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Inventory of medium-sized and large mammals in the wetlands of Laguna de Terminos and Pantanos de Centla, Mexico

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Abstract

Wetlands are one of the most productive ecosystems in the world. However, they have received little attention in the tropics. Biodiversity data from the Terminos-Centla wetlands is limited despite the conservation efforts to protect these wetlands. In this study we list the medium-szied and large mammals from 8 sites within the Terminos-Centla wetlands. We recorded 30 native and 1 introduced species, representing 9 orders, 14 families, and 27 genera. Four of the recorded species are Threatened, 9 Endangered, and 1 under special protection under Mexican legislation. Compared with other sites of southeastern Mexico, the area of the Terminos-Centla wetlands has a many more species. Our results highlight the Terminos-Centla wetlands as one of the most important systems of Mesoamerica for the medium-sized and large mammals and and underlines the urgent need to develop conservation strategies for the area.

Key words

Tabasco; Campeche; Natural Protected Areas; deforestation; inventories.

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Introduction

Wetlands are among the ecosystems with the highest primary productivity of the world, yet in the tropics, they have received much less scientific attention than rainforests and other forested ecosystems (Ellison 2004). Tropical wetlands, in general, are highly threatened (Junk 2002), although in Mexico, coastal mangroves, a type of wetland, have legal protection. However other inland freshwater wetlands have much weaker legal protection (Landgrave and Moreno-Cassasola 2012).

The main strategy for protecting wetlands in Mexico has been the declaration of Natural Protected Areas (NPA). The Terminos Lagoon Flora and Fauna Protection Area (TLFFPA) and Pantanos de Centla Biosphere Reserve (PCBR; hereafter called Terminos-Centla wetlands) are two NPAs created fundamentally to protect the wetlands in the region of the Gulf of Mexico. Together

they form the most important coastal ecological unit of Mesoamerica (Rivera-Arriaga and Villalobos-Zapata 2005). Despite their declaration as NPAs and conservation efforts to protect these wetlands, they have suffered considerable destruction in the last 50 years. From 1990 to 2000, the forest, composed of *Bucida buceras* in Pantanos de Centla, decreased by 8%, while the remnants of the *Haematoxylum campechianum* forest decreased almost 100% (Guerra-Martínez and Ochoa-Gaona 2008). From 1974 to 2001, Terminos Lagoon lost 12% of its mangroves (11,000 ha) and 31% of its forests (62,000 ha; Soto-Galera et al. 2010) mainly due to the expansion of cattle ranching, wetland drainage, deforestation for agricultural development (mostly oil palm and rice), oil drilling, and recent tourism developments (Tudela 1989, Rivera-Arriaga and Villalobos-Zapata 2005, Guerra-Martínez and Ochoa-Gaona 2008, Barba-Macías et al. 2014). Despite these threats, the Terminos-Centla wetland still conserves an important portion of its biodiversity and ecological functions (Ayala-Pérez 2010, Barba-Macías et al. 2015).

Research on the mammals of the Terminos-Centla wetlands is scarce (Escalante et al. 2002). The largest efforts to determine the region's mammal species were made during the development of management plans of the NPAs. It was estimated that PCBR could potentially harbor around 104 species of mammals (INE 2000), with 32 being medium-sized and large species (i.e. mammals whose adult weight exceeds 500 g). In TLFFPA, the management plan estimated the presence of 86 species, though it did not provide their identity or the source of this information (INE 1997). After the declaration of the PCBR as an NPA, disturbed areas within and surrounding the reserve were studied, and 4 medium-sized and large mammals were confirmed (*Didelphis virginiana* Linnaeus, 1758; *D. marsupialis* Kerr, 1792; *Procyon lotor* (Linnaeus, 1766); and *Nasua narica* (Linnaeus, 1758)). Through interviews with the local people, at least 8 other species were recorded (Sánchez-Hernández et al. 2001). In the TLFFPA and its surroundings, Rangel-Negrin et al. (2014) documented 11 medium-sized and large mammals, and biodiversity expeditions have confirmed other species such as *Tayassu pecari* (Link, 1795) (Hidalgo-Mihart and Contreras-Moreno 2012, Hidalgo-Mihart et al. 2015), *Spilogale angustifrons* Howell, 1902 (Hidalgo-Mihart et al. 2014a), *Panthera onca* (Linnaeus, 1758) (Hidalgo-Mihart et al. 2015), *Canis latrans* Say, 1822 (Hidalgo-Mihart et al. 2013), as well as populations of introduced species such as wild boars (*Sus scrofa* Linnaeus, 1758; Hidalgo-Mihart et al. 2014b).

Given the lack of information on mammals in this region, there is an urgent need to generate an updated list of species (Escalante et al. 2002). Because the Terminos-Centla wetlands present a highly heterogeneous landscape, a regional list is more appropriate. The heterogeneity is due to the constant environmental pressures, including differences in the level and duration of flooding, microtopography, and soil and vegetation types (Barba-Macías et al. 2006, Lara-Lara et al. 2008), but also the intensity and type of dominant human activities (e.g. cattle ranching, agriculture of oil palm or rice, oil extraction, and subsistence fishing and hunting; Córdova-Ávalos et al. 2009). Land tenure and whether its located within the NPA polygon also adds to this heterogeneity. The objective of our study is to produce a list of medium-sized and large mammal species obtained through camera-trap studies, literature searches, and direct observations in 8 different sites distributed within the Terminos-Centla wetlands.

Methods

Study area. The study area lies in the protected coastal wetlands of the TLFFPA (18°25′00″ N, 091°50′00″ W and PCBR (18°22′00″N, 092°28′00″ W), as well as in the adjoining areas not included in the NPA. The study area is located on the coastal plain of the Gulf of Mexico, in northeastern Tabasco state, Mexico, southwest of Campeche state (Fig. 1). The area is within the physiographic subprovince of Pantanos and Llanuras Tabasqueñas (INEGI 2015a, 2015b).

The study area is between 0–5 m above sea level, and most of the region is subject to seasonal floods that can last from 2 to 8 months (June to February), depending on the topography, rate of discharge from the regional fluvial system, and the tide in the areas close to the sea. The seasonal floods are followed by a drier season when higher areas partially or completely dry (March to May; Barba-Macias et al. 2014). The temporal variations in the levels of flooding are apparent in the gradient of vegetation from the most flooded areas to the least flooded areas. The vegetation is heterogeneous, and comprises hydrophilic vegetation, flooded savannah, mangroves, sub-evergreen flooded rain forests, and tropical deciduous flooded forests (Ocaña and Lot 1996, Guerra-Martínez and Ochoa-Gaona 2008, Barba-Macias et al. 2014). Flooding in the region also influences the degree and type of human activities that vary from intense extractive activities such as fishing, hunting, and logging in the wettest areas to extensive cattle ranching in savannahs and unnatural grasslands. The ecosystems, particularly tropical forest, are also impacted by subsistence maize crops and irrigated agriculture, mostly of rice and more recently, oil palm. Oil and natural gas exploitation takes place in the western portion of the Terminos-Centla wetlands and includes a vast network of wells, artificial waterways used for navigation, and access roads (Rivera-Arriaga and Villalobos-Zapata 2005). Additionally, in the eastern Terminos-Centla wetlands 2 large tourist hotel complexes were built recently.

