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Responses of two sympatric species of peccaries (*Tayassu pecari* and *Pecari tajacu*) to hunting in Calakmul, Mexico

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Abstract

The white-lipped peccary (*Tayassu pecari*) and the collared peccary (*Pecari tajacu*) are social ungulates of great ecological and economic importance. Both species represent important sources of animal protein in the diet of indigenous and rural communities in Neotropical forests, which has contributed to reducing their populations throughout their geographic distribution. It is still not well understood how the social ecology of peccaries is affected by hunting. This study analyzed the relationship between hunting and group size, group composition, daily activity patterns, and the relative abundance of the two peccary species. Camera-traps and direct observation were used from February 2014 through February 2015 in two sites differing in their degree of protection and hunting pressure: the first was Calakmul Biosphere Reserve (a site with no hunting) and the second was the community of Nuevo Becal (a hunting site). Our analyses suggest that hunting negatively affects group size, structure, composition and the relative abundance of both peccary species. We propose that management and conservation plans, particularly for key resources such as water, and monitoring and hunting controls in the habitats of both peccary species, might ensure their survival in the Calakmul region.

Keywords

White-lipped peccary, *Tayassu pecari*, collar peccary, *Pecari tajacu*, group size, activity patterns, hunting effect, water source, Calakmul

Introduction

Subsistence hunting in the tropics is focused on large species, mainly ungulates (Di Bitetti, Paviolo, Ferrari, De Angelo, & Di Blanco, 2008; Fa, Peres, & Meeuwig, 2002). Peccaries are among the prey species preferred by hunters in the Neotropics (Escamilla, Sanvicente, Sosa, & Galindo, 2000; Fang et al., 2008; Montiel, Arias, & Dickinson, 1999; Reyna-Hurtado & Tanner, 2007). Needless to say, hunting has a significant impact on their activity patterns as well as resulting in a reduction of their populations (Escamilla et al., 2000; Peres, 2000). It has resulted, too, in a reduction of the total biomass of ungulate species, as well as in an increase of smaller species populations, which are not targeted by hunters (Peres & Palacios, 2007). The constant pressure of subsistence hunting in the Neotropics has caused 'empty forest syndrome' due to the local extinction of hunted species, including the white-lipped peccary (WLP) (*Tayassu pecari*) and the collared peccary (CP) (*Pecari tajacu*) (Redford, 1992; Stoner, Vulinec, Wright, & Peres, 2007). This type of hunting is on-going, and it is not well known how it affects local peccary populations. Therefore, understanding the effect of hunting on peccary populations has important implications for their conservation and management (Di Bitetti et al., 2008; Harrison et al., 2013).

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There are three known species of peccaries (Tayassuidae family, Sowls, 1997) and two of them live in Mexico. The white-lipped peccary is considered to be in a vulnerable state throughout its distribution area (IUCN, 2013) and it is endangered in Mexico, where its distribution area has decreased by 84% (Altrichter, Taber, Beck, Reyna-Hurtado, & Keuroghlian, 2012). White-lipped peccaries usually form groups of 10 to 300 individuals (De Almeida Jácomo et al., 2013; Fragoso, 1998; Reyna-Hurtado, Naranjo, Chapman, & Tanner, 2010; Sowls, 1997), but there are also historical reports of the presence of herds of over 1000 individuals (Mayer & Wetzel, 1987). Studies show that the white-lipped peccary is a selective species using specific and extensive habitat such as evergreen forests in areas subject to conservation and low flooded forests in areas where they are under pressure from hunting (Briceño-Méndez, Reyna-Hurtado, Calme, & García-Gil, 2014; Reyna-Hurtado & Tanner, 2007).

The state of the collared peccary is of lower concern throughout its distribution area (IUCN, 2011, 2013). This species persists in disturbed habitats such as secondary forests near agricultural sites and in areas under high pressure from hunting (Reyna-Hurtado & Tanner, 2007). Little is known about group composition, activity patterns and hunting effects on peccaries in parts of their distribution ranges, especially in corridors connecting major conservation areas (Naranjo, Amador-Alcalá, Falconi-Briones, & Reyna-Hurtado, 2015). March (1993) observed that smaller peccary groups are probably a result of hunting pressure. Reyna-Hurtado et al. (2010) found that in hunting areas group sizes were smaller than in conservation sites in the Calakmul region, Mexico. Briceño-Mendez et al. (2014) also found lower abundances in hunting areas than in conservation areas. In our study we used camera-traps and direct observation to compare two contrasting sites: the Calakmul Biosphere Reserve, a protected site, and Nuevo Becal, a community forest where there is subsistence hunting, occasional sport hunting, logging, and extraction of non-timber forest products. Our aim was to explore the potential responses of white-lipped peccary and collared peccary populations and their group structure to hunting pressure.

Methods

Study sites

The Calakmul Biosphere Reserve (CBR) is the largest protected area of tropical forest in Mexico with an area of 7,231.25 km^2, of which approximately 4,000 km^2 are located to the south of the Chetumal-Escárcega highway in the state of Campeche (Morales & Magaña, 2001). Precipitation increases from North to South. Vegetation ranges from tropical deciduous forest in the North, with trees up to 18 m high, to evergreen tropical forest in the south, where trees reach over 35 m in height (Pennington & Sarukhán, 1998). The most abundant forest is the semi-evergreen tropical forest with trees between 18 m and 25 m in height, of which approximately 25% shed their leaves during the dry season. Some intermediate associations are low flooded forests, locally known as "lowlands" or "akalches" in Mayan, which are forests with trees between 8 m and 15 m in height which are seasonally flooded because they are located on depressions in clay soils. The climate of the CBR is warm and sub-humid with a mean annual temperature of 24.6 °C (Garcia-Gil, 2003). There is a rainy season between June and October with an annual rainfall average of 1,076 mm, varying from 700 mm in the northern part to more than 2000 mm in the southern part. Most of the rainwater percolates into the underground while the rest is superficially drained in temporary streams (or semi-permanent) and stored in small reservoirs, locally known as "aguadas". These reservoirs are the only source of water for wildlife and various human communities during the dry season (Reyna-Hurtado et al., 2010).

The Nuevo Becal Community (NBC) is located 30 km from the municipal town of Xpujil on the north-eastern side of the CBR. The population is comprised of people from the states of Veracruz, Tabasco and Campeche. It has an area of 520 km^2 (18° 40' 07.7" N, 89° 12' 34.3" W). Approximately 80% of the area is still forested (Reyna-Hurtado, 2009), including: 1) medium semi-evergreen forest; 2) semi-evergreen flooded lowland forest (commonly known as "flooded forest" or locally as "*bajos*") that has dominant trees under 15 m in height; 3) lowland dry forest with trees heights under 15 m, where 75-100% of the dominant trees lose their leaves during the dry season; and 4) secondary vegetation that develops once the original vegetation has been removed either by human activities or by natural processes (Pennington & Sarukhán, 1998).

