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Unveiling activity patterns of the deer *Odocoileus virginianus* (Artiodactyla: Cervidae) and its predators in Mexico's Arid Region

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ABSTRACT

Introduction: Size, predator presence, and habitat nutritional quality influence herbivorous species' activity patterns and resource utilization.

Objective: To determine the relative abundance and activity patterns of white-tailed deer (*Odocoileus virginianus*) and their main predators.

Methods: The study was conducted in the WMU "Bienes Comunes Santa Cruz Nuevo" in Totoltepec de Guerrero, Puebla, Mexico. Twenty-two quadrants were randomly selected, and camera traps were installed. Over two years (2018-2020), wildlife visits were recorded to estimate the relative abundance index (RAI), activity patterns, and overlap coefficient (Dhat1) of white-tailed deer and their predators based on their activity schedule.

Results: The estimated RAI for deer was 7.2 %, while it was 3.4 % for coyotes (*Canis latrans*), 2.3 % for bobcats (*Lynx rufus*), and 0.14 % for pumas (*Puma concolor*). White-tailed deer were observed in 31 % of the camera traps, while coyotes were captured in 68 % of them. The overlap of the activity schedule, Dhat1, between deer and coyotes was 0.18. In contrast, the activity overlap between foxes and deer was higher (Dhat1: 0.2979; EE 0.037) based on the analysis of variance. The activity pattern of coyotes indicated they were crepuscular, with increased activity during the afternoon and night. However, an increase in activity synchronized with deer's patterns was also observed. The bobcat coincided with deer in 10 % of the cameras, but due to the limited number of observations, it was not possible to estimate the activity overlap between these species.

Conclusions: The activity overlap between white-tailed deer and foxes is more significant than that of deer and coyotes in this region. The activity overlap between deer and coyotes is lower compared to other parts of the world.

Key words: abundance; camera traps; deer habitat use; Tehuacán-Cuicatlán valley; *Lynx rufus*.



RESUMEN

Revelando patrones de actividad del venado *Odocoileus virginianus* (Artiodactyla: Cervidae) y sus depredadores en la región árida de México

Introducción: El tamaño, la presencia de depredadores y la calidad nutricional del hábitat influyen en los patrones de actividad y utilización de recursos de las especies herbívoras.

Objetivos: Determinar la abundancia relativa y los patrones de actividad del venado cola blanca (*Odocoileus virginianus*) y sus principales depredadores.

Métodos: El estudio se realizó en la UMA “Bienes Comunes Santa Cruz Nuevo” en Totoltepec de Guerrero, Puebla, México. Se seleccionaron al azar 22 cuadrantes y se instalaron cámaras trampa. Durante dos años (2018-2020), se registraron las visitas de fauna silvestre para estimar el índice de abundancia relativa (IAR), los patrones de actividad y el coeficiente de superposición (Dhat1) del venado cola blanca y sus depredadores en función de su horario de actividad.

Resultados: El IAR estimado para venado fue de 7.2 %, mientras que para coyote (*Canis latrans*) de 3.4 %, el gato montés (*Lynx rufus*) 2.3 % y puma (*Puma concolor*) 0.14 %. Se observaron venados cola blanca en el 31 % de las cámaras trampa, mientras que se capturaron coyotes en el 68 % de ellas. La superposición del programa de actividad, Dhat1, entre venados y coyotes fue de 0.18. En contraste, la superposición de actividad entre zorros y venados fue mayor (Dhat1: 0.2979; EE 0.037). El patrón de actividad de los coyotes indicó que eran crepusculares, con mayor actividad durante la tarde y la noche. Sin embargo, también se observó un aumento en la actividad sincronizada con los patrones de los venados. El gato montés coincidió con el venado en el 10 % de las cámaras, pero debido al limitado número de observaciones, no fue posible estimar el traslape de actividad entre estas especies.

Conclusiones: La superposición de actividades entre venados cola blanca y zorros es más significativa que entre venados y coyotes en esta región. El traslape de actividad entre venados y coyotes es menor en comparación con otras partes del mundo.

Palabras clave: abundancia; cámaras trampa; uso de hábitat del venado; valle Tehuacán-Cuicatlán; *Lynx rufus*.

