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ECOLOGÍA DEL VENADO COLA BLANCA (*Odocoileus virginianus*) EN HÁBITATS TROPICALES DEL SURESTE DE MÉXICO.

TESIS QUE PARA OBTENER EL GRADO DE DOCTOR EN CIENCIAS EN ECOLOGÍA Y MANEJO DE SISTEMAS TROPICALES

PRESENTA:

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Abstract

The white-tailed deer is the most hunted species in the tropics of Mexico. However, information on daily movements, the size of the home environment, as well as the seasonality of antlers and times of birth in tropical sites is scarce. In this study we analyzed the factors that influence the daily distances travelled, the size of the home environment and the temporality of antlers and fawning of the white-tailed deer distributed in southeastern Mexico between the states of Tabasco and Campeche. Using satellite telemetry data, daily movement data were obtained, as well as the area of deer activity. Using trap camera data, the timing of antlers and the time of fawning of white-tailed deer were analyzed. We found that the daily movements of the white-tailed deer in the study area are less than reports from studies in central and northern Mexico. Movements recorded are longer during the dry season and shorter during the wet season. Similarly, the home environment recorded in this study was similar to that recorded in other tropical sites for the species but differs from home environments recorded in sites where animals were translocated or reintroduced. Physical factors such as temperature did not show any influence on daily movements, but food scarcity is likely to include the time of birth, as well as longer daily movements of deer. In addition, the results indicate that the breeding season in the Campeche wetlands is different from that in the northern latitudes of Mexico and the southern United States. It was found that the timing of the development of hard white-tailed deer antlers in the study area does not coincide with the official hunting season established in Mexico.
Keywords: Animal movement, Campeche, fawning season, flood, tropical deer, wetlands, Southeastern Mexico.

Resumen

El venado de cola blanca es la especie más cazada en las zonas tropicales de México. Sin embargo, la información sobre los movimientos diarios, el tamaño del ámbito hogareños, así como la estacionalidad de astas y épocas de nacimientos en sitios tropicales es escasa. En este estudio se analizaron los factores que influyen en las distancias recorridas diarias, tamaño del ámbito hogareño y la temporalidad de astas y nacimientos del venado cola blanca que se distribuye en el sureste de México entre los estados de Tabasco y Campeche. Utilizando datos de telemetría satelital se obtuvieron datos de movimientos diarios, así como el área de actividad de venados. Y utilizando datos provenientes de cámaras trampa se analizó la temporalidad de astas, así como la época de nacimientos de venados cola blanca. Encontramos que los movimientos diarios del venado cola blanca en el área de estudio son menores a los reportes de estudios en el centro y norte de México. Los movimientos registrados son más largos durante la estación seca y más cortos durante la estación húmeda. De igual forma el ámbito hogareño registrado en este estudio fue similar a lo registrado en otros sitios tropicales para la especie, pero difiere con ámbitos hogareños registrados en sitios donde los animales fueron translocados o reintroducidos. Factores físicos como la temperatura no mostraron ninguna influencia en los movimientos diarios, pero es probable que la escasez de alimento incluya en la época de nacimientos,

así como en movimientos diarios más largos de los venados. Además, los resultados indican que la temporada de reproducción en los humedales de Campeche es diferente de la que ocurre en las latitudes septentrionales de México y el sur de los Estados Unidos. Se comprobó que el momento en que se desarrollan las astas duras de venado de cola blanca en el área de estudio no coincide con la temporada oficial de caza establecida en México.

Palabras clave: Movimiento animal, Campeche, Epoca de nacimientos, inundación, venado tropical, humedales, Sureste de México.

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CAPÍTULO 1

INTRODUCCIÓN GENERAL

El venado cola blanca (*Odocoileus virginianus*) es el cérvido con la distribución más amplia en el continente americano, extendiéndose desde el sur de Canadá hasta Sudamérica (Halls 1984), en México su distribución abarca casi todo el país, con excepción de la Península de Baja California (Villarreal 2006).

En cuanto al uso, el venado aparece como una especie muy utilizada por las diversas culturas atraves del tiempo, hallazgos en códices y piedras talladas, indican que ha sido cazado y venerado desde épocas prehispánicas (Mandujano et al. 2014). Principalmente en ceremonias religiosas, danzas típicas, y como alimento (Weber 2014).

En cuanto al estado al estado de conservación, *O. virginianus* no es considerado en ninguna categoría de riesgo en el país (NOM-059-SEMARNAT-2010), por lo que bajo el esquema de manejo de UMA (Unidades de Manejo para la Conservación de la Vida Silvestre) el aprovechamiento de los venados es permisible.

Su importancia económica es principalmente como resultado de la derrama por actividades de cacería deportiva, ya que es una de las presas de caza preferidas a nivel mundial (SCI 2014a,b), al respecto en México, la caza deportiva de venados de cola blanca representa una actividad importante, particularmente en la parte norte del país donde los cazadores brindan importantes beneficios económicos a los habitantes locales (Guajardo-Quiroga y Martínez-Muñoz 2004; Contreras-Gil et al. 2010; Villarreal 2013). En algunos estados del sur de México, ha habido un desarrollo significativo de las actividades de caza deportiva de venados de cola blanca (CONABIO 2012), pero hasta ahora, en pocas ocasiones, esta actividad ha permitido a los habitantes locales accedan a los beneficios económicos (García-Marmolejo et al. 2008).

Sin embargo, a pesar de la importancia cinegética, la mayoría de las investigaciones se han enfocado a seis subespecies que se distribuyen en sitios semidesérticos y templados, precisamente las subespecies que se consideraban (hasta antes del 2012) las especies trofeo de interés, siendo las subespecies tropicales las menos estudiadas (Gallina et al. 2010, Mandujano 2011). Afortunadamente y gracias a la gestión del Capítulo Monterrey del Club Safari Internacional, a partir de 2012 han sido aprobadas 7 nuevas categorías de trofeos de venado cola blanca mexicanos, lo que permite que las subespecies mexicanas tengan un reconocimiento mundial como trofeos de caza con el consecuente beneficio económico (Viejo 2012).

Aun hoy en día existen necesidades que no se han cubierto en cuanto al conocimiento de muchas especies de fauna silvestre, por ejemplo, el venado cola blanca, aun con la importancia que representa para las diferentes culturas, los estudios sobre esta especie en el sureste de México son escasos, aun cuando en décadas pasadas el venado se encontraba ampliamente distribuido en la cuenca del Usumacinta (Reyes 1981). En general las investigaciones se han enfocado principalmente a determinar aspectos poblacionales como la abundancia, densidad, distribución y preferencias de hábitat (Contreras-Moreno et al. 2015a, b) aprovechamiento (Reyna-Hurtado y Tanner 2010) y simpatría con otras especies de venados (Weber 2014). Pese a los estudios realizados, aún se desconocen muchos aspectos ecológicos del venado cola blanca en sitios tropicales del sureste, datos que son indispensables para poder hacer un manejo adecuado de la especie, ya sea para aprovechamiento o conservación. Este estudio tiene como objetivo describir aspectos de la ecología del venado cola blanca (*O. v. thomasi*), la subespecie que se distribuye que en la actualidad no se conocen en el sureste de México.

El venado de cola blanca es la especie de caza más importante en México (Mandujano et al. 2014). Sin embargo, los estudios de los patrones de movimiento sobre la especie son escasos en el país, particularmente, no hay información sobre el tema en las áreas tropicales. Razón la cual en el Capítulo 2 de este estudio se pretendió determinar el efecto que las variables ambientales (estacionalidad de la lluvia y la temperatura) y el estado reproductivo (temporada de nacimiento) tuvieron en las distancias diarias del venado cola blanca en una zona de humedales tropicales del sureste de México. En el Capítulo 2, se utilizaron datos de telemetría satelital para determinar las distancias diarias que viajan los venados en el sureste de México. Este capítulo fue publicado en un capítulo del libro "Movement Ecology of Neotropical Forest Mammals: Focus on Social Animals", en el formato de Estilo Básico de libros de Springer.

Así mismo, dado la importancia comercial del venado cola blanca para las comunidades rurales, a través de la cacería deportiva, se considera, que es indispensable determinar las diferencias que se dan en las temporadas de cría y reproducción entre las poblaciones de venados cola blanca, tanto del sur como del norte de México, con el fin de lograr un mejor manejo de la especie. Los principales objetivos de la actividad de caza deportiva son los machos con astas, y dado que la temporada en la que están disponibles en el sur (en zonas tropicales), podría no coincidir con la temporada de caza establecida actualmente. Se consideró necesario establecer el calendario estacional de reproducción y nacimiento de venados en el sur de México y determinar si el calendario de caza actual es adecuado para cumplir con las condiciones regionales. Por lo que en el Capítulo 3, el objetivo fue determinar la estacionalidad del desarrollo de las astas y la temporada de nacimiento de los venados cola blanca en una zona de humedales de Campeche y evaluar su congruencia con el calendario de caza actual. En el Capítulo 3, se utilizaron datos provenientes de cámaras trampa con los que se identificaron los diversos estadios de los venados machos, así como la presencia de crías. Este Capítulo 3, corresponde a un artículo publicado en formato de European Journal of Wildlife Research.

La determinación del tamaño del rango de origen del venado de cola blanca ha sido identificada como una de las prioridades de investigación para la especie en México, principalmente porque ayudará a mejorar la conservación y el manejo del venado de cola blanca (Ortega-S. et al. 2011). Determinar el efecto de las condiciones ambientales y el estado reproductivo de los individuos en el área de distribución de los venados de cola blanca en el área de la Laguna de Términos, es de gran importancia ya que la subespecie que se distribuye en Campeche y Tabasco (*O. virginianus thomasi*) se incluyó en el Premio Hubert Thummler para el venado en México (Villarreal 2013; SCI 2014a, b) y debería fomentar el desarrollo de iniciativas de caza deportiva sostenibles en la región. Razón por la cual en el Capítulo 4, el objetivo fue determinar el efecto de la estacionalidad en el tamaño del área de ámbito hogareño del venado cola blanca en los humedales de la región de Laguna de Términos, en el sureste de México. En el Capítulo 4, donde se analiza el ámbito hogareño del venado cola blanca, utilizando datos de telemetría satelital, de venados de una UMA del sur de Campeche, México. Este capítulo corresponde a un manuscrito con formato Journal of Mammalogy.

Finalmente, en el capítulo 5 se discute de forma general los resultados encontrados en este estudio.

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CAPÍTULO 2

Daily traveled distances by the white-tailed deer in relation to seasonality and reproductive phenology in a tropical lowland of Southeastern Mexico

Chapter 8
Daily Traveled Distances by the White-Tailed Deer in Relation to Seasonality and Reproductive Phenology in a Tropical Lowland of Southeastern Mexico

Fernando M. Contreras-Moreno, Mircea G. Hidalgo-Mihart, and Wilfrido M. Contreras-Sánchez

8.1 Introduction

Movement is the process by which animals make behavioral decisions to select resources in space and time (Turchin 1998). Animal movement reflects a wide range of phenomena, including habitat use, foraging and depredation (Gurarie et al. 2011), dispersal and migration (Delgado et al. 2010), social and territorial behaviors (Moorcroft et al. 1999), as well as coexistence with competitors (Keeling and Grenfell 1997) and community interactions (Hanski 1998). Animal movement usually is influenced by different factors, including the individual (age, sex, size, reproductive status), population (density and abundance, social interactions) as well as habitat characteristics (availability of resources, quality and quantity of resources, geographic barriers), and intensity of human activities (Webb et al. 2010; Salek et al. 2015).

Few studies have documented fine-scale temporal movements (i.e., daily trav- eled distances) of ungulate species (Pépin et al. 2004; Webb et al. 2010). In the case of the white-tailed deer (*Odocoileus virginianus*), the study of movement has focused on how movements of white-tailed deer vary at different spatial scales, from large-scale dispersal and migration to small-scale movements within home ranges and habitats (Webb et al. 2009). Movement of white-tailed deer (*Odocoileus virginianus*) could be influenced by many ecological, environmental, and behav- ioral variables such as hunger, reproduction, physiological condition, habitat, and predators or human activity (Ferguson et al. 1998; Phillips et al. 2004). Many stud- ies of white-tailed deer have examined both large-scale movements (e.g., dispersal and migration) and movement within home ranges and among habitat types. These different types of movement occur at different hierarchical spatial scales (Webb

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et al. 2009). Small-scale movements, such as space-use patterns within a home range, may be influenced by physical habitat features, resource availability, or the distribution of conspecifics (Crist et al. 1992; McIntyre and Wiens 1999). Large-scale movements, such as dispersal, may be influenced by landscape structure or behavior as it relates to gene flow or population dynamics (Long et al. 2005).

The white-tailed deer movement ecology has been an important research subject in the United States and Canada (e.g., Webb et al. 2010; Long et al. 2005). However, in the southern portion of the distribution of the species, the information about the movement ecology is practically unknown, especially in tropical areas. It has been observed that in the northeastern arid lands of Mexico, the daily traveled distances of the white-tailed deer depended on the environmental temperature and precipitation (Delfín et al. 1998; Gallina et al. 2003), and deer moved longer distances during the fawning season (Bello et al. 2004). Also, in the tropical dry forests of the Pacific slope of the country, the daily traveled distances were longer during the wet season of the year (June–November) corresponding to the fawning season (Sánchez-Rojas et al. 1997).

The extensive wetland system located on western Campeche state in Mexico is subject to severe seasonal changes, with a marked dry season with temperatures above 40 °C (Instituto Nacional de Estadística y Geografía 2013), followed by long flooding season that can least for more than 8 months (Rivera-Monroy and Twilley 1996). These climatic conditions probably had a strong effect on the resource and habitat availability for the wildlife inhabiting the area (Hidalgo-Mihart et al. 2017) and are one of the possible causes that had produced that the fawning season of white-tailed deer synchronizes with the dry months of the year (February–June, Contreras-Moreno 2018).

Determining the effect of the environmental conditions and physiological status of individuals on the movement patterns of the white-tailed deer in this area of Mexico will help to understand how this species could be affected by the changes that are already occurring in the region, where it is anticipated a general decrease in mean precipitation and an increase in drought (Imbach et al. 2012; Chiabai 2015) with a strong effect on the wildlife (Reyna-Hurtado et al. 2010). Also, the sea level increase from global warming will produce longer periods of flooding as a result that most of this coastal area is in a very low terrain, with some areas even under the sea level (Yañez-Arancibia et al. 2014). This will probably have severe impact in the movement patterns of the white-tailed deer, as has already been detected in ungulates from the Amazon basin (Bodmer et al. 2018).

White-tailed deer is the most hunted species in Mexico (Mandujano et al. 2014). However, the study of movement patterns on the species is scarce in the country and specially on the tropical areas. The objective of this study was to determine the effect that environmental variables (rain seasonality and temperature) as well as reproductive status (fawning season) had on the daily traveled distances of the female white-tailed deer in a tropical lowland of southeastern Mexico.