We surveyed for medium-sized and large mammals in 8 sites in the Terminos-Centla wetlands (Western Centla; Eastern Centla; Atasta; North Palizada; South Palizada; Chekubul; Sabancuy; Chenkan; Fig. 1, Table 1). The location of these study sites was established according to the information needs of the managers of the NPA. However, the distribution of sites allowed for a good

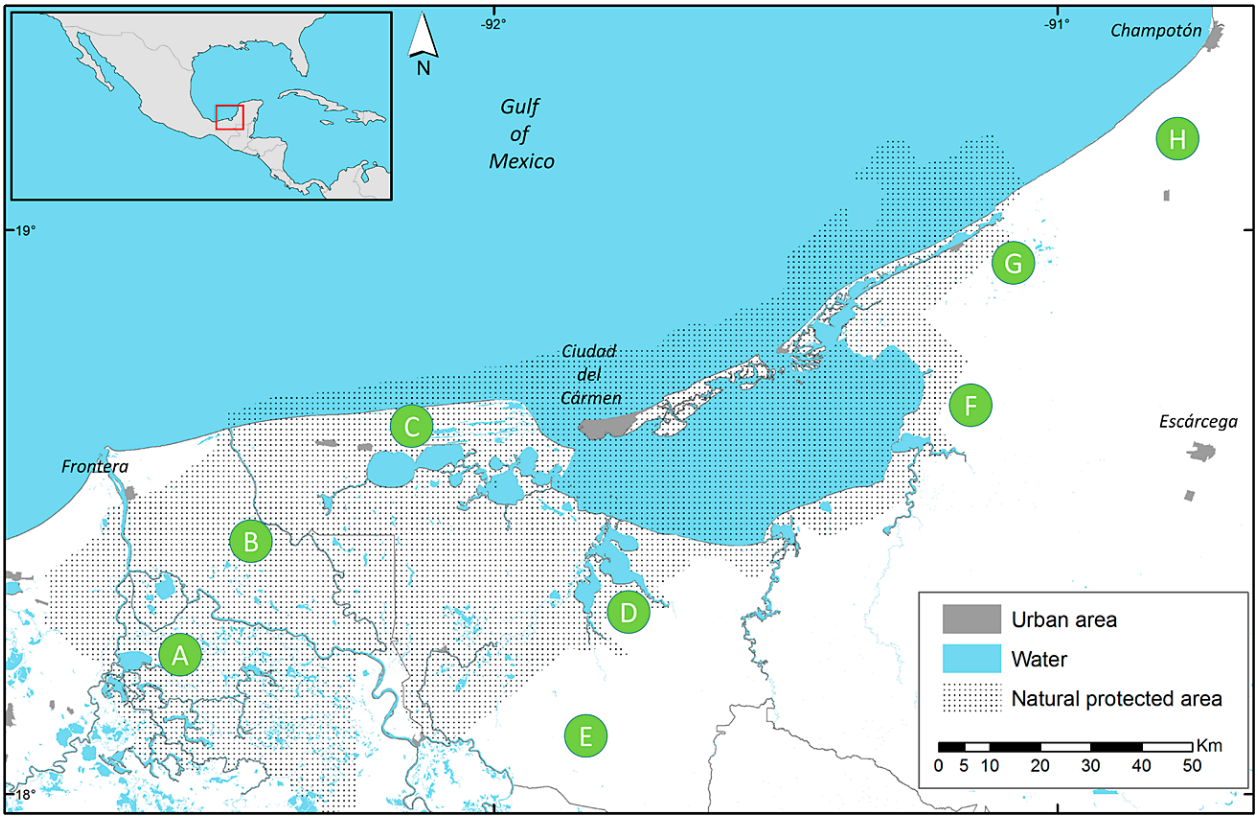


Figure 1. Location of the Terminos-Centla wetlands in southeastern Mexico. The letters correspond to the sites where the species richness of medium-sized and large mammals were studied: (A) West Centla, (B) East Centla, (C) Atasta, (D) North Palizada, (E) South Palizada, (F) Chekubul, (G) Sabancuy, (H) Chenkan. The datum of the map is WGS84.

Table 1. Location, natural, and anthropogenic characteristics of the 8 regions studied in the Terminos-Centla wetlands.

Natural and anthropogenic characteristics	Region/location							
	West Centla	East Centla	Atasta	North Palizada	South Palizada	Chekubul	Sabancuy	Chenkan
	18°24′50″ N, 092°37′50″ W	18°31′25″ N, 092°26′25″ W	18°38′50″ N, 092°08′25″ W	18°19′50″ N, 091°45′50″ W	18°03′00″ N, 091°51′50″ W	18°45′50″ N, 091°05′50″ W	19°00′00″ N, 091°02′00″ W	19°10′50″ N, 090°45′00″ W
Natural vegetation								
Hydrophilic vegetation	X	X	X					
Natural savannah		X	X	X	X	X	X	X
Mangrove	X	X	X	X		X	X	X
Tropical deciduous forest				X	X	X	X	X
Tropical semi-deciduous forest	X			X	X	X	X	X
Flooding season (months)	> 8	> 8	6-8	6	3	6	6	6
Human activities								
Forestry			X	X		X	X	X
Fishing	X	X	X	X				
Cattle ranching	X	X	X	X	X	X	X	X
Seasonal agriculture (maize)	X	X	X	X	X	X	X	X
Industrial agriculture (rice and oil palm)					X	X	X	X
Oil extraction	X	X	X					
Tourism							X	X
Land tenure								
Communal (Ejido)	X	X	X	X	X	X	X	X
Private		X	X	X	X		X	X
Natural Protected Area	PCBR[1]	PCBR[1]	LTFFPA[2]	Partially in LTFFPA[2]	No	Partially in LTFFPA[2]	Partially in LTFFPA[2]	No

[1]Pantanos de Centla Biosphere Reserve.
[2]Laguna de Terminos Flora and Fauna Protection Area.

representation of the vegetation types within the Terminos-Centla wetland system, driven by flooding activity, vegetation types, human activity, and land tenure (Table 1; INE 1997, 2000).