INTRODUCTION

The Mixtec is a mountainous area between Puebla and Oaxaca in Southeastern Mexico. There converges a chain of mountains named the “Sierra Madre Oriental,” the Neo volcanic Axis, and another chain of mountains named the “Sierra Madre del Sur.” Its elevation ranges from 167 to 3 347 meters above sea level, making it an area with a predominance of mountains interspersed with canyons, ravines, valleys, and plateaus (Hernández-Aguilar et al., 2017). One of the essential valleys within this zone is the Tehuacán-Cuicatlán valley, located Southeast of Puebla. This valley is the arid or semi-arid zone with North America’s most extraordinary biological diversity. It has the densest columnar cacti forests on the planet, which form a unique landscape associated with agaves, yuccas, holm oaks, bromeliads, and burserae (UNESCO, 2018). Under these conditions, accurately estimating deer habitat use and abundance can be difficult because they are

in ecosystems with dense vegetation, thus making detection difficult (Urbanek et al., 2012).

However, obtaining reliable estimates of terrestrial herbivore abundance can be used to assess the management of wild species with ecological and economic value. Within these estimates, abundance makes it possible to evaluate conservation efforts, establish hunting quotas, estimate prey availability for carnivores, and evaluate the management of the area in question (Palmer et al., 2018). Under these conditions, camera traps are used in wildlife estimates due to their objectivity, ease of use, and ability to generate information on large numbers of species. Camera traps are primarily designed to document species richness, occupancy, and abundance indices; estimate the abundance of individually identifiable species in a capture-recapture framework; and determine their activity patterns (Tanwar et al., 2021). A central issue in wildlife management is understanding how species respond to environmental changes. Their distribution is

increasingly affected by anthropogenic stressors as habitat fragmentation, urban development, and accelerating global climate change (Combe et al., 2022). These alterations, together with the presence of predators (Higdon et al., 2019) and the nutritional quality of the habitat, have shown that the activity patterns and the use that a herbivorous species makes of this resource change depending on its size (Roque et al., 2021).

Regarding activity patterns, there is extensive research on white-tailed deer in temperate and cold ecosystems (Michel et al., 2020; Pustilnik et al., 2021). In these habitats, the activity pattern of the white-tailed deer (*Odocoileus virginianus*, var. *texanus*) is associated with the presence of the coyote (*Canis latrans*), which is considered the predator par excellence of this species in the United States (Crawford et al., 2021). In South America, the habitat use, and abundance of white-tailed deer vary widely. However, habitat use patterns generally reflect the quality and abundance of resources in focal areas, influencing variations in habitat use and deer fitness in a landscape (Duquette et al., 2020).

In Mexico, some researchers evaluated the activity patterns in the country's north and south (Gallina & Bello Gutierrez, 2014; Retana Guascón et al., 2015). However, they did not describe the interaction of the activity pattern concerning the presence of predators. It is likely that because the size of the white-tailed deer (*Odocoileus virginianus* var. *mexicanus*) is smaller than that of the *Texanus* (Villarreal-Espino et al., 2011), the type of predator with which this pattern is associated in the center of the country may be different from the coyotes. Additionally, and due to the physiographic characteristics of the Mixtec, the activity patterns of white-tailed deer are likely different; thus, the work aimed to determine the effect of the presence of predators on the pattern of activity in white-tailed deer and the relative abundance of mammals and birds in the area.

MATERIALS AND METHODS

Study area: We carried out this research at the Wildlife Management Unit (WMU) at Santa Cruz Nuevo, in Totoltepec de Guerrero, Puebla (18°17'44" N & 97°48'35" W). The prevailing climates are semi-warm sub-humid with summer rains (Aw -Köppen classification; INEGI, 2021) and temperate sub-humid with summer rains (Cfa-Köppen classification; INEGI, 2021). The area is part of the Balsas River hydrological region (Villarreal-Espino et al., 2011), presenting a marked seasonality. The range of inclination of the slope is between 20 and 70 %, with shallow soils from 0 to 25 cm (INEGI, 2021). The types of vegetation present are low deciduous forest, xeric scrub, Central Mexican submontane mixed desert scrub, medium scrub, and medium thorny sub deciduous forest (Barrera-Salazar et al., 2015).

