

Chapter 3

White-Lipped Peccary Home-Range Size in the Maya Forest of Guatemala and México

AUT José Fernando Moreira-Ramírez, Rafael Reyna-Hurtado, Mircea Hidalgo-Mihart, Eduardo J. Naranjo, Milton C. Ribeiro, Rony García-Anleu, Roan McNab, Jeremy Radachowsky, Melvin Mérida, Marcos Briceño-Méndez, and Gabriela Ponce-Santizo

3.1 Introduction

Understanding the spatial requirements of animals is crucial for addressing effective conservation planning, especially for endangered species that have important socio-economic values for rural communities and play key ecological roles, such as seed dispersers and seed predators (Beck 2006; Keuroghlian et al. 2009a, b). Habitat loss and overhunting are two of the main activities affecting wildlife in protected and communal areas (Bodmer et al. 1997; Fritz et al. 2009). Hunting in tropical forests

J. F. Moreira-Ramírez (✉) · R. Reyna-Hurtado
El Colegio de la Frontera Sur, Ciudad Industrial, Lerma,
Ciudad de Campeche, Campeche, México

Wildlife Conservation Society, Programa para Guatemala, Flores. Petén, Guatemala
e-mail: jfmoreira@ecosur.edu.mx

M. Hidalgo-Mihart
División Académica de Ciencias Biológicas, Universidad Juárez Autónoma de Tabasco,
Villahermosa, Tabasco, Mexico

E. J. Naranjo · M. Briceño-Méndez
El Colegio de la Frontera Sur, Carretera Panamericana y Periférico Sur s/n,
San Cristóbal de Las Casas, Chiapas, Mexico

M. C. Ribeiro
Laboratório de Ecologia Espacial e Conservação, Departamento de Ecologia, Universidade
Estadual Paulista, Rio Claro, São Paulo, Brazil

R. García-Anleu · R. McNab · M. Mérida · G. Ponce-Santizo
Wildlife Conservation Society, Programa para Guatemala, Flores. Petén, Guatemala

J. Radachowsky
Wildlife Conservation Society, Bronx, New York, USA

can exert a strong effect on the behavior and abundance of ungulates (Peres 2000; Naranjo and Bodmer 2007; Reyna-Hurtado and Tanner 2007; Endo et al. 2010; Reyna-Hurtado et al. 2010). Previous studies documented that hunting can have a negative impact on vertebrate populations and combined with habitat destruction can decrease Neotropical prey species to the point of causing local population extinction (Alvard et al. 1997; Reyna-Hurtado and Tanner 2007; Andrade Melo et al. 2015). In contiguous forests, where the persistence of populations in the sink habitat depends on their migration from high-quality source habitats (Pulliam 1988), the establishment of reserves can function as wildlife refuges for prey populations (Naranjo and Bodmer 2007), which is vital for the survival of hunted species (Peres 2001). Additionally, primary forests distant from human settlements are effective in maintaining biodiversity, even if not officially protected (Peres et al. 2003; Peres and Palacios 2007). Hunters often seek out larger animals, such as white-lipped peccaries (*Tayassu pecari*, Link 1795), which are favorite prey among hunters in the Neotropics (Peres 1996; Reyna-Hurtado and Tanner 2007; Santos-fita et al. 2012). White-lipped peccaries are social ungulates that form large and cohesive groups between 10 and 300 individuals (Altrichter et al. 2012; Moreira-Ramírez et al. 2015; Reyna-Hurtado et al. 2016). White-lipped peccaries are confined to the Neotropical Region, from southeastern Mexico to northern Argentina and Rio Grande do Sul in southern Brazil, moving across large areas of up to 200 km² (Fragoso 1998; Altrichter et al. 2012), and they are an important seed predator with a unique role as an ecosystem engineer (Beck 2006; Keuroghlian et al. 2009b). Local populations have declined at alarming rates throughout Mesoamerica in the last 20 years as a result of hunting pressure, habitat loss, and forest fragmentation (Peres 1996; Escamilla et al. 2000; Endo et al. 2010; Reyna-Hurtado et al. 2017), and the species is now confined to few large tropical forest reserves (Altrichter et al. 2012; Reyna-Hurtado et al. 2017). Currently, it is listed as vulnerable throughout all its distributional range (Keuroghlian et al. 2013).

In the Maya Forest of Mexico, hunting of white-lipped peccaries occurs mainly in the dry season (Reyna-Hurtado et al. 2010), resulting in lower abundances and smaller group sizes than in protected areas (Reyna-Hurtado and Tanner 2007; Reyna-Hurtado 2009; Briceño-Méndez et al. 2016). Previous studies have analyzed the home-range sizes of the white-lipped peccaries in fragmented and protected areas (Fragoso 1998; Carrillo et al. 2002; Keuroghlian et al. 2004, 2015; Reyna-Hurtado et al. 2009; Jacomo et al. 2013); however the effect of hunting on the groups' movement pattern is unknown. The only study carried out in the Calakmul Biosphere Reserve focused on estimating the home-range size and habitat preferences of white-lipped peccary (Reyna-Hurtado et al. 2009). This study showed that peccaries will undertake long-range movements to locate preferred types of habitats and water ponds on a landscape scale. To understand how the landscape dynamics of this region influence space use by white-lipped peccaries, we investigated, using GPS satellite collars, whether group home-range size is influenced by season and hunting. The present study reports white-lipped peccary's home-range sizes for four groups at three sites in the Maya Forest, and for the first time, information on the temporal and spatial movements of white-lipped peccaries in a hunting site is described. We explored the following question: Are there differences in home-range size between seasons in hunted and non-hunted sites? We hypothesized

that home ranges would be larger in the rainy season compared to the dry season and that home ranges would be larger in protected areas than the hunted site.

3.2 Materials and Methods

3.2.1 Study Site

The Maya Forest is the largest continuous remaining tropical rainforest in Mesoamerica. The area includes a ~31,000 km² protected forest that stretches across Belize, northern Guatemala, and throughout Mexico's Yucatan Peninsula. The forest is extensive and diverse, supporting large populations of many rare and endangered species such as white-lipped peccaries, jaguars (*Panthera onca*, Linnaeus, 1758), and tapirs (*Tapirus bairdii*, Gill 1975). Guatemala's 21,100 km² Maya Biosphere Reserve is adjacent to Mexico's 7238 km² Calakmul Biosphere Reserve to the north.

