

Analysis of the male annual antler cycle, reproductive behavior and spotted fawn presence in the tropical white-tailed deer

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The rutting season of the white-tailed deer (*Odocoileus virginianus*) is seasonal in North America, but in tropical latitudes it occurs year-round with peaks locally variable. Reproductive cycle of this species in Costa Rica is variable, clearly seasonal in San Lucas Island but continuous with two birth peaks in Palo Verde and Santa Rosa national parks in northwestern Costa Rica. In Hacienda y Refugio de Vida Silvestre Curú in the Nicoya Peninsula, a site south of these parks but in a different life zone, we observed males with hard antlers in 2015 but only from July to November. We therefore hypothesized that white-tailed deer have a continuous reproductive cycle during the year in Curú because the rainfall pattern is the same as in Palo Verde and Santa Rosa. We visited Curú every month and recorded the status of white-tailed deer antler growth: nubs, velvet, and hard, from January 2016 to December 2019. We also recorded other rut behaviors and the presence of spotted fawns. We recorded 1,134 observations of the status of antler growth, 13 observations on reproductive behavior and 133 observations of spotted fawns. The antler cycle was seasonal in the four years of study. Male antler casting took place from mid-November to mid-February and the growth of new antlers began in mid-December and lasted until mid-March. Velvet shedding occurred in April, May and June, and by July males had hard antlers. The rutting season lasted three months from mid-June to mid-August. Small spotted fawns were observed from the middle of the dry season to the beginning of the rainy season. All this highly contrasts with the reproduction pattern observed in Santa Rosa. Lack of seasonal variation in the photoperiod is likely an important factor that allows deer to reproduce throughout the year in these protected areas, but this variation does not exist in Curú either, where the species is seasonal. The reproductive patterns of white-tailed deer in Central and South America may have evolved in response to seasonal fluctuations in specific food availability, competition, or predation, all of which may be directly related to rainfall patterns. Greater knowledge of the link between rainfall patterns and food availability for deer would be of great help to further our understanding of factors driving the reproduction cycle of the White-tailed deer.

La temporada de reproducción o brama del venado cola blanca (*Odocoileus virginianus*) es estacional en América del Norte, pero en latitudes tropicales ocurre durante todo el año con picos variables localmente. El ciclo reproductivo de esta especie en Costa Rica es variable, claramente estacional en la isla San Lucas, pero continuo con dos picos de nacimientos en los parques nacionales Palo Verde y Santa Rosa en el noroeste de Costa Rica. En Hacienda y Refugio de Vida Silvestre Curú en la Península de Nicoya, un sitio al sur de estos parques, pero en una zona de vida diferente, observamos machos con astas duras en 2015, pero solo de julio a noviembre. Por lo tanto, planteamos la hipótesis de que el venado cola blanca tiene un ciclo reproductivo continuo durante el año en Curú porque el patrón de lluvia es igual al de Palo Verde y Santa Rosa. Visitamos Curú todos los meses y registramos el estado del crecimiento de las astas de los venados de enero de 2016 a diciembre de 2019. También registramos otros comportamientos de celo y la presencia de cervatillos manchados. Registramos 1,134 observaciones del estado del crecimiento de las astas, 13 observaciones sobre el comportamiento reproductivo y 133 observaciones de cervatillos manchados. El ciclo de las astas fue estacional en los cuatro años de estudio. Los machos botaron las astas de mediados de noviembre a mediados de febrero y el crecimiento de las nuevas astas inició a mediados de diciembre y se prolongó hasta mediados de marzo. La caída del terciopelo ocurrió en abril, mayo y junio y a partir de julio los machos tenían astas duras. La brama duró tres meses, desde mediados de junio hasta mediados de agosto. Observamos cervatillos manchados pequeños desde la mitad de la estación seca hasta el inicio de la temporada de lluvias. Todo esto contrasta con el patrón de reproducción observado en Palo Verde y Santa Rosa. La falta de variación estacional en el fotoperiodo es probablemente un factor importante que permite que los venados se reproduzcan durante todo el año en estas áreas protegidas, pero esta variación tampoco existe en Curú, donde la especie es estacional. Los patrones reproductivos del venado cola blanca en América Central y del Sur pueden haber evolucionado en respuesta a fluctuaciones estacionales en la disponibilidad de alimentos específicos, la competencia o la depredación, todo lo cual puede estar directamente relacionado con los patrones de lluvia. Un mayor conocimiento del vínculo entre los patrones de lluvia y la disponibilidad de alimentos para los venados sería de gran ayuda para comprender mejor los factores que impulsan los ciclos de reproducción del venado cola blanca.

Keywords: Antler status; dry forest; humid forest; nubs; reproduction; rut; velvet.

Introduction

White-tailed deer (*Odocoileus virginianus*) has the widest distribution and is the most abundant of all New World cervids (Teer 1994). Its distribution extends from south-eastern Alaska in North America to northern South America with up to 38 recognized subspecies (Mattioli 2011). There is controversy regarding whether there is only one species or several species (Molinari 2007). In the latter case, the species found in Central America corresponds to *Odocoileus cariacou* of wide distribution on the Neotropical region (Molinari 2007).

Endogenous recognition of photoperiod changes drives seasonal reproductive cycles (Bronson 2009). A decrease in the daylight-darkness ratio triggers the onset of the reproductive cycle. Since the photoperiod is related to latitude (Ditchkoff 2011), the rutting season of white-tailed deer progresses along a continuum from November in most of North America, to January to March in northern México (Mattioli 2011), and from January to April in central and southern México (Weber et al. 1994; Contreras-Moreno et al. 2019). The annual cycle of antlers is related to the reproductive cycle with variation in the reproductive chronology linked to environmental variables mainly associated with latitude, especially photoperiods and food availability (Goss 1983; Price et al. 2005a; Hanon et al. 2008; Contreras-Moreno et al. 2019).