Wildlife monitoring: We randomly selected twenty-two sites and established 50 m² plots (Anderson et al., 2013). We recorded the Altitude (Meters above sea level; masl) and quantified basal and escape coverage within these areas. In each of them, we installed a camera trap and recorded through the programming of the equipment, the location, date, and time; with the recorded ecological data, we estimated the sampling duration (Effort) (Bowler et al., 2017). We checked the cameras every 16 weeks for approximately two years (2018 to 2020). We carefully observed each photographic sequence to determine the independent captures. When we could not identify with certainty the gender, class, age, and unique body markings of the photographed animals, we considered successive captures (with an interval of fewer than five minutes) of the same species a single event. Also, we considered an independent capture if another individual of a different species appeared within two continuous sequences of less than five minutes. We used the free access software Wild.ID (Mandujano



& Morteo-Montiel, 2018) to facilitate ordering the photographic folders derived from the sampling. Also, we determined the presence-absence (number of individuals and species) by observing the captured images.

Data analysis: We realized these analyses using R software version 4.3.1 (Crawley, 2013) and we estimated the activity patterns of deer and predators (coyote, fox, and bobcat) and graphed based on the activity hours. We used the `overlap` Plot and `overlap Est` package to graph them in RStudio (Meredith & Ridout, 2009) using the “Kernel density estimator,” which is a non-parametric method that allows for estimating the probability density function of a random variable from a finite number of observations (samples) and for modeling the habitat use curve throughout a day. This program estimates the overlap coefficient (Dhat1); the delta value goes from 0 to 1, where 1 implies a significant coincidence of schedules and 0 implies that the activity patterns are entirely different (Mandujano, 2019). With the estimated Dhat1 values for each site where the overlap of deer with foxes or coyotes occurred and the mean obtained from the resampling (bootstrap) carried out by the same subprogram, we carried out an analysis of variance with a completely random model using both determined and estimated values of Dhat1 for each type of overlap as repetitions and deer-fox (T1) and deer-coyote (T2) overlap as treatments. We performed Stepwise Discriminant Analysis considering the escape cover, the basal cover of the area, and the altitude. We carried out these last analyses with the JMP8 program from SAS (Sall et al., 2017).

The relative abundance index (RAI) estimate was derived from recording the presence and absence of all species caught, assuming that estimates of observed abundance are proportional to the number of detections per site and that variation between sites is unknown (Duquette et al., 2020). Therefore, the RAI of each species was calculated as the number of independent photo-capture events of the same, divided by the sum of the total sampling effort of all the cameras multiplied by 100 (Gronwald

& Russell, 2021), under the following considerations: the RAI considers a positive linear relationship between the abundance of the population and the same index; it assumes that individuals of the same species behave similarly in different localities and seasons of the year; and it assumes a constant probability of detection and that it is not affected by the location of the cameras (Mandujano, 2019).

RESULTS

A total of 347 *Urocyon cinereoargenteus* (gray fox records), 105 white-tailed deer records, fifty coyote records, thirty-four bobcat records, and two cougar records were obtained. White-tailed deer were present in 36 % of the camera traps (Fig. 1), while predators had a greater distribution in the area: the coyote was captured in 68 %, the bobcat in 54 %, the puma only in 4.5 %, and the fox in 90 % of them.

The gray fox converged in 48.2 % of the sites with the coyote and in 24 % of the sites with the white-tailed deer; it is important to point out that in all the places where the gray fox and the white-tailed deer converged, either the coyote or the bobcat was always present. The results of this work show a greater abundance of foxes than coyotes in a ratio of 1.6:1.

Estimation of the RAI of deer and predators: Table 1 shows the RAI and the frequency of occurrence in camera traps. The RAI estimate for white-tailed deer was 6.06 %. Rabbits and rodents have a higher abundance (53.17 and 21.92 % on average). Rodents are commonly distributed in disturbed natural ecosystems or have changed their homogeneous landscape matrix by activities derived from land use change, mainly by agricultural activities.

