# Activity patterns of the white-tailed deer (*Odocoileus virginianus*) in a neotropical dry forest: changes according to age, sex, and climatic season

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Mammalian daily activity is shaped by a combination of intrinsic and extrinsic factors. Age influences activity rhythms due to energy requirements, while physiological and reproductive traits cause differences between genders. In ecosystems with marked climatic seasonality, such as the seasonally dry tropical forest (SDTF), activity patterns adapt to extrinsic factors like resource availability and environmental stress. This study investigates how intrinsic factors, specifically age and sex, influence the white-tailed deer's (*Odocoileus virginianus*) daily activities, and how these vary between dry and rainy seasons. Between 2015 and 2018, we conducted a camera trapping study to monitor the daily activity of a population of white-tailed deer in the Arenillas Ecological Reserve, southwestern Ecuador. We estimated individual daily activity based on four parameters: total and diurnal relative abundance index (RAI), activity directionality, and activity overlap between groups. We used generalized linear models to evaluate the changes in RAI based on age-classes and sex of the individuals. The Watson test was employed to assess differences in directional patterns during activity hours, while the Wald test was utilized to evaluate significant variations in activity overlap. The same analyses were also performed to assess changes in daily activity between the dry and rainy seasons. The daily activity patterns of white-tailed deer varied by age and sex. Fawns were predominantly diurnal, whereas adults displayed continuous activity throughout the 24 hours of the day, with males being more active during the night than females. Females did not show significant differences in the activity pattern compared to fawns and juveniles. The daily activity pattern of white-tailed deer varied between seasons. Overall, there was an increase in daily activity during the dry season, but significant only for males. Females were the only group that showing seasonal variation in activity directionality, with more morning activity during the dry season. The daily activity patterns of white-tailed deer in the dry forest exhibit slight differences compared to those observed in other ecosystems, with extended daily activity periods. During the rainy season, reproductive and post-reproductive behaviors, rather than resource abundance, predominantly shaped the white-tailed deer's daily activity patterns. In contrast, the dry season presented a notable rise in overall activity and daily activity, accompanied by partition between groups. This partition likely stems from diminished resource accessibility and increased intraspecific competition. Given the slight differences in the white-tailed deer's daily activity from those noted in other regions, these insights are crucial for formulating management and conservation strategies tailored to specific environmental conditions.

Los patrones de actividad diaria de los mamíferos están determinados por diferentes factores. La edad puede determinar diferentes ritmos de actividad como respuesta a requerimientos energéticos, mientras que las características fisiológicas y reproductivas marcan diferencias entre sexos. En ecosistemas con una marcada estacionalidad climática, los ritmos de actividad pueden variar temporalmente en respuesta a cambios en la disponibilidad de recursos o factores de estrés ambiental. Este estudio analiza en qué medida los factores intrínsecos, como la edad y el sexo, determinan los patrones de actividad diaria del venado de cola blanca (*Odocoileus virginianus*), y si estos patrones cambian como consecuencia de la estacionalidad climática del bosque tropical estacionalmente seco (BTES). Entre 2015 y 2018 se monitoreó mediante fototrampeo la actividad diaria del venado de cola blanca en la Reserva Ecológica Arenillas, Ecuador. Se usaron modelos lineales generalizados para evaluar cambios en el índice de abundancia relativa (RAI) según la edad y el sexo del individuo. Se utilizó la prueba de Watson para evaluar diferencias en la direccionalidad en las horas de actividad y la prueba de Wald para evaluar diferencias en el solapamiento de la actividad entre grupos y entre estación seca y lluviosa. Los patrones de actividad diaria de *O. virginianus* variaron según la edad y sexo. Los cervatillos fueron predominantemente diurnos, mientras que en la etapa adulta la actividad se distribuyó durante todo el día. Además, el patrón de actividad diaria cambió entre estaciones, siendo los machos significativamente más activos durante la estación seca. Las hembras mostraron diferencias en la direccionalidad de la actividad diaria entre estaciones, con una mayor actividad durante las primeras horas de la mañana en la época seca. El patrón de actividad diaria de los venados en el BTES es ligeramente distinto al observado en otros ecosistemas, con patrones de actividad diaria más extendidos a lo largo del día. En el BTES, los cambios en la disponibilidad de recursos y de comportamiento de los venados entre estaciones generan cambios en el patrón de actividad diaria. Durante la época lluviosa los patrones de actividad diaria estuvieron definidos por el comportamiento reproductivo y post-reproductivo antes que por la alta disponibilidad de recursos. En la época seca hubo un aumento general de la actividad y de los periodos de actividad diaria, con una partición en los períodos de actividad entre grupos, lo que podría explicarse como una consecuencia de la reducción del acceso a los recursos y el incremento de la competencia intraespecífica. Considerando que la actividad diaria de *O. virginianus* puede diferir ligeramente de los patrones observados en otros ecosistemas, estos hallazgos son importantes para plantear medidas de manejo y conservación adaptadas a las condiciones propias de la localidad.

# Introduction

The daily activity patterns of species are natural responses to various biological, physiological, behavioral, and survival processes (Hut *et al.* 2012). For many species, these activity cycles follow patterns called circadian rhythms, repeating every 24 hours, allowing anticipation of and response to biotic and abiotic conditions (Halberg 1960; Dodd *et al.* 2005; Bradshaw and Holzapfel 2010; Libert *et al.* 2012; Spoelstra *et al.* 2016). Understanding these cycles is essential for managing vulnerable species or those that are key to the ecosystem.

The activity patterns exhibited by a species result from a complex balance between processes that maximize species success and reduce energy expenditure. Studies have shown that daily activity patterns can be determined by intrinsic factors such as sex, age, and physiological state, or by external factors such as forage availability and habitat quality (Beier and McCullough 1990; Main *et al.* 1996; Yearsley and Pérez-Barbería 2005; Fuller *et al.* 2020). Among intrinsic factors, changes in activity patterns at the demographic level enable adaptation to specific activities of different age groups, such as searching for shelter, food, or mates (Beier and McCullough 1990; Scheibe *et al.* 1999; Berger *et al.* 2002). In herbivores, activity patterns are closely related to feeding behavior since digestive processes impose cyclic activity patterns of less than 24 hours (Scheibe *et al.* 1999, 2009). These patterns result from the interaction between daily behavioral rhythms and digestive physiology (Scheibe *et al.* 1999, 2009; Berger *et al.* 2002; Owen-Smith and Goodall 2014). In large gregarious herbivores, having different activity patterns helps distribute their temporal niche for resource consumption and meet their energy needs, avoiding the energy expenditure that intraspecific competition can entail (Fortin *et al.* 2004; Valeix *et al.* 2007). The activity peaks of male and female ungulates may differ mainly due to their energy requirements (Beier and McCullough 1990). Males have higher energy needs; therefore, they cover more territory. However, their activity during the day and throughout the year may vary depending on the climatic conditions of each season (Webb *et al.* 2010; Gallina and Bello 2010; Massé and Côté 2013). In the case of fawns, the activity patterns are similar to those of their mothers since they depend on them for feeding, at least in the first months of the offspring's life (Ozoga and Verme 1986).

Furthermore, studies focused on deer species indicate that daily activity patterns change in response to extrinsic factors, such as environmental conditions (Mandujano and Gallina 1995; Sánchez-Rojas *et al.* 1997; Gallina and Bello 2010). It is known that in the tropics, ungulates carry out most of their activities at twilight (dawn and dusk), when climatic conditions are favorable, and it is possible to avoid energy and water loss due to high temperatures (Leuthold and Leuthold 1978; Beier and McCullough 1990; Galindo Leal and Weber 1998; Owen-Smith 1998; Gallina and Bello Gutierrez 2014). Since these conditions can vary between seasons, it is expected that these activity patterns will change according to climatic conditions. It has been reported that during the rainy season, deer are active throughout the day due to an increase in food availability, while during the dry season, when the availability and quality of food and water are very low (Arceo *et al.* 2005; Gallina-Tessaro 2019), they are more active during twilight hours (Mandujano and Gallina 1995; Sánchez-Rojas *et al.* 1997; Gallina and Bello 2010). Finally, changes in activity patterns between seasons could also be a consequence of mating behavior. Thus, during the breeding season, which matches with the rainy season, greater activity is expected than in the post-breeding period, which coincides with the dry season (Holzenbein and Schwede 1989; Beier and McCullough 1990; Fuller *et al.* 2020).

