should be considered in areas with a high abundance of free-ranging dogs and the presence of threatened species. Of the three areas studied, the San Bartolo Tutotepec (*S. aureogaster* area) has shown a high diversity of mesocarnivores, some threatened, and a very high abundance of free-ranging dogs, being the most abundant species. Furthermore, it has been shown that the distance to human settlements was the most critical factor in the abundance and conservation of the *S. oculatus* in Central Mexico, suggesting the importance of domestic carnivore predation near settlements (Tobajas et al., 2020). Although the abundance of free-living dogs in Spain can be considered lower compared to Mexico (Sykes et al., 2020), and no studies have evaluated the potential impact on squirrels species, it has been documented impacts on wildlife (Duarte et al., 2016; Millán et al., 2011). These data show that a conservation problem probably exists for many preys and mesocarnivore species due to the high abundance of feral and free-ranging dogs in many areas worldwide. This threat is receiving much attention with the increase in scientific knowledge on the adverse effects of feral and free-ranging dogs on native species (Callan et al., 2020; Carrasco-Román et al., 2021; Doherty et al., 2017; Martínez-Sotelo et al., 2022; Wierzbowska et al., 2016; Zapata-Ríos & Branch, 2016). However, despite this increasing evidence of the adverse effects of free-ranging dogs on biodiversity, there is a lack of management actions to reduce its effects. Therefore, we urge public administrations to create management plans for feral and free-ranging dogs in areas of high biodiversity.

Acknowledgments

Conflict of interest

The authors declare no conflict of interest.

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