The analysis of variance showed that the activity overlaps between fox and deer is higher than that between deer and coyote (Dhat1; 0.2979, SE 0.037 vs Dhat1; 0.1869 SE 0.034; $\alpha < 0.05$). Fig. 2 shows the activity overlaps between the white-tailed deer and the gray fox: it can be observed that the behavior of the gray fox is very similar at both elevation levels. In

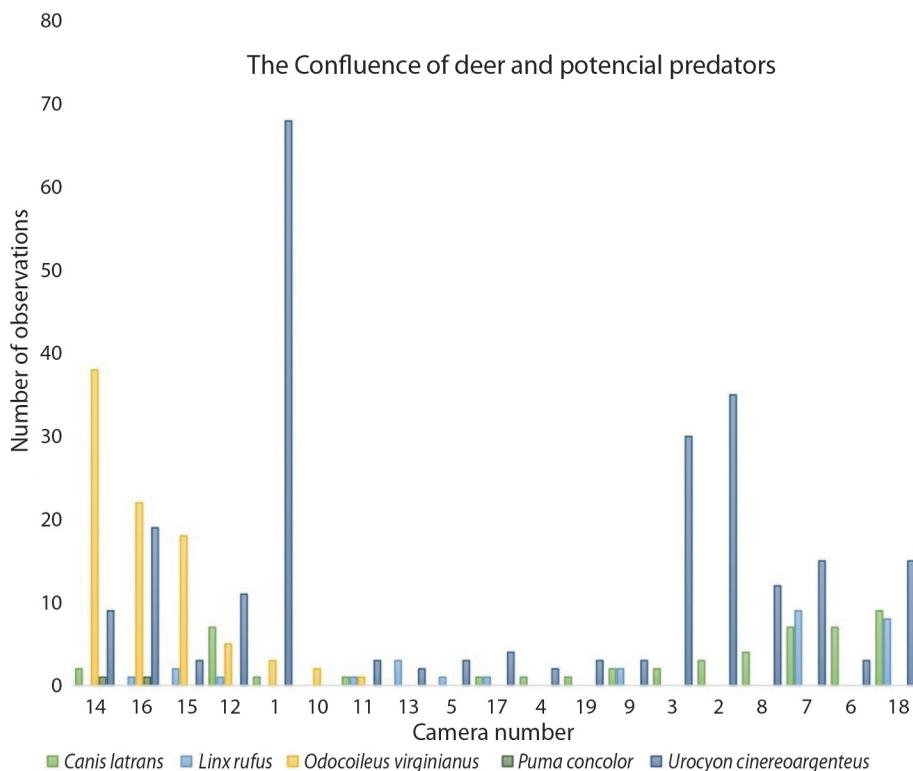


Fig. 1. Distribution of white-tailed deer and potential predators in camera traps.

Table 1
Relative abundance index and frequency of appearance in camera traps.

Genus / Species	Common name	No. of observations	RAI %	No. of cameras	Frequency %
<i>Oryctolagus cuniculus</i>	Rabbit	824	56.63	7	86.36
<i>Rattus novaeguineae</i>	Rat	366	25.15	2	22.73
<i>Peromyscus mekisturus</i>	Mouse	354	24.33	26	63.64
<i>Urocyon cinereoargenteus</i>	Grey Fox	347	23.85	1	90.91
<i>Bos primigenius</i>	Cow	154	10.58	3	36.36
<i>Odocoileus virginianus</i>	White-tail deer	105	7.22	4	31.82
<i>Canis lupus familiaris</i>	Dog	66	4.54	15	9.09
<i>Procyon lotor</i>	Raccoon	54	3.71	14	45.45
<i>Mephitis mephitis</i>	skunk	52	3.57	5	77.27
<i>Canis latrans</i>	Coyote	50	3.44	8	68.18
<i>Lynx rufus</i>	Bobcat	34	2.34	2	54.55
<i>Didelphis virginiana</i>	opossum	9	0.62	2	9.09
<i>Homo sapiens</i>	Man	6	0.41	12	22.73
<i>Bassariscus astutus</i>	Ringtails	5	0.34	3	13.64
<i>Nasua narica</i>	coati	5	0.34	17	18.18
<i>Herpailurus yagouaroundi</i>	jaguarundi	3	0.21	25	4.55
<i>Spilogale angustifrons</i>	Southern skunk	2	0.14	5	4.55