8.2 Methods

Study Area Our research was conducted at the Nicte-Ha UMA (Wildlife Management and Conservation Unit per its Spanish initials; hereafter called Nicte-Ha), located in southwestern Campeche, México (91°43′56″ W, 18°19′56″N), and adjacent to the Laguna de Términos Flora and Fauna Protected Area (Fig. 8.1). The area is a 2300 ha tract of tropical lower coastal plain habitat situated between −1 and 3 m asl. The climate in the region is warm-humid, with a mean temperature of 27 °C and up to 2000 mm of precipitation per year (Instituto Nacional de Estadística y Geografía 2013). Rainy season in the area usually began at mid-June and finished by November–December and is followed by a dry season that least for around 5 months (January–May). Due to the intense rainy season and the plain terrain, most of the Nicte-Ha area is subject to seasonal floods that can be as high of 0.5 m and last for 7 months (July–January). The vegetation types of the area vary from hydrophilic vegetation, flooded savannas, mangroves, sub-evergreen flooded rain forests, tropical deciduous flooded forests, secondary growth forests, agricultural areas, and induced grasslands for cattle grazing (Ocaña and Lot 1996).

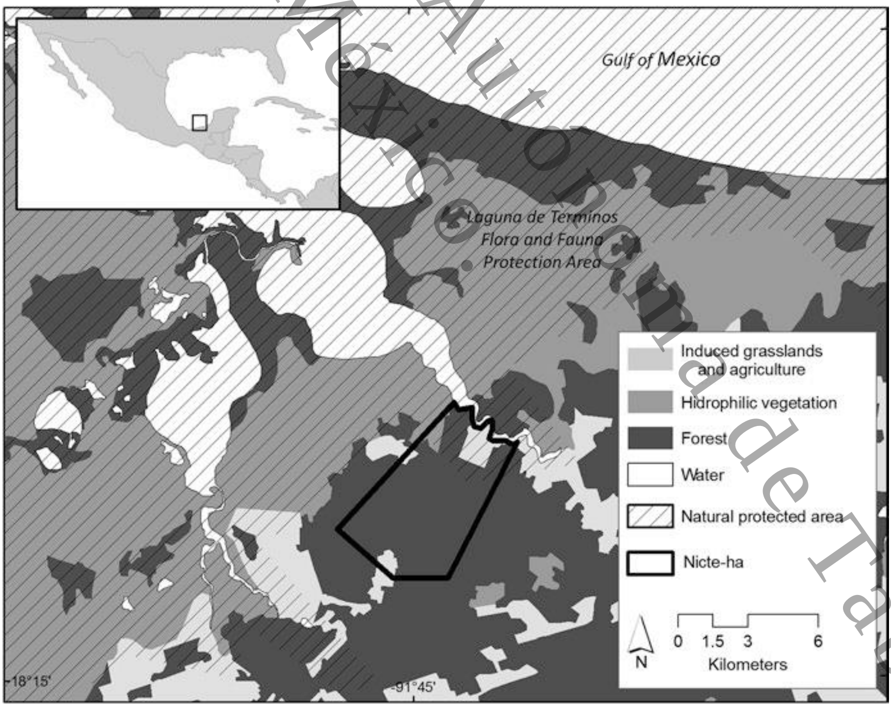

Fig. 8.1 Location of the study area in the tropical lowlands of Campeche, México. The Nicte-Ha area is located outside of the Laguna de Terminos Flora and Fauna Protected Area

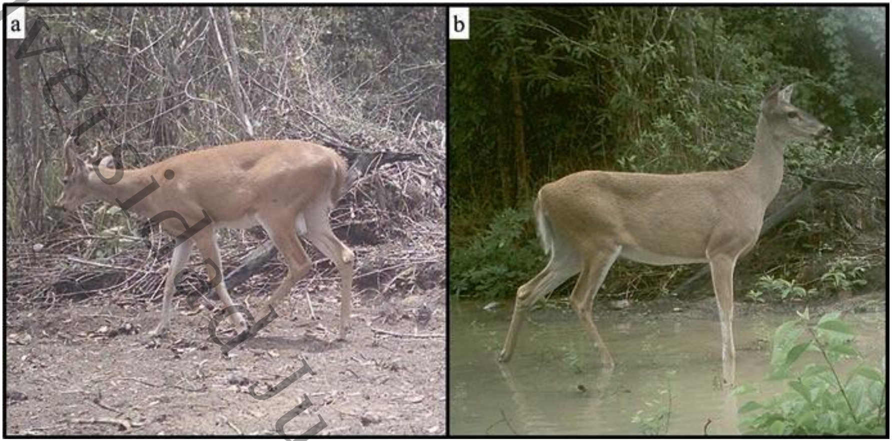

Fig. 8.2 Photograph of white-tailed deer in Nicte-Ha during the dry season (**a**) and the wet season (**b**). Nicte-Ha is located in a tropical lowland area that is subject to a severe drought during the dry season (2016) followed by a long flooding season. The white-tailed deer in Nicte-Ha should adapt their movement behavior to the changing environmental conditions during the year

In 2010, the owners of Nicte-Ha remove all the cattle from the ranch, and since then, the area has been used exclusively for sustainable white-tailed deer hunting. As in other parts of the Yucatan Peninsula, water is probably the most limiting factor for wild ungulates in the area during the dry season (Reyna-Hurtado et al. 2010; Fig. 8.2). To improve the white-tailed deer habitat quality, six water holes were built along Nicte-Ha area, to offer water to the wildlife during the dry season. However, in occasions due to a very strong drought such as the one that occurred at the end of the dry season in 2017 (late May–early June), most of the artificial water sources were dry, and the only water source for the wildlife on Nicte-Ha was the Rio del Este.

Capture and Radio Tracking During May of 2016, five adult female white-tailed deer were captured using a 20 × 20 m drop net (Ramsey 1968). Once captured, the deer were physically restrained, and conventional measurements and mass were obtained. Each deer was fitted with a VERTEX Survey Iridium Collar (Vectronic Aerospace GmbH, Berlin, Germany) and released immediately on the capture site (Fig. 8.3). The capture, management, and collaring of the white-tailed deer were carried out under the collection permit SGPA/DGVS/01097/16 (10-Febrero-2016) granted to Mircea Gabriel Hidalgo Mihart by the Dirección General de Vida Silvestre, SEMARNAT, México, following the capture and management guidelines of the American Society of Mammalogists (Sikes and Gannon 2011). Radio collars were programmed to take fixes at 2-h intervals and transmitting to the Iridium system every 24 h the date, time, position, and temperature of each fix.

Data Analysis To determine the daily traveled distance by each deer, we selected only those 24-h periods that had 12 GPS fixes to derive estimates of daily travel

Fig. 8.3 Photograph of a radio-collared female deer in Nicte-Ha drinking from an artificial water hole. In the Nicte-Ha area, white-tailed deer are exposed to a severe drought during the dry season. Artificial water holes were built to improve the habitat quality for the deer inhabiting the area

distance from the five radio-collared deer. For each day, the distances between sequential GPS fixes were measured and added up to calculate total distance traveled. Distance moved between two successive locations was estimated by using HRT, Home Range Tools, in ArcGIS 9 (Rodgers et al. 2007).

We arranged the daily traveled distance data per deer in a bimester basis from May–June 2016 to May–June 2017. We obtained the mean values of daily traveled distances per deer at each bimester and use them to perform a one-way analysis of variance (ANOVA) for repeated measures to determine for differences in the daily traveled distance per bimester (Zar 1999). Tukey HSD tests were conducted a posteriori to determine which bimesters were different (Zar 1999). All statistical analyses were performed using the Statgraphics Centurion®, v XVIII, ($\alpha < 0.05$).

Environmental Variables To determine the daily temperature that each individual deer was exposed during the 24 h period when we estimated the daily travel distance, we average the temperature obtained from the radio collar on each fix, for each one of the complete 24 h periods. To determine if daily traveled distances were associated with average daily temperature, we performed a linear regression analysis between these two variables (Zar 1999), first relating all the daily traveled distances from all the deer with all the average daily temperatures and second with the mean values of daily traveled distances per deer at each bimester with the mean average temperature per deer per bimester.

We collected the precipitation data from the nearest meteorological stations to the study area (Toluca, Carmen, Campeche and Jonuta, Tabasco; Instituto Nacional de Investigaciones Forestales Agricolas y Pecuarias 2018) to determine the rainy and dry season during the studied period for the study area. We define that the rainy season began when we have a 15-day period with at least 10 days with an accumulated daily rain of 25 or more mm. The end of the rainy season was defined as the time when we had a 30-day period with and accumulated rain of less than 50 mm.

Fawning Season We follow Contreras-Moreno (2018) to determine the fawning season for white-tailed deer in the study area. Accordingly, we fix the beginning of the fawning season on February and at the end of June.

8.3 Results

All the radio-collared deer were alive by February 2018, 20 months after the initial deployment of the radio collars. Radio collars were originally projected to work for 24 months, but due to collar malfunction, two collars sent information to the Iridium system for 12 months, two for 14 months, and one for 16 months (Table 8.1). We obtained 461 daily traveled distances for the five radio-collared deer (36–129). The mean daily traveled distance along the year was 1044.06 m (SD ± 501.00 m) with a minimum of 302 m and a maximum 4831 m. The precipitation data showed that the rainy season began on the second half of June and finished by the first half of November.

In order to include only bimesters with data of more than one individual deer, we only include on the analysis 427 daily traveled distances, corresponding to the period May–June 2016 to May–June 2017 (Table 8.1). When we relate the observed seasonality of the study area to the average daily traveled distances per bimester for all deer (Fig. 8.4) and we observed the individual average distance per deer (Fig. 8.4b), we notice that the lowest values corresponded to the rainy season, while the highest values coincide with the dry season. We observed that the longest daily traveled distances were during the fawning season compared with the post-reproductive season (Fig. 8.4a, b).

There were differences between bimesters (*Fobs* = 16.36; *g.l.* = 24, 6; $p < 0.001$), while no differences were detected between individual deer (*Fobs = 0.91*, *g.l.* = 34,4; $p = 0.47$; Fig. 8.4a, b). The Tukey TSD showed that there were no differences between June–August 2016, September–October 2016, and November–December 2016 ($p > 0.05$) which had the lowest average observed deer daily traveled distances (± SD; 676.024 ± 160.053; 778.024 ± 240.003; and 876.136 ± 220.995 m, respectively; Fig. 8.4). We found differences between the bimesters with highest daily traveled distances May–June 2017 (1531.72 m ± 1151.71) followed by the bimesters May–June 2016 and March–April 2017 (1201.23 ± 460.547 and 1240.96 ± 377.787 m, respectively; Fig. 8.4).

Table 8.1 Bimonthly average daily distance (m) moved per each individual female white-tailed deer studied at Nicte-ha, Campeche, México, during the years 2016 and 2017.The number in parenthesis indicates the number of complete daily cycles during each bimester

Individual	2016				2017				
	May–Jun	Jul–Aug	Sep–Oct	Nov–Dec	Jan–Feb	Mar–Apr	May–Jun	Jul–Aug	Sep–Oct
17,796	1207 (20)	680 (12)	745 (16)	900 (13)	1104 (28)	978 (24)			
17,797	987 (23)	672 (20)	727 (7)	932 (12)	850 (10)	1389 (18)	1358 (9)		
17,798	1193 (8)	866 (12)	792 (3)	978 (6)	952 (7)	1242 (23)	1553 (14)	736 (8)	918 (3)
17,800	1307 (14)	918 (9)	554 (3)	1104 (2)	1357 (7)	1277 (1)			
17,801	1438 (16)	811 (29)	554 (12)	688 (11)	1037(24)	1355 (31)	1741 (6)		

Even the linear regression analysis between daily traveled distances and the aver- age daily temperature was significant (Fobs = 12.48, g.l. = 426, $p < 0.001$); the explained variance of the model was low ($r^2 = 2.85\%$). We found that the linear regression between the mean values of daily traveled distances per deer at each bimester with the mean average temperature per deer per bimester was not significant (Fobs = 1.47, g.l. = 30, $p = 0.24$).

8.4 Discussion

The mean daily distances traveled by the white-tailed deer in Nicte-Ha (1044.06 ± 501 m) were shorter than those recorded in most of the studies in northern portions of the distribution of the species, where the usual daily traveled distances are above 1700 m (e.g., Sparrowe and Springer 1970; Ozoga et al. 1982; Schwede et al. 1993; Bertrand et al. 1996; Webb et al. 2009, 2010). Also, the mean daily traveled distances were shorter than those reported from the northwestern arid lands of Mexico (7016 ± 354 m; Gallina et al. 2003) and even in the tropical dry forest of the Pacific slope (1440 m in the dry season and 2580 m in the rainy season; Sánchez-Rojas et al. 1997).

Movement of white-tailed deer could be influenced by many ecological, environmental, and behavioral variables (Webb et al. 2010), and the differences we found between Nicte-Ha compared with studied sites should be reflecting the local adaptation of the deer in Nicte-Ha to the resource availability, as well the environmental conditions of the area. However, it is important to notice that to calculate the daily distance traveled by the deer, we are using a 2-h interval between fixes, which is a longer period than what has been used in other studies (e.g., Webb et al. 2010; Gallina et al. 2003) and could be underestimating the calculated movement distances