The main productive activities change depending on the time of the year and include farming, beekeeping, livestock production and coal mining. However, hunting is practiced year-round (Briceño-Méndez, 2012; Escamilla et al., 2000; Reyna-Hurtado & Tanner, 2007; Santos, Naranjo, & Salazar, 2012; Weber, 2000). Previous studies have shown that the collared peccary is the most frequently hunted prey in the region (Weber, 2000), and that whole groups of white-lipped peccaries can be exterminated in a single dry season (Reyna-Hurtado et al., 2010). Despite the high human impact on the forests of this region, the original biodiversity is still present, including large predators such as the jaguar (*Panthera onca*) and puma (*Puma concolor*) (Amador, Naranjo, & Jimenez, 2013), as well as another four species of ungulates: Baird's tapir (*Tapirus bairdii*), red brocket deer (*Mazama temama*), Yucatan brocket deer (*Mazama pandora*), and white-tailed deer (*Odocoileus virginianus*) (Escamilla et al., 2000; Reyna-Hurtado & Tanner, 2007).

Characterization of the study sites

In the Calakmul region, wildlife protection efforts have increased during recent years and hunting is now illegal. However, subsistence hunting is socially accepted and it is common to observe local people in the region carrying firearms when going to their farms. People commonly spend up to 15 days in the forest extracting sapodilla (*Manilkara zapota*) sap for chewing gum manufacturing, or sometimes they go to the jungle to take care of their livestock, protecting it from predators, mainly jaguars (Amador, Naranjo, & Jimenez, 2013). Different parameters were used in order to characterize the sites according to their level of hunting. First, accessibility to the sites was considered. The only access to the biosphere reserve that reaches up to Calakmul archaeological site is restricted by three checkpoints. The first corresponds to the Conhuas communal authority area, which covers the buffer zone of the reserve. The second comes under the control of the National Commission on Protected Areas (known as CONANP, its acronym in Spanish), which has forest-guards patrolling year-round. The third is regulated by the National Institute of Anthropology and History (INAH is its Spanish acronym), which controls direct access to the Calakmul archaeological site. For 17 years one of the authors of this article (RRH) has been conducting studies in this reserve and to date has not observed any kind of hunting activities at this site.

Second, all signs that demonstrated hunting activity during the study period were quantified at both sites. In the Nuevo Becal community30 sounds of gunshot, 33 traces of people, 12 bullet shells, 16 dogs, 9 photographs of people with weapons registered on the camera-traps, and 66 encounters with hunters were recorded. In contrast there were no signs of hunting activities recorded in the reserve. Moreover, information available in other studies of wildlife utilization and abundances in the region demonstrates that hunting was common in the Nuevo Becal community (Briceño-Méndez et al., 2014; Escamilla et al., 2000; Reyna-Hurtado & Tanner, 2007; Santos et al., 2012). Therefore we can assume with confidence that the Calakmul Biosphere Reserve is effectively protected from hunting while the Nuevo Becal community remains a hunting area (Figure 1).

Group size and age structure

Ten camera-trap monitoring stations (Reconyx PC800 Hyperfire Professional IRTM and PC600 Hyperfire Pro White FlashTM; Reconyx, Inc., Holmen, Wisconsin, USA) were established at each study site. Each monitoring station was set at the edge of a water body frequented by wildlife mainly in the dry season. The cameras were positioned at a minimum distance of 1.5 km from each other at a height of up to 50 cm from ground level ensuring that the focus would be in the direction of a wildlife trail. The photo capture period was scheduled to remain active for 24 hours with picture intervals every second. This capture sequence enabled all the individuals passing in line or in groups to be counted (Maffei, Cuellar, & Noss, 2002). Photographic records were considered to

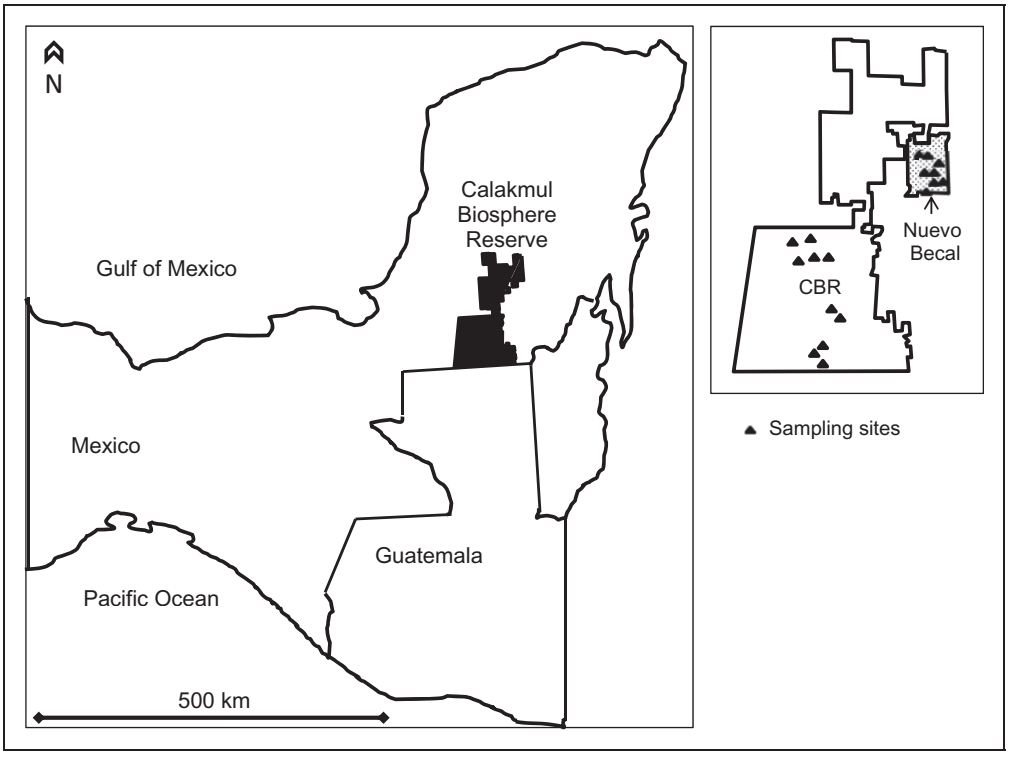

Figure 1. Yucatan Peninsula, Calakmul Biosphere Reserve, sampling sites and camera-traplocations in the Calakmul region, Campeche, Mexico.

be independent if 24 hours had passed between recordings or when two or more individuals were observed in a photo. The position of each station was geo-referenced with a Garmin 62 s® GPS and the time and date was recorded on each picture. Cameras, batteries, and memory cards were checked monthly to ensure they were functioning properly. Total sampling effort was 3510 and 3200 camera days in the areas with no hunting and the hunting areas, respectively.