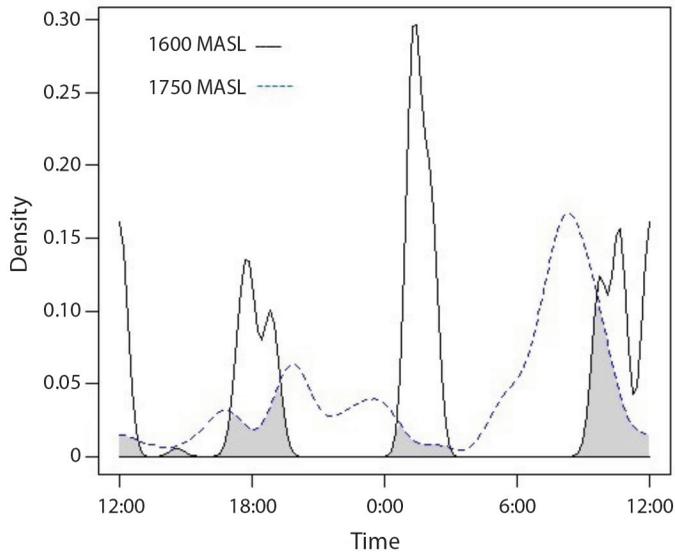


Fig. 2. Activity schedule of *Odocoileus virginianus* in WMU Santa Cruz Nuevo, Totoltepec de Guerrero, Puebla.

contrast, the white-tailed deer shows very different behaviors related to the elevation. Due to these changes in white-tailed deer activity, activity overlap was less when MBSL was low and increased when elevation was higher, at 1 650 m (Dhat1 1 600 = 0.18 vs. Dhat1 1 750 = 0.29, EE 0.03; α 0.05; $t=2.08$).

Stepwise Discriminant Analysis revealed that basal cover (amount of plant material covering the ground) was one of the essential components of the variance; this analysis showed that it modifies ($P < 0.02$; Table 2) the

overlap of activity patterns of white-tailed deer and coyote.

Fig. 3A shows that the activity pattern when the deer is around 1 600 masl has different peaks of activity approximately every six hours, while at a higher altitude (1 750 masl; Fig. 3B), it shows a higher diurnal activity (6:00 to 12:00). These activity patterns are entirely contrasting and only match about 25 %.

Fig. 4A and Fig. 4B show that both coyote and white-tailed deer tend to modify their activity depending on elevation; however, they

Table 2
Stepwise Discriminant Analysis between the habitat variables and activity overlap.

Overlap: White-tailed deer:coyote (Dhat1)						
Variable	F Ratio	P value	Test	Value	Exact F	Prob > F
Altitude	207.098	0.00001	Wilks' Lambda	0.046	111.53	0.0001*
Escape Cover	1.180	0.302	Pillai's Trace	0.953	111.53	0.0001*
Basal Cover	6.958	0.023	Hotelling-Lawley	20.279	111.53	0.0001*
			Roy's Max Root	20.279	111.53	0.0001*
Overlap: White-tailed deer:gray fox (Dhat1)						
Variable	F Ratio	P value	Test	Value	Exact F	Prob > F
Altitude	35.303	0.0003	Wilks' Lambda	0.184	35.303	0.0003*
Escape Cover	0.420	0.537	Pillai's Trace	0.815	35.303	0.0003*
Basal Cover	0.604	0.462	Hotelling-Lawley	4.412	35.303	0.0003*
			Roy's Max Root	4.412	35.303	0.0003*