This work studied the daily activity patterns of white-tailed deer (*Odocoileus virginianus*), a widely distributed ungulate mammal species in the American continent. These animals have significant ecological and cultural importance (McShea 2012). Besides being an important prey for predators, they play a fundamental role in seed dispersal and forest regeneration (Crawford *et al.* 2019; Jara-Guerrero *et al.* 2018; Rooney and Waller 2003). Therefore, conserving this species is paramount for maintaining ecosystem health and preserving biodiversity. By understanding their circadian rhythms and associated moments of activity, appropriate management strategies can be recommended, promoting their conservation and ensuring the balanced functioning of the species and the ecosystems they inhabit. Understanding the activity patterns will allow informed decisions on deer habitat management, hunting control, and prevention of threats that may affect their survival.

With this background, we are interested in understanding to what extent the age class and sex of white-tailed deer determine daily activity patterns, and if these change as a consequence of the climatic seasonality characteristic of the seasonally dry tropical forest (SDTF). This ecosystem is characterized by strong climatic seasonality, with a dry season of six to eight months, during which more than 70 % of woody species lose their leaves, and the herbaceous layer disappears (Sierra 1999). This condition implies a reduction in resource availability for different herbivore species (Davis 1990; Mandujano *et al.* 2004; Arceo *et al.* 2005). It is proposed that the activity pattern of the white-tailed deer would be a consequence of the balance between physiological constraints, reproductive and post-reproductive behaviors, and intraspecific competition for resources. During the rainy season, activity patterns among groups could show temporal partitioning or overlap depending on which factor is dominant, resource availability or behavior. Thus, i) if the balance favors resource availability, daily activity patterns should differ among groups as a consequence of intraspecific competition (Owen-Smith and Goodall 2014). The greater availability of resources would allow a stratification of activity hours that minimize potential conflicts between different age groups. ii) Conversely, if reproductive and post-reproductive behavior is more important,

we expect daily activity among groups to be similar. The interaction between males and females should increase as a consequence of the mating behavior that occurs at the end of the rainy season (Mandujano and Gallina 1996). While the activity between the initial development stages (juveniles and fawns) and their mothers should be more coincident because the breeding season coincides with the rainy season (Hawkins and Klimstra 1970; Mandujano and Gallina 1996).

In the dry season, the temporal partitioning or overlap is expected to depend on the balance between physiological constraints due to drought and intraspecific competition for resources. Thus, iii) if physiological constraints influenced by drought predominate, the daily activity patterns of different groups should align. These patterns would aim to minimize energy expenditure and water loss, maximizing activity during twilight hours as a strategy to cope with water stress (Mandujano and Gallina 1995; Sánchez-Rojas *et al.* 1997; Gallina and Bello 2010), thereby reducing differences in activity patterns among groups. Conversely, iv) if the availability of resources is the dominant factor, a temporal partition in the daily activity of the groups is expected. The dry season implies a significant reduction in resources for these animals (Davis 1990; Arceo *et al.* 2005),

potentially increasing intraspecific competition (Bowyer 2004; Donohue *et al.* 2013), leading different groups to exploit resources at distinct times.

## Materials and methods

*Study area.* The study was conducted in the Arenillas Ecological Reserve (REAr), a key remnant of Ecuador's seasonally dry forests, located in El Oro province, southwestern Ecuador (Espinosa 2012; Sierra 1999; Figure 1). Spanning 131.7 km² (Ministerio del Ambiente 2014a), the reserve lies between 3° 27' 30.94" and 3° 39' 37.49" S latitude and 80º 9' 18.65" to 80º 9' 47.93" W longitude, with elevations ranging from 4 to 160 meters above sea level (Luna-Florin *et al.* 2022). It has an average annual temperature of 25.9 °C and precipitation of 661 mm, featuring a distinct rainy season from January to May and a dry season from June to December during which precipitation does not exceeds 40 mm (Espinosa *et al.* 2018; Figure 1). The area is characterized by deciduous forests and shrublands (Luna-Florin *et al.* 2022), rich in Fabaceae family plants (Espinosa 2012), which are crucial to the diet of white-tailed deer (Arceo *et al.* 2005; Vasquez *et al.* 2016), especially their fruits during the dry season (Arceo *et al.* 2005; Jara-Guerrero *et al.* 2018).

The REAr is surrounded by a matrix of rural human settle-
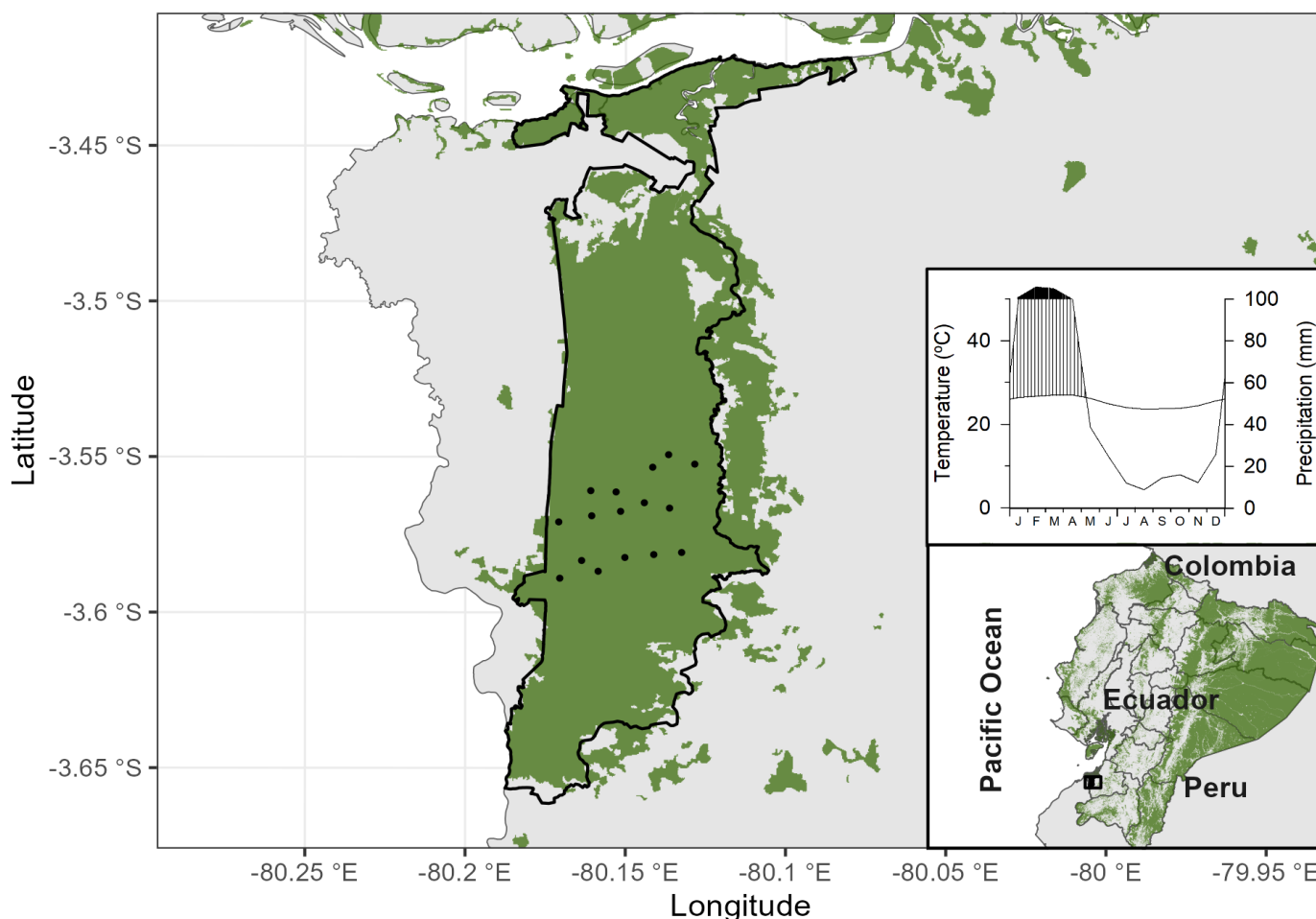