The annual phases of primary development of the testes, the complete production of sperm, and the rest period (Robinson et al. 1965) are associated with the onset of antler growth, shed of velvet, and antlers fall off, respectively (Verme and Ullrey 1984). The photoperiod acts through melatonin to modulate the secretion of reproductive hormones, mainly testosterone (Goldman 2001; Hanon et al. 2008) and regulates antlers cycle in white-tailed deer (Price et al. 2005a; Price et al. 2005b). However, because there is only a change in photoperiod in the tropics with a weak temporal association with seasonal climatic changes, it results that this environmental factor could have a reduced influence in controlling antler development in Southern México (Contreras-Moreno et al. 2019).

In temperate and cold regions of North America, severe weather and food availability are the critical environmental factors that dictate the timing of the birth season (Lincoln 1992; Price et al. 2005b). The reproductive cycle of white-tailed deer in these regions of North America is seasonal (Verme and Ullrey 1984; Mattioli 2011). The status of the antlers is associated with the growth and secretion cycle of testosterone by the testicles (Vasantha 2016). The testosterone cycle is governed largely by photoperiod (Loudon and Curlew 1988; Tomás 1995). The decrease of daylight and the increase in testosterone cause antlers to mineralize and shed their velvet (Tomás 1995). In contrast, increased daylight and decreased testosterone cause antler casting (Vasantha 2016). On the opposite, there is little information about the reproductive aspects of white-tailed deer in the Neotropics (Contreras-Moreno

et al. 2019). The birth of fawns and the development and casting of male antlers attracted the interest of the first naturalists working in the region (Rodríguez and Solís 1994). They speculated that fawns are born throughout the year and that there is no annual cycle in the growth and shedding of antlers due to the lack of seasonality in tropical and subtropical regions (Rodríguez and Solís 1994). However, studies conducted in the 1980s concluded that there may be some degree of synchrony in the growth of antlers and the birth of fawns in some places (Klein 1982; Branán and Marchinton 1987; Rodríguez and Solís 1994). Nonetheless, even in sites located nearby, the results seem contradictory because births occur in any season and the time of the year in which males shed their antlers is a function of individual age (Webb and Nellis 1981; Brox 1984; Rodríguez 1994; Fuller et al. 2020).

Studies on the reproductive cycle of white-tailed deer in Costa Rica have yielded contrasting results with clearly seasonal cycles at San Lucas Island (Rodríguez and Solís 1994) and continuous cycles with two birth peaks in Palo Verde and Santa Rosa national parks (Rodríguez 1994; Fuller et al. 2020). In the Nicoya Peninsula in northwestern Costa Rica, a peninsular site south of these areas and a different life zone, we observed males with hard antlers in 2015 but only from July to November. As a result, we made extensive, regular field observations from 2016 to 2019 to analyze the antler cycle in a white-tailed deer population in this area. We also recorded fawn birth periods in these four years. We hypothesize that white-tailed deer have a continuous reproductive cycle during the year in Curú because the rainfall pattern in this area is the same as in Palo Verde and Santa Rosa National Parks, where this species has an almost continuous annual reproductive pattern.

Material and methods

Study site. The Hacienda y Refugio de Vida Silvestre Curú (Curú) combines private and public lands totaling 1,496 ha: 312 ha dedicated to cattle ranching and 1,184 ha dedicated to conservation and ecotourism (Schutt and Vaughan 1995). It is located on the Nicoya Peninsula in northwestern Costa Rica (9° 47' 23" N, -84° 55' 28" W; Figure 1). Curú vegetation belongs to the Tropical Humid Forest Life Zone (Holdridge 1967; Bolaños et al. 2005).

Although the refuge is relatively small it is part of a continuum mosaic of cattle ranching operations and forest remnants along most of the south of the peninsula. Adjacent to Curú there is a secondary forest of over 5,000 ha located at the Peninsula de Nicoya Protected Zone. Curú is known to contain a high level of biodiversity due to the presence of several habitat types and its protection status (Schutt and Vaughan 1995). Seventy-eight species of mammals, 232 species of birds, 87 species of reptiles, and at least 500 species of plants have been identified in the refuge (McKinney 2014). Annual precipitation averaged 1,957 mm for the period 1970-2005, but it was 2,177 mm during our study (MN 2020a; IMN 2020b).