In addition to the camera-trap data, direct observations were made. Walking trips were performed every month for 12 days on average. Each trip lasted 9 hours (7:00-16:00 h) on average starting in the morning and following fresh trails of peccaries in order to find the herds. Both direct observations and photographic records were used to estimate the age structure of each group by classifying the individuals into three categories depending on size and fur coloration: mature adult, young adult, and juvenile (Reyna-Hurtado et al., 2010).

Relative abundance and activity patterns

The relative abundance of both peccary species was estimated using two methods. The first was an index based on the number of peccary footprints observed per kilometer (Reyna-Hurtado & Tanner, 2007) along 20 km of line transects walked between February and November 2014 at both study sites. Transects in Nuevo Becal were established in forested locations at least 7 km from the village. In the unhunted site, transects were randomly established in the southern portion of CBR, following the main access road to the Calakmul archaeological site. Transects were walked every month and all peccary tracks found within 1 m on each side of the transect centerline were recorded. Transect samplings were carried out with the help of local people and trained students at a speed of 1 km per hour. When two or more footprints were found together, they were counted as a single track to avoid overestimations (Reyna-Hurtado & Tanner, 2007). The second method consisted of the number of independent records obtained through photographs at each station (Lira, Galindo, & Briones, 2012). Sampling effort was obtained by multiplying the number of cameras by the total sampling days (Lira et al., 2012; Medellín et al., 2006). Activity patterns were assessed by using photographic records of both peccary species obtained within 2-hour periods at each station. Activity was considered either diurnal (08:00 h-18:00 h) or nocturnal (20:00 h-06:00 h) (Lira et al., 2012; Monroy-Vilchis, Zarco-González, Rodriguez-Soto, Soria-Díaz, & Urios, 2011).

Statistical analysis

Group sizes between peccary species and study sites were compared using Mann-Whitney's U tests. The proportions of records of activity (nocturnal or diurnal) at the hunted and unhunted sites were analyzed using contingency tables and x^2 tests. For the analysis, the SPSS (Statistical Program for Social Sciences, version 17.0, Chicago, USA) package was used.

Results

A total of 101 collared peccary group records (N = 603 individuals) and 94 white-lipped peccary group records (N = 2187 individuals) were obtained between February 2014 and February 2015 in the study area. More groups and individuals of both species were observed at the unhunted site (CP: 88, 554; WLP: 59, 1512) than at the hunted site (CP: 13, 49; WLP: 35, 675) (Table 2). Similarly, group sizes were significantly greater at the unhunted site (CP median = 5.3, SD = 2.9, n = 88; WLP median = 21.6, SD = 6.6, n = 59) than at the hunted site (CP median = 2.6, SD = 1.4, n = 13; WLP median = 18.3, SD = 4.1, n = 35) for both species (Mann-Whitney tests $P < 0.001$; Figures 2 and 3).

The age structures of collared peccary populations were determined based on 554 individuals at the unhunted site and the following proportions were found: mature adults 90.1%, young adults 6.5%, and juveniles 3.4%. At the hunted site, age structure was estimated based on 49 individuals and the following proportions were calculated: mature adults 77.6%, young adults 12.2%, and juveniles 10.2% (Table 1). The white-lipped peccary age structure was estimated based on 1512 individuals at the unhunted site finding 92.9%

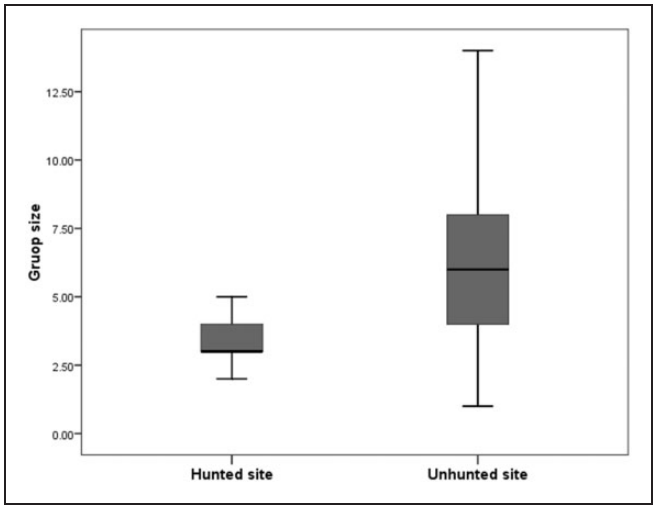

Figure 2. Collared peccary (*Pecari tajacu*) group size in two study sites of Calakmul, Campeche, Mexico. Bold horizontal lines within boxes indicate mean group size; gray areas show standard deviations around means, and vertical bars illustrate group size confidence intervals (95%).

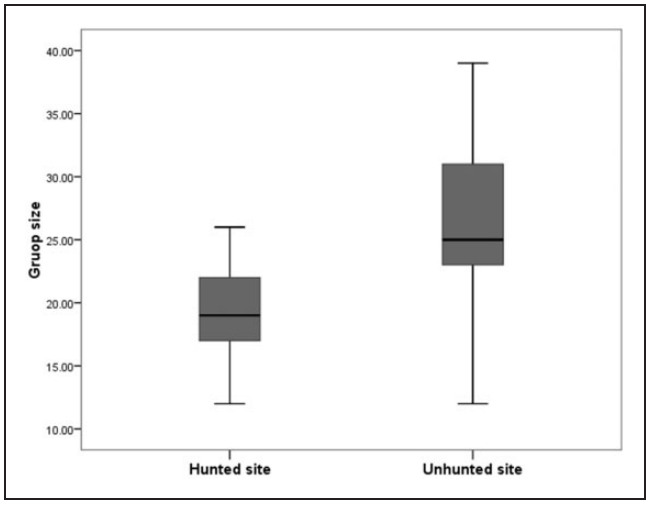

Figure 3. White-lipped peccary (*Tayassu pecari*) group size in two study sites of Calakmul, Campeche, Mexico. Bold horizontal lines within boxes indicate mean group size; gray areas show standard deviations around means, and vertical bars illustrate group size confidence intervals (95%).