The study was carried out in three areas of the Maya Forest: Laguna del Tigre National Park (LTNP) in Guatemala and Calakmul Biosphere Reserve (CBR) and "ejido" Nuevo Becal (NB) in Mexico. An *ejido* is defined as a piece of land farmed communally under a system supported by the Mexican state. The LTNP and CBR are protected areas without the presence of hunting, and NB is a communal forest with human presence and where hunting is common (Fig. 3.1). Laguna del Tigre National Park is located to the west of the Maya Biosphere Reserve (MBR) in the vicinity of latitude 17°10'30" N and longitude -90°25'22" W. It has an extension of 3370 km², being the largest Core Zone of the MBR and the largest National Park in Guatemala. When the MBR was established in 1990, LTNP was declared a national park and became a Ramsar site (Moreira-Ramírez et al. 2016). The mean temperature in the dry season and rainy season is 30 °C and 25 °C, respectively. The accumulated rainfall for the year 2015 was 1483 mm (Estación Meteorológica Mactún, San Andrés, Petén, Instituto de Sismología, Vulcanología, Meteorología e Hidrología). The altitude varies between 40 and 200 m. There are two climatic seasons: the dry season is from December to May and the rainy season from June to November (Moreira-Ramírez et al. 2016). The LTNP faces serious threats in the center and west side of the park, as forest fires in the dry season are caused primarily by unplanned human settlements, land speculation for agriculture and ranching, and oil activities without mitigation (Consejo Nacional de Áreas Protegidas and Wildlife Conservation Society 2015).

The CBR, which was established in 1989, covers an area of 7238 km² and conserves the largest tropical forest in Mexico. It is located in the southeastern corner of the state of Campeche in the vicinity of latitude 18°07'21" N and longitude 89°48'56" W (García-Gil 2003). In this region, subhumid warm climate prevails; the average annual temperature is 24.6 °C. The rainy season is between June and November with an annual rainfall average of 1076 mm, varying from 900 mm in the northern part to more than 1400 mm in the southern part (Martínez and Galindo-Leal 2002). The accu-

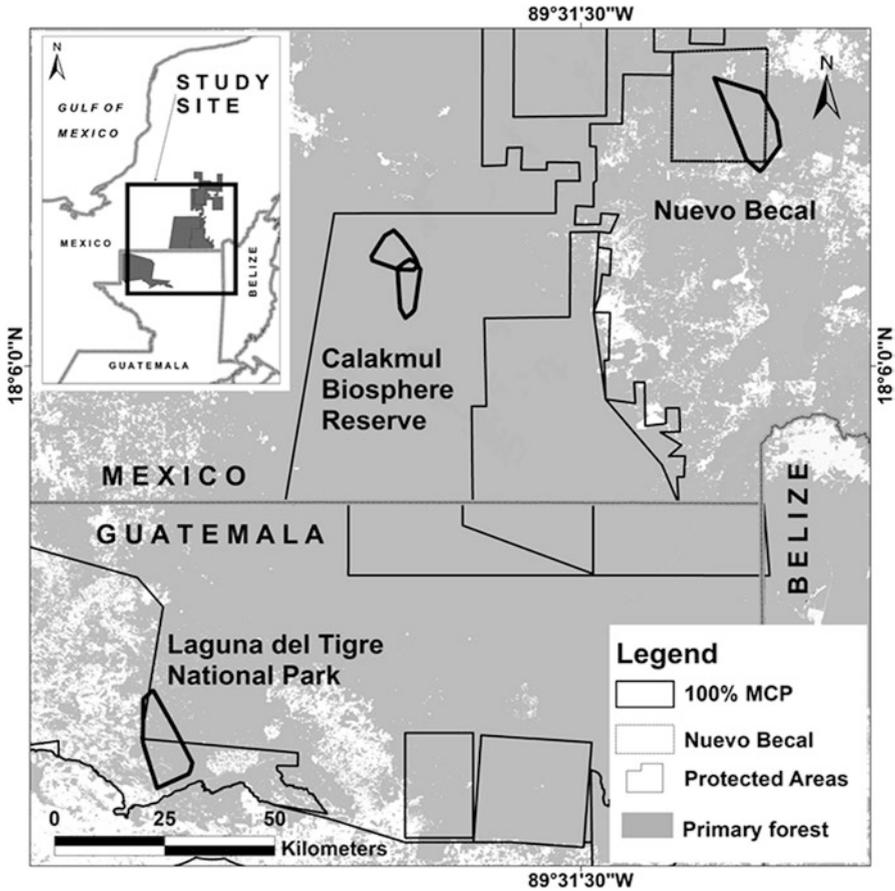


Fig. 3.1 Location of Laguna del Tigre National Park, Guatemala, and Calakmul Biosphere Reserve and “ejido” Nuevo Becal, Mexico, with the minimum convex polygon (100% MCP) home ranges of four white-lipped peccary groups

mulated rainfall in 2015 was 633 mm (Conhuás Weather Station, Calakmul, Comisión Nacional del Agua). The topography in the area is very flat (approximately 250 m above mean sea level) with the highest hills reaching 340 m above sea level. Since 1989, hunting has not been allowed within the CBR, and human activities inside the reserve are limited to tourism and research (Reyna-Hurtado and Tanner 2007).

The *ejido* NB is located in the vicinity of 18°40'07" N, 89°12'34" W, adjacent to the CBR. Nuevo Becal has an extension of 520 km², of which half is under forest management. The altitude varies between 100 and 380 m. The predominant climate is warm subhumid with summer rains and less than 60 mm of precipitation in the driest month. The annual average temperature is 25 °C, and the average

annual rainfall ranges from 1200 to 1500 mm in the center and 1500–2000 mm in the south (García-Gil 2003). The accumulated rainfall for 2015 was 762.7 mm (Zoh Laguna Weather Station, Calakmul, Comisión Nacional del Agua). Approximately 80% of the land is still forested (Reyna-Hurtado 2009). The main productive activities include farming, beekeeping, livestock production, and coal production. However, hunting is practiced year-round (Escamilla et al. 2000; Reyna-Hurtado and Tanner 2007; Santos-fita et al. 2012). Previous studies have shown that white-lipped peccary hunting occurs frequently in this community, which has resulted in smaller group sizes and relative abundance of this species in NB in comparison to CBR (Reyna-Hurtado and Tanner 2007; Briceño-Méndez et al. 2016).