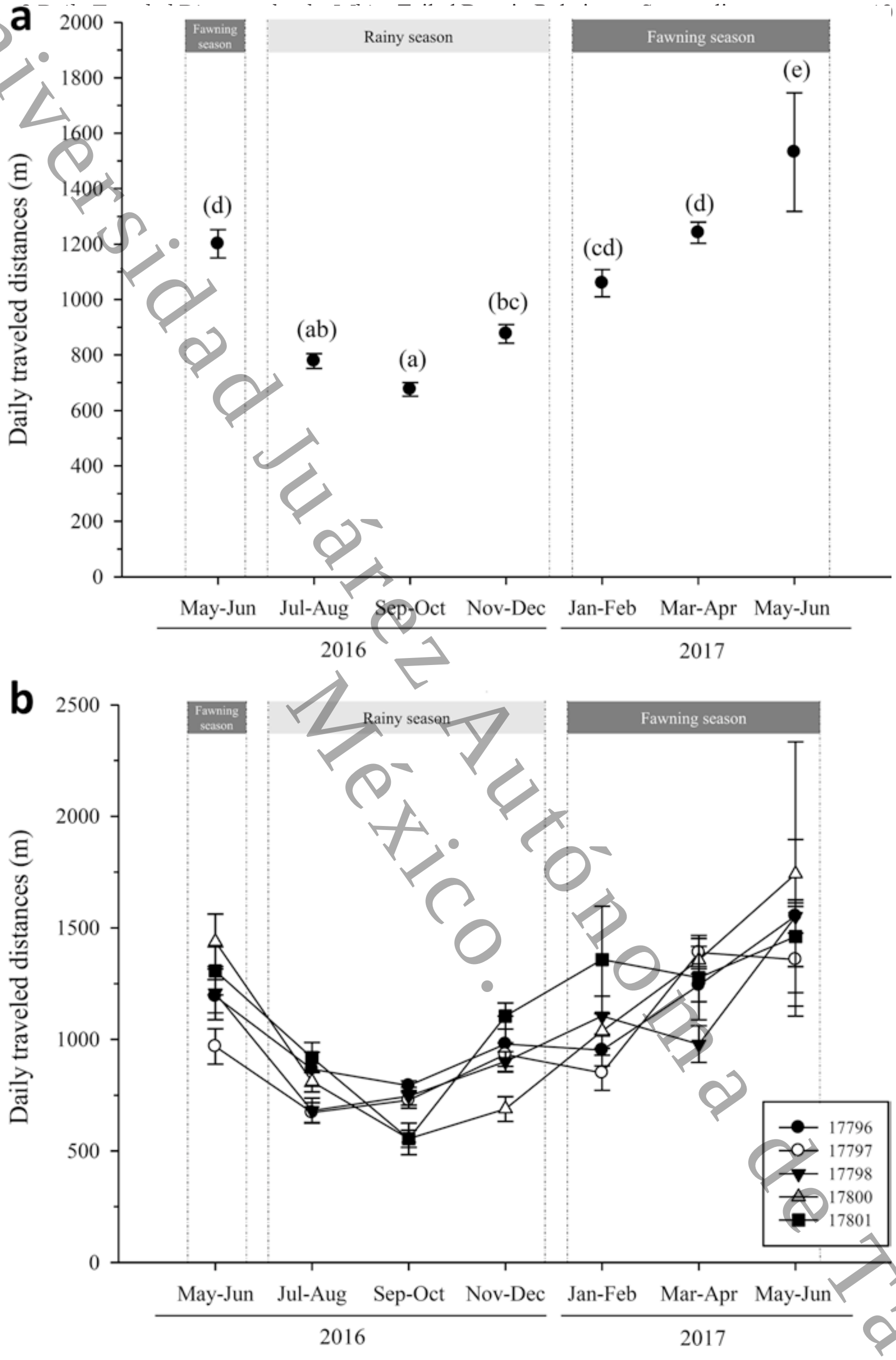

Fig. 8.4 (**a**) Average daily traveled distances (± EE) covered by all female white-tailed deer in Nicte-Ha per bimester during the study period (May 2006 and June 2017). Different letters over the values indicate statistically significant differences ($p < 0.05$). (**b**) Average daily traveled distances (± EE) covered by specific deer in Nicte-Ha per bimester during the study period (May 2006 and June 2017). The numbers in the label box indicate the identification number for each deer. The light-shaded area shows the approximate dates for the rainy season in 2016. The dark shaded areas indicate the fawning season in the Nicte-Ha area according to Contreras-Moreno (2018)

(Mills et al. 2006) because we are not capturing a more realistic movement distance produced by tortuous movement paths (Webb et al. 2010).

Several factors influence deer movements including physiology, which includes breeding and parturition, general changes in season and daylength, and environmental influences such as weather (Webb et al. 2010). In our study, the daily distances traveled by the deer showed differences throughout the study period. This suggests that environmental conditions or physiological traits of the deer that change over the course of the year influenced the behavior and the need of the deer to increase or decrease their activities. We found an increase in the traveled distances by the female deer during the dry season of 2016 and 2017, which corresponded also with the fawning season.

Delfín et al. (1998) and Sánchez-Rojas et al. (1997) found that in areas of semi- arid and dry tropical forest, respectively, deer traveled shorter distances during the dry season, when temperatures were high, probably to reduce energy consumption. However, in both these areas (Northwest arid Mexico and tropical dry forest of the Pacific slope), the dry season corresponded to a post-reproductive season, and the females are not under the pressure to satisfy the fawn needs. Contrary, in Nicte-Ha, the dry season coincides with the fawning season (Contreras-Moreno 2018). In general, during the fawning season, the activity of the female white-tailed deer increases (e.g., Bello et al. 2004; Gallina et al. 2010; Gallina and López-Arévalo 2016), and the longer daily traveled distances of the females in Nicte-Ha could be related to the presence of fawns during the dry season, even taught it is the hottest time of the year.

In the Yucatan Peninsula, the dry season produced that herbivores like the white-lipped peccary (*Tayassu pecari*) and the tapir (*Tapirus bairdii*) concentrate their activities around the water ponds (Reyna-Hurtado et al. 2009; Pérez-Cortez et al. 2012). Due to the intense seasonality on Nicte-Ha, it was possible to expect that the white-tailed deer should concentrate their activities around the water sources reducing the daily traveled distance. During 2017, several of the artificial water holes in Nicte-Ha were dry because of the intense drought. This could cause that white-tailed deer increased the daily distance traveled during the May–June period, to travel to other water sources. However, in 2016 the drought was not as intense, and water holes do not get dry, but the deer still traveled longer distances than in the rainy season. This indicates that the reduced amount of water during the dry season is probably not the main cause of the longer traveled distances, supporting the hypothesis that the increase in the metabolic needs during the fawning produced that the female deer walk for longer distances.

The dry season brings about phenological changes that affect the diversity and availability of resources for herbivores, thereby prolonging natural periods of scarcity. As a result, herbivores must make decisions and modifications to their behavior, with some adjustments to their diets (Keuroghlian and Eaton 2008). In the region, diet of the white-tailed deer is comprised mostly by leaves and stems year-round and is richer in plant species during the wet season and much more restricted during the dry season (Weber 2005). Temporal variation in patch productivity has been observed to directly influence spatial use and deer movements (Van Beest et al. 2011). The reduction in available leaves and stems (the quality and quantity of natural fodder produced by the available biomass) in Nicte-Ha could be a factor that motivates deer females to travel longer distances, in search of food, to supplement their metabolic needs, and during the fawning season, there is an increase in energy needs due to the demands of breastfeeding.

The results of this study indicated that there is no relationship between temperature and the daily movements of the deer, although deer moved longest daily distances during the hottest months of the year (March–June). This is contrasting with other studies (e.g., Gallina et al. 2003; Webb et al. 2010) where there has been a correlation between activity and temperature. We still considered that the temperature could be affecting the white-tailed deer movement rate on Nicte-Ha. Rodríguez-Boza (2015) found that white tailed-deer was more active during the sunset and sunrise in Nicte-Ha and the activity was greatly reduced during the evening, the hottest time of the day. It is probable that the lack of relation between distance moved and the temperature could be because the use of average daily temperatures and daily distances moved by the deer is hiding the detailed movement pattern in relation to temperature that occurs during specific times of the day. Further studies should consider these problems to help to determine the relationship between deer movement and temperature in Nicte-Ha.

The flooding season in Nicte-Ha is coincident with the time when the deer in Nicte-Ha moved shorter distances. This behavior could be produced because it is the time when the fawning season is over (Contreras-Moreno 2018) and the meta- bolic needs for the female deer due to lactation are reduced. We did not detect that the white-tailed deer in Nicte-Ha migrate to higher ground areas during the flooding season, and even during the high flooding levels (July–October), the deer still stand on their home ranges. It is possible that the increased flooding levels reduced the mobility of the deer and they should concentrate their activities in areas of their home ranges where the flooding level is lower, as occurs in other wetland areas such as in the Florida Everglades (Fleming et a. 1994).

Nicte-Ha, as a most of the Campeche state coastal area, is in a high risk of flood- ing due to sea level rise, according to the current climate change scenarios (Ortiz and Méndez 1999; Yañez-Arancíbia et al. 2014). The reduced daily traveled dis- tances during the flooding season by female white-tailed deer observed on this study indicate that the flooding season affected the movement of the individuals. The increase on flooding levels because of sea level rise in Nicte-Ha could have important effects on this species, as already happened in the Amazon where increase on water levels due to flooding had affected the mammal communities (Bodmer et al. 2018). Under these circumstances, the continuation of studies on the movement ecology of the species would help us to clarify how this species will adapt to the climate change scenarios in Nicte-Ha where longer flooding seasons with contrasting extreme drought are expected (Ortiz and Méndez 1999; Imbach et al. 2012; Chiabai 2015).

Although the number of radio-tracked individuals during this study was low, this is the first time that white-tailed deer movement is studied by satellite telemetry in the tropical portion of the distribution of the species. We hope that this study encourages other researchers to increment the knowledge of the species in the region, especially because it is probably the most hunted by subsistence and sport hunters and their importance for the natural communities.

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CAPÍTULO 3

Seasonal antler cycle in white-tailed deer in Campeche wetlands in Southeastern Mexico

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ORIGINAL ARTICLE

Seasonal antler cycle in white-tailed deer in Campeche wetlands in Southeastern Mexico

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Abstract

Hunting activity in Mexico is regulated by the Secretaria de Medio Ambiente y Recursos Naturales (SEMARNAT), a Federal agency which also approves management plans and annual harvest rates. The official calendar for white-tailed deer hunting season in Mexico comprises a single season that runs from November to March. To determine the congruence of the current hunting calendar with the seasonal timing of hard antlers of white-tailed deer in the wetlands of Campeche in southeastern Mexico, we used data obtained from 10 camera trap surveys performed from 2010 to 2017. In the pictures of white-tailed deer, we identified the timing of the presence of different antler developmental stages (velvet, hard antlers, and no antlers) as well as the occurrence of fawns. We obtained 1071 pictures of deer with antlers in velvet stage, 128 with hard antlers, 16 with no antlers, and 414 pictures of fawns. We observed that pictures of deer with antlers in velvet stage occurred from February to July, hard antlers from May to October, and no antlers from the second part of November to January. We also observed that the fawning season ran from February to June. Our results indicate that the reproductive season in Campeche wetlands is different from what occurs in the northern latitudes of Mexico and southern USA. Because the timing of the white-tailed deer antler development in our study area does not coincide with the official hunting season established in Mexico, we believe it is necessary to modify the official hunting season for the Campeche wetland area. Sport hunting should be permitted from August to October, based on the timing of deer with hard antlers.

Keywords Camera traps · Campeche · Fawning season · Sport hunting · Wetlands

Introduction

White-tailed deer occurs from South America to Canada (Heffelfinger 2011), and populations of the species display extensive variation in phenotypic and physiologic traits throughout their range (Demarais et al. 2000). In most of the species' range, there is variation in the timing of reproduction among regions, where populations within regions are similar or vary in a clinal fashion (Severinghaus and Cheatum 1956; Webb and Nellis 1981; Bronson 1989; Loe et al. 2005). Usually, white-tailed deer mating season in temperate latitudes occurs so that parturition coincides with periods of favorable weather and maximum forage quality (Greig 1979; Clutton-Brock et al. 1982; Bronson 1989). For example, in the north, central, and western portions of Mexico, white-tailed deer are consistently born from July to September (Mandujano et al. 1994; Mandujano and Gallina 1996; Galindo-Leal and Weber 1998; Villarreal 2006; Buenrostro et al. 2008; Gallina et al. 2010), coinciding with times of greatest water and food avail-ability. In accordance with this fawning season, the reproduc-tive season and the time for hard antlers to form in males extend from November to January (Galindo-Leal and Weber 1998; Gallina et al. 2010).

There is practically no information about the reproductive aspects of white-tailed deer in the southern portion of their distribution. Like most mammals, variation in the species'

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reproductive chronology has been associated with latitude (Webb and Nellis 1981; Goss 1983; Verme and Ullrey 1984; Richter and Labisky 1985; Bronson 1989; Lincoln 1992; Loe et al. 2005). In tropical latitudes, the lack of change in day light should produce year-round reproduction in the white-tailed deer; nevertheless, reproduction is usually timed to co-incide with resource availability (Heffelfinger 2011). This suggests that the species in the southern portion of the distri-bution could still have a regional reproductive season associ-ated with the availability of local resources.

Historically, there has been a series of reports suggesting that the white-tailed deer reproductive season could be differ-ent in the southern and northern portions of their distribution. Several authors incidentally reported that in southern Mexico, the fawning season occurs from April to June (Allen 1904; Gaumer 1917; Villa 1954; Leopold 1959; Weber 2014) and the reproductive season finishes in November (Villa 1954). Also, in Central and South America, a fawning season has been recorded from January to May in Costa Rica (McCoy-Colton and Vaughan-Dickhaut 1985), Panamá (Allen 1904), Peru (Brokx 1984), and Venezuela (Weber 2014). Extreme situations have also been recorded in Colombia where the fawning season goes from September to March, peaking from December to February (Blouch 1987; Blanco and Zabala 2005). Given the large variation in the fawning season in the southern portion of the distribution, some authors suggest that white-tailed deer do not have specific reproductive seasons in these areas (Geist 1998; Weber 2014).

Sport hunting of white-tailed deer (Odocoileus virginianus) has been a successful practice for many years in North America (Leopold 1959; Chapman 1975), mostly driven by the opportunity to harvest antlered bucks (Adams and Hamilton 2011). In Mexico, white-tailed deer sport hunting represents an important activity, particularly in the northern part of the country where hunters give significant economic benefits to local inhabitants (Guajardo-Quiroga and Martínez-Muñoz 2004; Contreras-Gil et al. 2010; Villarreal 2013). In some southern states of Mexico, there has been a significant development of white-tailed deer sport hunting activities (CONABIO 2012), but so far, on few occasions has the activ-ity allowed local inhabitants to gain access to the economic benefits (García-Marmolejo et al. 2008).

In 26 of the 32 states of Mexico, white-tailed deer sport hunting is regulated by the Ministry of Environment and Natural Resources (SEMARNAT; Secretaría de Medio Ambiente y Recursos Naturales 2017b). Only Baja California Norte, Chihuahua, Sonora, Nuevo León, Coahuila, and Tamaulipas in northern Mexico have a state-level wildlife management regulation. In the remaining 26 states, SEMARNAT is responsible for determining policies, harvest rates, and hunting seasons for the species (Retana 2006; Contreras-Gil et al. 2010). SEMARNAT determined that white-tailed deer sport hunting season comprises a single date that runs from mid-November to the end of March in these 26 states. The election of this hunting period is based on the opinions received by each one of the SEMARNAT state offices (SEMARNAT 2017a). However, in practice, these dates are determined by the mating season and occurrence of hard antlers of the white-tailed deer subspecies living in north-ern Mexico (e.g., O. virginianus texanus and O. virginianus couesi; Villarreal 2006) and parallels the dates in the southern USA (Gallina et al. 2010; Mandujano et al. 2014) but may be inappropriate for more southerly populations of the species.

The difference in the fawning and reproductive seasons between the southern and northern white-tailed deer popula-tions is important for the management of the species. The main drivers of the hunting activity are the antlered bucks, and the season in which these are available in the south may not coincide with the current established hunting season. Given this scenario, it is necessary to establish the reproduc-tive and fawning seasonal timing in southern Mexico and determine if the current hunting calendar is adequate to fulfill regional conditions. The objective of this work was to deter-mine the seasonal timing of antler development and fawning season of white-tailed deer in the Campeche wetland area in Mexico and to evaluate its congruence with the current hunt-ing calendar.