In this study, we define medium-sized and large mammals as those whose adult body weight exceeds 500 g (Reid 2009). Records of these species in the 8 sites were obtained from camera-traps, other photographs of live animals, skeletal material and road kill specimens, published data, and scientific collections.

Camera traps. Camera traps have been widely used to survey mammals in the Neotropics (e.g. Silveira et al. 2003, Tobler et al. 2008). In the case of the Centla-Terminos wetlands, camera-traps have been effective in recording the presence of threatened mammals (Hidalgo-Mihart et al. 2012) and invasive species (Hidalgo-Mihart et al. 2014b). Therefore, we used camera traps as a reliable method for sampling the species in our study. From 2009 to 2016, a combination of at least 20 digital camera traps of different models (Wildview, Wild View Web Products Inc., Greenfield, MN, USA; Cudddeback, Non Typical Inc., De Pere, WI, USA; Moultrie, Moultrie Products, LLC, Birmingham, Al, USA; Acorn, LTL Acorn Outdoors, Green Bay, WI, USA; Pantheracam Model IV and V; Olliff et al. 2014) were placed for a minimum of 45 days during the dry season of each year in the study areas. The sampling effort at each of the sites varied according to the support and information needs of the management of the NPA. Consequently, Atasta and Chekubul were sampled during 1 season, South Palizada during 2 seasons, and East and West Centla, North Palizada, and Chenkan during 4 seasons. The number of camera traps varied at each site and over the study period due to equipment failures and losses because of vandalism and flooding. However, the minimum sampling effort per site and season was 15 camera traps working continuously for a minimum of 45 days.

Cameras were separated from each other by at least 1 km and placed 50 cm above the ground on trees. Camera traps were placed close to trails where we found evidence of use by medium-sized or large mammals and programmed to take pictures 24 h per day. In front of each camera we placed a partially open can of sardines approximately 5 m from the camera to attract species that feed on this type of food.

Mammals photographed by the cameras were identified using the field guide by Reid (2009) and pictures were stored in Camera Base (Tobler 2015). To obtain the sampling effort per site, we calculated the number of camera days that each individual camera functioned in the field by counting the number of days from when the camera was active to the date of the last picture taken. We considered a camera day as a period of 24 h during which the camera was operating. The total sampling effort was obtained by adding the number of camera days that every camera operated in each region during all study periods.

Field observations. The detection of mammals with camera-traps can vary depending on the habits of the species (e.g. arboreal species; Srbek-Araujo and Chiarello 2005), their size (Anile and Devillard 2016), as well as the location of the cameras (Harmsen et al. 2010). Because of these possible biases, it is necessary to use complementary methods to generate a thorough species inventory (Srbek-Araujo and Chiarello 2005). With the objective of improving the species inventories obtained with camera-traps, we opportunistically recorded our observations of species in the study area. We considered all our observations of living animals and carcasses as well as animals killed by hunters or ran over by vehicles. Observations of living animals were identified using Reid (2009) and skeletal remains using the identification keys by Álvarez-Castañeda et al. (2015).

Literature and scientific collections records. Information obtained from mammal collections and published literature can be used to complement mammal inventories (e.g. Illoldi-Rangel et al. 2004, Ortega-Huerta and Peterson 2004). To complete our inventory of the Terminos-Centla wetlands, we conducted an extensive search of mammal records in collection databases and in published field studies performed in the area.

We searched for recent records from Global Biodiversity Information Facility (GBIF; http://www.gbif.org) for all potential medium-sized and large terrestrial mammals of Terminos-Centla wetlands according to the distribution maps of Reid (2009). Because we are interested in obtaining a recent inventory, we only considered records made after 2000.

We also searched in books, and scientific articles using Google Scholar (http://www.scholar.google.com/) for verified records of medium-sized and large mammals in the Terminos-Centla wetlands. We used the scientific and common names of the species with the keywords Tabasco or Campeche + Centla swamps or Terminos lagoon. In all cases, we searched the terms in English and Spanish. In a similar way to our search of GBIF records, we only considered published records obtained after the year 2000. We used the georeferenced information of the mammal collection obtained through GBIF and the published literature to assign the species record to 1 of the 8 areas studied.

Taxonomic identification of the species and conservation status. With the objective of standardizing all information on the mammals of the Terminos-Centla wetlands, including that gathered from other studies, we used the taxonomic nomenclature proposed by Ramirez-Pulido et al. (2014) for Mexican mammals. The conservation status of the mammal species in our study was obtained using the Norma Oficial Mexicana-SEMARNAT-059-2010 (SEMARNAT 2010) and the IUCN Red List of Threatened Species (2017).

Data analysis. To verify the similarity of the medium-sized and large mammal species composition among the Terminos-Centla wetlands we constructed a similarity

dendrogram with the presence/absence of species at each site using the Jaccard's Similarity Coefficient and the Unweighted Pair-group Methods Average (UPGMA) as the classification method (Sneath and Sokal 1973). We evaluated the resulting clustering solution using the cophenetic correlation. All the analyses were performed in PAST ver. 2.07 (Hammer et al. 2001).

Results

Throughout the 6 years of work in the Terminos-Centla wetlands we obtained a sampling effort of 32,285 camera days and recorded 29 species of medium-sized and large mammals (Figs 2–33; Table 2). In addition to the data obtained from camera-traps, we added 2 species to our list based on direct observations (1 alive and 1 road kill; Figs 2–33; Table 2). We did not find additional species by searching the literature or scientific collections. Thus, in total we recorded 31 species belonging to 9 orders, 14 families, and 27 genera (Table 2). Of these, 30 are native and 1 is introduced.

The sampling effort varied between sites, from a maximum of 13,852 camera days in North Palizada to only 450 in Atasta (Table 2). Interestingly, the site with more species recorded (26 species) was Chenkan even though we only had 2,386 camera-days of sampling. The next site with most species recorded was North Palizada (25 species and 13,852 camera-days), followed by South Palizada (24 species and a 2,735 camera-days), Sabancuy (22 species and 2,157 camera-days), Chekubul (21 species and 2,465 camera-days), East Centla (15 species and 4,546 camera-days), West Centla (14 species and 3,786 camera-days), and finally Atasta (11 species and 450 camera-days).

Of the species recorded, 4 species are Threatened, 9 are Endangered, and 1 is given special protection by Mexican legislation (SEMARNAT 2010). In the IUCN Red List (2017), 24 species are categorized as Least Concern, 2 as Data Deficient, 3 as Endangered, 2 as Near Threatened, and 1 as Vulnerable (V) (Table 2).