Table 1. Age structure of collared peccary *(Pecari tajacu)* and white-lipped peccary *(Tayassu pecari)* groups in the Calakmul region, Campeche, Mexico. February 2014-February 2015.

	Collared peccary		White-lipped peccary	
Age structure	Unhunhted site (%)	Hunted site (%)	Unhunted site (%)	Hunted site (%)
Mature adults	90.10	77.55	92.85	93.03
Young adults	6.50	12.24	5.16	2. 82
Juveniles	3.40	10.21	1.98	4.15
Total number of individuals	554	49	1512	675

were mature adults, 5.1% young adults, and 2% juveniles. At the hunted site, of 675 individuals 93% were mature adults, 2.8% young adults, and 4.2% juveniles (Table 1).

The relative abundance estimated from both transect sampling and camera-trapping was higher for both species at the unhunted site. For the collared peccary, 0.95 tracks/km (N = 190 records) and 27.5 pictures/1,000 camera-days were estimated at the unhunted site versus 0.56 tracks/km (N = 112 records) and 3.70 pictures/1,000 camera-days at the hunted site. These values were statistically different (*t*-test, $p = 0.01$) (Table 2). For the white-lipped peccary, 0.16 tracks/km (N = 32 records) and 18.43 pictures/1000 camera-days were obtained at in the unhunted site versus 0.11 tracks/km (N = 23 records) and 9.97 pictures/1,000 camera-days at the hunted site. These

Table 2. Mean relative abundances of peccaries in the Calakmul region, Campeche, Mexico. February 2014-February 2015.

Species	Unhunted site	Standard error	Hunted site	Standard error	P value
Collared peccary	0.13	0.72	0.08	0.04	0.01[a]
(*Pecari tajacu*)	2.7	1.62	0.37	0.30	0.01[b]
White-lipped peccary	0.02	0.03	0.01	0.01	0.55[a]
(*Tayassu pecari*)	1.84	1.23	0.98	0.36	0.14[b]

[a]P value for relative abundances estimated through transect sampling.
[b]P value for relative abundances estimated through camera-trapping.

differences were not significant (Table 2). The main activity time for peccaries was during the day at both sites and it did not differ significantly between them ($X^2 = 9.57$, d. f = 1, $P = < 0.001$. The greatest number of records occurred between 08:00 h-10:00 h and 12:01 h-14:00 h (Figure 4).

Discussion

The expected responses to hunting by peccary populations in this study were lower abundances, reduced group sizes, different group composition and altered activity patterns in a hunted site (Nuevo Becal) compared to an unhunted site (Calakmul Biosphere Reserve). Group sizes of both species and the abundance of collared peccaries were certainly lower at the hunted site. However, group composition, activity patterns, and white-lipped peccary abundances did not differ between sites. Some of the most relevant arguments aiming to explain our results follow.

In tropical forests, the collared peccary group size usually comprises fewer than 20 individuals (March & Mandujano, 2005; Robinson & Einsenberg, 1985). However, in the Southwestern United States groups may have up to 50 individuals. In Venezuela, an average group size of 36.6 ± 6 individuals has been estimated, which divides into average groups of 14 individuals (Castellanos, 1983). Our study found smaller group sizes than previously reported for the species. In addition, we found significant differences between group sizes and study sites. These results are similar to those reported by Mandujano (1999) for Chamela, Jalisco, Mexico, and by Naranjo, Gallina, Mandujano, and Weber, (2008) for El Eden Reserve in Quintana Roo, Mexico. However, the average group size found in this study at both sites is higher compared to that reported by Naranjo (2002) for the Lacandon rainforest, Chiapas, Mexico (mean = 2.3) with frequent groups of up to 15 individuals.

White-lipped peccary group sizes found in this study were generally smaller than those reported in other Neotropical sites. For instance, Baur (1999) estimated

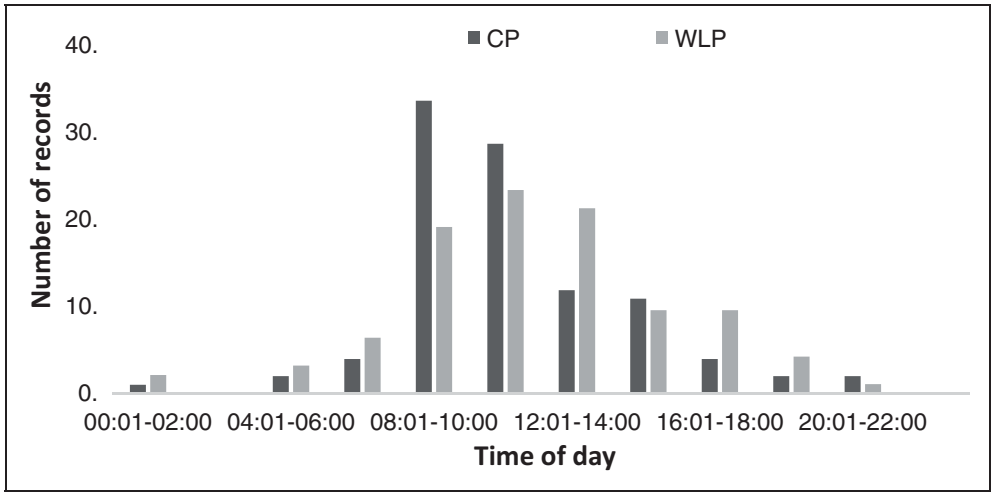

Figure 4. Daily activity patterns in two peccary species in the Calakmul region, Campeche, México (Collared peccary, N = 101 records), (White-lipped peccary, N = 94 records).

an average size of 50.1 individuals per herd in the community forestry concession of Carmelita, in the Maya Biosphere Reserve of Guatemala. Similarly, Moreira, Lopez, Garcia Anleu, Cordova, and Dubon (2015) estimated an average group size of 39.8 individuals in a temporary lagoon within the Mirador-Rio Azul National Park, Guatemala. Larger group sizes at both areas compared to groups of the Calakmul Biosphere Reserve may be attributed to the greater availability of water present in the Guatemalan study sites. In the dry forests of Northern Argentina, Altrichter (2005) estimated an average of 23 individuals per group, a number comparable to that observed in the Calakmul Biosphere Reserve. Both sites are seasonal and water is a limiting factor during the dry season. Average group sizes found in previous studies (Reyna-Hurtado et al., 2010, 2016) for this region are similar to those found in this study, which demonstrates the direct effect of hunting on white-lipped peccary group size variation, as noted in other study areas (Altrichter & Boaglio, 2004; Naranjo & Bodmer, 2007; Peres, 1996; Reyna-Hurtado & Tanner, 2007). In the Amazon forests of Peru, Bolivia and Brazil, white-lipped peccary groups had more individuals than those in Guatemala, Mexico and Argentina (Fragoso, 1998; Kiltie & Terborgh, 1983; Sowls, 1997). However, it is important to consider the effect that excessive increases in livestock farming activities in the Calakmul region could be having on peccary populations.