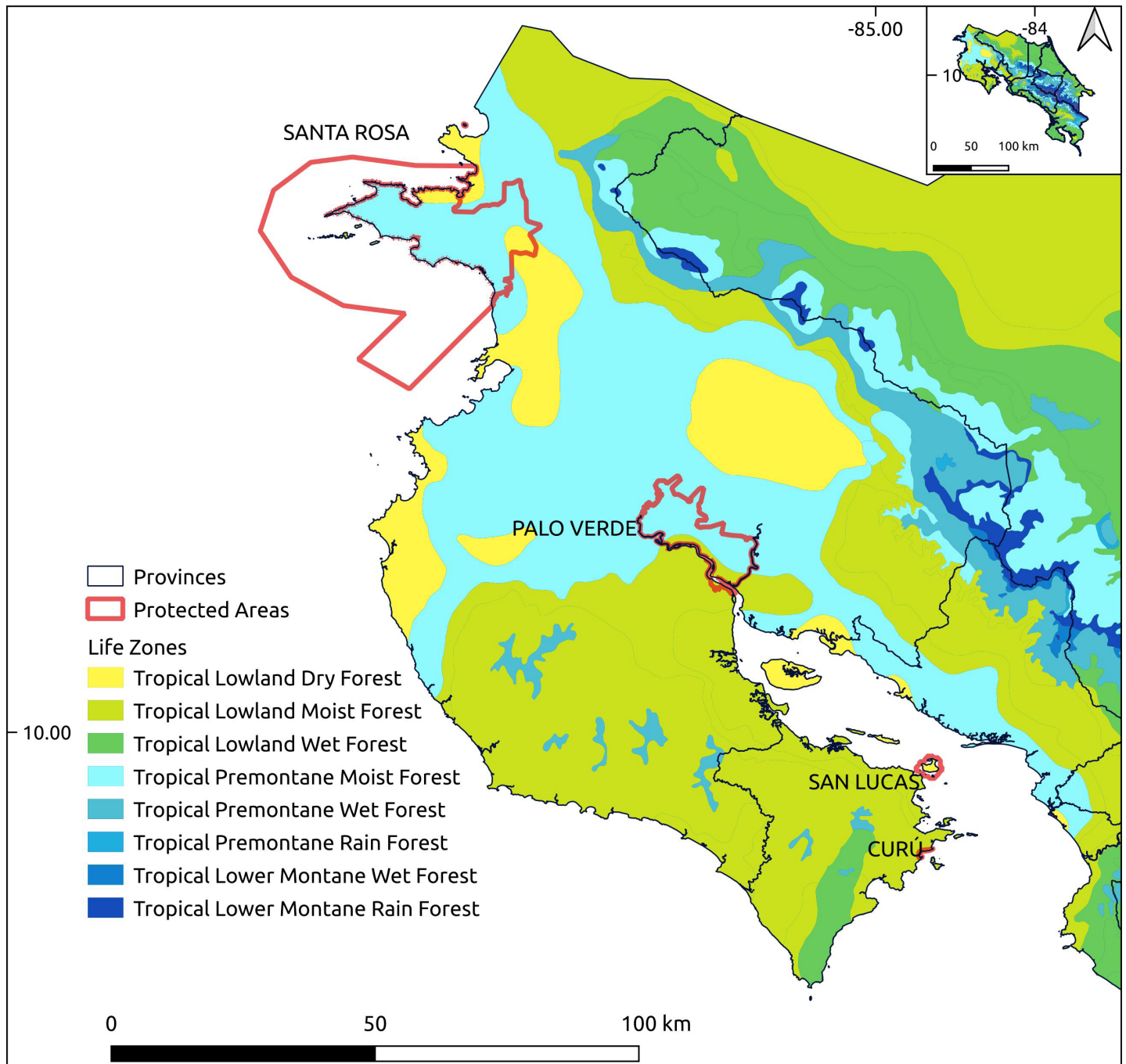


Figure 1. Life zones in Guanacaste province at Northwestern Costa Rica, and the four study sites mentioned in the text. The Hacienda y Refugio de Vida Silvestre Curú is located at the extreme southeastern portion of the Nicoya Peninsula in the Tropical Lowland Moist Forest. Map by G. Chaves (Cachi).

The dry season occurs from December to March when only 4 % of total annual rainfall accumulates. The transition to the rainy season is in April and by the third week in May, the rainy season is typically well established (IMN 2020). The first rainy period occurs between May and August when 50 % of the annual total precipitation accumulates. The first maximum of rains occurs in June as the southeastern trade winds intensify causing local storms and heavy downpours. The northeast trade winds intensify again causing a brief dry season between July and August called the “Pacific summer” or “canicula”. A second rainy season extends from September to November. The

greatest amount of rain, 46 % of the annual total, falls during September and October due to the greater influence of Caribbean cyclonic events. The transition to the dry season occurs in November (IMN 2020).

Data collection. We visited Curú once a month between January 2016 and December 2019, except in September 2016 and September 2019 when it was impossible to enter the area due to flooding and landslides on the access road. However, this did not affect our study since September is not of high significance for our purposes. We looked for deer on two transects: the main road (2,090 m) and a secondary road (1,958 m). We walked each transect in the

morning (6:00 h to 9:00h) and the afternoon (15:00h to 17:00h) every month. We recorded deer data using 10 x 50 binoculars and a digital camera.

Every time we observed a deer we recorded the sex and age group (fawn, yearling, adult) of each individual. We classified adult males by the presence of antlers and testicles and adult females by the absence of antlers and testicles, as well as by the presence of one or two fawns. Juvenile deer were classified as males or females based on body size and by the presence or absence of pedicels and testicles, respectively. Fawns were identified by the presence of spots on their fur. Both researchers have vast experience identifying and classifying deer by age.

Each time we observed an adult male we took a digital photograph for a database on the monthly growth status of deer antlers. For individual recognition of males and to avoid double-counting, we considered: 1) antlers size, 2) antler shape (number of tips, malformations) and 3) physical characteristics of each animal (presence of scars and wounds). Later we classified adult males as 1) nubs (no antlers or just one antler, pedicels in velvet), 2) velvet (growing antlers covered in velvet with rounded tine ends), and 3) hard (fully formed antlers, velvet-less; Figure 2). Additionally, we recorded rubs, odor marks, nonaggressive sparring, fights matching dominant bucks, chasing, and tending bucks, and bucks scraping the ground and leaving odor marks locally known as “rascaderos” (Rodríguez 2015). Although we also recorded the presence of adult females in the field, we made no effort to identify them individually. At each visit, we also counted spotted fawns and recorded them as small and large spotted fawns (see below).

Data interpretation and assumptions. All data were analyzed by month and year, however, for this report, the data were grouped for the whole study period: 2016 to 2019. To identify the reproductive seasonality of deer, we made the following assumptions concerning deer morphology and development based on a literature review. Antlers are shed annually (Sauer 1984). Antler’s growth lasts six months, and velvet dries and falls. Adult males keep hard antlers for about six months and then shed them (Sauer 1984). Testis’s cycle has three phases: 1) primary development, 2) full sperm production, and 3) resting period (Verme and Ullrey 1984). These phases are associated with the onset of antler growth, velvet shedding, and antler casting respectively (Verme and Ullrey 1984). Adult males are fertile only during the hard antler period. Female gestation varies among subspecies and ranges from 187 to 222 days, with a mean of 202 days (Smith 1991). Fawns spend most of their time hidden away from their mothers for three to four weeks (Marchinton and Hirth 1984), but gradually fawns spend more time with their mothers.