Because the sampling effort in Atasta was considerably less than that of the other sites, we decided not to include this site in the classification dendrogram. Therefore, the dendrogram was built using only 7 sites. The results of the dendrogram (Fig. 34) show that the sites in East and West Centla present a species composition different from the other study sites. Also, among the other 5 sites, the ones that resemble each other most are South Palizada and Sabancuy, followed by North Palizada and Chenkan. The Chekubul site shows a species composition that is different from these last 4 sites. The observed cophenetic correlation of the cluster solution (0.899) was considered adequate (McGarigal et al. 2000).

Taxonomic identity of the observed specimens

Philander opossum (Linnaeus, 1758)

Material examined. Table 2; Figure 2.

Medium-sized opossum, smaller than *Didelphis* spp., slightly woolly and with dense fur. It has a blackish head with contrasting cream-colored spots above the eyes and cheeks. *Philander opossum* is often mistaken with *Chironectes minimus* (Zimmermann, 1780), but the distinctive 4 broad black bands on the dorsum are absent in *P. opossum.*

***Didelphis* sp.**

Material examined. Table 2; Figure 3.

The species could be *Didelphis marsupialis* Linnaeus, 1758 or *Didelphis virginiana* Kerr, 1792. In the study area, there are potentially both species, and although the morphological characteristics allow for the distinction between them (white cheeks and black portion of tail longer than white portion in *D. virginiana* than in *D. marsupialis*; Reid 2009), this distinction is not evident in photographs obtained from infrared-illuminated camera-traps. Therefore, we decided to report these 2 species as *Didelphis* sp.

Dasypus novemcinctus Linnaeus, 1758

Material examined. Table 2; Figure 4.

Dasypus novemcinctus is the only species of dasypodid in Mexico (Hall 1981). This species has an armored body with 8 or 9 conspicuous scutes that make it distinct from any other mammal of the region (Reid 2009).

Tamandua mexicana (Saussure, 1860)

Material examined. Table 2; Figure 5.

Tamandua mexicana is the only species of its genus in Mexico and Central America (Hall 1981). The long-tapered snout and a blotchy, almost naked prehensile tail, in addition to the sparse golden-brown fur and the powerful forelimbs with 2 large and 2 small claws make this species unique in the region (Reid 2009).

Cyclopes didactylus **(**Linnaeus, 1758)

Material examined. Table 2; Figure 6.

Cyclopes didactylus is the only species of the *Cyclopes* genus in Mexico (Hall 1981). The small size, prehensile tail, and golden hair make this species distinct from any other species in the region (Reid 2009).

Ateles geoffroyi Kuhl, 1820

Material examined. Table 2; Figure 7.

Ateles geoffroyi is the only species of the *Ateles* genus in Mexico (Hall 1981). The very long, thin limbs, small head, and long prehensile tail make this species distinct from any other species in the region (Reid 2009).

Alouatta villosa (Gray, 1845)

Material examined. Table 2; Figure 8.

The study region is close to the area where *A. villosa* and *A. palliata* (Gray, 1849) are sympatric and where the *A. villosa* × *A. palliata* hybrid has been described (Kelaita and Cortés-Ortíz 2013). We only observed entirely black howler monkeys without the long yellowish fur on the flanks that is characteristic of *A. palliata* (Reid 2009). For this reason, we assigned all the howler monkey observations to *A. villosa.* However, we acknowledge that *A. villosa* x *A. palliata* hybrids could

be present in our study area.

The species is commonly called *A. pigra*, but there is extensive evidence to support *A. pigra* the correct name (Brandon-Jones 2006). However, we used *A. villosa* following Ramirez-Pulido et al. (2014).

Sylvilagus floridanus (Allen, 1890)

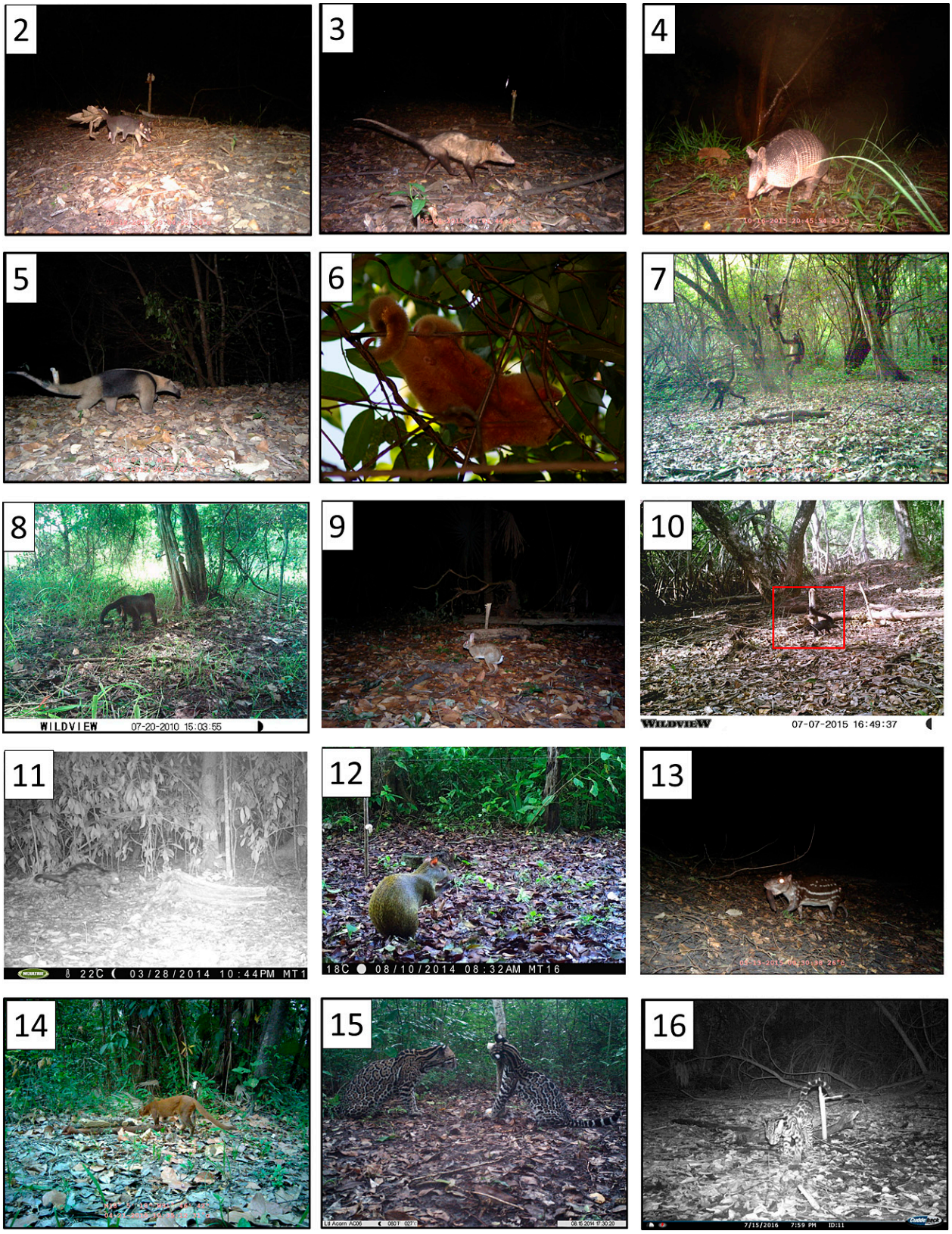
Material examined. Table 2; Figure 9.