Materials and methods

Study site

The study area is located in c.a. 800 km^2 of the wetlands of the state of Campeche, in southeastern Mexico (Fig. 1). The climate in the region is warm-humid, with a mean temperature of 27 °C and up to 2000 mm of precipitation a year (INEGI 2015). The study area is between 0 and 5 m above sea level, and most of the region is subject to seasonal floods that can last from 2 to 8 months (June to December), depending on the topography, rate of discharge from the regional fluvial system, and the tide in the areas close to the sea. The seasonal floods are followed by a drier season when higher areas are partially or completely dry (January to May; Barba-Macías et al. 2014). The temporal variations in the flooding level are apparent in the gradient of vegetation from the most flooded to the least flooded areas. The vegetation is het-erogeneous: it comprises hydrophilic vegetation, flooded savannah, mangroves, sub-evergreen flooded rain forests, and tropical deciduous flooded forests (Ocaña and Lot 1996). Flooding in the region also influences the degree and type of human activities that vary from intense ex-tractive activities such as fishing, hunting, and logging in the wettest areas to extensive cattle ranching in savannahs and induced pastures. The ecosystems, particularly

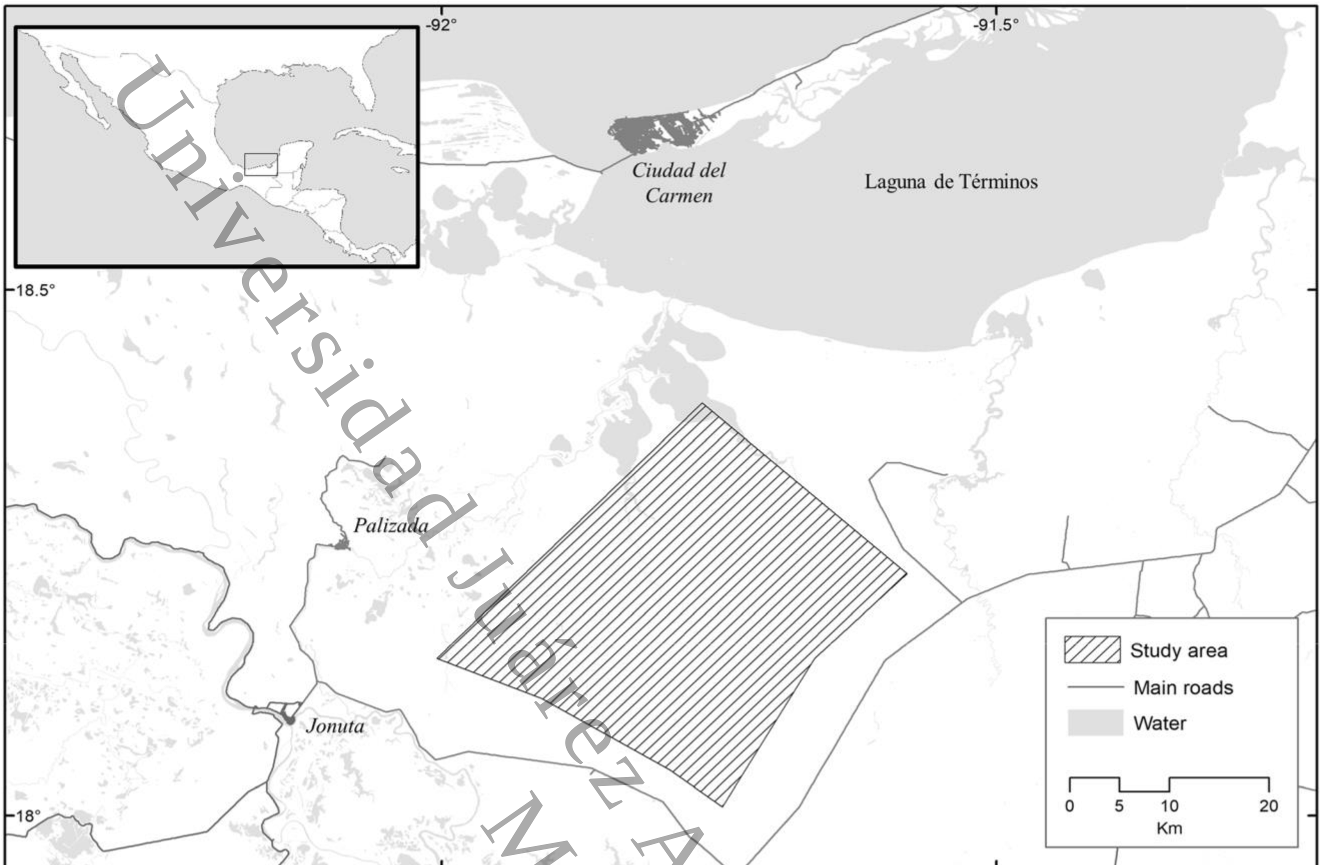

Fig. 1 Location of the study area in the Campeche wetlands in southeastern Mexico

tropical forests, are also impacted by subsistence maize crops and irrigated agriculture, mostly of rice and, more recently, oil palm.

Camera trapping

The use of camera traps to study ecological attributes and behavioral aspects of white-tailed deer is extensive. Camera traps have been useful in identifying white-tailed deer population characteristics (e.g., McKinley et al. 2006; McCoy et al. 2011) and have allowed for the identification of some temporal developmental phases such as the presence of offspring, pregnant females, and the moment in which the hard antlers of the males become apparent (e.g., McKinley et al. 2006; Soria-Días and Monroy-Vilchis 2015). Some studies have even made possible the identification of individual males based on antler configurations (Jacobson et al. 1997).

From 2010 to 2017, we performed 10 camera trap surveys along in the wetlands of southwestern Campeche with the aim of determining the richness and abundance of medium-sized and large mammals of the study area (see Hidalgo-Mihart et al. 2017 for a review). The location, intensity, and timing of the surveyed areas were established according to the information required by the managers of the natural protected areas in the region. Each one of the camera trap surveys consisted of at least 20 digital camera traps of different models (Wildview, Wild View Web Products Inc., Greenfield, MN, USA; Cudddeback, Non Typical Inc., De Pere, WI, USA; Moultrie, Moultrie Products, LLC, Birmingham, Al, USA; Acorn, LTL Acorn Outdoors, Green Bay, WI, USA; Pantheracam Models IV and V) operating for a minimum of 45 days. The final number of operating camera traps and camera trap days (we considered a camera trap day as a period of 24 h during which a single camera was continuously operating) varied at each survey and over the study period due to equipment failures and losses because of vandalism and flooding. During each one of the surveys, we tried to place the cameras at least 1 km apart from one another and 50 cm above the ground on trees. Camera traps were placed close to trails where we found evidence of use by medium-sized or large mammals, and they were programmed to take pictures 24 h per day. We considered a white-tailed deer pho-tograph as independent when the time between sequential photographs was > 6 h. Because the surveyed areas (Nicte ha, Palizada and Zapata) were located only 20 km away from each other, and the environmental characteristics of the three areas were very similar, we grouped the pictures of all the surveys into a single area.

To determine the seasonal timing of antlers and fawn occurrence of the white-tailed deer in the study area, we revised all the independent photographs that we obtained during all our surveys. The first stage of the analysis was to determine the sex of the observed deer and the presence of the fawns. We considered that a photographed deer was a male when antlers at any stage were present or when the surface of the exposed antler pedicle was fully identified (absent where the antler should be) in the form of a wound or scar (Price et al. 2005b) or when it was possible to observe sexual traits such as testis. In the case of fawns, we considered photographed individuals to be fawns when they presented a reddish-brown color, with a series of white lateral and dorsal spots; juveniles and adults do not present these spots (Reid 2009) as they disappear at 3–4 months of age (Hesselton and Hesselton 1982). During this stage of the analysis, we also eliminated the photographs where the head of the adult deer was not visible, or when the area of the head where the antlers should be was not observable (e.g., the deer turned in the opposite direction of the camera). We also eliminated blurred pictures or pictures with poor image quality due to camera malfunction or when the time stamp was not accurate.

Once we obtained the final list of usable photographs, we categorized the photographs of males according to three differentiable antler development stages: (1) velvet: photographs where the deer's antlers evidently showed the presence of velvet (specialized skin with velvet appearance that covers the antlers during development; Bubeník 1990). We consid-ered under this category all the antler velvet stages, from their appearance until well developed (Fig. 2): (2) hard antlers: photographs where fully developed antlers are visible, without evidence of velvet (Fig. 2); (3) no antlers: photographs in which the surface of the exposed pedicle was fully identified (empty where the antler should be) in the form of a wound or scar (Price et al. 2005b; Fig. 2). In the case of fawn pictures, we did not make any attempt to classify them by age or size, due to the possible subjectivity of this classification; we instead grouped them into a single fawn category. Once we categorized the pictures according to the antler status and the presence of fawns, we grouped the pictures from the 10 surveys in semi-monthly periods (c.a. 15 days each) according to the time when the picture was obtained in order to determine the seasonal timing of antler development and the fawning season. In 2833 photographs (31.02% of the white-tailed deer pictures obtained during the study), we observed incomplete images of the photographed deer, which did not allow us to determine the status of the antler (even in several occasions when the presence of sexual characteristics allowed us to iden-tify that the photographed deer was a male). Because the un-certainty of the antler stage identification in such a consider-able number of photographs could have an effect in the esti-mation of aspects such as relative abundance of deer under a particular antler stage (i.e., number of pictures under a particular antler stage/camera trap effort), we decided not to perform statistical analysis on the data. We only indicate the proportion of the different antler stages from the total number of identifiable photographs during semi-monthly periods (c.a. 15 days each) along the year.

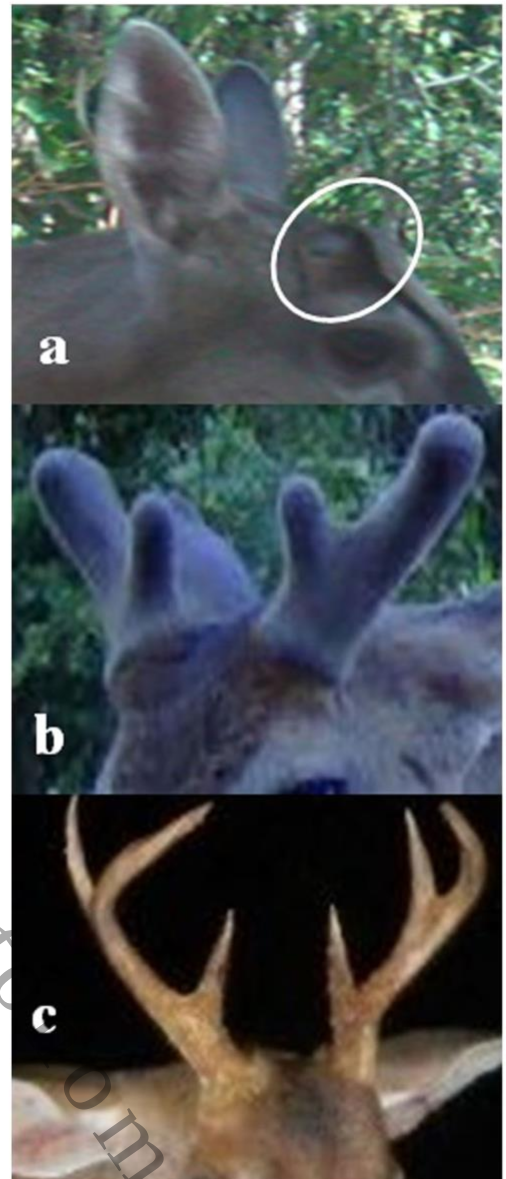

Fig. 2 Examples of the three white-tailed deer antler development stages in which the photographs were categorized. a No antlers stage. b Velvet stage. c Hard antlers stage

Results

Antler developmental timing

During the 10 surveys performed throughout the 8 years of study, we obtained 9131 photographs of white-tailed deer in

30,475 camera trap days. Because the area is affected by an intense flooding season, most of the survey effort was per-formed during the dry season (January to June; 19,950 trap days; Fig. 3) and the first part of the rainy season (July to August; 4725 camera trap days), with a reduced effort during the late rainy season which is the time of the highest flooding levels (September to December; 5800 camera trap days; Fig. 3). We excluded 7920 (86.74%) white-tailed deer photo-graphs from the antler analysis; because the observed deer was identified as a female or a fawn (4961 photographs), it was not possible to observe the head of the photographed deer (2833 photographs) or the quality of the picture did not allow for a proper identification of antler status (63 photographs). Only in 1211 photographs we were able to identify the status of the antler. We obtained 1071 pictures of deer in the velvet antler status, 128 pictures with hard antlers, and 16 with no antlers.

We observed deer in the velvet stage from the second part of January until the second part of July, out of which the highest frequency was observed from the first part of March to the second part of May (Figs. 3 and 4). In the case of hard antlers, the observations took place from the second part of May until the second part of October, with the highest fre-quency of observations from the second part of July to the second part of October (Figs. 3 and 4). Finally, even though we had a small number of observations in the category of deer with no antlers, (mostly because in order to determine if a deer was under this category it was necessary to have a clear picture of the head), they were observed from the second part of November to the first part of January (Figs. 3 and 4).

Fawning season

We obtained 414 pictures of fawns. We observed that the first fawn pictures were taken during the first part of February, and the last record was taken during the second part of June (Fig. 3). We did not obtain pictures of fawns with white lateral and dorsal spots after June, indicating that by this date, most of the fawns lost this characteristic and progressed to the next developmental stage (Fig. 5). Most of the records of fawns in this region were photographed from the first part of April to the second part of May (Fig. 3).

Discussion

Our results show that the hard antler season for white-tailed deer in Campeche area seems to occur from July to October and the fawning season from February to June. This observation is different from what occurs in the north, central, and western portions of Mexico where the fawning season goes from July to September (Villarreal 2006; Galindo-Leal and Weber 1998; Gallina et al. 2010; Mandujano et al. 1994; Mandujano and Gallina 1996; Buenrostro et al. 2008), and the hard antlers are present from mid-November to the end of January (Villarreal 2006; Gallina et al. 2010; Mandujano et al. 2014), supporting the hypothesis that the timing of re-production is different between other parts of Mexico and our study area.

We are aware that due to logistical reasons, most of our survey efforts in the study area were performed during the dry season (January to June) and early rainy season (July–August) and that we had reduced survey efforts during the late rainy season when flooding levels are higher (September to December). The result of this survey effort deficiency is reflected in the reduced number of photographs of deer with hard antlers. However, because we had a very clear velvet season in which we did not find any deer with hard antlers (late January to early June), and because from July to October only deer with hard antlers were apparent, we are very confi-dent that we are able to describe the antler seasonality of the white-tailed deer in the study area. The results of this study showed that the seasonality of the white-tailed deer antler development in the study area is different from other parts of Mexico. Particularly, the hard antler timing does not coincide with the official hunting season established for the area (mid-November to end of March; SEMARNAT 2017a). Our results showed that even though the hunting season is the result of the information provided by the SEMARNAT's regional offices, the absence of local information about the species in southern Mexico has resulted in a determination of the hunting season which is only based on available data obtained from northern Mexico.

As in other parts of the white-tailed deer distribution, the main driver of their sport hunting in southern Mexico is the presence of males with hard antlers (trophies).