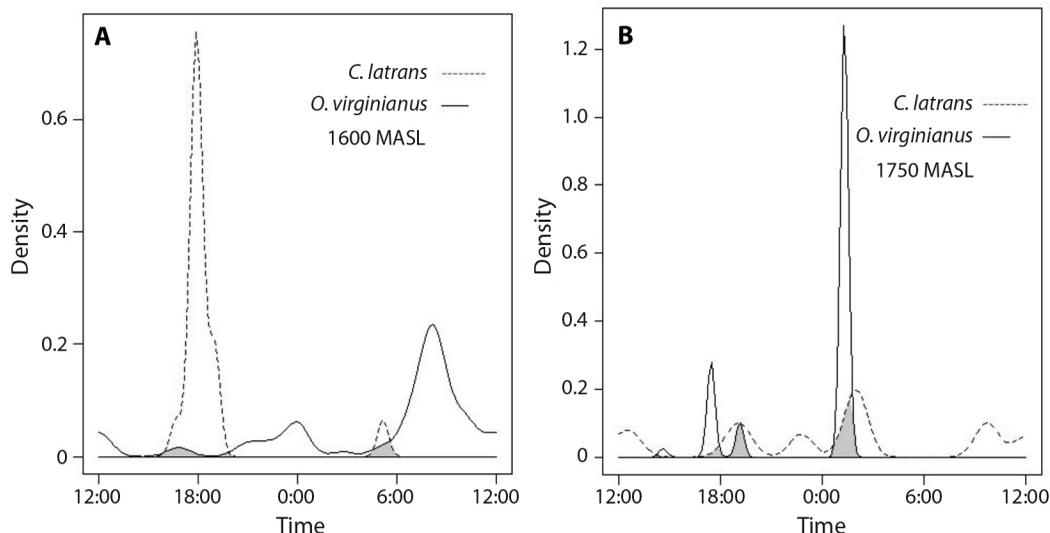


Fig. 3. A. Activity overlap (Dhat1) between the deer and the coyote at 1 600 MASL. B. Activity overlap (Dhat1) between the deer and the coyote at 1 750 masl.

always maintain a shallow level of overlap. When confidence intervals were estimated using the bootstrap function, they were 0.1016 to 0.3837 for activity overlap of these species at 1 600 masl and -0.00274 to 0.11380 when found at more than 1 750 masl.

DISCUSSION

Estimation of the RAI of deer and predators: It is important to note that the RAI is modified mainly by the number of captures in such a way where if there are many sightings in a relatively low number of camera traps, it will result in a high RAI (Mandujano & Morteo-Montiel, 2018), which is what happens in the particular case of the white-tailed deer.

Among the potential predators that interact with the white-tailed deer, based on the body size of the prey, the coyote (*Canis latrans*; 3.32 % RAI), the bobcat (*Lynx rufus*; 2.52 % RAI), and the cougar (*Puma concolor*; 0.14 % RAI) are expected. The abundance of *Urocyon cinereoargenteus* (gray fox) in the habitat is the highest of the carnivores (24.71 %); although this predator probably does not attack adult deer, the young white-tailed deer could be

targets of their predation. In contrast to the work of, Cruz-Jácome et al. (2015) where neither the presence of cattle nor people were reported and they only mentioned the puma, in this work, the effect of changes in habitat use was manifested in the presence of cattle, dogs, and people. This is relatively expected because generally in the diversified livestock system, cattle are expected to contribute a part of the economic income (Villarreal Espino-Barros et al., 2008). The greater abundance of the gray fox can be explained by the high number of rodents and rabbits in the area and by the habitat preferences of this species. Gallina et al. (2016) reported that this species prefers habitats with a low density of people and that dirt roads positively improve the presence of this species because they can consume poultry and waste; additionally, the data suggest that the puma stayed away from the core of the population.

Overlap of deer and predator activity schedules: As previously mentioned, the gray fox converged in 48.2 % of the sites with the coyote and in 24 % of the sites with the white-tailed deer; it is important to point out that in all the places where the gray fox and the