Sylvilagus floridanus is a medium-sized rabbit with a cotton-white tail (Reid 2009). The study area is at the edge of the distribution range of *S. brasiliensis* (Linnaeus,

Table 2. Species list of medium-sized and large land mammals detected with camera traps in eight sites along the Terminos-Centla wetlands. Conservation status according to the IUCN Red List (2014) and Mexican legislation (SEMARNAT 2010). IUCN categories: (LC) Least Concern, (DD) Data Deficient, (NT) Near Threatened, and (V) Vulnerable. NOM- 059: (Th) Threatened, (En) Endangered, and (SP) Special protection. The method by which the species registration was obtained in the study sites is indicated by a P when it was obtained through camera traps, L when it was obtained through literature, and O when it was obtained by direct observation (of living animals or organic remains from traffic accidents or found in the field). In the cases where literature was the information source, the superscript indicates the specific citation.

Species list	Conservation status		Study sites								No. of sites where found
	IUCN	NOM 059	West Centla (3768)[1]	East Centla (4546)[1]	Atasta (450)[1]	North Palizada (13852)[1]	South Palizada (2735)[1]	Chekubul (2465)[1]	Sabancuy (2157)[1]	Chenkan (2396)[1]	
Didelphimorphia											
Didelphis sp.	LC		P,L[2]	P	O	P	P	P	P, L[3]	P	8
Philander opossum	LC		P,L[2]	P		P	P	P	P	P	7
Cingulata											
Dasypus novemcinctus	LC					P	P	P	P	P	5
Pilosa											
Tamandua mexicana	LC	En	P	P	O	P	P	P	O	R	8
Cyclopes didactylus	LC	En	O								1
Primates											
Ateles geoffroyi	EN	En				P	P	O	P	O	5
Alouatta villosa	EN	En	P	P	O	P	P	P, L[3]	O, L[3]	O	8
Lagomorpha											
Sylvilagus floridanus	LC					O	P	L[3]			2
Rodentia											
Sciurus sp.	LC		P	P	P	P	P	P	O, L[3]	O	8
Coendou mexicanus	LC	Th	P	O			P	P	P, L[3]		5
Dasyprocta punctata	LC					P	P		P	P	4
Cuniculus paca	LC		P	P		P	P	P	P	P	7
Carnivora											
Herpailurus yagouaroundi	LC	Th	P			P	P	O		P	5
Leopardus pardalis	LC	En	P	P	P	P	P	P	P	P	8
Leopardus wiedii	NT	En		P			O	O	P		4
Puma concolor	LC					P				P	2
Panthera onca	NT	En		P	L[4]	P	P	P	P	P	7
Canis latrans	LC		P	O	P	P	P	P	P	P	7
Urocyon cinereoargenteus	LC					P	P		P,L[3]	P	4
Conepatus semistriatus	LC	SP				P	P		P,L[3]	P	4
Spilogale angustifrons	LC									P	1
Lontra longicaudis	NT	Th	P	P	L[5]	P					4
Eira barbara	LC	En				P	P	P	P	P	5
Galictis vittata	LC	Th				P	P		L[3]	P	4
Nasua narica	LC		P, L[2]	P	P	P	P	P	P, L[3]	P	8
Procyon lotor	LC		P, L[2]	P	P	P	P	P, L[3]	P, L[3]	P	8
Artiodactyla											
Dicotyles crassus	LC					P	P	P	P, L[3]	P	5
Tayassu pecari	V	En				P				P	2
Mazama temama	DD							P		O	2
Odocoileus virginianus	LC		P	P	P	P	P	P	P	P	8
Sus scrofa						P, L[6]	P, L[6]				2
Perisodactyla											
Tapirella bairdii	EN	En								O, L[5]	1
Total no. of species per site			**15**	**15**	**11**	**25**	**24**	**21**	**22**	**26**	

[1]Number of camera days per site. [2]Sánchez-Hernández et al. (2001). [3]Rangel-Negrín et al. (2014). [4]Hidalgo-Mihart et al. (2015). [5]Santiago-Plata et al. (2013). [6]Hidalgo-Mihart et al. (2014).



Figures 2–15. Photographs of the medium and large–sized mammal species recorded in the Terminos- Centla wetlands, in southeastern Mexico. **2.** *Philander opossum*. **3.** *Didelphis* sp. **4.** *Dasypus novemcinctus*. **5.** *Tamandua mexicana*. **6.** *Cyclopes didactylus*. **7.** *Ateles geoffroyi*. **8.** *Alouatta villosa*. **9.** *Sylvilagus floridanus*. **10.** *Sciurus* sp. **11.** *Coendou mexicanus*. **12.** *Dasyprocta punctata*. **13.** *Cuniculus paca*. **14.** *Herpailurus yagouaroundi*; **15.** *Leopardus pardalis*. **16.** *Leopardus wiedii*.

1758). However, *S. floridanus* and *S. brasiliensis* are distinguishable because *S. floridanus* had a white tail and *S. brasiliensis* had a brown color tail. All our photographs of *Sylvilagus* specimens are *S. floridanus.*

***Sciurus* sp.**

Material examined. Table 2; Figure 10.

Our records could be *Sciurus aureogaster* Cuvier, 1829, *S. deppei* Peters, 1863, or *S. yucatanensis* Allen,

1877, all species potentially in the study area. Although morphological characteristics allow for the distinction between these 3 species. (*S. aureogaster* is slightly larger than *S. yucatanensis* and these 2 species are larger than *S. depeii*; Reid 2009, Koprowski et al. 2017), this distinction is difficult to observe in camera-trap photographs. The fur color of *S. aureogaster,* varying from completely black to combinations of black with reddish brown or gray, may produce confusion with the other 2 species in camera-trap photographs (Reid 2009, Koprowski et al. 2017). Therefore, to avoid misidentification we decided to report our records only as *Sciurus* sp.

Coendou mexicanus **(**Kerr, 1792)

Material examined. Table 2; Figure 11.