3.2.2 *White-Lipped Peccary Monitoring*

In the dry season, white-lipped peccaries visit ponds frequently in search of water, mud, and food (Moreira-Ramírez et al. 2016). This behavior allowed us to capture peccaries in ponds near field camping sites (5–15 km) in the three study areas. The capture was done by chemical immobilization using ketamine (7.7 mg/kg) and xylazine hydrochloride (4.3 mg/kg) delivered by a dart rifle (Telinject Inc., Santa Clarita, California, and Pneu-Dart Inc., Williamsport, Pennsylvania) from a tree nearby a pond (Reyna-Hurtado et al. 2009). We weighed and recorded the age and sex of each animal, as well as standard morphometric measurements. All animals were captured and handled following the guidelines of the American Society of Mammalogists (Sikes et al. 2011) and from El Colegio de la Frontera Sur. We used satellite global positioning system (GPS) collars. We captured and radio-collared four and two white-lipped peccaries in the dry season of 2015 and 2016, respectively. The radio-collared animals belonged to 4 different groups corresponding to 1 in LTNP (minimum group size 46 individuals), 2 in CBR (each minimum group size: 30 individuals; CBR1, CBR2), and 1 in NB (minimum group size 25 individuals). We fitted 2 individuals with Telonics collars model TGW-4470-4 (1 in CBR and 1 in LTNP; Telonics Inc., Mesa, Arizona) and 4 with Vectronic collars model GPS PLUS Vertex Survey (1 in CBR, 2 in LTNP and 1 in NB; Vectronic Aerospace GmbH, Berlin, Germany). Animals recovered from immobilizations within 1–1.3 h, after which they usually rejoined their original group 1–3 days after capture. GPS collars were programmed to acquire a location every 2 h (12 locations/day, Telonics collars) and 12 h (2 locations/day, Vectronic collars) and to send data through the IRIDIUM and Globalstar system every 2 and 4 days for Telonics and Vectronic collars, respectively. Telonics collars included a programmable release mechanism (model CR-2A, Telonics Inc.), and we scheduled the drop-off mechanism to release 11–12 months after capture. The GPS collars were recovered when possible using the mortality locations obtained through the IRIDIUM and Globalstar system and by searching the VHF pulse of the collars using a receiver (Daninject Dart Guns, Austin, Texas). We were unable

to recover the GPS collar of the peccary captured in NB, and therefore we were unable to download additional fixes stored onboard. Due to this we obtained a variation in the fixes for this group.

3.2.3 *Home-Range Estimation and Analysis*

Many problems and limitations in home-range estimation were overcome by the recently developed autocorrelated kernel density estimates (AKDE) that can handle large autocorrelated movement datasets without the need of thinning the data or excluding inherent information from the data structure (Fleming et al. 2015). Autocorrelated kernel density estimate (AKDE) home ranges were calculated using R 3.3.2, package *ctmm* 0.3.6 (R Development Core Team 2012; Fleming et al. 2015; Calabrese et al. 2016; Moßbrucker et al. 2016), following the procedure of Fleming et al. (2015). After visualizing the autocorrelation structure to obtain starting values for the variance and autocorrelation timescales, we fitted three different continuous-time movement models to each white-lipped peccary dataset: (i) independent and identically distributed (IID), (ii) Ornstein–Uhlenbeck (OU, including autocorrelation in location; Dunn and Gipson 1977), and (iii) Ornstein–Uhlenbeck-F (OUF, including autocorrelation in both location and velocity; Fleming et al. 2014). From these three models, we selected the one with the best fit by comparing second-order Akaike information criterion values and then proceeded to calculate AKDE home ranges and confidence limits (Calabrese et al. 2016). These data were managed and stored in Movebank (<http://www.movebank.org> Wikelski and Kays 2017). We also used the fixed kernel estimator (KDE) (Kernohan et al. 2001), as this estimator is the recommended for investigations focusing on home-range boundaries (Millspaugh and Marzluff 2001) and has previously used to estimate the white-lipped peccaries (WLP): home range in Mexico (Reyna-Hurtado et al. 2009) and Brazil (Jacomo et al. 2013). KDE home ranges were estimated with the bandwidth (h) selected using the least square cross-validation method (LSCV; Seaman and Powell 1996; Seaman et al. 1999). For AKDE and KDE analyses, we considered 50% and 95% of the locations, the former to represent the core area of a peccary group's home range, the latter to represent its full range (Harris et al. 1990). Because of this differential spatial sampling effort and to facilitate comparisons with other studies, we further estimated home ranges for groups of white-lipped peccary by the minimum convex polygon (MCP) using the full dataset (100% of fixes). Both KDE and MCP were calculated using Geospatial Modelling Environment (Beyer 2012). We defined the dry season as December–May and the rainy season from June to November. Seasonal 95% and 50% KDE home ranges were estimated for both the dry and rainy seasons in 2015 and 2016 only for LTNP group. For groups CBR1 and CBR2, we estimated the home range only for the dry seasons of 2015 and 2016, respectively. For NB we estimated the home range for rainy season of 2015 and the dry season 2016. We compared home-range size during the dry and rainy

seasons with a Mann-Whitney-Wilcoxon Test and evaluated if the home-range sizes were influenced by the number of fixes obtained per individual using Spearman's correlation analysis. All spatial data were prepared and compiled using ArcMap 10 (ESRI 2011) and R software (R Development Core Team 2017) performed to the 0.05 confidence level.

3.3 Results

The monitoring of four groups of white-lipped peccary over periods of 2–16 months resulted in a total of 1322 GPS localizations available for analysis (Table 3.1). Mean error was 2.5 ± 1.6 m for localizations of Telonics collars and 2 ± 0.6 m for Vectronic collars. After recovering the collars and downloading the data stored, there we found that the fix success of the two Telonics collars varied between 85.1% and 96.3%. For the four Vectronic collars, the fix success was much lower and varied between 3.7% and 56.7% (mean = 21.7%). The home-range sizes of the LTNP and NB white-lipped peccaries groups when plotted against the number of tracking months (LTNP: 17 months; NB: 13 months) indicated that our sampling effort was adequate to describe the annual 100% MCP home-range sizes for these groups (Fig. 3.2). The home

Table 3.1 Satellite telemetry period, continuous-time movement model selection for autocorrelated kernel density estimation (AKDE) using the difference for finite sample size-corrected Akaike information criterion (Δ AICC) among the three models, independent and identically distributed (IID), Ornstein–Uhlenbeck (OU), and Ornstein–Uhlenbeck-F (OUF), and home-range estimates in Km² for four groups of white-lipped peccaries using 95% AKDE, including the 50% core area and confidence limits Cllow and Clup, the 95% kernel density estimation (KDE; including the 50% core area), and the 100% minimum convex polygon (MCP) estimates

Group	Telemetry period	Δ AICC IID	Δ AICC OU	Δ AICC OUF	95% AKDE {50% core area} (Cllow, Clup) [km ²]	95% KDE {50% core area} [km ²]	100% MCP [km ²]
LTNP	March 2, 2015–July 4, 2016	2548.97	0	2.05	156 {31} (96, 231) $n = 508$	99 {17}	138
CBR1	March 12, 2015–June 10, 2015	138.09	0	2.88	142 {28} (92, 203) $n = 102$	77 {15}	47
CBR2	March 15, 2016–May 13, 2016	ND	36.73	0	62 {15} (39, 89) $n = 682$	40 {7}	54
NB	May 10, 2015–June 19, 2016	34.88	0	3.1	312 {80} (178, 483) $n = 30$	140 {38}	154