**Figure 1.** Location of study area. The forest remnants in 2022 are highlighted in green (Geoportal MAATE), and the border of the Arenillas Ecological Reserve is shown as a black line. A black spot represents the location of each camera trap. The climate diagram was elaborated using the meteorological station data from Arenillas (1965 to 2012), provided by the Instituto Nacional de Meteorología e Hidrología de Ecuador (INAMHI; Espinosa *et al.* 2018).

ments and farmlands. Unlike other dry forest areas where livestock farming is common, no human activities such as livestock are conducted within the reserve (Jara-Guerrero *et al.* 2019). Although there are instances of illegal hunting, these are limited due to its status as a protected area. Despite human pressures, the reserve maintains high ecological integrity, with significant diversity and no evidence of pressures that could be filtering specific mammal groups (Espinosa *et al.* 2016). The vegetation cover and structure meet the criteria for natural forests proposed by Jara-Guerrero *et al.* (2019) for the SDTF, with low to no human disturbance inside the reserve.

*Data collection.* Sixteen trail cameras were installed, including eight Bushnell model M-990i and eight Moultrie model Trophy Cam HD Max cameras. They were active from July 2015 until January 2018 and were placed on natural trails within a grid, with approximately 1000 meters separating each camera (Rovero and Marshall 2009).

The cameras operated continuously throughout the day, set to take three photos per trigger with a 5-second reload time (Ahumada *et al.* 2013). Cameras were checked monthly for battery replacement and memory card exchange.

*Data Processing.* Images were uploaded and processed using the free Wild.ID software, which extracts the date and time from each photo. Images were categorized by climatic season, with January to May as the rainy season and June to December as the dry season (Espinosa *et al.* 2018; Figure 1). Deer photos were classified by age class based on morphological characteristics: juveniles were identified by longer limbs relative to body size, smaller and less branched antlers; fawns by white spots on their fur, smaller body size, proportionally larger ears, and always being near their mother. When fawns appeared with their mother, presence data were recorded for both age classes. Adults were differentiated by the presence of testicles and antlers, visible in the images (Gaillard *et al.* 2000; Monteith *et al.* 2009; Flinn *et al.* 2015). Photos where sex or age class couldn't be identified were excluded.

To minimize overestimation of individual abundance, consecutive images separated by at least 30 minutes were considered independent records. From these, the Relative Abundance Index (RAI) was calculated to standardize data to records per 100 trap days. This was done by dividing the number of independent records by the number of camera activation days and multiplying by 100. (Balme *et al.* 2010). RAI served as a measure of overall activity throughout the day for each group.

*Statistical Analyses.* To analyze the activity patterns of the white-tailed deer, three metrics were utilized: total RAI and diurnal RAI, directionality, and overlap. Total RAI sums all independent records across the day, while diurnal RAI calculates the daytime vs. nighttime records proportion. Directionality measures average daily activity per hour. Overlap quantifies the daily activity overlap between two groups. Changes in total and diurnal RAI across age classes and seasons were examined using generalized linear models. As RAI is continuous but not normally distributed, a Gamma error distribution and log link function were applied. Additionally, differences in diurnal activity probability among age classes were assessed using a generalized linear model with a binomial error distribution. Record counts during day (6:00 to 18:00 hrs.) and night for each camera were compared using pairwise tests with Bonferroni correction via the "emmeans" package (Lenth *et al.* 2023).

Changes in the directionality of daily activity among all pairs of age classes, genders, and climatic seasons were tested using the two-sample Watson homogeneity test. This test assesses whether two samples come from populations with the same mean, based on the t-test statistic, which compares the means of the two samples and evaluates if there is sufficient evidence to reject the null hypothesis that the means are equal (Agostinelli and Ulric 2022).

To evaluate the overlap between different age classes, the "overlap" package was used, calculating the overlap coefficient Δ as a descriptive measure of the degree of overlap between two density curves. This coefficient fits the camera trap data to a non-parametric circular kernel density function and estimates probabilities of temporal activity overlap, which can range from 0, indicating no overlap in activity patterns, to 1, indicating complete overlap in activity patterns (Ridout and Linkie 2009; Rowcliffe *et al.* 2014; Lashley *et al.* 2018; Meredith *et al.* 2018).

Overlap was defined as the area under the curve, determined by taking the minimum value of two density curves at each time point. We used the Δ4 estimator for sample sizes comparing categories (sex, age, and between seasons) greater than 50 observations (Ridout and Linkie 2009; Meredith *et al.* 2018; Saisamorn *et al.* 2019). To assess the reliability of the Δ4 estimator and estimate a 95 % confidence interval, we performed 1,000 iterations of smoothed bootstrapping (Meredith *et al.* 2018). The "activity" package was used to compare activity level estimates and determine significant differences in activity patterns using the Wald Test, which assesses if the differences between category estimates are significantly different from 0 (Rowcliffe *et al.* 2014; Rowcliffe and Rowcliffe 2016). All statistical analyses were conducted using R Studio (R Core Team 2022)

## Results

Over 32 months of sampling and 14,272 trap-days, 7,633 deer records were obtained: 5,446 adults, 1,085 juveniles, 1,047 fawns, with 55 unclassified records. Among adults, 3,335 were females and 2,111 males.

Generalized linear models indicated age stage significantly affected relative abundance indices, with fawns significantly lower than other stages (Figure 2a). Diurnal activity was highest in fawns and lowest in adult males, with only fawns showing significantly different diurnal activity (Figure 2b).
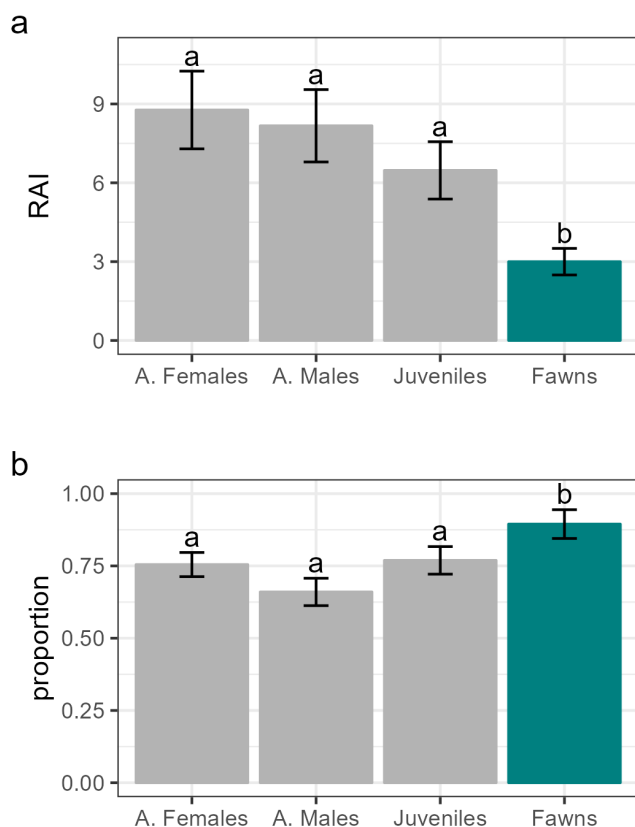
a



b



**Figure 2.** Activity index (a) and proportion of diurnal activity (b) for different sex, and age classes of white-tailed deer. The pairwise test with Bonferroni correction is shown in letters and with dark cyan color bar.