Coendou mexicanus is the only erethizontid in southern Mexico (Hall 1981). The presence of spines on most of the body make this species unique in the region (Reid 2009). We classify this species as *Coendou mexicanus* and not *Sphiggurus mexicanus* following Voss et al. (2013) and Ramirez-Pulido et al. (2014).

Dasyprocta punctata Gray, 1842

Material examined. Table 2; Figure 12.

Dasyprocta punctata is a large orange-brown rodent with a rounded back and long skinny legs. The study area is at the edge of this species' distribution range (Hall 1981). However, there is a second potential species, *D. mexicana* Saussure, 1860 which differs from *D. punctata* by its black, rather than orange-brown fur. All our photographs of *Dasyprocta* belong to *D. punctata.*

Cuniculus paca (Linnaeus, 1766)

Material examined. Table 2; Figure 13.

Cuniculus paca is the only cuniculid species in Mexico (Hall 1981). It is a large and stocky rodent with a pig-like body and brown pelage with whitish spots along the sides, which makes it readily distinguishable from any other species in the region (Reid 2009).

Herpailurus yagouaroundi (É. Geoffroy Saint-Hilaire, 1803)

Material examined. Table 2. Figure 14.

Herpailurus yaguaroundi is a small, short-legged, felid with an elongate body and proportionally small head with low, rounded ears. The only felid that could be confused with *H. yaguaroundi* is *Puma concolor* (Linnaeus, 1771). However, the smaller body size, the elongate body and long tail of *H. yaguaroundi* prevents confusion. The animals in our study had the most common pelage patterns of the species in the area, chocolate brown to near black phenotype and a rust or reddish-brown color (Reid 2009). Recently this species has been classified in the genus *Puma* (Johnson et al. 2006), but we follow Ramirez-Pulido et al. (2014) in keeping the name *Herpailurus yaguaroundi*.

Leopardus pardalis (Linnaeus, 1758)

Material examined. Table 2; Figure 15.

Leopardus pardalis is a medium-sized spotted cat that can be confused in the study area only with *L. wiedii*, but is larger and heavier than that species (Reid 2009).

Leopardus wiedii (Schinz 1821)

Material examined. Table 2; Figure 16.

Leopardus wiedii is a medium-sized spotted cat that can be confused in the study area only with *L. pardalis*. However, *L. wiedii* is smaller and has a bushy tail that is longer than the hind legs (Reid 2009).

Puma concolor (Linnaeus, 1771)

Material examined. Table 2; Figure 17.

Puma concolor is a large cat with a relatively small head and long legs (Reid 2009). It may only be confused with *H. yaguaroundi*. However, *P. concolor* is considerably larger than *H. yaguaroundi*.

Panthera onca (Linnaeus, 1758)

Material examined. Table 2; Figure 18.

Panthera onca is a very large and large-headed spotted cat (Reid 2009) and the only large spotted cat in the study region (Hall 1981). It cannot be confused with any other species (Reid 2009).

Canis latrans Say 1823

Material examined. Table 2; Figure 19.

Canis latrans is the only dog-like species native to the area (Hall 1981). This species could be confused with domestic dogs, but domestic dogs usually have shorter legs and shorter fur (Reid 2009).

Urocyon cinereoargenteus (Schreber 1775)

Material examined. Table 2; Figure 20.

Urocyon cinereoargenteus is the only fox-like canid occurring in the study area (Hall 1981). It is a small, slender fox with a bushy tail that cannot be confused with any other species in the region (Reid 2009).

Conepatus semistriatus (Boddaert 1758)

Material examined. Table 2; Figure 21.

Conepatus semistriatus is a large and stocky skunk with a black body and 2 narrow white stripes that run from the forehead to the upper rump. It has a large pig-like snout (Reid 2009). *Conepatus semistriatus* could be confused with other skunk species (*Spilogale angustifrons* Howell, 1902 or *Mephitis macroura* Lichtenstein, 1832) that potential occur in the region, but the large and stocky body are sufficient to distinguish this species.

The study region is close to the area where *C. semistriatus* and *C. leuconotus* (Lichtenstein, 1832) are sympatric (Hall 1981). However, *C. semistriatus* has 2 narrow white stripes on the back compared with *C. leuconotus* which only has a single, broad white stripe from the forehead to the tail (Reid 2009). All our photographs of *Conepatus* are *C. semistriatus*.

Spilogale angustifrons Howell, 1902

Material examined. Table 2; Figure 22.

Spilogale angustifrons is a small, short-legged and slim-bodied skunk that is mostly black with a complex pattern of white stripes and spots. This species could be

Figures 17–31. 17. *Puma concolor*. **18.** *Panthera onca*. **19.** *Canis latrans*. **20.** *Urocyon cinereoargenteus*. **21.** *Conepatus semistriatus*. **22.** *Spilogale angustifrons*. **23.** *Lontra longicaudis*. **24.** *Eira barbara*. **25.** *Galictis vittata*. **26.** *Nasua narica*. **27.** *Procyon lotor*. **28.** *Dicotyles crassus*. **29.** *Tayassu pecari*. **30.** *Mazama temama*. **31.** *Odocoileus virginianus*.

confused with other skunk species (*C. semistriatus* or *M. macroura*), both potentially present in the region, but the small size and complex pattern of white stripes and spots make this species unique.

Lontra longicaudis (Olfers, 1818)

Material examined. Table 2; Figure 23.

Lontra longicaudis is a semiaquatic otter with a long, stocky body and short legs with broad feet and webbed

Figures 32, 33. 32. *Sus scrofa* (introduced species). **33.** *Tapirella bairdii*.

toes (Reid 2009). In the study area, this species cannot be confused with any other mammals.

Eira barbara (Linnaeus, 1758)

Material examined. Table 2; Figure 24.

Eira barbara is a large, long-legged weasel with a long bushy tail. It has a black body, tail, and legs. In Mexico, Belize, and Guatemala, the head and neck are pale yellow or gray-brown (Reid 2009). In the region, this species cannot be confused with any other mammals.

Galictis vittata (Schreber, 1776)

Material examined. Table 2; Figure 25.

Galictis vittata is a medium-sized, gray weasel having a mostly black face with a white line across the forehead to the ears and down the sides of neck (Reid 2009). This species cannot be confused with any other mammal in the region.

Nasua narica (Linnaeus, 1766)

Material examined. Table 2; Figure 26.

Nasua narica is a medium-sized, dark brown, reddish orange, or yellow brown procyonid that has a long slender tail with a series of black bands (Reid 2009). This is the only species of coati in the region.

Procyon lotor (Linnaeus, 1758)

Material examined. Table 2; Figure 27.

Procyon lotor is a medium-sized, gray procyonid having a distinctive face with a black mask extending onto the cheeks, bordered with white eyebrows and sides of the muzzle (Reid 2009). This is the only raccoon to occur in continental Mexico.