ND No Data

n number of relocations available for analysis

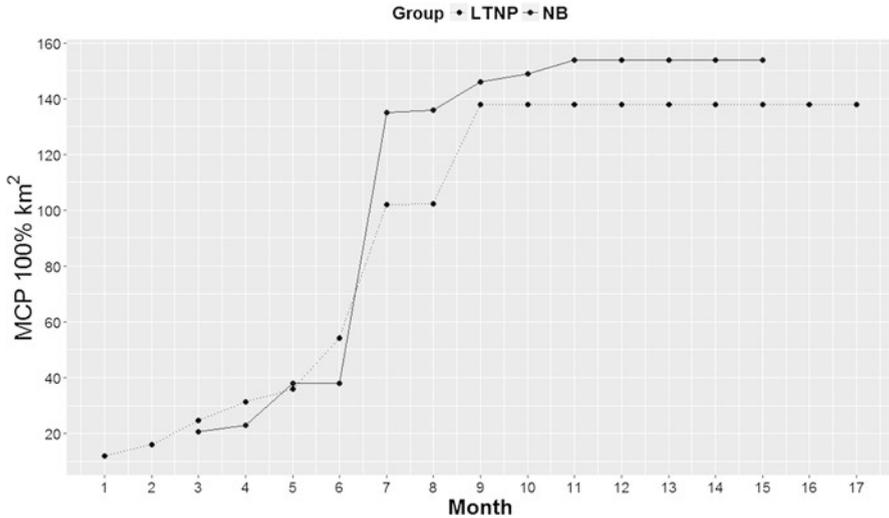


Fig. 3.2 The 100% minimum convex polygon home ranges of Laguna del Tigre National Park (LTNP, dotted line) and Nuevo Becal (NB, solid line) groups that were tracked in the Maya Forest obtained by cumulative sequential samples and then plotted versus the number of months tracked

ranges for CBR1 and CBR2 were likely underestimated because they were only monitored for 4 and 2 months, respectively. Of three groups, we were able to recover the collars to download the stored localizations. The collar from the NB group was not retrieved in the field because it did not generate a mortality signal possibly due to the battery running out. This collar only sent sporadic locations, on average three locations per month. This could be due to several factors, such as canopy cover, mud in the collar antenna, or simply failure to connect with the satellites. In spite of this situation, we considered that the number of locations obtained for this group and the time span tracked allowed for a reliable home-range estimate of the NB group.

AKDE were obtained for all four white-lipped peccary groups (Fig. 3.3, Table 3.1), with the model OU performing best for all but one group (CBR2, Table 3.1), for which the OUF model reached a smaller AKDE value, most likely owing to the more continuous movements observed for this particular group and for the shorter time interval that it was followed. The home-range estimation using AKDE, KDE, and MCP was lower for the three groups of the non-hunted sites than that of the group at the hunted site. The 95% AKDE area estimates for non-hunted sites ranged from 62 km² (C_{low} = 39, C_{up} = 89) for CBR2 to 156 km² (C_{low} = 96, C_{up} = 231) for LTNP. For the hunted site (NB), AKDE estimate was 312 km² (C_{low} = 178, C_{up} = 483). Core area estimates using the 50% AKDE in non-hunted sites ranged from 15 km² for CBR2 to 31 km² for LTNP and were smaller than that of the hunted site in NB (80 km²). The 95% KDE home-range area estimates for non-hunted sites ranged from 40 km² (CBR2) to 99 km² (LTNP). Considering the estimate from LTNP as more reliable due to the fact that this group was monitored

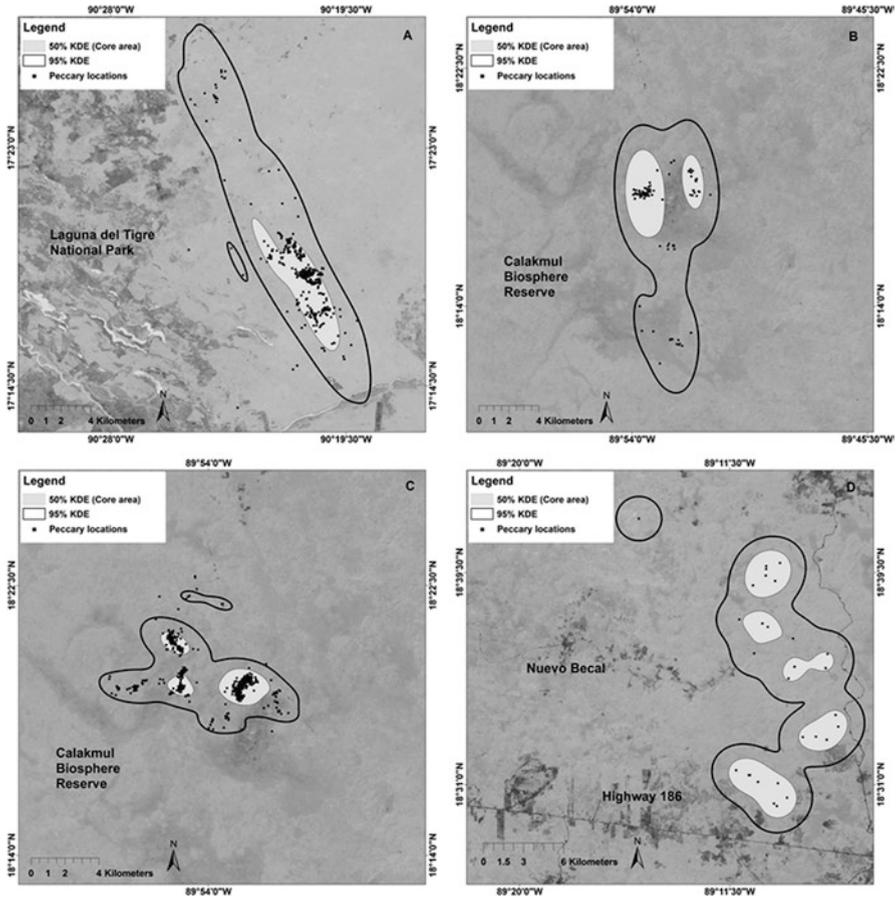


Fig. 3.3 Kernel density estimation (95% KDE) home ranges and 50% core area of four white-lipped peccary groups. (a) Laguna del Tigre National Park. (b) Calakmul Biosphere Reserve 1. (c) Calakmul Biosphere Reserve 2. (d) Nuevo Becal

for more than a year, we still found this estimate substantially smaller than the hunted site with 140 km². Core area estimates using the 50% KDE in non-hunted sites ranged from 7 km² for CBR2 to 17 km² for LTNP and were smaller than that of the hunted site in NB with 38 km². Similarly, the 100% MCP area estimates for non-hunted sites varied between 47 km² (CBR1) and 138 km² (LTNP), which were substantially smaller than the MCP area estimates at the hunted site with 154 km² (Table 3.1). When we compared the two sites where movement data exceeded 10 months, we observed that in the NB area, where the level of hunting pressure was higher, the 95% AKDE, 95% KDE, and 100% MCP home-range estimates were 156 km² (100%), 41 km² (41%), and 16 km² (12%) larger, respectively, than the non-hunted site in LTNP. In addition, when we compared the 95% KDE home-range size between the LTNP and NB groups only for the rainy season of 2015 and