Watson tests revealed significant daily activity mean differences between males and females, males and juveniles, and juveniles and fawns (*P* value < 0.05; Figure 3). Females peaked in activity between 15:00 to 18:00 hrs, differing

in directionality from males, who had a more distributed activity pattern. Juveniles were most active in the late afternoon (16:00 to 18:00 hrs), and fawns in the morning (6:00 to 12:00 hrs). Circular kernel analyses showed significant activity pattern overlaps between age classes, notably between juveniles and fawns, females and juveniles, and males and juveniles (Figure 3).

Circular kernel analysis revealed significant differences in daily activity pattern overlap between age classes, specifically between juveniles and fawns, females and juveniles, and males and juveniles (Wald test; Figure 4).

*Seasonal changes.* Overall, increased activity was observed during the dry season, except for fawns, which were more active during the rainy season. The only statistically significant difference was found in males (deviance 2.067, *P* = 0.036), showing less activity in the rainy. Significant differences in activity among age class states were only found during the dry season, with fawns being significantly less active than other categories (Figure 5a, c). No significant differences were observed in diurnal activity across seasons or within each season for any group, although males were less diurnal during the rainy season and juveniles during the dry season (Figure 5b, d).

Directionality of daily activity patterns between seasons only significantly changed for females, with increased afternoon activity and reduced early morning activity during the rainy season (06:00 to 09:00 hrs). The dry season presented more significant changes in activity directionality among age classes (Figure 6). Watson tests indicated significant directionality differences between males and females, and males and juveniles, with males showing a strong activity peak in the late afternoon (16:00 to 17:00 hrs) and juveniles
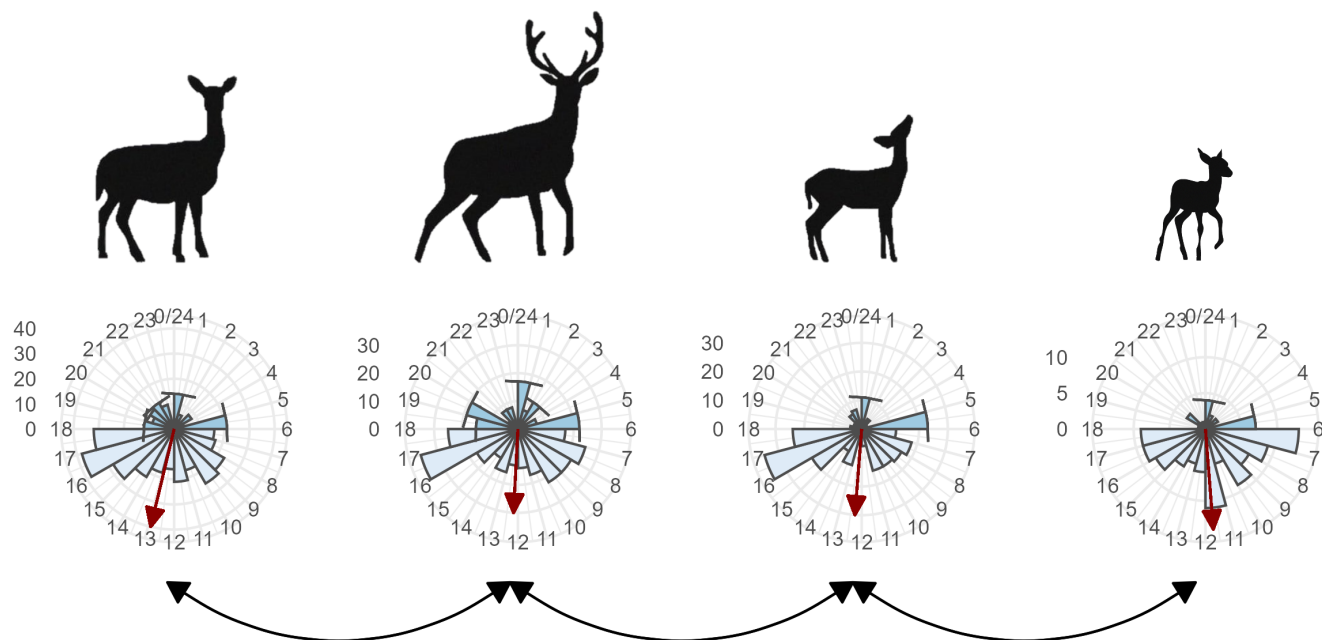


**Figure 3.** Directionality of daily activity of different sexes and age classes in order females, males, juveniles, and fawns. The red arrows show the average daily activity, and the black arrows between groups indicate significant differences in directionality. The x-axis scale, represented as a circle, shows hours in 24 hours, while the y-axis is shown outside the circle and represents the frequency of activity.
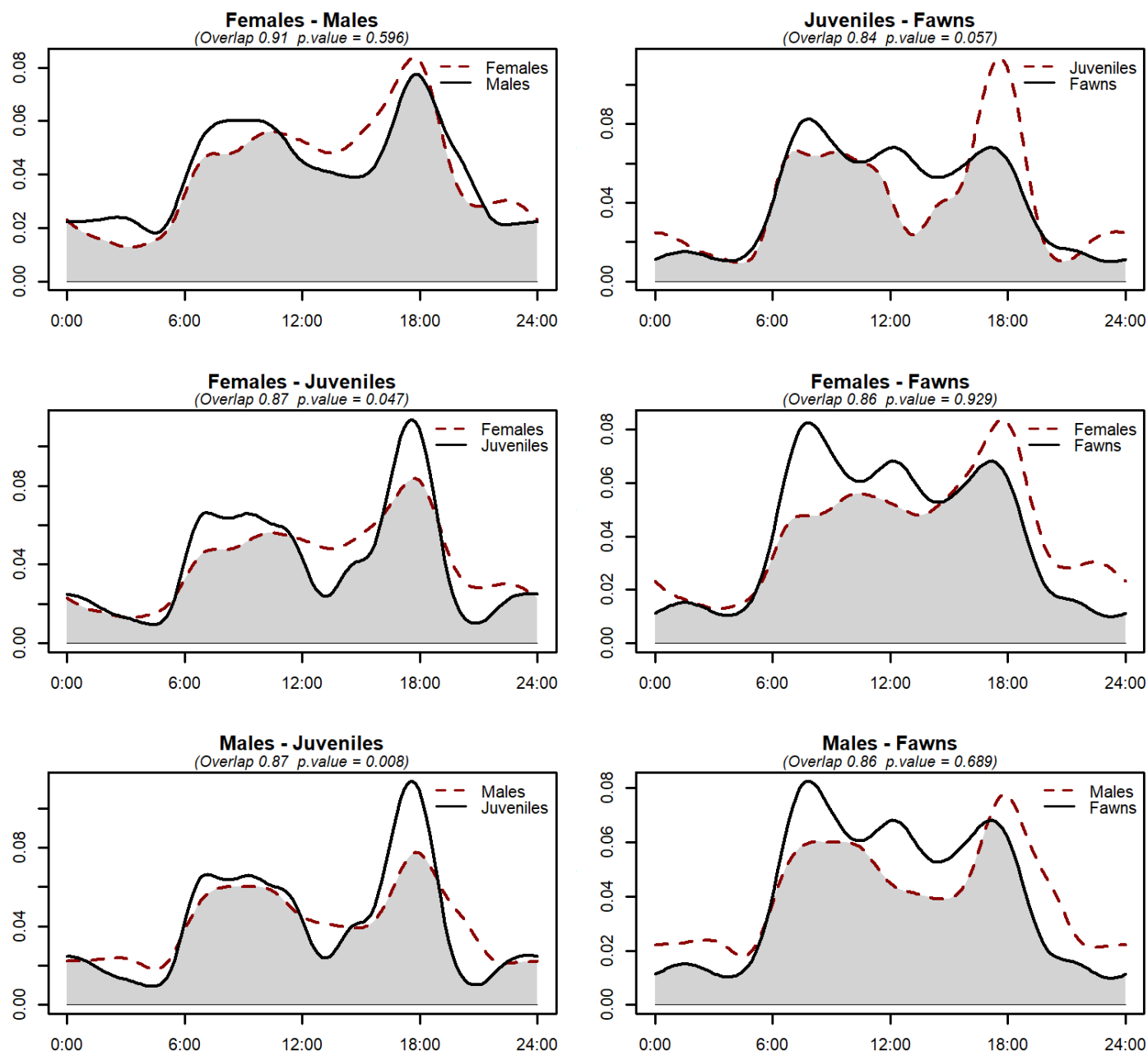
**Figure 4.** Daily activity density curves and overlap between different sexes and age classes of white-tailed deer in the Arenillas Ecological Reserve. The gray color represents the area of overlap of daily activity.