It is not possible to know the date of birth of the fawns in the field. Therefore, we classified spotted fawns into two groups: 1) small spotted fawns were two weeks to two months old, they do not reach the height of the mother’s

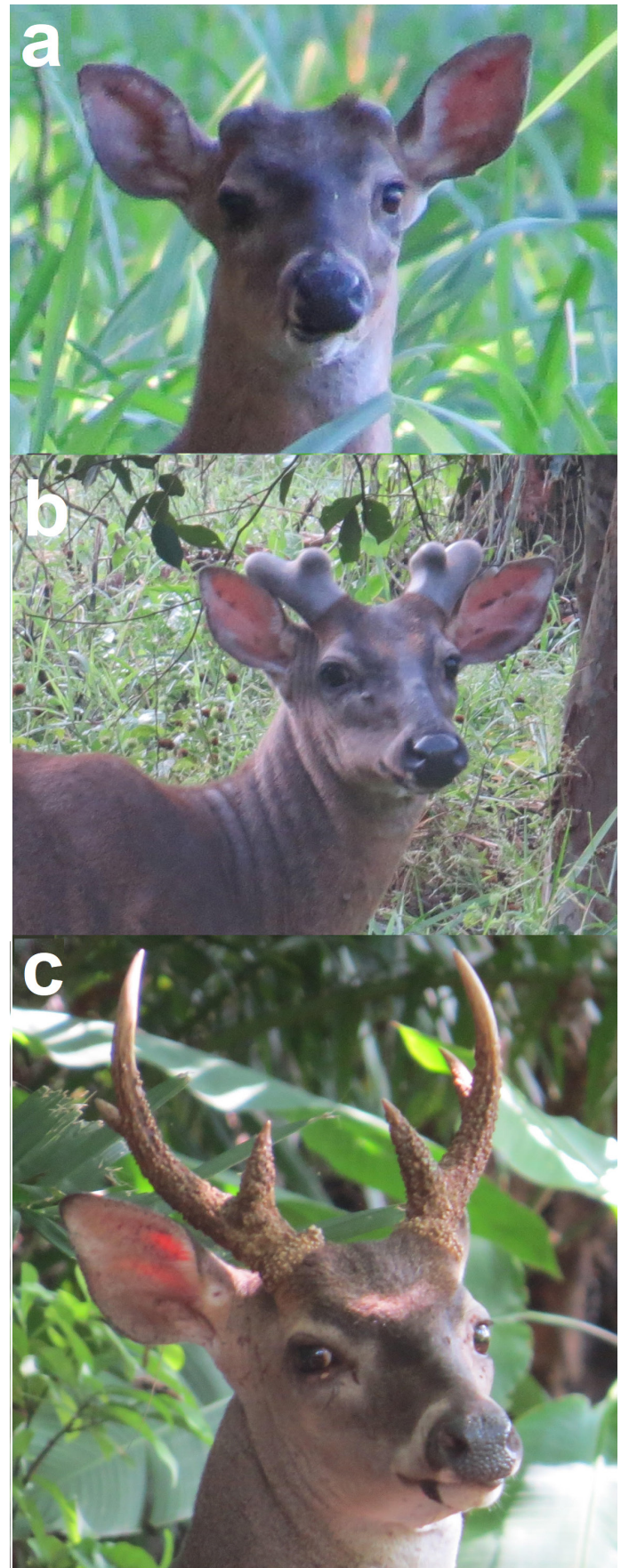


Figure 2. Antler growth stages of white-tailed deer (*Odocoileus virginianus*) at Hacienda y Refugio de Vida Silvestre Curú, Northwestern Costa Rica: a) nubs, b) velvet, c) hard.

belly, and they are generally observed alone in the forest or accompanied by the mother, and 2) large spotted fawns were three to four months old, they exceed the height of the mother's belly, and they are usually accompanied by the mother and other deer.

To test for the independence between the status of antler growth and the month of the year (which are related to the amount of rain) we analyzed the data with a Chi Square Test. We compared the absolute number of white-tailed deer (1,134) according to antler status per month. We used the adjusted residuals of the Chi Square Test as a posteriori test to evaluate in which cells of the contingency table it is observed more or less frequently than is expected at random. The critical value is the range from -1.96 to 1.96, so the values outside this range differ from the frequency expected by pure chance (Table 2).

Results

We totaled 1,134 observations of the status of antler growth of male white-tailed deer at Curú ($n = 233$ in 2016, $n = 367$ in 2017, $n = 294$ in 2018 and $n = 240$ in 2019; Table 1). The way we walked the transects and our knowledge of the area reduced the probability to count any male more than once. Additionally, we recorded 13 observations on reproductive behavior and 133 observations of spotted fawns.

Antlers. The antler cycle of the white-tailed deer at Curú was seasonal in the four years of study ($\chi^2 = 970$, d.f. = 22, $P < 0.001$). Antlers casting occurred over a three-month period that began in mid-November and ended in mid-February, during the first part of the dry season. The earliest antlerless or single-antlered deer were observed on 19 November 2017. The last single-antlered deer was observed on 5 February 2017. Antlerless or single-antlered males were not observed in any other month. Antlers grew during the dry season from mid-December to mid-March. A hundred percent of the males had velvet antlers in March in the four years of study (Figure 3a, Table 1).

Velvet shedding started in April and lasted through May and June, just at the beginning of the rainy season. In July less than 5 % of the males presented velvet antlers. We did not observe males with velvet antlers from August to October. We observed males with hard antlers from April until January or February of the following year. From July to October, 100 % of the males had hard antlers (Figure 3a, Table 1).