Table 3.2 White-lipped peccary home-range estimates for four groups in the Maya Forest of Guatemala and Mexico in dry and rainy seasons using 95% kernel density estimation (KDE)

Group	95% KDE {50% core area} [km ²]			
	Dry season 2015 {50% core area}	Rainy season 2015 {50% core area}	Dry season 2016 {50% core area}	Rainy season 2016 {50% core area}
LTNP	36 {8}	106 {42}	4 {1}	14 {3}
CBR1	57 {11}	ND	ND	ND
CBR2	ND	ND	40 {7}	ND
NB	ND	103 {15}	132 {29}	ND

ND No data

between the LTNP, CBR2, and NB groups only for the dry season of 2016, the hunted site still presents a larger home-range size compared with the two non-hunted sites (Table 3.2).

There was no correlation between the home-range size and the number of fixes obtained per group for 95% AKDE ($\rho = -0.8$, $S = 18$, $P = 0.33$), 95% KDE ($\rho = -0.8$, $S = 18$, $P = 0.33$), and 100% MCP ($\rho = -0.4$, $S = 14$, $P = 0.75$). There were no significant differences in home-range size between the AKDE and KDE estimators (50%: Mann-Whitney-Wilcoxon Test $W = 11.5$, $P = 0.38$; 95%: Mann-Whitney-Wilcoxon Test $W = 3$, $P = 0.2$). For the LTNP and NB groups, we obtained an asymptote in the 100% MCP size for 7 and 5 months, respectively, because we were able to obtain information on the movements of the two groups for more than 12 months. The LTNP group showed an annual pattern of seasonal movements by visiting the capture pond at the beginning of February 2016, 1 year after the first white-lipped peccary was captured. Later they moved 18 km toward the northwest in August. The group in LTNP, a non-hunted site, increased their home-range movements substantially during the rainy season (Table 3.2). We estimated a home range of 36 km² and 106 km² for the 2015 dry season and 2015 rainy season, respectively, for the LTNP group using 95% KDE. This same pattern was observed in 2016 in the same place where we estimated a home range of 4 km² and 14 km² for the dry season and rainy season, respectively. In contrast, the NB group (hunted site) presented a larger home range in the dry season (132 km²) compared to the rainy season (103 km²). After capture, the NB group made a displacement of 12 km southeast of the *ejido*, remaining in that area from May to August. In September, the group traveled further south, staying just 3 km away from federal highway 186, which may have served as a barrier. At the end of March, the group returned to the central area of their home range, remaining there until June, when contact was lost with the group. However, we did not find significant differences in home-range sizes between the two seasons for non-hunted sites (Mann-Whitney-Wilcoxon Test; $W = 3$, $P = 0.8$). At non-hunted sites, we recorded white-lipped peccary group sizes as 46 individuals in LTNP and 30 individuals in CBR, both slightly larger than the estimated group size of 25 individuals at the hunted site NB.

3.4 Discussion

Home-range size of white-lipped peccary groups in non-hunted sites (CBR and LTNP) was smaller than in the group of the hunted site (NB), contrary to our hypothesis. This movement pattern suggests that the hunting has some influence on the behavior of this group in NB. A similar pattern was found in Mato Grosso do Sul, Brazil, where the impact of forest deforestation and fragmentation on mammals was compared by analyzing home ranges of two white-lipped peccary groups between a pristine and a disturbed area. In the disturbed habitat, the home-range area was 51% larger than that of the pristine area because animals resorted to changing their routes and using larger areas to find enough resources (Keuroghlian et al. 2015).

In the Maya Forest of México, previous studies showed that the status of white-lipped peccary populations outside the protected areas is of special concern due to several factors such as overhunting (Reyna-Hurtado and Tanner 2007; Reyna-Hurtado 2009; Reyna-Hurtado et al. 2010). Estimates of white-lipped peccary group sizes in protected areas were bigger than in areas heavily used by humans, where there is hunting pressure by subsistence and sport hunters (Briceño-Méndez et al. 2016). The hunting season occurs mainly in the dry season when this species is highly vulnerable because groups congregate in the remaining water ponds that did not dry up. Subsistence hunting harvest rates are probably larger than is sustainable for this population (Reyna-Hurtado 2009; Briceño-Méndez et al. 2016).

In order to compare our results with other studies, we relied on the KDE values, as this method was better adjusted to the white-lipped peccary biology in our study area and showed a more precise contour of the areas where the groups move. Our home-range estimates in non-hunted sites (95% KDE: 40–99 km²) were similar to those previously determined at CBR, between 39 and 98 km² using 95% fixed kernel and 23–122 km² using 100% MCP (Reyna-Hurtado et al. 2009), and at a relatively pristine area of the southern Pantanal, Mato Grosso do Sul, Brazil, where home ranges were estimated between 46 and 55 km² using 95% kernel method and the 95% harmonic mean (Keuroghlian et al. 2015). Home ranges observed in our study were larger than estimates from most other studies. At the Bladen Nature Reserve, Belize, home range was estimated at 55 km² for a single group using 95% AKDE (Hofman et al. 2016). In a fragmented area of the Atlantic Forest of Brazil, average home range was estimated to be 18.7 km² for three to four groups using a 90% harmonic mean estimator (Keuroghlian et al. 2004). In Corcovado National Park, Costa Rica, annual MCP home ranges were reported between 32 and 38 km² for one group (Carrillo et al. 2002). In Maracá Island, Roraima, Brazil, white-lipped peccaries' (WLP) home range was 21.8 km² (Fragoso 1998). In Panama in the Darien National Park, Meyer et al. (2018; this book) estimated between 42 and 76 km²: studies that reported similar or larger home ranges compared to our study have also had larger group sizes, ranging from 56 to 130 individuals. Examples include the Cerrado ecosystem in Goiás State, Brazil (277, 147, and 91 km² for groups of 65, 70, and 110 individuals, respectively—Jacomino et al. 2013); the southern Pantanal, Mato Grosso do Sul, Brazil, where the level of disturbance due to

deforestation was higher (80 km² using 95% MCP for a group of 56 individuals—Keuroghlian et al. 2015); and Maracá Island, Roraima, Brazil with a home range of 110 and 200 km² using 100% MCP for groups of 130 and >200 individuals, respectively (Fragoso 1998, 2004).