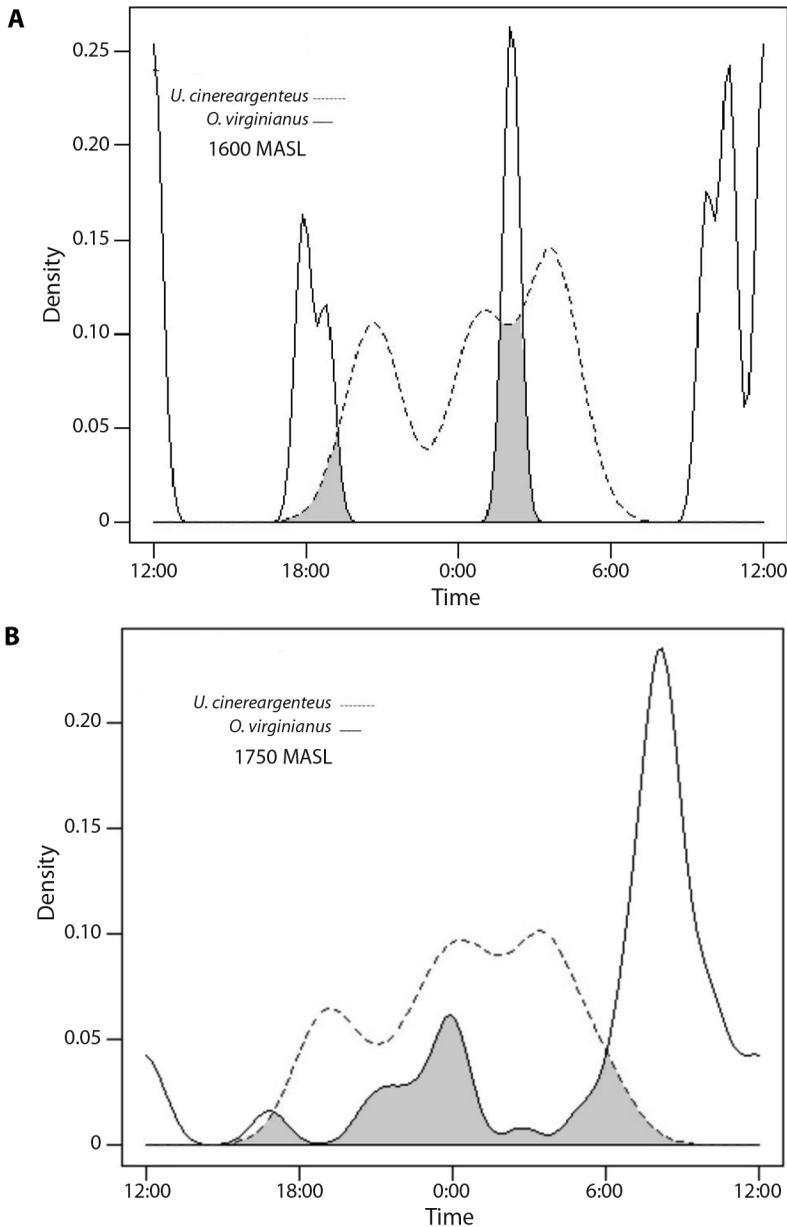


Fig. 4. A. Activity overlap (Dhat1) between the deer and the gray fox at 1 600 MASL. **B.** Activity overlap (Dhat1) between the deer and the gray fox at 1 750 MASL.

white-tailed deer converged, either the coyote or the bobcat was always present. The coexistence of these three species has already been reported and is considered normal because the fox is omnivorous, so there is no direct competition between them and other predators

(Veals et al., 2021). As previously mentioned, this carnivore was the most abundant in the area. However, many studies show a negative interaction between the coyote and this species and that the presence of the coyote reduces its abundance (Egan et al., 2021). The coexistence

between the three species can be explained based on the presence of trees in the sampling areas, which the fox can use due to its ability to climb trees to seek refuge from potential predators (Deuel et al., 2017). The results of this work show a greater abundance of foxes than coyotes in a ratio of 1.6:1.

The analysis of variance showed that the activity overlap between fox and deer (Dhat1; 0.2979, EE 0.037) is higher than that between deer and coyote (Dhat1; 0.1869 EE 0.034; $\alpha < 0.05$). Fig. 2 shows the activity overlaps between the white-tailed deer and the gray fox; it can be observed that the behavior of the gray fox is very similar at both altitude levels, while the white-tailed deer shows very different behaviors. Of these changes in white-tailed deer activity, activity overlap was less when MASL was low and increased when MASL was higher, at 1 750 m (Dhat1 1600 = 0.18 vs. Dhat1 1750 = 0.29, EE 0.03; $\alpha < 0.05$; $t = 2.08$). It is essential to point out that the gray fox is considered a generalist species with very marked preferences in its diet, so it is assumed that, at least in the Northern part of the country, it does not consume any species of the Artiodactyl category; therefore, it does not consume deer (Rodríguez-Luna et al., 2021). The fact that deer do not form part of the fox's diet could explain the increased daytime activity of both species, when both are dedicated to foraging. The activity overlap between deer and coyote in this work is much lower than that reported by Higdon et al. (2019); they showed an overlap from 0.68 to 0.72 depending on the size or gender of the animal. The reduction in activity overlap between coyotes and deer can be explained by how the prey can minimize predation risk through behavioral changes that reduce the probability that the predator will find it (Smith et al., 2019).