Dicotyles crassus Linnaeus, 1758

Material examined. Table 2; Figure 28.

Dicotyles crassus is a medium-sized mammal with a large triangular head, stocky body, and thin legs. Its fur is mostly dark gray-brown but this species is characterized by a cream-colored collar from the shoulders to the chest. The only similar species is *Tayassu pecari*, but *D. crassus* can be easily differentiated because *T. pecari* is larger, has darker fur, and has a white patch on its cheek and lower jaw. We use *D. crassus* instead of the commonly used *Pecari tajacu* following Ramirez-Pulido et al. (2014).

Tayassu pecari (Link, 1795)

Material examined. Table 2; Figure 29.

Tayassu pecari is a medium-sized mammal with a large triangular head and slim legs. It is mainly blackish brown and has a white patch along its lower jaw, cheek, and throat (Reid 2009). This species could be confused with *Dicotyles crassus,* but *D. crassus* is smaller and does not have the white patch (Reid 2009).

Mazama temama (Kerr, 1792)

Material examined. Table 2; Figure 30.

Mazama temama is a small, reddish brown deer having a rounded body with arched back and slim legs and neck (Reid 2009). In the eastern portion of the study region *M. temama* is almost sympatric with *M. pandora* Merriam, 1901 (Medellin et al. 1998). The main differences between these species are their size and color (larger and a paler in *M. pandora*) (Reid 2009). In previous studies, *Mazama* spp. were observed at very low abundance in the wetlands of Campeche (Contreras-Moreno et al. 2016). We only have 1 photograph of *Mazama spp.* in our study, and recorded a second record of a deer killed by a subsistence hunter. Both individuals were identified as *M. temama* by their reddish-brown fur.

Odocoileus virginianus (Zimmermann, 1780)

Material examined. Table 2; Figure 31.

Odocoileus virginianus is a medium-sized slim deer with long legs, a flat back, and a long narrow head (Reid 2009). The only similar species in the region is *M. temama*. However, *O. virginianus* is larger and has a white belly, distinctive antlers, has and a flat back compared with the arched back of *M. temama*.

Sus scrofa Linnaeus, 1758

Material examined. Table 2; Figure 32.

Sus scrofa is a swine native to Europe, Africa, and Asia and introduced to the study area (Hidalgo-Mihart et al. 2015). With great individual variation in body size and pelage color, *S. scrofa* could be confused with *D. crassus* and *T. pecari*, but *S. scrofa* is usually larger. Depending on the genetic origin of individuals and their relationship with domestic forms, they can have multicolored hair or be totally hairless. Using the criteria proposed by Hidalgo-Mihart et al. (2015), we determined that the specimens photographed were from wild stock.

Tapirella bairdii (Gill, 1865)

Material examined. Table 2; Figure 33.

Tapirella bairdii is the only species of the order Perisodactyla in Mexico and Central America, and it is the largest land mammal in the region (Reid 2009). This spe-

cies is unique and cannot be confused with other species in the region.

This species is usually named as *Tapirus bairdii,* but Ruíz-Garcia et al. (2012) called used *Tapirella* for this species. However, a recent revision called this species *Tapirus bairdii* (Cozzuol et al. 2013). In following Ramirez-Pulido et al. (2014), we use *Tapirella.*

Discussion

Our study found that the Terminos-Centla wetlands contains the largest number of species of medium-sized and large mammals detected in any study using camera-traps in the southern Mexican wetlands. We detected 31 native species, compared to 20 species in other wetlands in the state of Tabasco (Gordillo-Chávez et al. 2015) and 15 species in the Petenes (Hernández-Pérez et al. 2015). Moreover, 5 of the individual sites that we sampled (Chenkan, North Palizada, South Palizada, Sabancuy, and Chekubul) contained a greater number of species than other wetlands in Campeche and Tabasco (Gordillo-Chávez et al. 2015, Hernández-Pérez et al. 2015; Tables 2, 3). This was not a surprise because there we sampled more intensively in the Terminos–Centla wetlands than had been done in other areas. Nevertheless, when comparing individual sites, it is of interest to find a greater number of species in sites such as Chenkan, South Palizada, Chekubul, and Sabancuy, because the sampling efforts were similar to the effort reported by Gordillo-Chávez et al. (2015) and Hernández-Pérez et al. (2015) in other wetlands. In comparison to camera-trap studies in non-wetland environments of southern Mexico and including the Yucatan Peninsula (Gordillo-Chávez et al. 2015, Hernández-Pérez et al. 2015; Table 3), we found that the Terminos-Centla region contains a greater number of species. Individual sites such as Chenkan and Palizada had a similar number of species as Zapotal (Faller-Menéndez et al. 2005) and the Petén in Guatemala (Thornton et al. 2011).

The similarity dendrogram resulted in the formation of 4 groups. There is a clear consistency in the species composition observed in Centla, probably associated with their geographical proximity and environmental characteristics. Nevertheless, geographical proximity cannot explain the similarity in the species composition observed in North Palizada and Chenkan as well as Sabancuy and South Palizada. The similarities between Chenkan and North Palizada are likely due to the similar environmental conditions in these sites. Both sites present a long flooding season (6 months) and relatively well-preserved natural ecosystems, dominated by mangroves, natural savannah and tropical semi-deciduous forest. In the case of Sabancuy and South Palizada, the similarities in species composition could also be the result of the environmental conditions. Both regions have been subject to considerable loss of the natural vegetation due to the transformation of forest to induced grasslands (Soto-Galera et al. 2010). This could result in the similar species composition observed in these 2 areas.

We observed that several of the species listed by the management programs of the PCBR and the TLFFPA were not detected in our study (INE 1997, 2000). In both NPAs, the management program mentions species that should be present, yet there are no specific locations or references. This is the case of *T. bairdii*, a species that was included in the species list in the management programs of both NPAs. However, we only recorded the species in the extreme eastern portion of the study