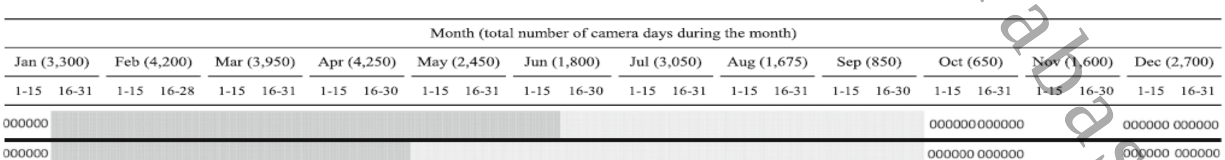

Fig. 3 Semi-monthly periods (c.a. 15 days each) when each one of the three white-tailed deer antler development stages was recorded. The ant-ler development stages are 1—velvet stage: dark gray; 2—hard antlers stage: light gray; 3—no antlers stage: circles. The total number of camera days indicates the total sum of camera days during the month

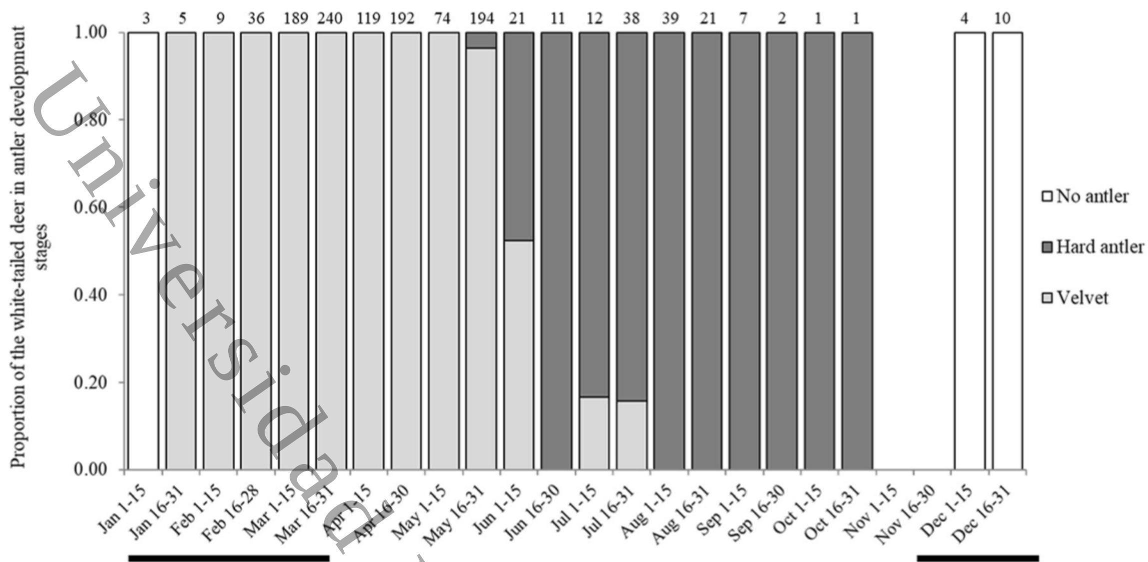

Fig. 4 Proportion of the white-tailed deer antler development stages (velvet, hard antlers and no antlers) observed in the study area in southeastern Mexico per semi-monthly periods (c.a. 15 days each). Numbers in top of each bar indicate the number of pictures where the antler development stage could be identified during the period. The continuous black line on the bottom of the graph represents the dates where white-tailed deer could be officially harvested in the study area according to the calendar proposed by Ministry of Environment and Natural Resources (Secretaría de Medio Ambiente y Recursos Naturales; SEMARNAT)

White-tailed deer sport hunting in Mexico is allowed only in wildlife management and conservation areas called UMAs (Unidades para el Manejo Sustentable de la Vida Silvestre), which are private or communal proprieties with a specific wildlife management plan authorized by the federal government through SEMARNAT (Valdez et al. 2006). Even though the UMAs of Campeche promote white-tailed deer as the most important species to be harvested on their lands (CONABIO 2012), the UMA strategy has not been very successful in the region mostly due to the deficiencies in the wildlife management and the failure of law implementation (Weber et al. 2006). Owners and managers of the UMAs in southern Mexico are aware that the hard antler season of white-tailed deer occurs from August to October and hunts according to this calendar, violating the hunting schedule established

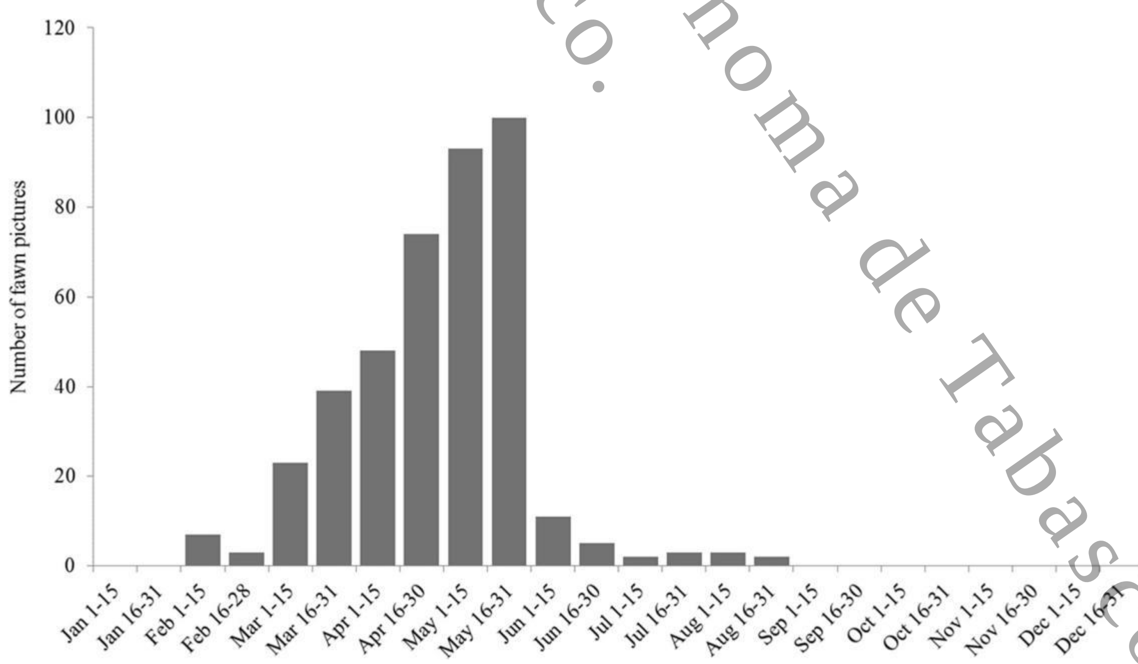

Fig. 5 Number of white-tailed deer fawn pictures in semi-monthly periods (c.a. 15 days each) obtained in the camera trap surveys performed in the Campeche wetlands in southeastern Mexico. Photographed white-tailed deer were considered as fawns when they presented a reddish-brown color, with a series of white lateral and dorsal spots

by SEMARNAT. The only way in which UMA owners and managers will avoid sanctions by the federal environmental authorities due to hunting outside of the authorized season is to modify the official hunting season for these states. A new season, adapted to local conditions, should be established which should run from August to October. This is especially important in a scenario where the white-tailed deer subspecies distributed in Campeche and Tabasco (O. virginianus thomasi) has been included in the Hubert Thummler Award for the Mexico deer slam (Villarreal 2013; SCI 2014a, 2014b) and should encourage the development of more UMA initiatives in the region, where the species is managed and harvested for sport hunting.

Variation in the reproductive chronology of the white-tailed deer has been linked to environmental variables associated with latitude such as photoperiods and food availability (Goss 1983; Lincoln 1992; Price et al. 2005a; Demarais and Strickland 2011). The photoperiod acts through melatonin to modulate the secretion of reproductive hormones (mostly testosterone; Goldman 2001; Hanon et al. 2008), regulating the antlers cycle in this species (Price et al. 2005a, 2005b); however, in view of the slight photoperiodic changes in the tropics (and their weak temporal association with seasonal climatic changes), this environmental factor could have a reduced influence in controlling antler development in our study area. This could mostly be happening because the development of the velvet antlers is taking place during February, when the duration of daylight increases, contrary to what occurs in high latitudes when the velvet antler stage is produced by the reduction in the day length (Goss 1983; Lincoln 1992). This situation suggests that in our study area, the conditions that determine the reproductive cycle of the species could be related to resource availability.

We found the earliest recorded fawns during the first part of February and the highest numbers were observed from March to May. Still, it is important to note that white-tailed deer fawns are under-represented in camera surveys during the first 2 months of their lives (McKinley et al. 2006), and so it could be possible that the fawning season begins earlier than February. Our observations partially resemble previous re-ports that the fawning season for the species in tropical areas occurs from April to June (Allen 1904; Gaumer 1917; Villa 1954; Leopold 1959; Brokx 1984; McCoy-Colton and Vaughan-Dickhaut 1985; Blouch 1987; Geist 1998; Blanco and Zabala 2005; Weber 2014), indicating that in the study area, the fawning season occurs earlier than in other tropical regions.

Because mid to late lactation is the most energetically costly period for female mammals, we would expect that white-tailed deer would have evolved adaptive mechanisms for matching peak energetic requirements to seasonal fluctuations in forage quality resulting in the weaning of the fawns at a time of maximal forage quality (Bronson 1989). This has been observed in the north, central and western portions of Mexico, where white-tailed deer are consistently born from July to September (Mandujano et al. 1994; Mandujano and Gallina 1996; G a l i n d o - L e al an d We b e r 1 99 8; Vi l l a r r e a l 20 0 6; Buenrostro et al. 2008; Gallina et al. 2010), coinciding with the times of greatest water and food availability. Though this is likely occurring in other tropical areas along the range of the species, our observed fawning sea-son from February to May matches the dry season in the area, a time characterized by a severe water deficiency and daily extreme temperatures exceeding 50 °C and when the forage availability for females is likely reduced due to the deciduousness of the tropical forests of the region. Instead, it is possible that in our study area, the fawning season is synchronized with seasonal changes in the hydrologic regime and occurs during the mid-dry sea-son months (April–May), when numerous dry sites are available for fawning. Fawns that are born during the dry season will be approximately 3+ months old when flooding season begins in June/July reducing the risk of neonatal mortality due to fawn drowning. This change in fawning season associated to flooding has been previously reported in white-tailed deer populations that occur in areas affected by severe flooding such as the Everglades in Florida (Fleming et al. 1994; Richter and Labisky 1985; Boulay 1992; MacDonald-Beyers and Labisky 2005) as well with other tropical cervid species that live in areas prone to flooding like the Chital Axis axis (Dinerstein 1980) and the Thamin Rucervus eldii (Aung et al. 2001).

Our results showed that in the Campeche wetland area there is a clear fawning season. White-tailed deer fawning and reproductive seasons could have important regional variations (e.g., local environmental conditions, origin of the herd; Richter and Labisky 1985; Sumners et al. 2015), and it is possible that there is not a single reproductive and fawning season in the tropical areas. It is necessary to perform local surveys to identify the local reproductive seasons for the species along the southern portion of its distribution. Camera trapping has been a popular method to survey the mammalian fauna in southern Mexico, Central America and northern South America (Ahumada et al. 2013) and as in our study, white-tailed deer are commonly photographed (e.g., Gonthier and Castañeda 2013; Meyer et al. 2015). Similar to our study, most of the camera trapping surveys were not designed to deter-mine antler and fawning times for white-tailed deer but were performed during long periods of time and probably captured fawns and deer undergoing different antler stages. We encourage the researchers to systematize the available information on white-tailed deer and describe the local reproduction times of the species as we have done for our study area.

Management implications

Our results show that the reproductive timing for white-tailed deer in our study area is different from previously studied areas in Northern, Western, and Central Mexico. We found that fawning in the Campeche wetlands runs from February to June and that hard antler formation runs from June to October. The hunting calendar for the study area authorizes hunting in UMAs from mid-November to end of March. Even though a few individuals probably still have antlers, this is the time when most of the male deer lose their antlers and thus the chances that a sport hunter can hunt a trophy deer are extreme-ly reduced. To help UMA owners and managers avoid sanc-tions by the federal environmental authorities due to hunting outside of the authorized season, we encourage the Mexican hunting regulation authorities (SEMARNAT) to modify the hunting calendar for white-tailed deer in Campeche allowing sport hunting to take place from August to October, based on the timing of deer with hard antler.

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CAPÍTULO 4

Seasonal home range size of the white-tailed deer (Odocoileus virginianus) in a tropical wetland area of southeastern Mexico

Seasonal home range size of the white-tailed deer (*Odocoileus virginianus*) in a tropical wetland area of southeastern Mexico

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Abstract.

Determining home-range size (HR) of a species is an important prerequisite to understand a species' behavior, ecology, and management. White-tailed deer (*Odocoileus virginianus*) HR size is one of the most studied aspects of the species biology. However, in the southern portion of distribution (Mesoamerican Mexico, Central America and northern South America), even the white-tailed deer is largely important for subsitence and sports hunting, the information about the HR is scarce, reducing the capacity of management of the species. To better understand how the HR of the species response to the sex (female vs. male) and seasonality (rain, transition and dry seasons) of a tropical area, from 2016 to 2019 we radiotracked 11 adult white-tailed deer (seven females and four males) in a tropical wetland of western Campeche, Mexico. We found that mean female HR varied from 12.67 ha (±3.52) in the transition season to 21.57 ha ((±18.14) during the dy seson, and for males HR varied from 37.31 ha (±16.93) for the dry season to 90.16 ha (±72.64) during the rainy season. We did not found differences between seasonal HR of males and females. However, we found that differences exist when we combine the sex and the seasonality of the area, showing that female home range size is similar among the year, and that males, have smaller home range sizes during the early and dry season than during the rainy season. Our results show that water availability during the dry season, and flooding levels during the rainy season could have significant effects on the home rage size and configuration of the white tailed deer in the study area.

Key words.

Laguna de Términos, Core area size, home range overlap, Campeche

INTRODUCTION

Home range (*i.e.* the area used by an animal to meets its needs of food, water, cover, social interactions and caring for young; Burt 1943) serves as the most fundamental index of space use by wildlife (Hemson et al. 2005). Therefore, determining home-range size of a species is an important prerequisite to understand a species' behavior, ecology, and management (Sanderson 1966). In North America (United States, Canada, and northern Mexico) white-tailed deer (*Odocoileus virginianus*) home range size and configuration, and the effect that numerous environmental (*e.g.* seasonality, landscape configuration, etc.) and/or anthropogenic factors (*e.g.* hunting pressure, urbanization, etc.) have on these ecological characteristics, is one of the most studied aspects of this species' ecology (see Stewart et al. 2011 for a review). However, in the southern portion of distribution (Mesoamerican Mexico, Central America and northern South America), the information about the home range is scarce, especially in tropical areas (see Supplementary material 1 for a review).