Spatially, prey species can alter habitat use and minimize exposure to predation risk. However, the reports on changes in deer behavior in the presence of predators are variable: some authors have reported that deer change the spatial use of their habitat when the coyote spread their hair (Seamans et al., 2002) or

bobcat urine repeatedly (Swihart et al., 1991). In contrast, more recent work has shown that the presence of predators such as wolves may not have a significant impact on deer behavior, since deer may mistake them for domestic dogs (van Ginkel et al., 2019). White-tailed deer and coyote have a confluence in 20.6 % of the sites, which suggests that deer avoid the same sites as coyotes, or they modify their hours of activity in such a way as to reduce the chances of capture further. The bobcat coincided with the deer in 10 % of the cameras; however, due to the low number of observations in them, it was not possible to estimate the activity overlap between this species and the white-tailed deer. Apparently, the white-tailed deer avoids this species more than the coyote, which can be explained by how although the bobcat is considered a general carnivore, recently published studies show that, at least in the Northern hemisphere, deer and opossum are two essential components of its diet (Landry et al., 2022).

Stepwise discriminant analysis revealed that basal cover was one of the most critical components of the variance; pairwise correlation showed that it modifies ($P < 0.02$; Table 2) the overlap of activity patterns of white-tailed deer and coyotes. This result is different from Henderson et al. (2020), who showed that the deer select their hiding areas based on the height and thickness of the vegetation. However, in their case, the basal cover modified the preference of the deer in those areas. The explanation for the negative correlation can be found in the field of deer herbivory; it has been reported that one of the effects of deer browsing is the reduction of both basal cover and plant richness (Royo et al., 2017). According to these authors, a more significant presence of deer would reduce plant cover.

The altitude modify the Dhat1 of the deer with the coyote ($P < 0.00001$); this effect is reflected in Fig. 3, which shows that the pattern of activity when the deer is around 1 600 m, they have different peaks of activity approximately every six hours, while at a higher altitude (1 750 MASL), they show more significant daytime activity (6:00 a.m. to 12:00 p.m.) so



that these activity patterns are entirely contrasting and only coincide in approximately 25 %.

Fig. 4 shows that both coyote and white-tailed deer modify their activity depending on altitude; however, they always maintain a shallow level of overlap. When confidence intervals were estimated using the bootstrap function, they were 0.1016 to 0.3837 for activity overlap of these species at 1 600 MASL and -0.00274 to 0.11380 when found at more than 1 750 MASL. In contrast, the works published by Dellinger et al. (2019) and Hinton et al. (2022) show that this variable modifies the use of white-tailed deer habitat due to the mechanisms they develop to escape from predators (maximum speed races); they consequently prefer areas with lower MASL. In this work, the effect of altitude was only manifested as an inverse trend, suggesting that the coyote is more abundant in areas with lower altitudes because it is in that area where the primary water sources are located. Works published long ago showed that the coyote stayed close to water sources and kept the deer away from them (Villarreal-Espino-Barros et al., 2012).

The activity overlaps between the white-tailed deer and the fox are greater than that of the white-tailed deer and the coyote. In this region, the activity overlap between the deer and the coyote is much less than that reported in other parts of the world. This variable is modified by basal cover but not by escape cover or altitude. However, the activity patterns of *O. virginianus* are modified by MASL.

Ethical statement: the authors declare that they all agree with this publication and made significant contributions; that there is no conflict of interest of any kind; and that we followed all pertinent ethical and legal procedures and requirements. All financial sources are fully and clearly stated in the acknowledgments section. A signed document has been filed in the journal archives.

This study complied with all the permits required by the ethics committee of the Universidad Autónoma Metropolitana and

the Secretary of the Environment and Natural Resources of Mexico.

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