in the early morning (5:00 hrs; Figure 3). No significant differences were observed among age classes during the rainy season.

The season did not significantly affect the overlap for any age class, with activity patterns remaining consistent throughout the year. A significant difference in overlap between juveniles and fawns was noted in both seasons (Figure 7).

## Discussion

White-tailed deer exhibit a broad distribution across various ecosystems along an extensive latitudinal range. While it is known that the species' daily activity pattern responds to changes in abiotic conditions and varies with age, these responses have predominantly been studied in temperate ecosystems. Despite the species' high occupancy in SDTF (Haro-Carrión *et al.* 2021), their daily activity patterns have not been thoroughly evaluated (but see Sánchez-Rojas *et al.* 1997).

This study found that the daily activity patterns of white-tailed deer in SDTF show predominantly crepuscular peaks, varying by age class, sex, and seasonality. Adult individuals follow the widely reported pattern for the species (Cornicelli *et al.* 1996; Webb *et al.* 2010; Gallina and Bello Gutierrez 2014), with higher activity peaks during twilight, while fawns are most active in the early morning hours. Adult activity is distributed over 24 hours, though males tend to be more active at night than females. According to Bowyer
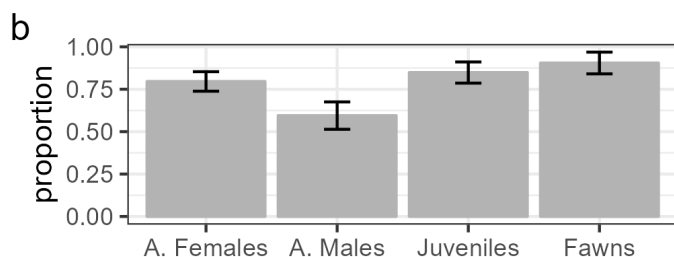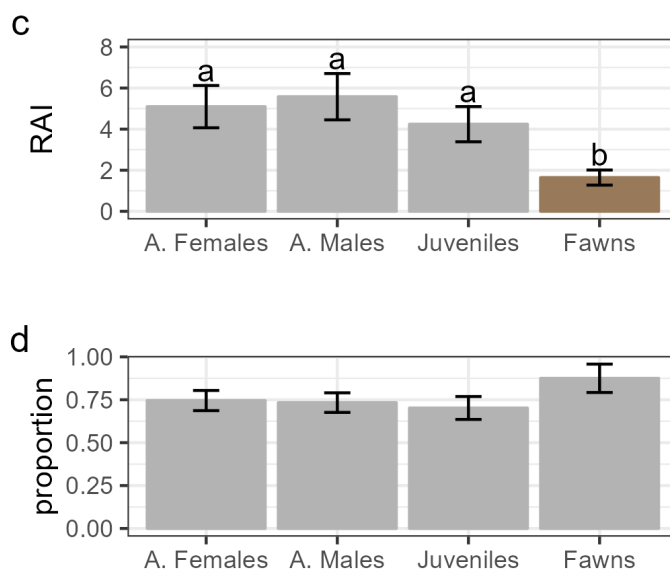
## Rainy season
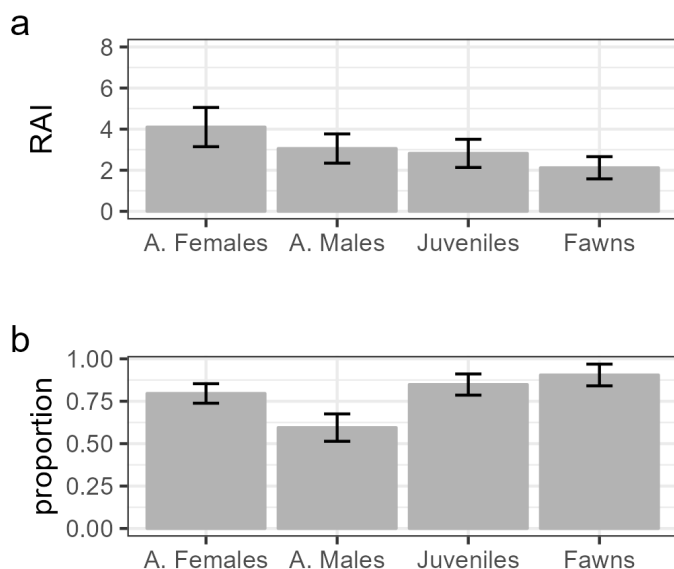


## Dry season

**Figure 5.** Activity index (a, c) and proportion of diurnal activity (b, d) during the dry and the rainy seasons for different sex, and age classes of white-tailed deer. The pairwise test with a Bonferroni correction is shown in letters and with brown color bar.

(2004) temporal segregation between sexes may reduce competition for resources when there are no differences in their diets. Furthermore, adult males, being larger, may be less susceptible to predation (Main *et al.* 1996; Fulbright and Ortega-Santos 2013; Lashley *et al.* 2014), allowing them to access resources at night.

Females showed no differences in their activity pattern compared to fawns. Although overlap with juveniles is less, the activity period of the latter falls within the females' activity period. This similarity in activity patterns between females, juveniles, and fawns is expected due to the lactation process and females being more tolerant of these groups in terms of access to food resources (Hawkins and Klimstra 1970). It has even been reported that juveniles may increase their feeding activity when adult females are present (Stone *et al.* 2017). On the other hand, juveniles tend to be most active at times different from higher-ranking adult males to avoid antagonistic encounters (Townsend and Bailey 1981; Donohue *et al.* 2013), which could explain the differences in activity patterns between these two groups. According to Cherry *et al.* (2015), many juveniles do not reach sexual maturity, so their activity budget would be primarily allocated to body growth rather than reproduction.

As expected, the daily activity pattern of white-tailed deer changed between seasons. During the rainy season, there was a general decrease in daily activity (Figure 5a). This could be because greater resource availability during this season reduces the need for exploratory behavior for adequate forage (Crimmins *et al.* 2015). Results also showed greater overlap and the same directionality in the activity of different groups during rainy season. This overlap could be explained by the mating and breeding season

coinciding with the rainy season (Mandujano and Gallina 1996; Gallina-Tessaro 2019). According to Mandujano y Gallina (1996), in SDTF, white-tailed deer breading occurs at the beginning of the rainy season, while mating happens towards the end. In other ecosystems, some studies suggest that during the mating season, activity patterns between females and males coincide (Holzenbein and Schwede 1989; Fuller *et al.* 2020), whereas during the rearing, fawns and juvenile females typically forage together with their mothers (Hawkins and Klimstra 1970; Mandujano and Gallina 1996). These results suggest that, during the rainy season, reproductive and post-reproductive behavior was more important than intraspecific competition.