Resource (i.e. food, water and cover) dispersion and seasonal availability are some of the most important environmental variables that influence on white-tailed deer home range size (Stewart et al. 2011). White-tailed deer living in areas where higher quality resources are abundant and well distributed tend to have smaller home ranges than deer that occupy less productive areas with unevenly distributed resources (Marchinton and Hirth 1984; Lesage et al. 2000; Stewart et al. 2011). Nevertheless, home ranges may decrease or expand seassonally as food or water change in availability (Hellickson et al. 2008; Stewart et al. 2011). In the case of the white-tailed deer that lives in the southern portion of the range, it has been observed that areas with extreme variations in temperature and precipitation (e.g. scrub lands in the northwest of Mexico or the tropical dry forests of the western portion of the country; Sánchez-Rojas et al. 1997; Bello et al. 2001), had strong effects on the white tailed deer home range size. However due to deficiency on information about this aspect, it is not possible to determine if this effect occurrs throughout other tropical and subtropical areas.

An example of these tropical areas is the extensive wetland system located on western Campeche state in Mexico, subject to severe seasonal changes, with a marked dry season with temperatures above 40 °C (Instituto Nacional de Estadística y Geografía 2013), followed by long flooding season that can last for more than eight months (Rivera-Arriaga and Villalobos-Zapata 2005). These climatic conditions have a strong effect on the resource availability for the wildlife inhabiting the area (Hidalgo-Mihart et al. 2017), in the case of white tailed-deer, the species respond to changing environmental conditions by increasing the daily distances traveled during the harshest portion of the dry season compared to the rainy season (Contreras-Moreno et al. 2019a).

Additionally, it has been fund that fawning sinchronize with the dry months of the year and the seasonality of the area is one of the possible causes of it (February-June; Contreras-Moreno et al. 2019b). Comprehending how do white-tailed deer home range size and configuration respond to the seasonality of the area, will help to know how this species could be affected by climate change in the region, a region that has experimented a general decrease in mean precipitation and an increase in drought in the last years (Imbach et al. 2012; Chiabai 2015).

White-tailed deer is the most hunted species in Mexico (Mandujano et al. 2014). White tailed deer hunting is commonly practiced for sport, subsistence, handcraft carving or as a part of the religious ceremonies of native cultures (Ortega-S. et al. 2011). Hunting also represents an important activity, particularly in the northern part of the country where hunters acquire significant economic benefits to local inhabitants (Guajardo-Quiroga and Martínez-Muñoz 2004; Contreras-Gil et al. 2010; Villarreal 2013). In some southern states of Mexico there has been a significant development of white tailed-deer sport hunting activities (CONABIO 2012), but so far, on few occasions has the activity allowed local inhabitants to obtain economic benefits (García-Marmolejo et al. 2008), mostly due to complications related to wildlife management and community organization (Weber et al. 2006).

Home range size determination of wildlife species has been identified as one of the research priorities for the species in Mexico, mostly because it will help to improve the conservation and management for the species (Ortega-S. et al. 2011). Understanding the effect of environmental conditions on the reproductive status of individual home ranges of white-tailed deer in the Laguna de Terminos Area, is a scenario of great importance because the white tailed-deer subspecies distributed in Campeche and Tabasco (*O. virginianus thomasi*) is included in the Hubert Thummler Award for the Mexican deer slam (Villarreal 2013; SCI 2014a, b) and should encourage the development of sustainable sport hunting initiatives in the region. Thus, the objective of this study was to determine the effect of seasonality on the home range size of white-tailed deer in the wetlands of Laguna de Terminos Area, in southeastern Mexico.

Materials and Methods

Study area. —Our research was conducted at the Nicte-Ha UMA (Wildlife Management and Conservation Unit per it Spanish initials; hereafter called Nicte-Ha), located in southwestern Campeche, México (91°43’56” W, 18°19’56” N) and adjacent to the Laguna de Terminos Flora and Fauna Protected Area (Fig. 1). The area is a 2,300 ha tract of tropical lower coastal plain habitat situated between -1 and 3 m asl. The climate in the region is warm-humid, with a mean temperature of 27°C and up to 2,000 mm of precipitation per year (INEGI 2013). The vegetation types of the area vary from hydrophilic vegetation, flooded savannas, mangroves, sub-evergreen flooded rain forests, tropical deciduous flooded forests, secondary growth forests, agricultural areas and induced grasslands for cattle grazing (Ocaña and Lot 1996). In 2010, the owners of Nicte-Ha removed all cattle from the ranch, and since then, the area has been used exclusively used for sustainable white-tailed deer hunting.

Water is probably the most limiting factor for wild ungulates during the dry season in the Yucatan Peninsula (Reyna-Hurtado et al. 2010). In Nicte-Ha, rain is concentrated in a single season that usually began at June and finish by November, followed by a dry season that lasts around six months (December-May). The intensity and seasonality of the rains in combination with a flat terrain, produces seasonal floods that can reach 0.5 m. The flood lasts for the entire rainy season, but once is over, water for ungulates becomes available and concentrated in numerous puddles along the area that usually dry out by mid-February. After this date, the only available free-standing water in Nicte-Ha is the Rio del Este river, and the artificial water holes that owners have built along Nicte-Ha area to improve the quality of habitats for white-tailed deer. However, in occasions due to a very extended drought such as the one that occurred at the end of the dry season in 2017, even the artificial water holes dry and the only water source for the wildlife on Nicte-Ha was the Rio del Este.

Capture and radio tracking. — During May of 2016 and May of 2018, eleven adult white-tailed deer (five males and one male in 2016, and two females and three males in 2018) were captured using a 20 x 20 m drop net (Ramsey 1968). Once captured, the deer were physically restrained, and conventional measurements and mass were obtained. Each captured deer during 2016 was fitted with a VERTEX Survey Iridium Collar (Vectronic Aerospace GmbH, Berlin, Germany), and those captured in 2018 with a VERTEX Survey Globalstar Collar (Vectronic Aerospace GmbH, Berlin, Germany). Once equipped, all the captured deer were released immediately on the capture site. The capture, management and collaring of the white-tailed deer was carried out under the collection permits SGPA/DGVS/01097/16 and SGPA/DGVS/003244/18 by the Dirección General de Vida Silvestre-SEMARNAT-México, and we followed the capture and management guidelines of the American Society of Mammalogists (Sikes et al. 2016). Iridium radio collars were programmed to take fixes every 6-h and the Globalstar every 12 h.

Home range calculation. — Although we captured and followed white-tailed deer in two different years (2016-2017 and 2018-2019), the small sample size precluded us to combine locations of individuals obtained in the different years of the study. We divided the location data into three seasons according to the availability of water for the white-tailed deer in Nicte-Ha 1.- Rainy season (June-November) when most of the area is flooded and water is freely available along Nicte-Ha; 2.- Transition season (December-February) in which eventual rains could occur and free water is available in puddles and water holes distributed along Nicte-Ha; 3.- Dry season (March-May) in which rain is extremely rare and free standing water is only available in artificial water holes and in the Río del Este. These seasons partially coincide with the reproductive cycle of the white-tailed deer in the study, where the antlered males are found from June-November, the antlerless males from November to February and the fawning season began in March and extended until June (Contreras-Moreno et al. 2019b).

Home range was estimated for each deer for each season (rainy season, transition season and dry season). We used HRT Home Range Tools in Arc GIS 9 (Rodgers et al. 2007) to estimate home range size and the core area with the Fixed Kernel method using 95% and 50% of the locations, respectively (Kernohan et al. 2001). The smoothing parameter (h) for each estimate was obtained using the least squares cross-validation method (Kernohan et al. 2001). In order to compare the white-tailed deer home range with other studies (Gula et al. 2013), we also calculated seasonal home rage size with the Minimum Convex Polygon (MCP) using 100% of the locations using The Animal Movement extension was in ArcView 3.2 (ESRI 1999; Hooge et al. 2001; Supplementary material 2).

To determine if there were differences in home-range sizes and core areas due to the seasonality of the study area and sex, we combined data from individuals of the different studied years. Temporal (rainy season, transition season and dry seasons) and sex (female white-tailed deer vs. male white-tailed deer) differences in home range size and core area, were analyzed using a general linear mixed model (GLMM; repeated measures analysis with random effects), with the seasonal home range size/seasonal core area size, and the sex as the explanatory variables using nlme in R (Pinheiro et al. 2019). Even though these analysis allow us to determine if the explanatory variables had an influence on the home-range size and the core area size of the white-tailed deer, because we combine the data of individuals from the different studied years, the differences resulting from inter-annual variations could not be tested and remained in the analysis as a source of error.

To quantify the degree of seasonal fidelity of the white-tailed deer to their home range, we calculated percent overlap of seasonal home ranges and core areas during consecutive seasons, i.e., the percentage of the home-range area utilized in a given season that was utilized again in the following one. We averaged percent overlap across seasons to determine average seasonal male and female percent overlap.

RESULTS

All the 11 captured deer where alive at the end of the one-year cycle, and their collars functioned properly during the three studies seasons. We obtained 5492 locations from the all the radio-collared deer during the study (range= 291 - 922; Table 1), distributed by 2361 locations during the rainy season (range 115-419), 1607 during the transition season (range= 94-258) and 1524 during the dry season (range= 78-275).

Home range.—The mean (± SD) home range size for females during the study was from 12.67 (±3.52) during the transition season to 21.57 (±27.44) in the dry season (Table 1). For males the mean home range size was from 37.31 (±16.93) during the dry season to 90.16 (±72.64) during the rainy season (Table 1). We found that in Nicte Ha, white-tailed deer home range size is larger for males than for females (χ^2=13.043, g. l.=1, p>0.001; Figure 3). Although, we did not found differences between seasonal home range sizes (χ^2=1.43, g. l.=1, p=0.23), we found that differences exist when we combine the sex and the seasonality of the area (χ^2=5.69, g. l.=1, p>0.0.171), showing that female home range size is similar among the year, and that males, have smaller home range size during the transition and dry seasons, than during the rainy season (Figure 3).

We found that the mean core area size (±SD) for females goes from 3.52 ha (±1.58 ha) during the transition season to 5.15 ha (±6.96 ha) during the dry season (Table 1). In the case of the males, mean core area size goes from 20.45 (±18.14 ha) during the rainy season to 7.91 ha (±5.52 ha) during the dry season (Table 1). When we compare the seasonal core area size between males and females, we found similar results that in home range size, with larger core area size for males than for females (χ^2=10.00, g. l.=1, p=0.002; Figure 3), and with out differences between seasonal core area size (χ^2=1.70, g. l.=1, p=0.19). However, we found differences in the core area size when we combine the sex and the seasonality of the area (χ^2=4.41, g. l.=1, p>0.03), showing that the core area size for females similar among the year, and males with larger core area size during the rainy season, compared with the transition and dry season, which is similar to our home range size results (Figure 3).

Seasonal home range overlap.- We found that the home range and core area overlap was for females was slightly larger from the rainy season to the transition season than during the transition season to the dry season (Table 2). However, even some seasonal changes occur (e.g. home range overlap of the male C during the rainy season to transition season), it is interesting to notice that for most of the radiotracked white-tailed deer in Nicte ha, both females and males remain on the same areas and maintain most of their home ranges and core areas during the year. Also, it is interesting to notice that even during the rainy season and the transition season some individuals (*e.g.* female C and males B,C and D) had separated home ranges from each (Figure 2), during the dry season, even they maintain portions of their separated home ranges, all they move portions of their home ranges to a single area around an artificial water hole.

DISCUSSION

Compared to the home range obtained in other areas along the distribution range of the white- tailed deer, our results tend to be smaller than those obtained for other subtropical areas such as desert scrublands (e.g. Bello et al, 2004; Hellickson et al. 2008) or even other wetlands (e.g. Labisky et al. 1999). White tailed deer home range size in areas with higher quality resources that are abundant and well distributed tend to have smaller home ranges than deer that occupy less productive areas (Marchinton and Hirth 1984; Lesage et al. 2000; Stewart et al. 2011). Productivity in tropical areas like Nicte-Ha is greater than in subtropical and temperate areas (Gillman et al. 2015). Higher productivity have a direct impact in the available food resources for ungulates (Mandujano and Naranjo 2010), and resulted that in Nicte-Ha, white-tailed deer were able to obtain all their basic needs in smaller home ranges compared to white-tailed deer home ranges in subtropical and temperate ecosystems.

The mean home range size for the female white-tailed deer in Nicte-Ha is similar to the home range areas observed in other tropical and subtropical areas in Mexico (Sánchez-Rojas et al. 1997; González-Pérez 2003; Table 1), but smaller than home ranges observed in Costa Rica, Colombia and Venezuela. However, is it important to notice that the animals monitored in Central and South America in all cases were hand-raised individuals released as adults or relocated individuals (e.g. Sáenz-Méndez and Vaughan-Dickhaut 1998; Camargo-Sanabria 2005; Table 1) and the large home ranges could have resulted from dispersal movements from the releasing area until a more stable home range is established (Nelson 2015). In the case of males, the observed home range in Nicte-Ha is similar to the home ranges of the deer in the Venezuela llanos (Correa-Viana 2000; Table 1) and tropical dry forests of Mexico (Sánchez-Rojas et al. 1997) and Colombia (Camargo-Sanabria 2005), but smaller than other areas of Colombia (Correa-Viana 2000). However, as with the females, most of the work made with white tailed deer in South America have been hand-raised or relocated individuals that probably were exploring the new habitat.

Forage quality and quantity for the deer in the Campeche area, had significant variations along the year in response to the seasonality of the region, with a drastic reduction in the available forage during the dry season compared with the rainy season (Granados et al. 2014). We found that home range size and core area size was similar along the year for the studied females, even during the fawning months (February to June; Contreras et al. 2019b), when the forage avaiability was reduced due to the dry season. These observations probably indicate that the forage availability and the fawning season are not the main factors that influenced the home range size of female white tailed deer in Nicte-Ha. Although there were not changes in the home rage size, the daily traveled distances for female deer were larger during the dry season (Contreras et al. 2019a), mostly driven by the search of water (including roundabout exploration movements to the Rio del Este longer than 2 km, followed by a return to their home range when the artificial water holes dried during the 2016-2017 dry season). Also, it is important to notice that for those females that during the three seasons occupy areas close to an artificial water hole, presented home rage very stable home ranges along the year, with a high home range overlap between seasons. The exception of this observation, were the females C and F, tht spend the rainy, and the transition seasons away from a water hole, but during the dry season they move their home range to areas close to a permanent water hole.