There was a significantly lower frequency of hard antlers than expected by chance in the first five months of the year, and significantly more frequency from June to December (Table 2). On the opposite, there was significantly higher frequency of antlers in velvet than expected from February to May and a lower frequency from July to January of the following year. Nubs were less frequent than expected in general during the year except in January and December, although differences were not significant in February, September, and November (Table 2).

Table 1. The absolute number of white-tailed deer (*Odocoileus virginianus*) according to antler status per month in the Hacienda y Refugio de Vida Silvestre Curú between January 2016 and December 2019. Nicoya Peninsula, Costa Rica.

Month	Antler status			n
	Hard	Velvet	Nubs	
Jan	33	37	47	117
Feb	4	106	9	119
Mar	0	96	0	96
Apr	7	93	0	100
May	25	78	0	103
Jun	75	42	0	117
Jul	88	2	0	90
Aug	82	0	0	82
Set	42	0	0	42
Oct	70	0	1	71
Nov	69	1	8	78
Dec	80	15	24	119
Total				1,134

$\chi^2 = 970$, d.f. = 22, $P < 0.001$.

Rutting season. The rutting season of white-tailed deer in Curú Refuge lasted three months from mid-June to mid-August. Rutting began when adult males were ready to reproduce, indicated by their hard antlers and reproductive

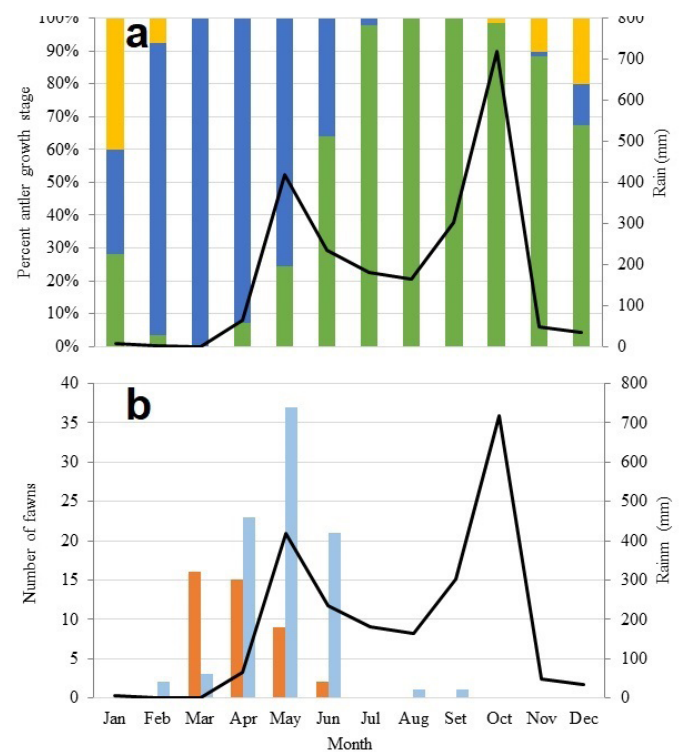


Figure 3. a) Monthly relative frequency (%) of antler status ($n = 1134$, monthly range 42-119). Hard (green), velvet (blue) and nubs (yellow). b) number of monthly observations of small spotted fawns (orange) and large spotted fawns (light blue) of white-tailed deer (*Odocoileus virginianus*) in Hacienda y Refugio de Vida Silvestre Curú between January 2016 and December 2019. Black lines indicate the average monthly precipitation (mm) in the same period at the Paquera Station: 2016 = 1,473.4 mm; 2017 = 2,475.8 mm; 2018 = 2,436.4 mm; 2019 = 2,327.8 mm (IMN 2020a), Nicoya Peninsula, Costa Rica.

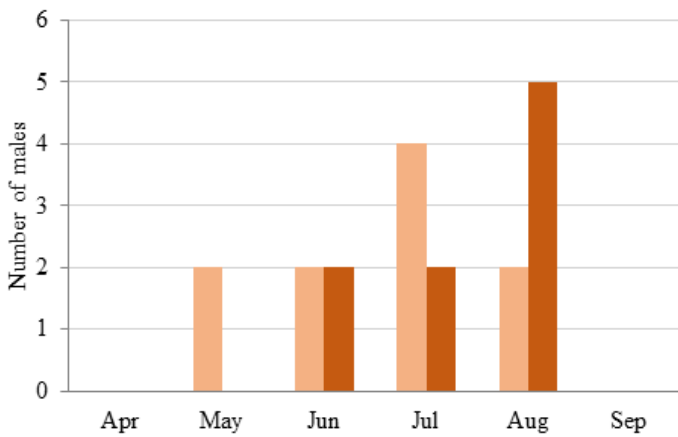


Figure 4. The number of males white-tailed deer (*Odocoileus virginianus*) per month that chased females, and the number of males per month that accompanied females, between January 2016 and December 2019 (other months have zero males engage in these activities). Hacienda y Refugio de Vida Silvestre Curú, Nicoya Peninsula, Costa Rica. Chasing deer males (pink) and tending deer males (brown).

behavior. In mid-June, males started rubbing antlers, scraping, and sparring. This behavior lasted for the first part of the rainy season. They adopted tending bond mating systems, courtship and copulating receptive does in August and September when males had hard antlers (Figures 3a, 4). The first males observed chasing does entering estrus were in August. We observed does accompanied by bucks in August and September, and by October neither chasing nor courtships were observed (Figure 4).

Fawning season. Small spotted fawns (Figure 5) were observed between March and June (Figure 3a); this is from the middle of the dry season to the beginning of the rainy season. During March most of the observations were of small spotted fawns (16 out of 19), while only three observations corresponded to large spotted fawns (Figure 3a). On the opposite, observations of large spotted fawns (Figure 5) predominated in April (23 out of 38).