The strong climatic seasonality characteristic of SDTF limits resource availability during the dry season, especially foliar biomass (Mandujano *et al.* 2004; Arceo *et al.* 2005; Gallina-Tessaro 2019) and increases stress for water and solar radiation (Jara-Guerrero *et al.* 2021). According to our hypotheses, the balance between intraspecific competition and environmental stress should define the overlap or temporal partitioning of the daily activity of white-tailed deer. Resource scarcity implies an increase in intraspecific competition for food and a possible temporal partitioning of daily activity. Conversely, increased environmental stress should lead to greater overlap among groups as all would avoid peak stress hours to reduce energy expenditure (Mandujano and Gallina 1995; Sánchez-Rojas *et al.* 1997; Gallina and Bello 2010). Our results show a general increase in activity and daily activity periods during the dry season, supporting the idea of decreased resources. Additionally, we found a partition in daily activity periods among groups (Figure 6), which could be explained by reduced resource access and increased intraspecific competition.
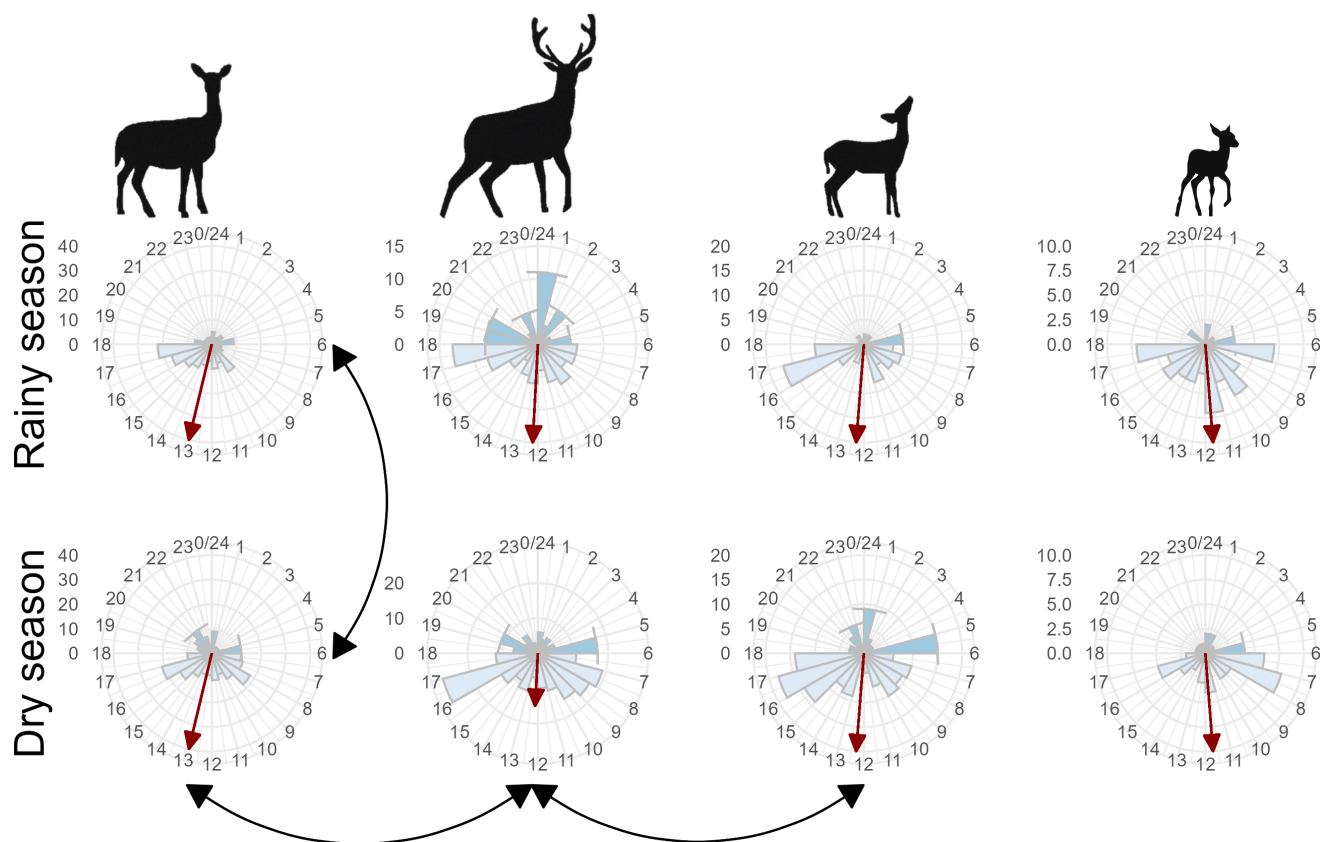
**Figure 6.** Seasonal changes in the directionality of daily activity of different sex, and age classes, in order females, males, juveniles, and fawns. The red arrows show the average daily activity, and the black arrows between groups indicate significant differences in directionality. The x-axis scale, represented as a circle, shows hours in 24 hours, while the y-axis is shown outside the circle and represents the frequency of activity.

Anthropogenic activities have been shown to impact large mammal populations, such as the white-tailed deer, altering their behavioral patterns and daily activity (Root et al. 1988; Osterhaus and Jensen 2019). Due to the narrow shape of the REA, ranging between nine and six km at the study site, human activities could be influencing deer activity patterns (Espinosa et al. 2016). In SDTF, human pressure mainly involves extensive use of the forest for activities such as livestock farming with free-range cattle, firewood and timber extraction, and hunting (Antongiovanni et al. 2020; Jara-Guerrero et al. 2019, 2021; Singh 1998). Throughout nearly three years of study, we found no records of domestic animals or livestock within the study site, except for three records of *Canis lupus familiaris*. These data, along with the substantially higher number of deer records compared to other similar reserves like Pacoche and Machalilla (Espinosa et al. 2016; Lizcano et al. 2016), suggest that the REA is subject to relatively low anthropogenic pressure.

Hunting is another pressure that could modify the activity patterns of white-tailed deer within the study area, although this effect would depend on the intensity of hunting pressure (Osterhaus and Jensen 2019). Osterhaus and Jensen (2019) found no effect of hunting on the activity pattern of white-tailed deer in Kansas, United States, attributing the lack of effect in their study to low levels of daily hunting activity (0.065 hours/ha) compared to levels reported by Root et al. (1988; 0.45 hours/ha per day) in a similar ecosystem in Missouri, United States, where an effect of hunting on deer activity patterns was observed. In our study area, based on human records from camera traps, we estimate that human daily activity was 0.03 hours/ha, a reduced pressure compared to other studies. These results allow us to propose that the activity patterns reported in this work are those expected under natural conditions. However, it is necessary to conduct studies to analyze deer behavior under different levels of hunting pressure in conditions with different anthropogenic pressures to better understand the impact of human activities on the daily activity of this important mammal.