We found that during the dry season in Nicte-Ha, the home range size of the males were smaller than during the other two seasons. Rut season in the area is coincident with the rainy season (June to October; Contreras et al. 2019b), and it is common that males during this time tend to have larger home ranges (e.g. Hellickson et al. 2008). The velvet season that occurrs from February to June is coincident with the last part of the transition season and the dry season. Male nutrient requirements during the velvet season increases in order to gain weight and cover the energy requiments for antler development (Dryden 2016). As a consequence of the dry season, the forage quality and quantity for deer in the study area is reduced (Granados et al. 2014). However, we observed that males reduced the home range during this time, and also relocate their home ranges and reduce the seasonal home range and core area overlap to use areas close to the artificial water holes. Restriction in water availability causes important reductions in food intake by deer (Lautier et al. 1988) and could generate a severe weight lost in deer (Jenks et al.1990). It is possible that as with the females, the intense dry season in Nicte-Ha generates that males instead of use larger areas to search for the available food, reduce their movements to areas close to the main water sources. Thus, the dry season produced that white tailed deer concentrate their activities around the water ponds as has been found for other large sized herbivores in the region like the white-lipped peccary (*Tayassu pecari*) and the tapir (*Tapirus bairdii*), (Reyna-Hurtado et al. 2009; Pérez-Cortez et al. 2012), making the water the most limiting resource for this mammal guild during this season.

We observed that during the rainy season and the consequent flooding of the area, white-tailed deer does not search for higher ground, and an increment in home range and core area overlap between the rainy and the transition seasons indicate that stay inhabiting the same areas after the flooding season. Increasing flooding levels reduce the mobility of the deer (Contreras-Moreno et al. 2019a) and probably they should concentrate their activities in areas of their home ranges where the flooding level is lower, as occurs in other wetland areas such as in the Florida (Fleming et al. 1994; Lopez et al. 2004).

Our results show that water availability during the dry season, and flooding levels during the rainy season could have significant effects on the home rage size and configuration of the white tailed deer in Nicte-Ha. It is of great importance to understand how the white-tailed deer could be affected by the changes that are already occurring the region. It is anticipated that the Nicte-Ha area will suffer for a general decrease in mean precipitation and an increase in drought (Imbach et al. 2012; Chiabai 2015), and in contrast, sea level rise due to global warming will produce longer periods of flooding on the costal low terrain of Nicte-Ha region (Yañez-Arancibia et al. 2014). This will probably have a severe impact in the white-tailed deer, as has already been detected in ungulates from the Amazon basin where extreme drought and flooding is already occuring (Bodmer et al. 2014).

Our results showed that during the dry season of the studied years of 2016-2017, and 2018-2019, we had 6 and 5 deer respectivly that established most of their home range in an area of 1 km^2 close to a single water hole. Also, we notice with camera traps located around this water hole, than less than 25% of the photographs of white-tailed deer were from animals equipped with radio-collars (Contreras-Moreno pers. Obs.). This is an indication that the number of white-tailed deer around this particular water hole should be substantially larger than those observed with the radio-collars. White-tailed deer density calculated in two ejidos (land tenure regime which is a form of property right based on common-use of resources by rural settlements) close to Nicte-Ha were 0.63 (±0.43) and 1.13 (± 0.44) deer/km^2 (Contreras-Moreno et al. 2015). This is much smaller than what we observed in Nicte-Ha. White tailed deer in southeastern Mexico is subject to an intense subsitence hunting regime (e.g. Santos-Fita et al. 2012; Weber 2014) which has produced the local extinction of the species in several areas (Weber 2014; Ortiz-Lozada et al. 2017). White-tailed deer sport hunting in Nicte-Ha is allowed because is a private proprietie under a management regime called UMA (Unidad para el Manejo Sustentable de la Vida Silvestre, that declares the propirietie as a wildlife and conservation area that has an specific wildlife management plan authorized by the federal government; Valdez et al. 2006). However, white tailed deer management harvest plan in Nicte-Ha is strictly enforced by the owners and manager of the property, with no subsistence hunting allowed, that resulted in a reduction in poaching. This probably has modify deer densities and behaviour in Nicte-Ha, from other areas of Campeche, where deer management is not strictly applied. Because of this, the results of this study should be take cautously when extrapolated to other areas where subsistence hunting is allowed and not regulated. It is of great relevance for the future management of the white tailed deer in southeastern Mexico, and especially in Campeche that future studies foucus on undertand the spatial ecology of white-tailed deer in areas subject to subsistence hunting.

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Table 1.- Home range size and core area size of the white-tailed deer followed in the Campeche wetlands in southeastern Mexico obtained using the Adaptive Kernel Method. Rainy season goes from June-November. Transition season goes from December to February. Dry season goes to March to May. HR.- Seasonal home range size (ha). CA.- Seasonal core area size (ha). N.- Seasonal number of locations used to determine the home range and core area size. SD.- Standard deviation. NA.- Not available

Sex	Id	Year	Weight on capture (kg)	Rainy season			Transition season			Dry season		
				HR	CA	N	HR	CA	N	HR	CA	N
Female	A	2016-2017	28.5	15.85	4.41	240	13.00	3.35	169	9.39	2.46	269
Female	B		32.6	9.98	2.61	303	6.35	1.91	203	12.55	2.56	253
Female	C		24.3	6.12	1.89	333	11.41	2.93	258	6.70	1.06	156
Female	D		28.8	13.88	5.05	419	12.65	3.48	228	12.87	2.70	275
Female	E		34.0	20.47	6.82	263	15.33	3.82	136	17.21	3.90	51
Male	A		31.0	29.58	6.91	129	26.45	6.85	96	21.28	5.23	61
Female	F	2018-2019	NA	21.43	6.08	134	21.86	6.80	94	83.33	20.83	76
Female	G		31.2	11.71	3.14	145	8.09	2.37	101	8.92	2.55	98
Male	B		31.7	71.47	14.18	115	64.11	16.40	98	41.15	5.44	78
Male	C		30.6	195.63	47.21	115	36.46	7.46	101	27.39	4.79	90
Male	D		31.2	63.96	13.50	165	45.24	12.85	123	59.44	16.18	117
Mean females (± SD)				14.20 (±5.53)	4.28 (±1.82)		12.67 (±3.52)	3.52 (±1.58)		21.57 (±27.44)	5.15 (±6.96)	
Mean males (± SD)				90.16 (±72.64)	20.45 (±18.14)		43.07 (±15.99)	10.89 (±4.55)		37.31 (±16.93)	7.91 (±5.52)	

Table 2.- Percentage of home range (HR) and core area (CA) seasonal overlap in white-tailed deer followed in the Campeche wetlands in southeastern Mexico. Rainy season goes from June-November. Transition season goes from December to February. Dryseason goes to March to May. HR.- Home range. CA.- Core area. SD.- Standard deviation

Sex	Id	Year	Seasonal overlap			
			Percent overlap rainy season-transition season		Percent overlap transition season-dry season	
			HR	CA	HR	CA
Female	A	2016-2017	62.55	27.96	38.67	17.01
Female	B		75.14	37.95	65.24	38.08
Female	C		54.91	18.69	88.93	32.20
Female	D		98.11	65.98	27.99	13.23
Female	E		74.57	42.36	77.11	39.66
Male	A		55.24	15.70	69.08	26.11
Female	F	2018-2019	85.91	55.95	26.23	38.28
Female	G		66.48	42.80	64.04	34.43
Male	B		67.82	52.63	30.87	0.00
Male	C		13.81	10.23	30.03	0.00
Male	D		49.47	31.71	95.32	61.07
Mean females (± SD)			73.95 (±14.58)	41.67 (±15.95)	55.46 (±24.66)	30.41 (±10.80)
Mean males (± SD)			46.59 (±23.16)	27.57 (±19.03)	56.32 (±31.74)	21.79 (±28.93)

FIGURE CAPTIONS

Figure. 1.- Location of the study area in the wetlands of Campeche in southeastern Mexico. Nicte-Ha located in the outskirts of the federal level natural protected area Laguna de Terminos.

Figure 1

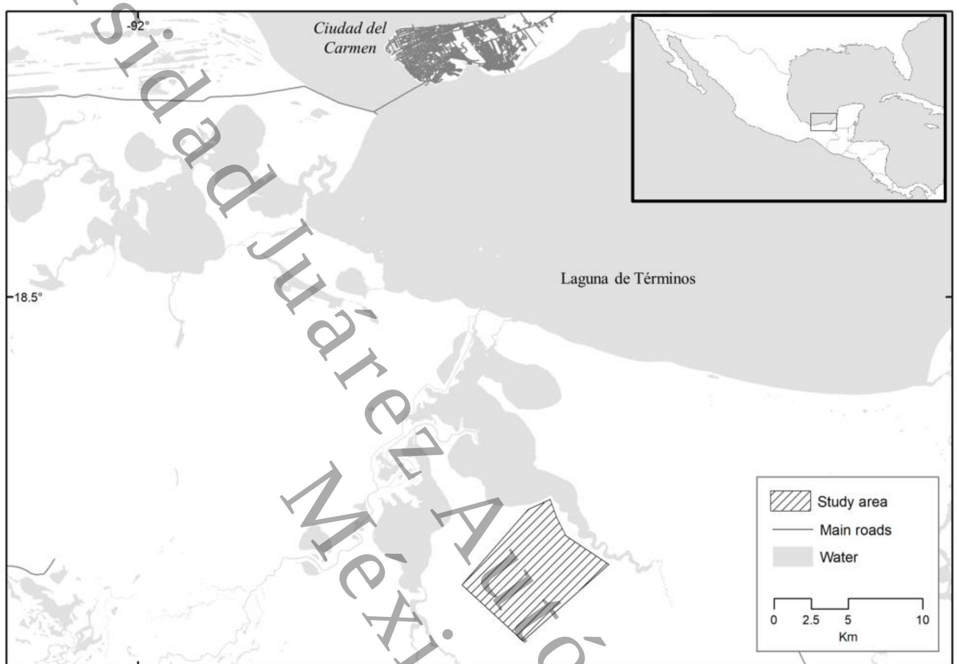


Figure 2.- Seasonal home range configuration of the white-tailed deer followed in the Nicte-Ha area. Six individuals (five females and one male) were followed during the 2016-2017 season and five (two females and three males) during the 2018-2019 season. A.- Home range configuration of the individuals followed during the 2016-2017 rainy season (June to November 2016). B.- Home range configuration of the individuals followed during the 2016-2017 transition season (December 2016 to February 2017). C.- Home range configuration of the individuals followed during the 2016-2017 dry season (March to May 2017). D.- Home range configuration of the individuals followed during the 2016-2017 rainy season (June to November 2018). E.- Home range configuration of the individuals followed during the 2016-2017 transition season (December 2018 to February 2019. F.- Home range configuration of the individuals followed during the 2016-2017 dry season (March to May 2019).

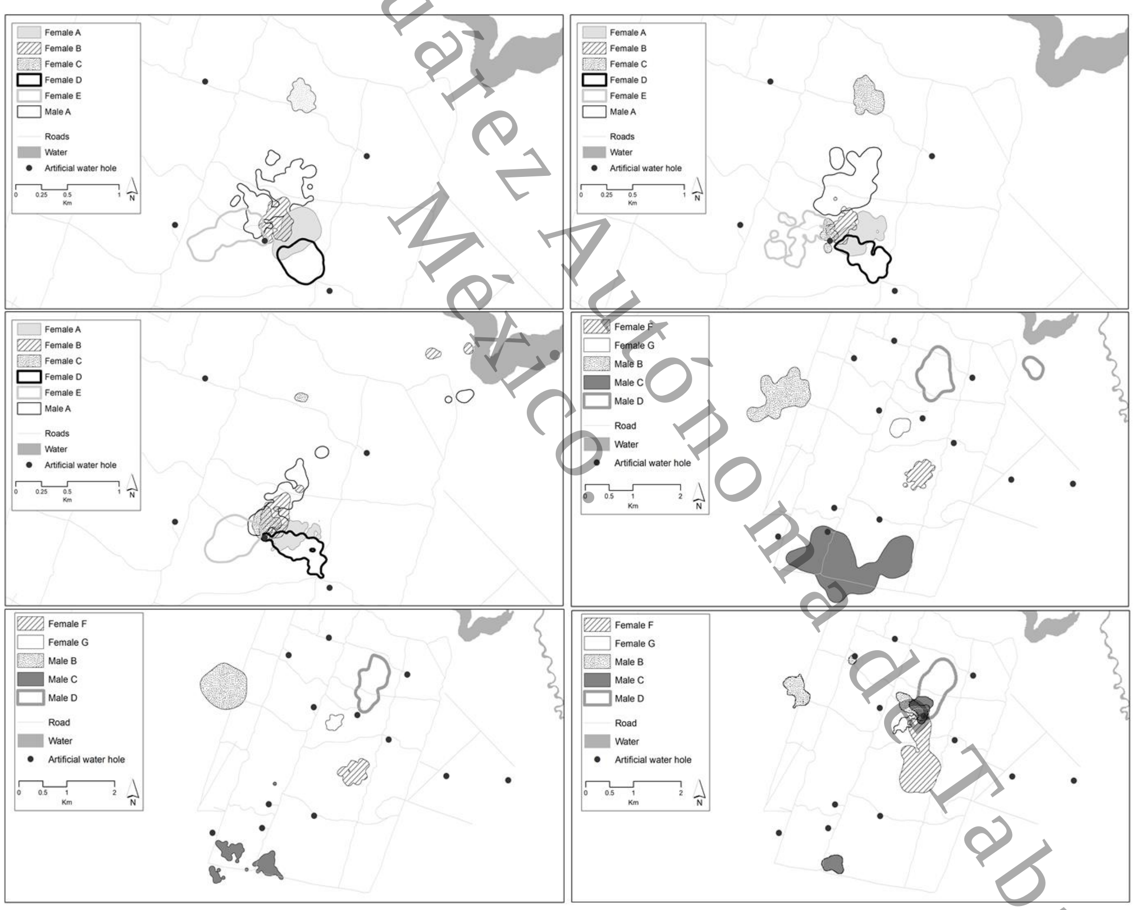
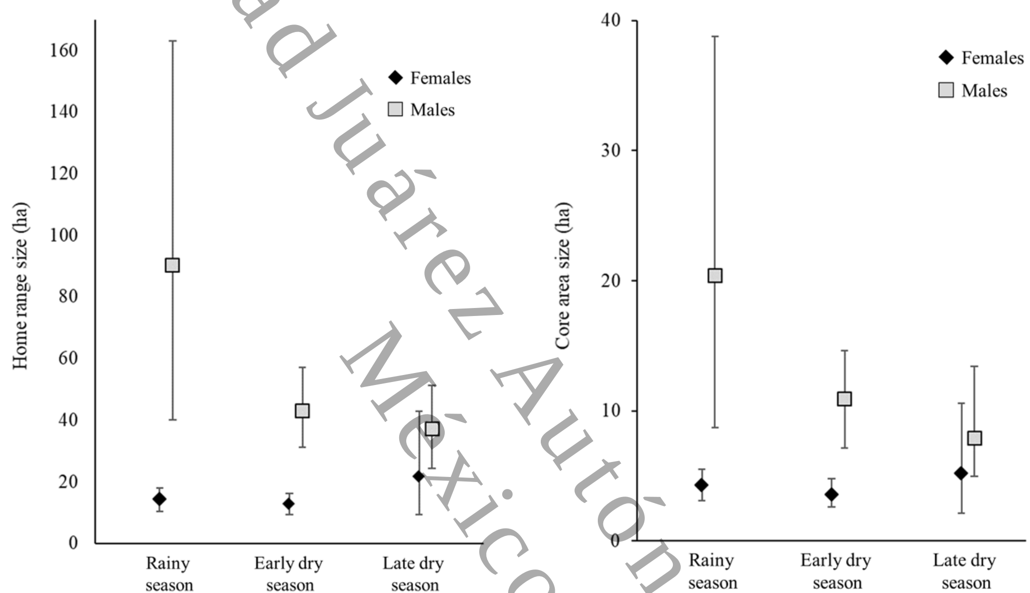


Figure 3.- Mean seasonal home range and core area sizes by sex of white-tailed deer in the wetlands of Campeche, southeastern Mexico. Error bars indicate the 95% confidence intervals; A.- Mean home range size and confidence intervals; B.- Core area size and confidence intervals.