Deforestation for livestock production implies habitat loss and potential alterations of group size and composition for both peccary species. In addition, the availability of resources such as water and food at each site evaluated is important. These factors might be influencing ecological strategies for group formation and their size in both peccary species. These are variables that must be evaluated in future research.

So far this is the first study that describes the age structure based on photographic records and direct observations of group composition of collared peccaries throughout its distribution range. Regarding the white-lipped peccary, the proportions of adults observed within the groups were similar to those previously reported for both in the Calakmul region (Reyna-Hurtado et al., 2010) and the Lacandon Forest in Chiapas, Mexico (Naranjo & Bodmer, 2007). However, in Calakmul we observed that a group was composed of 36 adults and five juveniles at the hunted site. This is an unusually high number of individuals for a white-lipped peccary group at a hunted site in this region (Reyna-Hurtado et al., 2010). This event could be because the observation site was in good condition and far from the nearest village. The site has two wildlife management units, which are subject to Community surveillance. This suggests that the study location, despite being a hunting site, may have favorable ecological conditions for the maintenance and conservation of peccary populations in the Calakmul region providing that hunting is regulated.

Our camera-trap sampling effort was slightly higher (9.8%) at the unhunted site compared to the hunted site. However, the differences in relative abundances between sites were considerably greater (7.4 and 1.8 times greater at the unhunted site for CP and WLP, respectively), which supports our assumption that hunting pressure has had an impact on peccary populations in Calakmul. The abundance estimated for the white-lipped peccary was relatively low. These results were similar to those reported in previous studies for this and other regions of Mexico (Briceño-Méndez et al., 2014; Naranjo, 2002; Reyna-Hurtado & Tanner, 2007). In a

study conducted by the first author (Briceño-Méndez et al., 2014) in 240 km of transects walked from August 2011 through January 2012, a relative abundance of 0.10 tracks/km was detected at the hunting site (N = 12 records), while 0.14 tracks/km were observed at the unhunted site (N = 17 records). Occasional interviews with residents of Nuevo Becal revealed that hunting was still prevalent in the community, with 93% of interviewees saying that they occasionally hunt white-lipped peccaries and other ungulates for subsistence (Briceño-Méndez, 2012). Contrary to our results, Lira et al. (Lira et al., 2012) found that the relative abundance of white-lipped peccaries in the Chimalapas region, Oaxaca, was the highest in Mexico. Their results may be attributed to high habitat quality, difficult access to the area, and lower hunting pressure than in the Calakmul region (Briceño-Méndez, 2012; Escamilla et al., 2000; Reyna-Hurtado & Tanner, 2007; Santos et al., 2012; Weber, 2000).

Collared peccaries may benefit from some kinds of human disturbance (Briceño-Méndez, Montes, Aguilar, & Pool, 2011; Mandujano, 1999; Naranjo, 2002; Reyna-Hurtado & Tanner, 2007). Yet, in some parts of their distribution range they can reach abundances that are appropriate for sustainable use, such as in the Nopala-Hualtepec region, Hidalgo, Mexico (Hernández, 2013), and in some regions of the Peruvian Amazon (Reyna-Hurtado & Tanner, 2007). Nevertheless, it is clear that in our study area hunting of this species lowers its abundance. Therefore, it is important to document the status of collared peccary populations at different spatial scales throughout the Calakmul region.

Previous studies showed that heavy hunting pressure at particular sites had a greater impact on white-lipped peccary populations than any other human activity (Keurohglian, Eaton, & Longland, 2004). Naranjo (2002) found that white-lipped peccary abundance was 7 times greater in an unhunted area compared to a hunted one in the Lacandon Forest, Chiapas, Mexico. Peres (1996), also reported that the white-lipped peccary was very rarely present in hunted areas near human settlements in the Peruvian Amazon.

Another aspect that should be addressed is the potential risk of disease transmission from domestic animals to peccaries, which may cause population declines, as reported by Fragoso (1997). So far only one study conducted in the Maya forest through photographic records has shown skin problems in white-lipped peccary groups (Reyna-Hurtado et al., 2014). Evaluating disease incidence in peccary populations is another important aspect that needs to be addressed in Calakmul and other regions of southern Mexico.

Another possible factor that could be influencing our results with respect to abundance is the movement patterns of white-lipped peccaries. For example, Vickers (1991) assessed wildlife harvest rates over a period of 10 years in the Amazon and found them to be highly variable, which was attributed to seasonal movements of peccary groups outside the evaluated area to less disturbed sites.

Several authors have indicated that peccaries are diurnal (Cuellar & Noss, 2003; Estrada, 2005; Maffei et al., 2002). Recent studies have shown that they may be active throughout the day and have presented three activity patterns classified according to (Medellín et al., 2006) as: (a) diurnal, when sunlight is observed in the photographs; b) nocturnal, when there is no sunlight, and c) twilight, when photographic captures are obtained early morning (6:00 h - 8:00 h) or in the evening (18:00 h - 20:00 h). These patterns have been reported in both peccary species in a study conducted in the Chimalapas region, Oaxaca, Mexico by Lira et al. (2012). These results are similar to those found in our study, since these three activity time periods were found in both study sites. However, the main activity time reported in this study according to frequency of records ranged between 8:00 and 14:00 h. This may be related to the presence of large predators such as the jaguar and the puma, as well as continuous human hunting pressure which occurs in Nuevo Becal during the night. The influence of hunting on deer activity patterns has been documented by Kilgo, Ronauld, and Fritzen (1998), noting that during the hunting season in sunlight hours, deer increased their nocturnal activity and avoided open areas.

This study provides new information on the daily activity patterns of two peccary species and the effect that hunting has on them by reducing their relative abundances and group sizes in Calakmul. This information may be valuable for designing hunting controls and conservation and management plans for both species, especially at critical times such as when water shortages occur and these mammals are more vulnerable.