A peak of spotted fawns was reached in May, although most of them were large-bodied spotted fawns (37 out of 46). Large-bodied spotted fawns (21 out of 23) also predominated in June when only two small spotted fawns were observed (Figure 3a). Fawns were five months old by July and had no spots. We did not see any spotted fawns after June, except by two large spotted fawns in August and September 2017, that were born probably by April-May given their sizes.

Discussion

Because there are comparatively few studies of white-tailed deer in the Neotropical region, a general conclusion emerged over time that white-tailed deer would be less seasonal in antler growth and casting in regions without strong seasonal changes in weather (Marchinton and Hirth 1984). The assumption was that the same would happen with other reproductive processes such as rut and fawn births. However, some studies challenge this generalization.

White-tailed deer reproduction seemed seasonal, lasting four to six months, as reported from limited observations in the Virgin Islands (Webb and Nellis 1981), Honduras (Klein 1982), Venezuela (Brokx 1984), Colombia (Blouch 1987) and Surinam (Branan and Marchinton 1987). A recent study in Campeche wetlands in Southeastern México, a tropical site, showed that the antler cycle of the white-tailed deer is seasonal (Contreras-Moreno *et al.* 2019).

Studies of white-tailed deer reproduction in Costa Rica have shown considerable variation in reproductive processes among relatively nearby populations. Rodríguez (1994) found no seasonality in antlers casting and growth or in fawn births in Palo Verde National Park in the mid- 1990s and recently Fuller *et al.* (2020) obtained similar results in a study in Santa Rosa National Park. However, on San Lucas Island, situated approximately 78 km in a straight line from Santa Rosa, the white-tailed deer life cycle had a marked seasonality (Rodríguez and Solís 1994). Antler growth occurred from March to June, velvet shedding in June and July, hard antlers from July to December, and antler casting in January and February (Rodríguez and Solís 1994). Antler status pattern, as well as fawn births, were even more seasonal in Curú than in San Lucas Island, the only real dry forest in Costa Rica included in this comparison (Figure 1). These processes took three months to complete in Curú. Some minor variations in the onset of antler casting and velvet shedding appear to be responses to variations in precipitation patterns between consecutive years. The first signs of the start of the rut appeared in June in Curú when antler velvet had dried and shed, and bucks had hard antlers (Figure 2c). Antler cycle as well all other processes were significantly seasonal (Table 2). Antler cycle seasonality in Curú coincides with the antler cycle of the white-tailed deer in a tropical site in southeastern México (Contreras-Moreno *et al.* 2019). In Curú, fawns were five months old by July and

Table 2. Value of adjusted residuals of the χ^2 test for antler status of white-tailed deer (*Odocoileus virginianus*) per month in the Hacienda y Refugio de Vida Silvestre Curú Nicoya Peninsula, Costa Rica, between January 2016 and December 2019. Residuals in bold indicate significant differences. The value of the sign indicates if the frequency is higher (+) or lower (-) than expected by chance.

Month	Antler status		
	Hard	Velvet	Nubs
Jan	-5.140	-2.277	13.728
Feb	-10.919	11.148	-0.122
Mar	-10.387	12.172	-2.988
Apr	-9.155	10.959	-3.056
May	-5.628	7.407	-3.106
Jun	3.061	-1.286	-3.333
Jul	9.309	-7.872	-2.885
Aug	9.270	-7.909	-2.744
Set	6.512	-5.556	-1.927
Oct	8.336	-7.322	-2.084
Nov	6.912	-7.462	0.819
Dec	3.810	-6.750	5.282

had no spots, which means they were born in February but were not observed sooner due to their hiding behavior during the first weeks of life (Rodríguez 2015).

Rain seasonality at Santa Rosa National Park (Fuller *et al.* 2020) is similar to that of Curú. Rainfall peaks in May - June, decrease in July – August, and peaks again with greater precipitation around October. That could explain why the phenology of Curú vegetation demonstrates similar patterns to those of other sectors in Northwestern Costa Rica where many dry forest species are deciduous and recover much of their foliage at the beginning of the rainy season in May and June (Castro *et al.* 2018). However, several tree species maintain foliage throughout the dry season, as do half of the shrubs, saplings, and seedlings (Frankie *et al.* 1974; Opler *et al.* 1980), and many animal species reflect these patterns (Rockwood 1975; Janzen 1993; Orkin *et al.* 2019).

Curú is located in a more humid life zone than Santa Rosa (Figure 1), but this seems to not affect the white-tailed deer reproductive cycle. Although the rainy season determines the availability of food, which is a proximate cause of high variation of the reproductive cycle in Santa Rosa during the year (Fuller *et al.* 2020), it does not seem to have a strong influence on the deer cycle in Curú. However, there was a coincidence between the peak of precipitation occurring in May and the highest number of fawns with spots (36, Figure 3a).

Lack of seasonal variation in the photoperiod is the decisive factor that likely favor deer reproduction throughout the year in Santa Rosa (Fuller *et al.* 2020). Yet this variation is identical in Curú, where the reproduction of the species is seasonal. The peak of births in February and March ensures the survival of the fawns, which will be weaned at the beginning of the rainy season when there is plenty of food. The high amount of rain in September and October, including flooding, will not affect the fawns because they are already grown up by this time of the year (Figure 3a). However, these severe rains and flooding could be an impacting seasonal factor on the fawning season at Curú. The association of flooding with changes in the fawning season has been reported in white-tailed deer populations that occur in areas affected by severe flooding such as the Everglades in Florida (MacDonald-Beyers and Labisky 2005).