CAPITULO 5

DISCUSIÓN GENERAL

Movimiento de los venados

En este estudio se registró que el promedio de distancias que recorren los venados cola blanca diariamente en la zona de Nicte-Ha (Laguna de Términos) es menor a lo que se ha estimado en sitios de Estados Unidos donde comúnmente superan los 1700 m, de igual forma estos recorridos diarios son menos aun que las estimaciones hechas para las tierras áridas del noroeste de México y para el bosque tropical seco de la vertiente del Pacífico.

El movimiento del venado cola blanca podría estar influenciado por muchas variables ecológicas, ambientales y de comportamiento (Webb et al. 2010), y las diferencias que encontramos en estudio en comparación con los sitios antes estudiados reflejan la adaptación local del venado en Nicte-Ha a la disponibilidad de recursos, así como las condiciones ambientales del área.

Diversos factores pueden estar influyendo en los movimientos de los venados, incluyendo la fisiología, que incluye la reproducción y el parto, los cambios generales en la estación y la duración del día, y las influencias ambientales como el clima (Webb et al. 2010). En este estudio, las distancias diarias recorridas por los venados mostraron diferencias a lo largo del periodo de estudio. Esto sugiere que las condiciones ambientales o rasgos fisiológicos de los venados que cambian a lo largo del año influyeron en el comportamiento y la necesidad de los venados de aumentar o disminuir sus actividades. Se registró un aumento en las distancias recorridas por las hembras de venado durante la estación seca de 2016 y 2017, lo que se correspondía también con la época de nacimientos.

En sitios de la región semiárida y bosque tropical seco, respectivamente, los venados viajaron distancias más cortas durante el período de la estación seca, cuando las temperaturas eran altas, probablemente para reducir el consumo de energía. En general en el norte de México durante la época de nacimientos, la actividad de la hembra del venado cola blanca aumenta, pero en Nicte-Ha pasa lo contrario, las mayores distancias diarias recorridas por las hembras podrían estar relacionadas con la presencia de cervatillos durante la estación seca, que coincide con el momento más caluroso del año.

La temporada de inundaciones en Nicte-Ha coincide con la época en que los venados de Nicte-Ha se movían a distancias más cortas. Este comportamiento podría producirse porque es el momento en que termina la temporada de nacimientos, de tal manear que y metabólicamente se reducen las necesidades de las hembras de venado debido a la lactancia. Algo muy interesante es que no se observó que los venados de cola blanca de Nicte-Ha migran a zonas más altas durante las inundaciones e incluso durante los altos niveles de inundación (julio-octubre). Es posible que el aumento de los niveles de inundación redujera el área de actividad de los venados de tal manera que deben concentrar sus actividades en sitios más pequeños.

Por otro lado, en cuanto al tamaño del ámbito hogareño que se estimó en Nicte-Ha, los resultados de este estudio tienden a ser menores que los obtenidos en otras áreas subtropicales como los matorrales desérticos o incluso en otros humedales. El tamaño del área de de actividad del venado cola blanca en áreas con recursos de mayor calidad, abundantes y bien distribuidos, tiende a tener áreas de distribución más pequeñas que los venados que ocupan áreas menos productivas (Stewart et al. 2011).

Productividad en las zonas tropicales como Nicte-Ha más grande que en áreas subtropicales y templadas (Field et al. 1998). La mayor productividad tiene un impacto directo en los recursos alimenticios disponibles para los ungulados (Mandujano y Naranjo 2010), y probablemente produjo que en Nicte-Ha, los venados cola blanca pudieran obtener todas sus necesidades básicas en áreas de distribución más pequeñas en comparación con las áreas de distribución del venado cola blanca observadas a lo largo de ecosistemas subtropicales y templados.

El tamaño medio del área de distribución del venado cola blanca en Nicte-Ha es similar a las áreas de distribución observadas en otros bosques tropicales y templados de México, pero menor que el área de distribución observada en Costa Rica, Colombia y Venezuela. Sin embargo, es importante notar que los animales seguidos en América Central y del Sur en todos los casos han sido individuos criados a mano y liberados como adultos o individuos reubicados y que las grandes áreas de distribución podrían ser el resultado de movimientos de dispersión desde el área de liberación hasta que se establezca un área de distribución más estable (Nelson 2015). En el caso de los machos, el área de distribución observada en Nicte-Ha es similar a las áreas de distribución de los venados en los llanos de Venezuela y los bosques tropicales secos de México y Colombia, pero más pequeña que otras áreas de Colombia. Sin embargo, al igual que con las hembras, la mayor parte del trabajo realizado con el venado de cola blanca en Sudamérica ha sido criado a mano o reubicado en individuos que probablemente estaban explorando el nuevo hábitat.

La calidad y cantidad de forraje para el venado en el área de Campeche, tuvo variaciones significativas a lo largo del año en respuesta a la estacionalidad de la región, con una drástica reducción en el forraje disponible durante la estación seca en comparación con la estación lluviosa (Granados et al. 2014). Encontramos que el tamaño del área de distribución del hogar y el tamaño del área núcleo fueron similares a lo largo del año para las hembras estudiadas, incluso durante los meses de parición, cuando la disponibilidad de forraje se redujo debido a la estación seca. Esta observación probablemente indica que la disponibilidad de forraje y la temporada de adulteración no son los principales factores que influyeron en el tamaño del área de distribución del venado hembra de cola blanca en Nicte-Ha.

La restricción en la disponibilidad de agua causa importantes reducciones en la ingesta de alimentos por parte de los venados (Lautier et al. 1988) y podría generar una severa pérdida de peso en los venados (Jenks et al.1990). Es posible que al igual que con las hembras, la intensa estación seca en Nicte-Ha genere que los machos, en lugar de usar áreas más grandes para buscar el alimento disponible, reduzcan sus movimientos a áreas cercanas a las principales fuentes de agua.

Se observó que, durante la temporada de lluvias y la consecuente inundación del área, el venado cola blanca no busca un terreno más alto, y que el elevado rango de hábitat y el área central se superponen entre la temporada de lluvias y la de transición, lo que indica que permanecen habitando las mismas áreas después de la temporada de inundaciones. El aumento de los niveles de inundación redujo la movilidad de los venados y probablemente deberían concentrar sus actividades en áreas de su área de distribución donde el nivel de inundación es más bajo, como ocurre en otras áreas de humedales como en los Everglades de Florida (Fleming et al. 1994).

Nuestros resultados muestran que la disponibilidad de agua durante la estación seca y los niveles de inundación durante la estación lluviosa podrían tener efectos significativos en el tamaño del ámbito hogareño y la configuración del venado de cola blanca en Nicte-Ha. Es de gran importancia entender cómo el venado de cola blanca podría ser afectado por los cambios que ya están ocurriendo en la región. Se prevé que el área de Nicte-Ha sufrirá una disminución general de las precipitaciones medias y un aumento de la sequía (Chiabai 2015), y en contraste, el aumento del nivel del mar debido al calentamiento global producirá períodos más largos de inundaciones en el terreno costero bajo de la región de Nicte-Ha (Yañez-Arancibia et al. 2014). Esto probablemente tendrá un impacto severo en el venado de cola blanca, como ya se ha detectado en ungulados de la cuenca amazónica, donde ya se están produciendo sequías e inundaciones extremas (Bodmer et al. 2014).

Productividad en las zonas tropicales como Nicte-Ha más grande que en áreas subtropicales y templadas (Field et al. 1998). La mayor productividad tiene un impacto directo en los recursos alimenticios disponibles para los ungulados (Mandujano y Naranjo 2010), y probablemente produjo que en Nicte-Ha, los venados cola blanca pudieran obtener todas sus necesidades básicas en áreas de distribución más pequeñas en comparación con las áreas de distribución del venado cola blanca observadas a lo largo de ecosistemas subtropicales y templados.

La calidad y cantidad de forraje para el venado en el área de Campeche, tuvo variaciones significativas a lo largo del año en respuesta a la estacionalidad de la región, con una drástica reducción en el forraje disponible durante la estación seca en comparación con la estación lluviosa (Granados et al. 2014). Encontramos que el tamaño del ámbito hogareño y el tamaño del centro de actividad fueron similares a lo largo del año para las hembras estudiadas, incluso durante los meses de parición (febrero a junio), cuando la disponibilidad de forraje se redujo debido a la estación seca. Esta observación probablemente indica que la disponibilidad de forraje y la temporada de nacimientos no son los principales factores que influyeron en el tamaño del ámbito hogareño de las hembras en Nicte-Ha.

Encontramos que durante la estación seca en Nicte-Ha, el tamaño del ámbito hogareño de los machos era menor que durante las otras dos estaciones. La temporada de lluvias en el área coincide con la temporada de lluvias (junio a octubre), y es común que los machos durante este tiempo tiendan a tener mayores áreas de distribución (por ejemplo, Hellickson et al. 2008). La temporada de terciopelo que se extiende de febrero a junio coincide con la última parte de la temporada de transición y la temporada seca. Los requerimientos de nutrientes masculinos durante la temporada de terciopelo aumentan para aumentar de peso y cubrir los requerimientos de energía para el desarrollo de las astas (Dryden 2016). Como consecuencia de la estación seca, la calidad y cantidad de forraje del venado en el área de estudio se reduce (Granados et al. 2014). Sin embargo, observamos que los machos redujeron el ámbito hogareño durante este tiempo, y también reubicaron sus áreas de distribución y redujeron el ámbito hogareño estacional y la superposición del núcleo para usar áreas cercanas a los pozos de agua artificiales. La restricción en la disponibilidad de agua causa importantes reducciones en la ingesta de alimentos por parte de los venados y podría generar una severa pérdida de peso en los venados. Es posible que al igual que con las hembras, la intensa estación seca en Nicte-Ha genere que los machos, en lugar de usar áreas más grandes para buscar el alimento disponible, reduzcan sus movimientos a áreas cercanas a las principales fuentes de agua.

Los resultados de este estudio muestran que la disponibilidad de agua durante la estación seca y los niveles de inundación durante la estación lluviosa podrían tener efectos significativos en el tamaño del ámbito hogareño y la configuración espacial del venado de cola blanca en Nicte-Ha. Es de gran importancia entender cómo el venado de cola blanca podría ser afectado por los cambios que ya están ocurriendo en la región. Se prevé que el área de Nicte-Ha sufrirá una disminución general de las precipitaciones medias y un aumento de la sequía (Chiabai 2015), y en contraste, el aumento del nivel del mar debido al cambio climático global, que producirá, períodos más largos de inundaciones en el terreno costero en la región de Nicte-Ha (Yañez-Arancibia et al. 2014). Esto probablemente tendrá un impacto severo en el venado de cola blanca, como ya se ha detectado en ungulados de la cuenca amazónica, donde ya se están produciendo sequías e inundaciones extremas (Bodmer et al. 2014).

Sobre la estacionalidad de astas y época de nacimientos de venado cola blanca

De igual forma en el presente estudio se analizó la temporada en que los machos de venado cola blanca tienen las astas duras (época en que se cazan trofeo para cacería deportiva) y la temporada en que suceden los nacimientos en la región de Laguna de Términos. Al parecer lo que sucede en Campeche es diferente de lo que ocurre en las partes norte, central y occidental de México, donde la temporada de nacimientos va de julio a septiembre, y los donde las astas duras están presentes desde mediados de noviembre hasta finales de enero (Villarreal 2006; Gallina et al. 2010; Mandujano et al. 2014), apoyando la hipótesis de que el momento de la reproducción es diferente entre otras partes de México y nuestra área de estudio.

Los resultados de este estudio mostraron que la estacionalidad del desarrollo de las astas de venado de cola blanca en el área de estudio es diferente de otras partes de México. Particularmente, la sincronización de las astas duras no coincide con la temporada oficial de caza establecida para la zona (mediados de noviembre a finales de marzo). Nuestros resultados demostraron que, aunque la temporada de caza es el resultado de la información proporcionada por las oficinas regionales de la SEMARNAT, la ausencia de información local sobre la especie en el sur del país México ha resultado en una determinación de la temporada de caza que sólo se basa en los datos disponibles obtenidos de los estados del Norte de México.

La variación en la cronología reproductiva del venado cola blanca se han relacionado a procesos bioquímicos tales como el fotoperiodo, de tal manera que este actúa a través de la melatonina para modular la secreción de hormonas reproductivas (en su mayoría testosterona; Hanon et al. 2008), regulando el ciclo de la astas en esta especie (Price et al. 2005a,b); sin embargo, después de analizar los ligeros cambios fotoperiódicos en el los trópicos (y su débil asociación temporal con las enfermedades estacionales de los cambios climáticos), este factor ambiental podría tener poca influencia en el control del desarrollo de los astas en el área de estudio.

Encontramos los primeros cervatillos registrados durante la primera parte de febrero y los números más altos se observaron de marzo a mayo. Nuestras observaciones se asemejan parcialmente a informes anteriores que mencionan a la época de nacimientos de la especie en áreas tropicales ocurre de abril a junio, indicando que en el estudio la temporada de nacimientos es más temprana que en otras zonas tropicales. Y puede deberse a la lactancia, media a tardía genera un alto costo energético pata los mamíferos, es de esperar que el venado de cola blanca habría desarrollado mecanismos de adaptación para adaptar las necesidades energéticas a las fluctuaciones en la calidad del forraje, lo que da como resultado el destete de los cervatillos en un momento de máxima calidad forrajera.

Nuestros resultados muestran que tanto el tiempo reproductivo como el uso espacial y movimientos diarios para el venado de cola blanca el venado en nuestra área de estudio es diferente de los previamente estudiados en el norte, oeste y centro de México. Para optimizar el manejo de la especie en el área de estudio, es necesario que se considere que patrones de uso y comportamiento, así como procesos fisiológicos suceden de forma diferente con respecto a lo que se conocía en estudios previos. Tanto los manejadores, como biólogos deberán considerar lo que se documenta en este estudio para poder hacer los ajustes a los métodos de monitoreo, así como a los diseños de muestreo. De igual forma animamos a las autoridades mexicanas, reguladoras de la caza (SEMARNAT) para que modifiquen el calendario de caza del venado cola blanca en el área de estudio con el fin de garantizar que se mantengan los procesos biológicos básicos de la especies y evitar un daño ambiental.

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