Implications for conservation

We consider our results relevant for promoting peccary conservation in southeast Mexico and similar sites across Central and South America. Peccaries are among the most important game species providing meat for villagers in Calakmul, the Yucatan Peninsula, and many other rural communities throughout the Neotropics (Altrichter, 2005; Briceño-Méndez et al., 2011; Santos et al., 2012; Sowls, 1997, Figure 5). They represent an important proportion of the animal protein consumed by hunters from many of the poorest tropical and subtropical areas in southeast Mexico and Central America (Naranjo, 2002; Santos et al., 2012). These ungulates are usually subject to heavy pressure from hunting and their population responses to this practice are still not well understood. Collared peccaries are widely perceived as

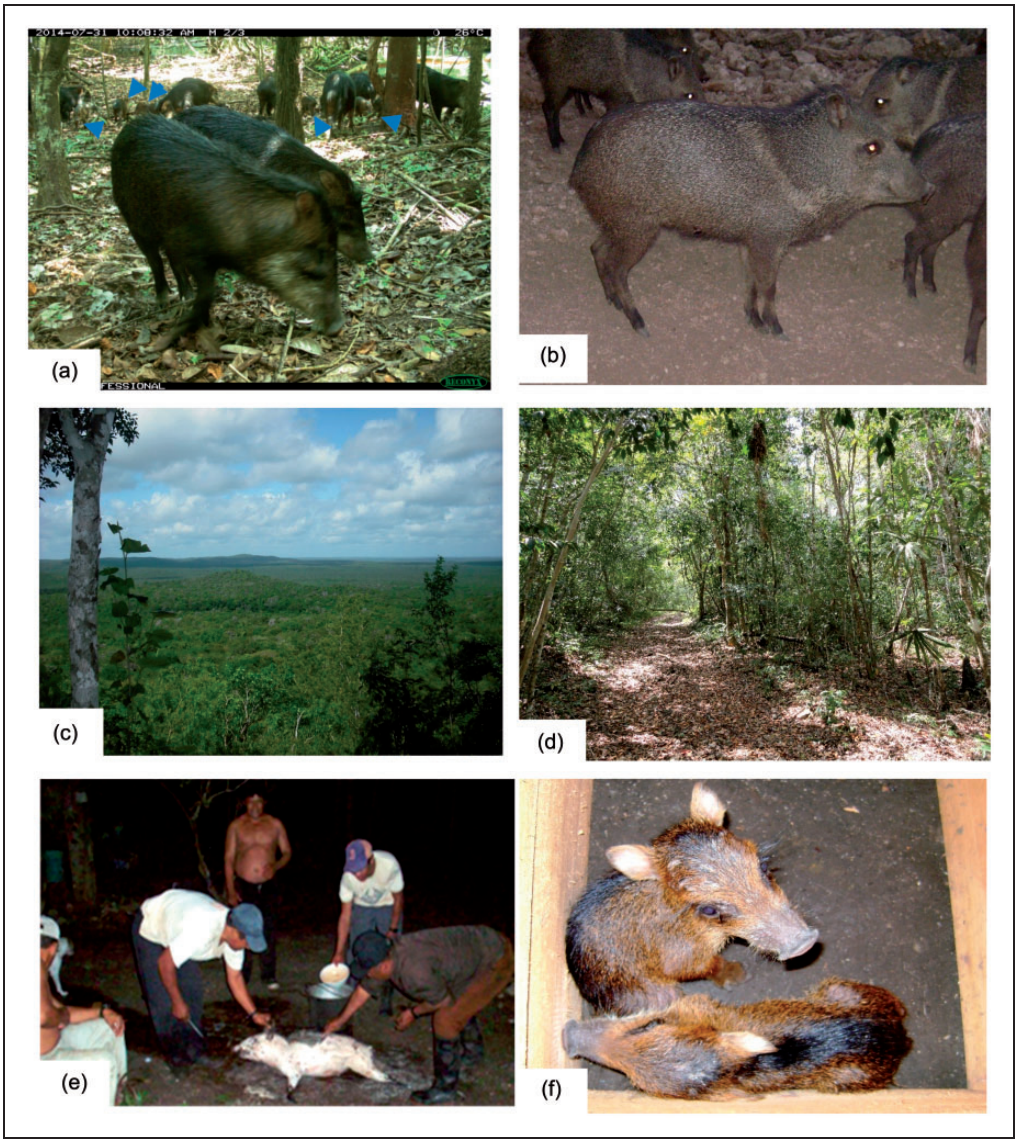

Figure 5. A,B: White-lipped peccaries and Collared peccaries in Calakmul Biosphere Reserve, Campeche, Mexico. C,D: Peccary habitat in Calakmul Biosphere Reserve and Ejido Nuevo Becal. E,F: Peccaries hunted and captured in Ejido Nuevo Becal. Photos: Marcos Briceño-Méndez and Eduardo J. Naranjo.

resilient to moderate hunting and habitat disturbance, whereas white-lipped peccaries are far more sensitive to human activity and rapidly disappear from forested areas which have been subject to increasing human presence and transformation into agriculture and grazing lands (Altrichter & Boaglio, 2004; Naranjo & Bodmer, 2007; Peres, 1996; Sowls, 1997). Thus, recommendations for population and habitat management based on sound scientific data are of the utmost importance if peccary populations are to persistin a context of human dominated landscapes. Such recommendations should also provide information to support husbandry efforts for poor families in villages neighboring protected areas. Peccary conservation would also be highly beneficial in Calakmul and other areas in order to maintain forest ecosystem processes in which they play a key role, such as seed dispersal and predation of many native trees. Furthermore, they arean important food source for large predators.

Most research on peccaries in Mexico has been done within protected areas where the best stocks are concentrated. In these areas peccary monitoring and management is usually easier than in unprotected areas because they are not subject to the constant pressure of human activities which potentially affect their behavior. Studying populations in areas with human activity is considerably more difficult. Information about the ecological and behavioral responses of peccaries to human disturbance is essential in order to identify habitat conditions that

allow their populations to persist and disperse between areas where water and food resources are more available. It is expected that this work will support future research efforts on peccary populations outside protected areas. We are confident that our results will help inform management plans and the conservation of peccaries in areas adjacent to large ecological reserves, and thus help ensure their survival in Mexico.

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References

Altrichter, M. (2005). The sustainability of subsistence hunting of peccaries in the Argentine Chaco. *Biological Conservation*, *126*, 351–362.

Altrichter, M., & Boaglio, G. L. (2004). Distribution and relative abundance of peccaries in the Argentine Chaco: Associations with human factors. *Biological Conservation*, *116*, 217–225.

Altrichter, M., Taber, A., Beck, H., Reyna-Hurtado, R., & Keuroghlian, A. (2012). Might the white-lipped peccary become ecologically extinct? A report of range-wide declines for a critical Neotropical ecosystem architect. *Oryx*, *46*, 87–98.