The reproduction pattern we observed in Curú is similar to the pattern on San Lucas Island, located in a dry forest at a distance less than 20 km in a straight line (Rodríguez and Solís 1984). What is different among the sites? The traditional or more commonly used system of ecosystem classification in Costa Rica is Holdridge's Life Zones (Bolaños *et al.* 2005). In this classification, Santa Rosa and Palo Verde are in the Pre-montane humid Forest Life Zone and Curú in the Tropical humid Forest zone, leaving San Lucas Island as the only one of the sites included in our comparison that is located in a tropical dry forest. This explains to some degree the highly seasonal reproductive process of the white-tailed deer in San Lucas, but it does not explain



Figure 5. a) Small spotted fawn and b) large spotted fawn of white-tailed deer (*Odocoileus virginianus*) at Hacienda y Refugio de Vida Silvestre Curú, Northwestern Costa Rica.

the seasonality pattern we found in Curú. However, Curú is even more humid than Santa Rosa and Palo Verde, even though all three of these sites as well as San Lucas have a marked dry season. Rainfall in Curú is higher than in Santa Rosa, and it may make a difference in year-round food availability, but severe rains and flooding by September and October can have a more determining impact on fawning seasonality.

The reproductive patterns of white-tailed deer in Central and South America may have evolved in response to seasonal fluctuations in specific food availability, competition, or predation, all of which may be related to rainfall patterns (Asher 2011). However, these factors do not explain why white-tailed deer reproduction is seasonal in some places, but not in others that are very close. Is there a direct relationship to weather or is some other factor that differs between the sites responsible for the differences in white-tailed deer reproduction? Are white-tailed deer more genetically related to North American forms that are more seasonal, or does another factor make them different from non-seasonal deer? It appears that white-tailed deer exhibit a very flexible and therefore variable reproductive pattern (Fuller *et al.* 2020). More research is needed to understand what factors more directly explain the observed pattern in the white-tailed deer reproduction.

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Literature cited

- ASHER, G. W. 2011. Reproductive cycles of deer. *Animal Reproduction Science* 124:170–175.
- BLOUCH, R. 1987. Reproductive seasonality of white-tailed deer on the Colombian Llanos. Pp. 339–343, *in* *Biology and management of the Cervidae* (Wemmer, C., ed.). Smithsonian Institution Press. Washington, U.S.A.
- BOLAÑOS, R., V. WATSON, AND J. TOSI. 2005. Mapa ecológico de Costa Rica (Zonas de Vida), según el sistema de clasificación de zonas de vida del mundo de L. R. Holdridge, Scale 1:750 000. Centro Científico Tropical. San José, Costa Rica.
- BRANAN, W., AND R. MARCHINTON. 1987. Reproductive ecology in white-tailed deer and red brocket deer in Suriname. Pp. 344–351, *in* *Biology and management of the Cervidae* (Wemmer, C., ed.). Smithsonian Institution Press, Washington, U.S.A.
- BROKX, P. 1984. South America. Pp. 525–546, *in* *White-tailed deer: ecology and management* (Halls, L. K., ed.). Stackpole Press. Harrisburg, U.S.A.
- BRONSON, F. H. 2009. Climate change and seasonal reproduction in mammals. *Philosophical Transactions of the Royal Society of London, B. Biological Sciences* 364:3331–3340.
- CASTRO, S. M., G. A. SÁNCHEZ-AZOFEIFA, AND H. SATO. 2018. Effect of drought on productivity in a Costa Rican tropical dry forest. *Environmental Research Letters* 13:045001.
- CONTRERAS-MORENO, F. M., ET AL. 2019. Seasonal antler cycle in white-tailed deer in Campeche wetlands in Southeastern Mexico. *European Journal of Wildlife Research* 65:53.
- DITCHKOFF, S. S. 2011. Anatomy and physiology. Pp. 43–73, *in* *Biology and management of white-tailed deer* (Hewitt, D. G., ed.). CRC Press/Taylor and Francis Group. Boca Raton, U.S.A.
- FRANKIE, G. W., H. G. BAKER, AND P. A. OPLER. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *Journal of Ecology* 62:881–919.
- FULLER, T. K., A. M. SILVA, V. H. MONTALVO, C. SÁENZ-BOLAÑOS, AND E. CARRILLO. 2020. Reproduction of white-tailed deer in a seasonally dry tropical forest of Costa Rica: a test of aseasonality. *Journal of Mammalogy* 101:241–247.
- GOLDMAN, B. D. 2001. Mammalian photoperiodic system: formal properties and neuroendocrine mechanisms of photoperiodic time measurement. *Journal of Biological Rhythms* 16:283–301.
- GOSS, R. J. 1983. Deer antlers – regeneration, function, and evolution. Academic Press. New York, U.S.A.
- HANON, E. A., ET AL. 2008. Ancestral TSH mechanism signals summer in a photoperiodic mammal. *Current Biology* 18:1147–1152.
- HOLDRIDGE, L. R. 1967. Life Zone Ecology. Tropical Science Center. San José, Costa Rica.
- IMN (INSTITUTO METEOROLÓGICO NACIONAL). 2020a. Boletín Meteorológico Mensual. San José, Costa Rica. <https://www.imn.ac.cr/boletin-meteorologico>. Accessed on 3 May 2020.
- IMN (INSTITUTO METEOROLÓGICO NACIONAL). 2020b. Clima en Costa Rica. <https://www.imn.ac.cr>. Accessed on 03 May 2020.
- JANZEN, D. H. 1993. Caterpillar seasonality in a Costa Rican dry forest. Pp. 448–477, *in* *Caterpillars – ecology and evolutionary constraints on foraging* (Stamp, N. E., and T. M. Casey, eds.). Chapman and Hall. New York, U.S.A.
- KLEIN, E. 1982. Phenology of breeding and antler growth in white-tailed deer in Honduras. *Journal of Wildlife Management* 46:826–829.
- LINCOLN, G. A. 1992. Biology of seasonal breeding in deer. Pp. 565–574, *in* *The biology of deer* (Brown, R. D., ed.). Springer Verlag. New York, U.S.A.
- LOUDON, A. S. I., AND J. D. CURLLEWIS. 1988. Cycles of antler and testicular growth in an aseasonal tropical deer (*Axis axis*). *Journal of Reproduction and Fertility* 83:729–738.
- MACDONALD-BEYERS, K., AND R. F. LABISKY. 2005. Influence of flood waters on survival, reproduction, and habitat use of white-tailed deer in the Florida Everglades. *Wetlands* 25:659–666.
- MARCHINTON, R., AND D. HIRTH. 1984. Behavior. Pp. 129–168, *in* *White-tailed deer: ecology and management* (Halls, L. K., ed.). Stackpole Press. Harrisburg, U.S.A.
- MATTIOLI, S. 2011. Family Cervidae (deer). Pp. 350–443, *in* *Handbook of the mammals of the world, volume 2: Hoofed Mammals* (Wilson, D. E., and R. A. Mittermeier, eds.). Lynx Edicions. Barcelona, Spain.
- MCKINNEY, T. 2014. Species-specific responses to tourist interactions by white-faced capuchins (*Cebus imitator*) and mantled howlers (*Alouatta palliata*) in a Costa Rican wildlife refuge. *International Journal of Primatology* 35:573–589.
- MOLINARI, J. 2007. Variación geográfica en los venados de cola blanca (Cervidae, *Odocoileus*) de Venezuela, con énfasis en *O. margaritae*, la especie enana de la Isla de Margarita. *Memoria de la Fundación La Salle de Ciencias Naturales* 167:29–72.
- OPLER, P. A., G. W. FRANKIE, AND H. G. BAKER. 1980. Comparative phenological studies of treelet and shrub species in tropical wet and dry forests in the lowlands of Costa Rica. *Journal of Ecology* 68:167–188.
- ORKIN, J. D., ET AL. 2019. Seasonality of the gut microbiota of free-ranging white-faced capuchins in a tropical dry forest. *The ISME Journal* 13:183–196.
- PRICE, J., C. FAUCHEUX, AND S. ALLEN. 2005a. Deer antlers as a model of mammalian regeneration. *Current Topics in Developmental Biology* 67:1–48.
- PRICE, J., S. ALLEN, C. FAUCHEUX, T. ALTHNAIAN, AND J. C. MOUNT. 2005b. Deer antlers: a zoological curiosity or the key to understanding organ regeneration in mammals? *Journal of Anatomy* 207:603–618.
- ROBINSON, M. R., J. W. THOMAS, AND R. G. MARBURGUER. 1965. The reproductive cycle of white-tailed deer in Central Texas. *Journal of Wildlife Management* 29:53–59.
- ROCKWOOD, L. L. 1975. The effects of seasonality on foraging in two species of leaf-cutting ants (*Atta*) in Guanacaste Province, Costa Rica. *Biotropica* 7:176–193.
- RODRÍGUEZ, M., AND V. SOLÍS. 1994. Ciclo de vida del venado cola blanca en la Isla San Lucas, Costa Rica. Pp. 63–71, *in* *Ecología y Manejo*