Our results suggest that in the Maya Forest, groups are smaller in size (25–46 individuals) and move in larger areas compared to other sites in the Neotropics. This pattern is similar to that reported previously by Reyna-Hurtado et al. (2009). In hunted areas, group sizes tend to decrease considerably, while the group occupies larger areas in comparison to most preserved, non-hunted regions, possibly because of the need to evade hunters, especially during the dry season. Water ponds in the Maya Forest are seasonal and are likely the dominant environmental resources contributing to nomadic movements of white-lipped peccary in this area (Reyna-Hurtado et al. 2009). Two groups of white-lipped peccaries in Roraima, Brazil (Fragoso 1998), and four groups in CBR, México (Reyna-Hurtado et al. 2009), visited the same pond on a regular basis over one or two seasons, respectively. This pattern was also observed for the group in the protected site (LTNP). In the 2015 and 2016 dry seasons, the LTNP group visited the same pond where we captured and collared the animals, as this is a year-round pond, providing surface water in this critical season of the year.

The white-lipped peccary group in the LTNP increased their home range in the rainy season, suggesting that water availability is the most important factor that determines the movements of this species and consistent with our hypothesis. This pattern is similar to that reported previously in CBR, where four groups increased their home ranges at the beginning of the rainy season (Reyna-Hurtado et al. 2009), suggesting that water availability in non-hunted sites in the Maya Forest is the key factor that determines the movement of this species (Reyna-Hurtado et al. 2012). In contrast, in NB, where hunting of ungulates is common, especially in the dry season (Reyna-Hurtado et al. 2010; Briceño-Méndez et al. 2016), the white-lipped peccary group modified their movement patterns during this time, resulting in slightly larger home ranges in the dry season compared to the rainy season (Table 3.2). This change in the movement pattern of the NB group in the dry season suggests that hunting pressure (Reyna-Hurtado et al. 2012) may influence the movement of this social species. In other studies, food resources appear to be the main driver for the movements of white-lipped peccaries. In Corcovado National Park, the home ranges of white-lipped peccaries were smaller from June to September, which encompassed the majority of the rainy season and produced an increased abundance of fruits (Carrillo et al. 2002). Likewise, in the Atlantic Forest, Brazil, it was found that the seasonal movements of white-lipped peccaries were apparently driven by the supply of key fruits, rare habitats, and riparian zones (Keuroghlian et al. 2004, 2009b; Keuroghlian and Eaton 2008). In the Cerrado ecosystem in Goiás State, Brazil, it seems that a combination of low food resources and reduction in the availability of surface water forced white-lipped peccary groups to occupy larger areas when foraging during the rainy season and to remain closer to the few water sources in the dry season (Jacomino et al. 2013).

The effect of hunting is demonstrated in a large-scale study across white-lipped peccary geographic distribution: hunting pressure, which was highly correlated with proximity to the nearest settlement, has a detrimental effect on group size and density for larger groups living in areas farther from human settlements (Reyna-Hurtado et al. 2016). In addition, it is important to address the potential risk of disease transmission by domestic animals to white-lipped peccaries, since they form large and cohesive groups which may speed up an epidemic outbreak with a reinfection cycle (Fragoso 2004). In the Maya Forest, white-lipped peccary skin problems have been reported through photographic records obtained with camera traps (Reyna-Hurtado et al. 2014). Assessment on the health and diseases in populations of white-lipped peccaries and domestic animals in close proximity to wildlife areas is an important subject to be addressed in the Maya Forest and Mesoamerica.

Our results indicate that although drier than NB, which has bigger water ponds that allowed people to colonize this area, CBR still maintains a greater group size than that of NB. While similar in water availability, the estimate for LTNP annual home range was smaller than and the group size was larger than the respective estimates for NB, perhaps due to the lack of hunting in LTNP. These results suggest that hunting in areas with human settlements puts greater pressure on the ecology of white-lipped peccary, resulting in smaller group sizes and use of larger home range compared with non-hunted sites.

Although we only monitored one group in NB and obtained relatively few GPS locations for several reasons, such as percent canopy cover, the results showed that the group has a large annual home range, increasing in the dry season when hunting is more frequent. In contrast, in non-hunted areas, the home ranges are smaller, and during the dry season, the groups remained close to water ponds, expanding their home range when the rainy season began. We recognize that our results could be biased by the small number of groups we monitored and that this sample size may not be representative of the population of white-lipped peccaries of our study area. Therefore, we consider that it is important to carry out further studies in areas with hunting pressure to estimate the movements of more white-lipped peccary groups to obtain higher fixes and compare them with our results and to promote conservation actions in protected and communities' areas. Our data suggest that white-lipped peccary groups required large areas to meet their spatial requirements in the Maya Forest. This has important implications for the management and conservation plans for this species at the landscape scale primarily because habitat destruction and fragmentation would have severe effects on white-lipped peccary population. Although the white-lipped peccary can persist in highly altered landscapes in South America (Jacomo et al. 2013), it prefers to use forested areas rather than sites close to human settlements and secondary forests associated with high human activities (Keuroghlian et al. 2015; Reyna-Hurtado et al. 2016).

White-lipped peccaries are experiencing population declines throughout their range (Altrichter et al. 2012; Reyna-Hurtado et al. 2017), specifically in Guatemala and México; its current distribution makes up only 10% and 16%, respectively, of its historical distribution (Altrichter et al. 2012; Moreira-Ramírez 2017). Due to the eminent threats to white-lipped peccaries and their habitat, we propose that efforts

should be taken to improve monitoring and surveillance in protected and communities' areas to decrease excessive hunting. Furthermore, joint conservation and monitoring strategies should be developed with government institutions and civil society in the three countries that are part of the Maya Forest. The Maya Forest in Guatemala, México, and Belize embraces the largest contiguous area of tropical forest habitat available for white-lipped peccary in Mesoamerica (Sanderson et al. 2002; Altrichter et al. 2012). Effective conservation at tri-national level of protected areas and integrating local communities will allow for the maintenance of viable populations of white-lipped peccaries in the future. Consistent communication with communities adjacent to protected areas is essential. Dialogue with community members about the current status of the peccaries, managing subsistence hunting, and declaring areas with strict protection for wildlife within their communal lands are initiatives that will contribute to the conservation of the species. Low-impact ecotourism should be promoted in water ponds of national parks and communal areas to observe large mammals, such as peccaries, to generate additional economic income. Our data suggest that the following conservation steps should be taken: protection against hunting, restrictions on road construction, reduction of large-scale agriculture and forest conversion for grazing, and landscape conservation of large, continuous, and ecologically diverse areas containing a mosaic of habitat types that guarantee the survival of this species. Finally, this study shed light in differences in home-range size and movement patterns of a species that is under hunting pressure. Evaluating changes in movement are a research priority for this highly mobile species as these changes can indicate the impact of human activities in wildlife.