In conclusion, white-tailed deer in dry forests exhibit a daily activity pattern slightly different from that observed in other ecosystems, with activity patterns more extended throughout the day. The overall analysis of activity showed different activity patterns for each age group; however, this difference changes when we analyze the activity pattern in each season. The results suggest that reproductive and post-reproductive behavior during the rainy season determine the overlap in activity among different age classes. Whereas, during the dry season, food availability and the consequent increase in competition lead to a partition in daily activity among the different groups.
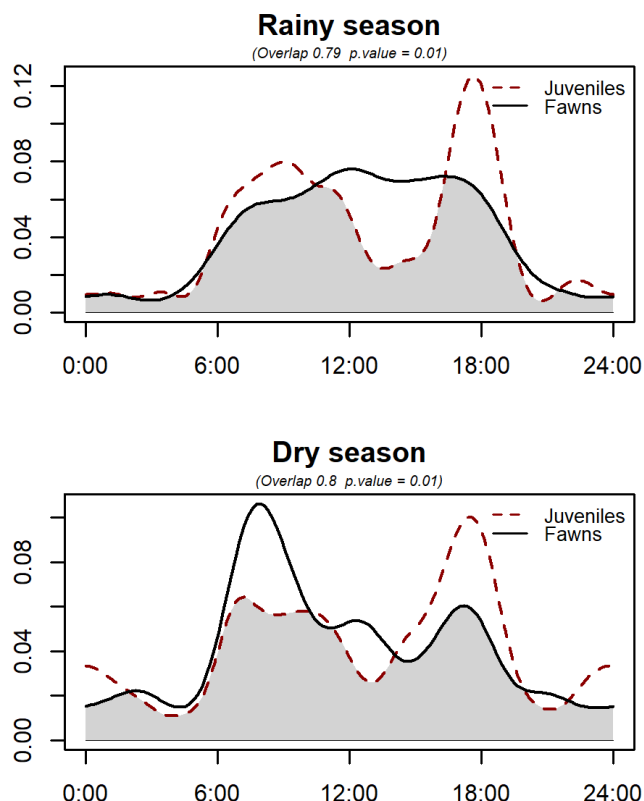
## Rainy season
*(Overlap 0.79  p.value = 0.01)*



## Dry season
*(Overlap 0.8  p.value = 0.01)*



**Figure 7.** Seasonal change in the daily activity density curves and overlap between different age classes of white-tailed deer in the Arenillas Ecological Reserve. The gray color represents the area of overlap of daily activity.

## Acknowledgments

## Literature cited

Agostinelli, C., and L. Ulric. 2022. R package "circular": Circular Statistics (version 0.4-95).

Ahumada, J. A., J. Hurtado, and D. Lizcano. 2013. Monitoring the status and trends of tropical forest terrestrial vertebrate communities from camera trap data: a tool for conservation. Plos One 8:e73707.

Antongiovanni, M., et al. 2020. Chronic anthropogenic disturbance on Caatinga dry forest fragments. Journal of Applied Ecology 57:2064–2074.

Arceo, G., et al. 2005. Diet diversity of white-tailed deer (*Odocoileus virginianus*) in a tropical dry forest in Mexico. Mammalia 69:159–168.

Balme, G. A., R. Slotow, and L. T. B. Hunter. 2010. Edge effects and the impact of non-protected areas in carnivore conservation: leopards in the Phinda-Mkhuze Complex, South Africa: Impact of edge effects on carnivore conservation. Animal Conservation 13:315–323.

Beier, P., and D. R. McCullough. 1990. Factors influencing white-tailed deer activity patterns and habitat use. Wildlife Monographs:3–51.

Berger, A., et al. 2002. Seasonal variation of diurnal and ultradian rhythms in red deer. Biological Rhythm Research 33:237–253.

Bowyer, R. T. 2004. Sexual segregation in ruminants: definition, hypotheses and implications for conservation and management. Journal of Mammalogy 85:1039–1052.

Bradshaw, W. E., and C. M. Holzapfel. 2010. What season is it anyway? circadian tracking vs. photoperiodic anticipation in insects. Journal of Biological Rhythms 25:155–165.

Cherry, M. J., L. M. Conner, and R. J. Warren. 2015. Effects of predation risk and group dynamics on white-tailed deer foraging behavior in a longleaf pine savanna. Behavioral Ecology 26:1091–1099.

Cornicelli, L., A. Woolf, and J. L. Roseberry. 1996. White-tailed deer use of a suburban environment in southern Illinois. Transactions of the Illinois State Academy of Science 89:93–103.

Crawford, D. A., et al. 2019. Chronology of reproductive investment determines predation risk aversion in a felid-ungulate system. Ecology and Evolution 9:3264–3275.

Crimmins, S. M., et al. 2015. Responses of female white-tailed deer home-ranges to increased resource availability. Northeastern Naturalist 22:403–412.

Davis, E. 1990. Deer management in the South Texas plains. Texas Parks and Wildlife Department, Texas.

Dodd, A. N., et al. 2005. Plant circadian clocks increase photosynthesis, growth, survival, and competitive advantage. Science, New Series 309:630–633.

Donohue, R. N., et al. 2013. Aggressive behavior of white-tailed deer at concentrated food sites as affected by population density. The Journal of Wildlife Management 77:1401–1408.

Espinosa, C., J. Camarero, and A. Gusmán. 2018. Site-dependent growth responses to climate in two major tree species from tropical dry forests of southwest Ecuador. Dendrochronologia 52:11–19.

Espinosa, C. I. 2012. Bosques tropicales secos de la región Pacífico Ecuatorial: diversidad, estructura, funcionamiento e implicaciones para la conservación. Ecosistemas 21:167–179.

Espinosa, C. I., et al. 2016. Arenillas ecological reserve; a refuge of biodiversity or an island of extinction? Ecosistemas 25.

Flinn, J. J., et al. 2015. Estimating age and antler traits of photographed male white-tailed deer. Journal of the Southeastern Association of Fish and Wildlife 2:135–143.

Fortin, D., M. S. Boyce, and E. H. Merrill. 2004. Multi-tasking by mammalian herbivores: overlapping processes during foraging. Ecology 85:2312–2322.

Fulbright, T. E., and J. A. Ortega-Santos. 2013. White-tailed deer habitat: ecology and management on rangelands. Texas A&M University Press.

Fuller, T. K., et al. 2020. Reproduction of white-tailed deer in a seasonally dry tropical forest of Costa Rica: a test of aseasonality. Journal of Mammalogy 101:241–247.

Gaillard, J.-M., et al. 2000. Body mass and individual fitness in female ungulates: bigger is not always better. Proceedings of the Royal Society of London. Series B: Biological Sciences 267:471–477.

Galindo Leal, C., and M. Weber. 1998. El Venado de la Sierra Madre Occidental: ecología, manejo y conservación. CONABIO-Ediciones culturales. Ciudad de México, México.

GALLINA, S., AND J. BELLO GUTIERREZ. 2014. Patrones de actividad del venado cola blanca en el noreste de México. Therya 5:423–436.

GALLINA, S., AND J. BELLO. 2010. El gasto energético del venado cola blanca (*Odocoileus virginianus texanus*) en relación a la precipitación en una zona semiárida de México. Therya 1:9–22.

GALLINA-TESSARO, S., (ED.). 2019. Ecology and conservation of tropical ungulates in Latin America. Springer International Publishing, Cham.

HALBERG, F. 1960. The 24-hour scale: a time dimension of adaptive functional organization. Perspectives in Biology and Medicine 3:491–527.

HARO-CARRIÓN, X., J. JOHNSTON, AND M. J. BEDOYA-DURÁN. 2021. Landscape structure and seasonality: effects on wildlife species richness and occupancy in a fragmented dry forest in Coastal Ecuador. Remote Sensing 13:3762.

HAWKINS, R. E., AND W. D. KLIMSTRA. 1970. A preliminary study of the social organization of white-tailed deer. The Journal of Wildlife Management 34:407.

HOLZENBEIN, S., AND G. SCHWEDE. 1989. Activity and movements of female white-tailed deer during the rut. The Journal of Wildlife Management 53:219.

HUT, R. A., ET AL. 2012. In search of a temporal niche. Pp 281–304, in The Neurobiology of Circadian Timing (Kalsbeek, A., M. Merrow, T. Roenneberg, and R. G. Foster, eds.). Elsevier. Amsterdam, The Netherlands.