Amador, A. S., Naranjo, E. J., & Jimenez, F. G. (2013). Wildlife predation on livestock and poultry: Implications for predator conservation in the rainforest of south-east Mexico. *Oryx*, *2*, 243–250.

Baur, E. (1999). *Estudio de la cacería de subsistencia en la concesión forestal de Carmelita, San Andrés, Petén*. Final report to Propetén-Conservation International, Flores, Guatemala.

Briceño-Méndez, M. (2012). *Preferencias de hábitat y abundancia relativa del pecarí de labios blancos (Tayassu pecari) en Calakmul, Campeche, México* (M.Sc. Thesis). Universidad Autónoma de Yucatán, Mérida, Yucatán, México.

Briceño-Méndez, M., Montes, R., Aguilar, W., & Pool, A. (2011). Cacería del pecarí de collar (*Pecari tajacu*) (Artiodactyla: Tayassuidae) en Tzucacab, Yucatán, México. *Revista Mexicana de Mastozoología*, *15*, 8–18.

Briceño-Méndez, M., Reyna-Hurtado, R., Calme, S., & García-Gil, G. (2014). Preferencias de hábitat y abundancia relativa de *Tayassu pecari* en un área con cacería en la región de Calakmul, Campeche, México. *Revista Mexicana de Biodiversidad*, *85*, 242–250.

Castellanos, H. G. (1983). Aspectos de la organización social del báquiro de collar *Tayassu tajacu* en el Estado Guarico, Venezuela. *Acta Biológica Venezolana*, *11*, 27–43.

Cuellar, E., & Noss, A. (2003). *Mamiferos del Chaco y de la Chiquitanía de Santa Cruz, Bolivia*. Santa Cruz, Bolivia: Editorial Fan.

De Almeida Jácomo, A. T., Malzoni-Furtado, M., Kashivakura, C. K., Marinho-Filho, J., Sollmann, R., Mundim-Tôrres, N., . . . Silveira, L. (2013). White-lipped peccary home-range size in a protected area and farmland in the central Brazilian grasslands. *Journal of Mammalogy*, *93*, 137–145.

Di Bitetti, M. S., Paviolo, A., Ferrari, C. A., De Angelo, C., & Di Blanco, Y. (2008). Differential responses to hunting in two sympatric species of brocket deer (*Mazama americana* and *M. nana*). *Biotropica*, *40*, 636–645.

Escamilla, A., Sanvicente, M., Sosa, M., & Galindo, C. (2000). Habitat mosaic, wildlife availability, and hunting in the tropical forest of Calakmul, México. *Conservation Biology*, *14*, 1592–1601.

Estrada, N. (2005). *Selección de hábitat y actividad diaria del chancho cariblanco Tayassu pecari en el Parque Nacional Corcovado: uso de trampas-cámara* (M.Sc. Thesis). Universidad Nacional de Costa Rica, Heredia, Costa Rica.

Fa, J. E., Peres, C. A., & Meeuwig, J. (2002). Bushmeat exploitation in tropical forest: An intercontinental comparison. *Conservation Biology*, *16*, 232–237.

Fang, T. G., Bodmer, R. E., Puertas, P. E., Mayor Aparicio, P., Perez Peña, P., Acero Villanes, R., & Hayman, D. T. (2008). *Certificación de pieles de pecaríes en la Amazonia Peruana*. Lima, Peru: Wust editions.

Fragoso, J. M. (1997). Desapariciones locales del báquiro labiado (*Tayassu pecari*) en la Amazonía: migración, sobre-cosecha o epidemia (extirpation of white-lipped peccary populations in Amazonia: Migration, overhunting or epidemic?). In T. Fang, R. Bodmer, R. Aquino, & M. Valqui (Eds.), *Wildlife management in Amazonia* (pp. 309–312). La Paz, Bolivia: United Nations Development Programme (UNEP).

Fragoso, J. M. (1998). Home range and movement patterns of white-lipped peccary (*Tayassu pecari*) herds in the Northern Brazilian Amazon. *Biotropica*, *30*, 458–469.

Garcia-Gil, G. (2003). *Colonización humana reciente y formación del paisaje agrario en la Reserva de la Biosfera de Calakmul, Campeche, México* (Ph.D. Dissertation). Universidad Nacional Autónoma de México, México, D. F.

Harrison, R. D., Tan, S., Plotkin, J. B., Slik, F., Detto, M., Brenes, T., . . . Novotny, V. (2013). Consequences of defaunation for a tropical tree community. *Ecology Letters*, *16*, 687–694.

Hernández, S. D. (2013). *Pecarí de collar (Pecari tajacu) L. en la región Nopala-Hualtepec, Hidalgo, México* (M.Sc. Thesis). Universidad Autónoma de Hidalgo, Pachuca, Hidalgo, México.

IUCN. (2011). *2011 Red list of threatened.* Retrieved from www.iucnredlist.org.

IUCN. (2013). *2013 Red list of threatened species*. Retrieved from www.iucnredlist.org.

Keurohglian, A., Eaton, D., & Longland, W. (2004). Area use by white-lipped and collared peccaries (*Tayassu pecari* and *Tayassu tajacu*) in a tropical forest fragment. *Biological Conservation*, *120*, 411–425.

Kilgo, J. C., Ronauld, R. F., & Fritzen, D. C. (1998). Influences of hunting on the behavior of white-tailed deer: Implications for conservation of the Florida panther. *Conservation Biology*, *6*, 1359–1364.

Kiltie, R., & Terborgh, J. (1983). Observations on the behavior of rain forest peccaries in Perú: Why do white-lipped peccaries form herds? *Thierpsychol*, *62*, 241–255.

Lira, T. I., Galindo, L., & Briones, M. (2012). Mamíferos de la Selva Zoque, México: Riqueza, uso y conservación. *Revista de Biología Tropical*, *60*, 781–797.

Maffei, L., Cuellar, R. L., & Noss, A. (2002). Uso de trampas cámara para la evaluación de mamíferos en el Ecotono Chaco-Chiquitanía. *Revista de Biología Tropical*, *11*, 55–65.

Mandujano, S. (1999). Variation in herd size of collared peccaries in a Mexican tropical forest. *The Southwestern Naturalist*, *44*, 199–204.

March, I. J. (1993). The white-lipped peccary (Tayassu pecary). In W. L. R. Oliver (Ed.), *Pigs, peccaries and hippos* (pp. 13–22). Gland, Switzerland: International Union for Conservation of Nature (IUCN).