Acknowledgments To the National Council of Science and Technology of Mexico for the grant offered to the first author to carry out his doctoral dissertation. We would like to give thanks to the American Society of Mammalogists, the Wildlife Conservation Society Research Fellowship Program, El Colegio de la Frontera Sur, Unidad Campeche, the Council of Science and Technology of Mexico (CONACYT) for the support of the Mexican research part through the project number 182386 to RR-H, to McGill University for providing cameras, and to the Rufford Foundation and Idea Wild for financial support. We would also like to thank the National Council of Protected Areas of Guatemala, the National Commission of Protected Natural Areas of Mexico, the *ejidatarios* of Nuevo Becal, the National Institute of Anthropology and History and Las Guacamayas Biological Station for the support, permits, and facilities provided. Lastly, we would like to thank N. Arias, G. Castillo, A. Hettena, W. Martínez, K. Sánchez, K. Tut, P. Pérez, C. Umaña, Y. Polanco, A. Xol, R. Chatá, and anonymous reviewers for their help. MCR is funded by FAPESP (process 2013/50421-2) and receives the research grant from CNPq (process 312045/2013-1).

References

- Altrichter M et al (2012) Range-wide declines of a key Neotropical ecosystem architect, the Near Threatened white-lipped peccary *Tayassu pecari*. *Oryx* 46:87–98
- Alvard MS, Robinson JG, Redford KH, Kaplan H (1997) The sustainability of subsistence hunting in the Neotropics. *Conserv Biol* 11:977–982

- Andrade Melo ÉR, Gadelha JR, da Silva M d ND, da Silva AP, Mendes AR (2015) Diversity, abundance and the impact of hunting on large mammals in two contrasting forest sites in northern amazon. *Wildl Biol* 21:234–245
- Beck H (2006) A review of peccary–palm interactions and their ecological ramifications across the Neotropics. *J Mammal* 87:519–530
- Beyer HL (2012) Geospatial modelling environment (version 0.7.3.0). www.spatial ecology.com/gme
- Bodmer RE, Eisenberg JF, Redford KH (1997) Hunting and the likelihood of extinction of Amazonian mammals. *Conserv Biol* 11:460–466
- Briceño-Méndez M, Naranjo EJ, Mandujano S, Altricher M, Reyna-Hurtado R (2016) Responses of two sympatric species of peccaries (*Tayassu pecari* and *Pecari tajacu*) to hunting in Calakmul, Mexico. *Trop Conserv Sci* 9:1–11
- Calabrese JM, Fleming CH, Gurarie E (2016) ctmm: an R package for analyzing animal relocation data as a continuous-time stochastic process. *Methods Ecol Evol* 7:1124–1132
- Carrillo E, Saenz JC, Fuller TK (2002) Movements and activities of white-lipped peccaries in Corcovado. *Biol Conserv* 108:317–324
- Consejo Nacional de Áreas Protegidas, Wildlife Conservation Society (2015) Monitoreo de la gobernabilidad en la Reserva de Biosfera Maya. Actualización a 2014 de la versión de septiembre de 2013. San Benito
- Dunn JE, Gipson PS (1977) Analysis of radio telemetry data in studies of home range. *Biometrics* 33:85–101
- Endo W et al (2010) Game vertebrate densities in hunted and nonhunted forest sites in Manu National Park. *Biotropica* 42:251–261
- Escamilla A, Sanvicente M, Sosa M, Galindo-Leal C (2000) Habitat mosaic, wildlife availability, and hunting in the tropical forest of Calakmul, Mexico. *Conserv Biol* 14:1592–1601
- ESRI (2011) ArcView GIS. Ver. 10.1. Environmental System Research Institute, Redlands
- Fleming CH, Calabrese JM, Mueller T, Olson KA, Leimgruber P, Fagan WF (2014) From fine-scale foraging to home ranges: a semivariance approach to identifying movement modes across spatiotemporal scales. *Am Nat* 183:E154–E167
- Fleming CH, Fagan WF, Mueller T, Olson KA, Leimgruber P, Calabrese JM (2015) A new autocorrelated kernel density estimator reports. *Ecology* 96:1182–1188
- Fragoso JMV (1998) Home range and movement patterns of white-lipped peccary (*Tayassu pecari*) herds in the Northern Brazilian Amazon. *Biotropica* 30:458–469
- Fragoso JMV (2004) A long-term study of white-lipped peccary (*Tayassu pecari*) population fluctuation in northern Amazonia. In: Silvius K, Bodmer RE, Fragoso JMV (eds) *People in nature, wildlife conservation in South and Central America*. Columbia University Press, New York, pp 286–296
- Fritz SA, Bininda-Emonds ORP, Purvis A (2009) Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. *Ecol Lett* 12:538–549
- García-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
- Harris S, Cresswell WJ, Forde PG, Trehwella WJ, Woollard T, Wray S (1990) Home range analysis using radio tracking data: a review of problems and techniques particularly as applied to the study of mammals. *Mammal Rev* 20:97–123
- Hofman MPG, Signer J, Hayward MW, Balkenhol N (2016) Spatial ecology of a herd of white-lipped peccaries (*Tayassu pecari*) in Belize using GPS telemetry: challenges and preliminary results. *Therya* 7:21–37
- Jacomo AT et al (2013) White-lipped peccary home-range size in a protected area and farmland in the central Brazilian grasslands. *J Mammal* 94:137–145
- Kernohan BJ, Gitzen RA, Millspaugh JJ (2001) Analysis of animal space use and movement. In: Millspaugh JJ, Marzluff JM (eds) *Radio tracking and animal populations*. Academic, San Diego, pp 125–166