JARA-GUERRERO, A., ET AL. 2018. White-tailed deer as the last megafauna dispersing seeds in Neotropical dry forests: the role of fruit and seed traits. Biotropica 50:169–177.

JARA-GUERRERO, A., ET AL. 2021. Chronic disturbance in a tropical dry forest: disentangling direct and indirect pathways behind the loss of plant richness. Frontiers in Forests and Global Change 4:723985.

JARA-GUERRERO, A., ET AL. 2019. Beyond the blame game: a restoration pathway reconciles ecologists and local leaders divergent models of seasonally dry tropical forest degradation. Ecology and Society 24:art22.

LASHLEY, M. A., ET AL. 2014. White-Tailed Deer Vigilance: The Influence of Social and Environmental Factors. PLoS ONE 9:e90652.

LASHLEY, M. A., ET AL. 2018. Estimating wildlife activity curves: comparison of methods and sample size. Scientific reports 8:1–11.

LENTH, R. V., ET AL. 2023. June 23. emmeans: Estimated Marginal Means, aka Least-Squares Means.

LEUTHOLD, B. M., AND W. LEUTHOLD. 1978. Daytime activity patterns of gerenuk and giraffe in Tsavo National Park, Kenya. African Journal of Ecology 16:231–243.

LIBERT, S., ET AL. 2012. Deviation of innate circadian period from 24 h reduces longevity in mice: Impact of circadian clock on longevity. Aging Cell 11:794–800.

LIZCANO, D. J., ET AL. 2016. Riqueza de mamíferos medianos y grandes del refugio de vida silvestre marina y costera Pacoche, Ecuador. Therya 7:135–145.

LUNA-FLORIN, A. D., ET AL. 2022. Ecological characterization of the flora in Reserva Ecológica Arenillas, Ecuador. Applied Sciences 12:8656.

MAIN, M. B., F. W. WECKERLY, AND V. C. BLEICH. 1996. Sexual segregation in ungulates: new directions for research. Journal of Mammalogy 77:449–461.

MANDUJANO, S., AND S. GALLINA. 1995. Comparison of deer censusing methods in tropical dry forest. Wildlife Society Bulletin 23:180–186.

MANDUJANO, S., AND S. GALLINA. 1996. Size and composition of white-tailed deer groups in a tropical dry forest in Mexico. Ethology Ecology and Evolution 8:255–263.

MANDUJANO, S., ET AL. 2004. Variación estacional del uso y preferencia de los tipos vegetacionales por el venado cola blanca en un bosque tropical de Jalisco. Acta Zoológica Mexicana 20:45–67.

MASSÉ, A., AND S. D. CÔTÉ. 2013. Spatiotemporal variations in resources affect activity and movement patterns of white-tailed deer (*Odocoileus virginianus*) at high density. Canadian Journal of Zoology 91:252–263.

MCSHEA, W. J. 2012. Ecology and management of white-tailed deer in a changing world: deer and eastern forests. Annals of the New York Academy of Sciences 1249:45–56.

MEREDITH, M., M. RIDOUT, AND M. M. MEREDITH. 2018. Package 'overlap.' Estimates of coefficient of overlapping for animal activity patterns 3:1.

MINISTERIO DEL AMBIENTE. 2014. Plan de Manejo de la Reserva Ecológica Arenillas. Quito, Ecuador. 68p.

MONTEITH, K. L., ET AL. 2009. Growth of male white-tailed deer: consequences of maternal effects. Journal of Mammalogy 90:651–660.

OSTERHAUS, D. M., AND W. E. JENSEN. 2019. Does activity of white-tailed deer (*Odocoileus virginianus*) vary between human-hunted areas and refugia? Transactions of the Kansas Academy of Science 122:235.

OWEN-SMITH, N. 1998. How high ambient temperature affects the daily activity and foraging time of a subtropical ungulate, the greater kudu (*Tragelaphus strepsiceros*). Journal of Zoology 246:183–192.

OWEN-SMITH, N., AND V. GOODALL. 2014. Coping with savanna seasonality: comparative daily activity patterns of african ungulates as revealed by GPS telemetry. Journal of Zoology 293:181–191.

OZOGA, J. J., AND L. J. VERME. 1986. Relation of maternal age to fawn-rearing success in white-tailed deer. The Journal of Wildlife Management 50:480.

R CORE TEAM. 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www. R-project. org/.

RIDOUT, M. S., AND M. LINKIE. 2009. Estimating overlap of daily activity patterns from camera trap data. Journal of Agricultural, Biological, and Environmental Statistics 14:322–337.

ROONEY, T. P., AND D. M. WALLER. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. Forest Ecology and Management 181:165–176.

ROOT, B. G., E. FRITZELL, AND N. GIESSMAN. 1988. Effects of intensive hunting on white-tailed deer movement. Wildlife Society Bulletin 16:145–151.

ROVERO, F., AND A. R. MARSHALL. 2009. Camera trapping photographic rate as an index of density in forest ungulates. Journal of Applied Ecology 46:1011–1017.

ROWCLIFFE, J. M., ET AL. 2014. Quantifying levels of animal activity using camera trap data. Methods in Ecology and Evolution 5:1170–1179.

ROWCLIFFE, J. M., AND M. M. ROWCLIFFE. 2016. Package 'activity.' Animal activity statistics R Package Version 1.

Saisamorn, A., *et al*. 2019. Spatial and temporal analysis of leopards (*Panthera pardus*), their prey and tigers (Panthera tigris) in Huai Kha Khaeng Wildlife Sanctuary, Thailand. Folia Oecologica 46:73–82.

Sánchez-Rojas, G., S. Gallina, and S. Mandujano. 1997. Área de actividad y uso del hábitat de dos venados cola blanca (*Odocoileus virginianus*) en un bosque tropical de la costa de Jalisco, México. Acta Zoologica Mexicana (n.s.) 72:39–54.

Scheibe, K. M., *et al*. 1999. Comparative analysis of ultradian and circadian behavioural rhythms for diagnosis of biorhythmic state of animals. Biological Rhythm Research 30:216–233.

Scheibe, K. M., *et al*. 2009. Variation of the phase of the 24-h activity period in different large herbivore species under European and African conditions. Biological Rhythm Research 40:169–179.

Sierra, M. 1999. Propuesta preliminar de un sistema de clasificación de vegetación para el Ecuador continental. Proyecto Inefan/Gef-Birf y Ecociencia.

Singh, S. P. 1998. Chronic disturbance, a principal cause of environmental degradation in developing countries. Environmental Conservation 25:1–2.

Spoelstra, K., *et al*. 2016. Natural selection against a circadian clock gene mutation in mice. Proceedings of the National Academy of Sciences 113:686–691.

Stone, D. B., *et al*. 2017. Breeding chronology and social interactions affect ungulate foraging behavior at a concentrated food resource. Plos One 12:e0178477.

Townsend, T. W., and E. D. Bailey. 1981. Effects of age, sex and weight on social rank in penned white-tailed deer. American Midland Naturalist 106:92.

Valeix, M., S. Chamaillé-Jammes, and H. Fritz. 2007. Interference competition and temporal niche shifts: elephants and herbivore communities at waterholes. Oecologia 153:739–748.

Vásquez, Y., *et al*. 2016. Variation in the diet composition of the white-tailed deer (*Odocoileus virginianus*) in the Tehuacán-Cuicatlán Biosphere Reserve. Revista Chapingo serie ciencias forestales y del ambiente 22:87–98.

Webb, S. L., *et al*. 2010. Measuring fine-scale white-tailed deer movements and environmental influences using GPS collars. International Journal of Ecology 2010:1–12.

Yearsley, J. M., and J. Pérez-Barbería. 2005. Does the activity budget hypothesis explain sexual segregation in ungulates? Animal Behaviour 69:257–267.