March, I., & Mandujano, S. (2005). *Pecarí de collar*. In G. Ceballos & G. Oliva (Eds.), *Los mamíferos silvestres de México* (pp. 524–527). México, D. F. CONABIO-Fondo de Cultura Económica.

Marín, G. R., Gallina, S., Mandujano, S., & Weber, M. (2008). Densidad y distribución de ungulados silvestres en la reserva ecológica el Edén, Quintana Roo, México. *Acta Zoológica Mexicana*, *24*, 73–93.

Mayer, J. J., & Wetzel, R. M. (1987). Tayassu pecari. *Mammalian Species*, *293*, 1–7.

Medellín, R. A., Maffei, L., Zarza, H., Bárcenas, H., Cruz, E., Legaria, R., Ávila, S. (2006). Censos y monitoreo.In C. Chávez & G. Ceballos (Eds.), *El jaguar Mexicano en el siglo xxi: Situación actual y manejo* (pp. 25–35). México, D. F.: CONABIO-WWF-Telcel-Universidad Nacional Autónoma de México.

Monroy-Vilchis, O., Zarco-González, M., Rodriguez-Soto, C., Soria-Díaz, L., & Urios, V. (2011). Fototrampeo de mamíferos en la sierra Nanchititla, México. *Revista de Biología Tropical*, *59*, 373–383.

Montiel, S., Arias, L., & Dickinson, F. (1999). La cacería tradicional en el norte deYucatán: una práctica comunitaria. *Revista de Geografía Agrícola*, *29*, 43–52.

Morales, R., & Magaña, S. (2001). *Fuentes de impacto, necesidades de investigación científica y monitoreo en Calakmul, Campeche*. México, D. F: Pronatura Península de Yucatán, A. C. and The Nature Conservancy.

Moreira, J. F., Lopez, J. E., Garcia Anleu, R., Cordova, F., & Dubon, T. (2015). Tamaño, composición y patrones diarios de actividad de grupos de pecari labios blancos (*Tayassu pecari*) en el Parque Nacional Mirador- Rio Azul, Guatemala. *Therya*, *6*, 469–482.

Naranjo, E. J. (2002). *Population ecology and conservation of ungulates in the Lacandon Forest*, *Mexico* (Ph.D. Dissertation). University of Florida, Gainesville.

Naranjo, E. J., & Bodmer, R. E. (2007). Source-sink systems and conservation of hunted ungulates in the Lacandon Forest, Mexico. *Biological Conservation*, *138*, 412–420.

Naranjo, E. J., Amador-Alcalá, S. A., Falconi-Briones, F. A., & Reyna-Hurtado, R. A. (2015). Distribución, abundancia y amenazas a las poblaciones de tapir centroamericano (*Tapirus bairdii*) y pecarí de labios blancos (*Tayassu pecari*) en México. *Therya*, *6*, 227–249.

Pennington, T., & Sarukhán, J. (1998). *Árboles Tropicales de México*. México, D. F: UNAM-Fondo de Cultura Económica.

Peres, C. A. (1996). Population status of white-lipped *Tayassu pecari* and collared peccaries *P. tajacu* in hunted and unhunted amazonian forest. *Biological Conservation*, *77*, 115–123.

Peres, C. A. (2000). Evaluating the impact and sustainability of subsistence hunting at multiple Amazonian forest sites. In J. Robinson & E. Bennett (Eds.), *Hunting for sustainability in tropical forests* (pp. 31–57). New York, NY: Columbia University Press.

Peres, C. A., & Palacios, E. (2007). Basin-wide affects of game harvest on vertebrate population densities in Amazonian forest: Implications for animal-mediated seed dispersal. *Biotropica*, *3*, 304–315.

Redford, K. H. (1992). The empty-forest syndrome. *BioScience*, *42*, 412–422.

Reyna-Hurtado, R. (2009). Conservation status of the white-lipped peccary (*Tayassu pecari*) outside the Calakmul biosphere reserve in Campeche, Mexico: A synthesis. *Tropical Conservation Science*, *2*, 159–172.

Reyna-Hurtado, R., & Tanner, G. (2007). Ungulate relative abundance in hunted and non-hunted sites in Calakmul forest (Southern Mexico). *Biodiversity and Conservation*, *16*, 743–756.

Reyna-Hurtado, R., Beck, H., Altrichter, M., Chapman, C., Tyler, R., Keuroghlian, A., . . . Naranjo, E. J. (2016). What ecological and anthropogenic factors affect group size in white-lipped peccaries (*Tayassu pecari*)? *Biotropica*, *48*, 246–254.

Reyna-Hurtado, R., Moreira, F., Briceño-Méndez, M., San vicente, M., Mcnab, R., García, R., . . . Hyeroba, D. (2014). White-lipped peccaries with skin problems in the Maya Forest. *Suiform Soundings*, *13*, 28.

Reyna-Hurtado, R., Naranjo, E. J., Chapman, C., & Tanner, G. (2010). Hunting patterns, population density, group size, and conservation of the white-lipped peccary (*Tayassu pecari*) in the Calakmul Region of Mexico. *Oryx*, *44*, 88–96.

Reyna-Hurtado, R., O'Farrill, G., Sima, D., Andrade, M., Padilla, A., & Sosa, L. (2010). Las aguadas de Calakmul, reservorios de fauna Silvestre y de la riqueza natural de México. CONABIO. *Biodiversitas*, *93*, 1–6.

Robinson, J. G., & Einsenberg, J. F. (1985). Group size and foraging habits of collared peccary (*Tayassu tajacu*). *Journal of Mammalogy*, *66*, 153–155.

Santos, D., Naranjo, E. J., & Salazar, J. L. (2012). Wildlife uses and hunting patterns in rural communities of the Yucatan Peninsula, Mexico. *Journal of Ethnobiology and Ethnomedicine*, *8*, 38.

Sowls, L. K. (1997). *Javelinas and the other peccaries: Their biology, management and use*. College Station, TX: Texas A&M University Press.

Stoner, K. E., Vulinec, K., Wright, S. J., & Peres, C. A. (2007). Hunting and plant community dynamics in tropical forests: A synthesis. *Biotropica*, *39*, 385–392.

Vickers, W. (1991). Hunting yields and game composition over ten years in an Amazon Indian territory. In: J. G. Robinson, & K. Redford (Eds.). *Neotropical wildlife use and conservation* Chicago, IL: University of Chicago Press, pp. 53–81.

Weber, M. (2000). *Effects of hunting on tropical deer populations in southeastern México* (M.Sc. Thesis). Royal Veterinary College, University of London, London, England.