- Keuroghlian A, Eaton DP (2008) Importance of rare habitats and riparian zones in a tropical forest fragment: preferential use by *Tayassu pecari*, a wide-ranging frugivore. *J Zool* 275:283–293
- Keuroghlian A, Eaton DP, Longland WS (2004) Area use by white-lipped and collared peccaries (*Tayassu pecari* and *Tayassu tajacu*) in a tropical forest fragment. *Biol Conserv* 120:411–425
- Keuroghlian A, Eaton DP, Desbiez ALJ (2009a) The response of a landscape species, white-lipped peccaries, to seasonal resource fluctuations in a tropical wetland, the Brazilian pantanal. *Int J Biodiver Conserv* 1:87–97
- Keuroghlian A, Eaton DP, Desbiez AL (2009b) The response of a landscape species, white-lipped peccaries, to seasonal resource fluctuations in a tropical wetland, the Brazilian pantanal. *Biodivers Conserv* 1:87–97
- Keuroghlian A et al (2013) *Tayassu pecari*. In: IUCN 2017. The IUCN Red List of Threatened Species. Version 2017.1. www.iucnredlist.org. Accessed 1 Aug 2017
- Keuroghlian A, Andrade Santos MDC, Eaton DP (2015) The effects of deforestation on white-lipped peccary (*Tayassu pecari*) home range in the southern Pantanal. *Mammalia* 79:491–497
- Martínez E, Galindo-Leal C (2002) La vegetación de Calakmul, Campeche, México: clasificación, descripción y distribución. *Bol Soc Bot Méx* 71:7–32
- Meyer N, Moreno R, Martínez-Morales MA, Reyna-Hurtado R (2018). Spatial ecology of a large and endangered tropical mammal: the white-lipped peccary in Darién, Panama. In: Reyna-Hurtado R, Chapman C (eds) *Movement Ecology of Neotropical Forest Mammals*. Springer Nature
- Millspaugh JJ, Marzluff JM (2001) Radio tracking and animal populations. Academic, San Diego
- Moreira-Ramírez JF (2017) Movimientos del pecarí de labios blancos en relación con la disponibilidad de agua y cacería en la Selva Maya de Guatemala y México. Ph.D. Dissertation, El Colegio de la Frontera Sur. Campeche, México
- Moreira-Ramírez JF, Lopez JE, García-Anleu R, Córdova F, Dubón T (2015) Tamaño, composición y patrones diarios de actividad de grupos de pecarí de labios blancos (*Tayassu pecari*) en el Parque Nacional Mirador-Río Azul, Guatemala. *Therya* 6:469–482
- Moreira-Ramírez JF et al (2016) Importance of waterholes for white-lipped peccary (*Tayassu pecari*) in the Selva Maya, Guatemala. *Therya* 7:51–64
- Moßbrucker MA, Fleming CH, Ali Imron M, Satyawan P, Sumardi (2016) AKDE C home range size and habitat selection of Sumatran elephants. *Wildl Res* 43:566–575
- Naranjo EJ, Bodmer RE (2007) Source-sink systems and conservation of hunted ungulates in the Lacandon Forest, Mexico. *Biol Conserv* 138:412–420
- Peres CA (1996) Population status of white-lipped *Tayassu pecari* and collared peccaries *T. tajacu* in hunted and un hunted Amazonian forests. *Biol Conserv* 77:115–123
- Peres CA (2000) Effects of subsistence hunting on vertebrate community structure in Amazonian forests. *Conserv Biol* 14:240–253
- Peres CA (2001) Synergistic effects on Amazonian forest vertebrates fragmentation. *Conserv Biol* 15:1490–1505
- Peres CA, Palacios E (2007) Basin wide effects of game harvest on vertebrate population densities in Amazonian forests: implications for animal mediated seed dispersal. *Biotropica* 39:304–315
- Peres CA, Barlow J, Haugaasen T (2003) Vertebrate responses to surface wildfires in a central Amazonian forest. *Oryx* 37:97–109
- Pulliam DW (1988) Sources, sinks, and population regulation. *Am Soc Nat* 132:652–661
- R Development Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna www.R-project.org/2009
- R Development Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org/, 2009
- Reyna-Hurtado R (2009) Conservation status of the white-lipped peccary (*Tayassu pecari*) outside the Calakmul Biosphere Reserve in Campeche, Mexico: a synthesis. *Trop Conserv Sci* 2:159–172

3 White-Lipped Peccary Home-Range Size in the Maya Forest of Guatemala...

- Reyna-Hurtado R, Tanner GW (2007) Ungulate relative abundance in hunted and non-hunted sites in Calakmul Forest (Southern Mexico). *Biodivers Conserv* 16:743–756
- Reyna-Hurtado R, Rojas-Flores E, Tanner GW (2009) Home range and habitat preferences of white-lipped peccaries (*Tayassu pecari*) in Calakmul, Campeche, Mexico. *J Mammal* 90:1199–1209
- Reyna-Hurtado R, Naranjo E, Chapman C a, Tanner GW (2010) Hunting and the conservation of a social ungulate: the white-lipped peccary *Tayassu pecari* in Calakmul, Mexico. *Oryx* 44:89
- Reyna-Hurtado R, Chapman CA, Calme S, Pedersen EJ (2012) Searching in heterogeneous and limiting environments: foraging strategies of white-lipped peccaries (*Tayassu pecari*). *J Mammal* 93:124–133
- Reyna-Hurtado R et al (2014) White-lipped peccaries with skin problems in the Maya Forest. *Suiform Soundings* 13:29–31
- Reyna-Hurtado R et al (2016) What ecological and anthropogenic factors affect group size in white-lipped peccaries (*Tayassu pecari*)? *Biotropica* 48:246–254
- Reyna-Hurtado R et al (2017) White-lipped peccary in Mesoamerica: status, threats and conservation actions. *Suiform Soundings* 15:31–35
- Sanderson EW, Jaiteh M, Levy M a, Redford KH, Wannebo AV, Woolmer G (2002) The human footprint and the last of the wild. *Bioscience* 52:891–904
- Santos-fita D, Naranjo EJ, Rangel-salazar JL (2012) Wildlife uses and hunting patterns in rural communities of the Yucatan Peninsula, Mexico. *J Ethnobiol Ethnomed* 8:38
- Seaman E, Powell RA (1996) An evaluation of the accuracy of kernel density. *Ecology* 77:2075–2085
- Seaman DE, Millspaugh JJ, Kernohan BJ, Brundige GC, Raedeke KJ, Gitzen RA (1999) Effects of sample size on kernel home range estimates. *J Wildl Manag* 63:739–747
- Sikes RS, Gannon WL, Care A, Committee U, Journal S (2011) Guidelines of the American Society of Mammalogists for the use of wild mammals in research guidelines of the American Society of Mammalogists for the use of wild mammals in research. *J Mammal* 92:235–253
- Wikelski M, Kays R (2017) Movebank: archive, analysis and sharing of animal movement data. www.movebank.org

Author Query

Chapter No.: 3 0004223406

Query	Details Required	Author's Response
AU1	Please confirm the affiliation details for all the authors.	