- jo del Venado Cola Blanca en México y Costa Rica (Vaughan, C., and M. A. Rodríguez, eds.). EUNA. Heredia, Costa Rica.
- RODRÍGUEZ, M. 1994. Ciclo de las astas del venado cola blanca en el Refugio Nacional de Vida Silvestre Palo Verde, Guanacaste, Costa Rica. Pp. 103–109, *in* Ecología y Manejo del Venado Cola Blanca en México y Costa Rica (Vaughan, C., and M. A. Rodríguez, eds.). EUNA. Heredia, Costa Rica.
- RODRÍGUEZ, M. A. 2015. El venado cola blanca en el bosque seco tropical de Costa Rica. Windmills Editions, California, U.S.A.
- SAUER, P. R. 1984. Physical Characteristics. Pp. 73–90, *in* White-tailed deer: ecology and management (Halls, L. K., ed.). Stackpole Press. Harrisburg, U.S.A.
- SCHUTT, A., AND C. VAUGHAN-DICKHAUT. 1995. Incorporating wildlife into development: the case of the Curú Wildlife Refuge and Farm, Costa Rica. Pp 250–254, *in* International Wildlife Management Congress (Bissonette, J. A., and P. R. Krausman, eds.). San José, Costa Rica.
- SMITH, W. P. 1991. *Odocoileus virginianus*. Mammalian Species 388:1–13.
- TEER, J. 1994. El Venado Cola Blanca: Historia Natural y Principios de Manejo. Pp. 33–47, *in* Ecología y Manejo del Venado Cola Blanca en México y Costa Rica (Vaughan, C., and M. A. Rodríguez, eds.). EUNA. Heredia, Costa Rica.
- TOMÁS, W. M. 1995. Seasonality of the antler cycle of pampas deer (*Ozotoceros bezoarticus leucogaster*) from the Pantanal Wetland, Brazil. *Studies on Neotropical Fauna and Environment* 30:221–227.
- VASANTHA, I. 2016. Physiology of seasonal breeding: A review. *Journal of Veterinary Science and Technology* 7:331.
- VERME J. L., AND D. E. ULLREY. 1984. Physiology and Nutrition. Pp. 91–118, *in* White-tailed deer: ecology and management (Halls, L. K., ed.). Stackpole Press. Harrisburg, U.S.A.
- WEBB, J., AND D. NELLIS. 1981. Reproductive cycle of white-tailed deer at St. Croix, Virgin Islands, USA. *Journal of Wildlife Management* 45:253–258.
- WEBER, M., P. ROSAS-BECEMIL, A. MORALES-GARCÍA, AND C. GALINDO-LEAL. 1994. Biología reproductiva del venado cola blanca en Durango, México. Pp. 111–127, *in* Ecología y Manejo del Venado Cola Blanca en México y Costa Rica (Vaughan, C., and M. A. Rodríguez, eds.). EUNA. Heredia, Costa Rica.

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