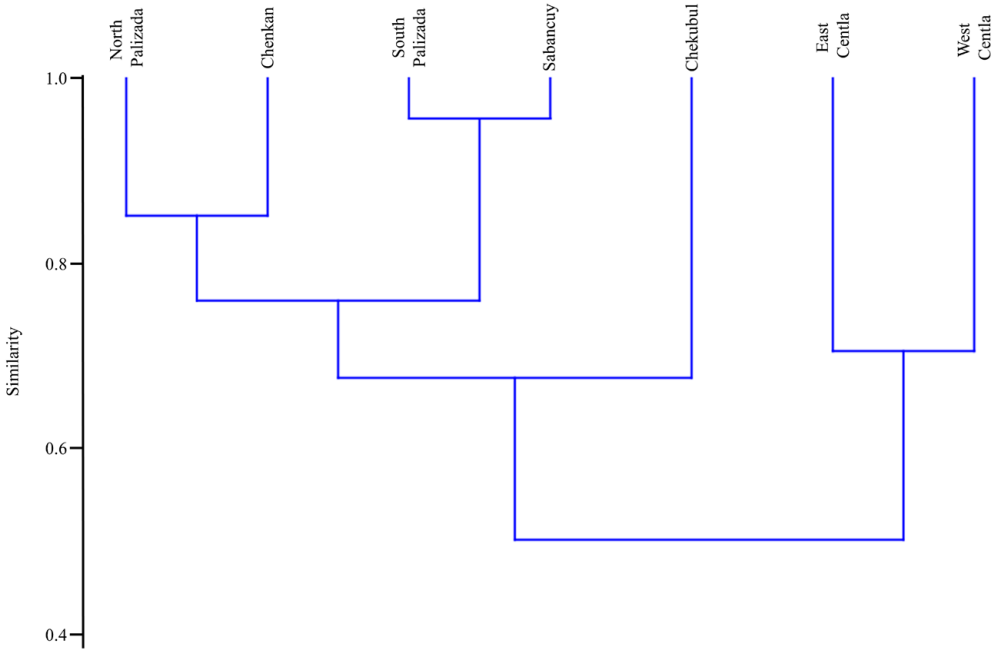


Figure 34. Similarity dendrogram comparing the species recorded in the study sites of the Terminos-Centla wetlands, Mexico. The dendogram represented the Similarity Jaccard's Coefficient and was constructed using the Unweighted Pair Group Average (UPGMA) as the classification method.

Table 3. Recent medium-sized and large mammal species inventories done in the tropical areas close to the Terminos-Centla wetlands . The predominant vegetation type of the study site is indicated in parenthesis. W, wetlands; TSF, Tropical semideciuous forest; TR, Tropical rainforest; TDF, Tropical deciduous forest.

Species list	Centla-Términos (W)[1, 3]	Los Petenes, Campeche (W)[2, 4]	El Zapotal, Yucatán (TSF)[1, 5]	Selva Lacandona, Chiapas (TR)[2, 6]	Chimalapas, Oaxaca (TR)[2, 7]	Chas Choc, Tabasco (W)[1, 8]	Distrito de Juchitán, Oaxaca (TDF)[2, 9]	Distrito de Tuxtepec, Oaxaca (TR)[2, 10]	Petén, Guatemala (Fragment-ed TSF)[1, 11]
Didelphimorphia									
Caluromys derbianus					X	X			
Didelphis virginiana						X	X	X	X
Didelphis marsupialis		X	X		X	X		X	X
Didelphis sp.	X								
Philander opossum	X	X		X	X	X	X	X	
Cingulata									
Dasypus novemcinctus	X	X		X	X	X	X	X	X
Cabassous centralis[12]				X					
Pilosa									
Tamandua mexicana	X		X	X			X	X	X
Cyclopes didactylus	X								
Primates									
Ateles geoffroyi	X	X	X						X
Alouatta villosa	X		X			X			X
Lagomorpha									
Sylvilagus brasiliensis					X			X	
Sylvilagus floridanus	X						X		
Sylvilagus sp.						X			
Rodentia									
Sciurus aureogaster					X	X			
Sciurus deppei		X	X			X			
Sciurus yucatanensis			X						
Sciurus sp.	X								
Coendou mexicanus	X		X			X	X	X	X
Dasyprocta punctata	X	X	X	X	X				X
Cuniculus paca	X	X	X	X	X	X		X	X
Carnivora									
Herpailurus yagoua-roundi	X		X	X	X	X		X	X
Leopardus pardalis	X	X	X	X	X	X	X	X	X
Leopardus wiedii	X	X	X	X	X			X	X
Puma concolor	X		X	X			X		X
Panthera onca	X		X	X			X		X
Canis latrans	X					X	X	X	
Urocyon cinereoar-genteus	X	X	X	X	X		X	X	X
Conepatus semis-triatus	X	X	X	X	X	X			X
Mephitis macroura							X		
Spilogale angusti-frons[13]	X								
Spilogale pygmaea[14]							X		
Lontra longicaudis	X					X			
Eira Barbara	X		X	X	X			X	X
Galictis vittata	X		X						
Mustela frenata			X						
Bassaricus astutus[15]									
Bassariscus sumi-chrasti			X				X		
Potos flavus			X						X
Nasua narica	X	X	X	X	X	X	X	X	X
Procyon lotor	X	X	X	X	X	X	X	X	X
Artiodactyla									
Dicotyles crassus	X	X	X	X	X		X	X	X
Tayassu pecari	X		X	X	X	X			X
Mazama americana				X				X	X
Mazama temama	X		X		X				
Odocoileus virginianus	X	X	X	X		X			X
Perisodactyla									
Tapirella bairdii	X			X	X				X
Total no. of species per site	31	15	27	21	20	20	17	18	25

[1]The study was performed using camera-traps and complimentary methods such as direct observations. [2]The study was performed only with camera traps. [3] This study. [4] Hernández-Pérez et al. (2015). [5] Faller et al. (2005). [6] Garmendia et al. (2013). [7] Lira-Torres and Briones-Salas (2012). [8] Gordillo-Chávez et al. (2015). [9] Cortes-Marcial and Briones-Salas (2014). [10] Pérez-Irineo and Santos-Moreno (2012). [11] Thornton et al. (2011). [12]*Cabassous centralis* (Miller, 1899). [13]*Spilogale angustifrons* Howell, 1902. [14]*Spilogale pygmaea* Thomas, 1898. [15]*Bassaricus astutus* (Lichtenstein, 1830).

area (Chenkan) as a roadkill, even though considerable camera trapping efforts were made, suggesting that the species could have very low abundance or not be present at all on the Terminos-Centla wetlands. Other examples are *D. novemcinctus*, *D. punctata*, *D. crassus*, *P. concolor*, and *E. barbara*. These 5 species were commonly detected in the eastern portion of the wetlands (North and South Palizada, Sabancuy, or Chenkan) and are listed on the PCBR management program but we were not able to record them on the Centla region (East and West Centla). These 5 species are known to survive in most of the ecosystems in the southeastern Mexico, even in areas with important anthropogenic alterations (Reid 2009). Besides, the anthropogenic alteration of Centla sites is relative, because even the natural vegetation of the region has notably decreased in recent years, large fragments of well-preserved vegetation still exist on the region (Guerra-Martínez and Ochoa-Gaona 2008). The most notable difference between the 2 Centla sites with the other wetlands in our study, is that Centla is flooded for longer periods and is mostly covered by hydrophilic vegetation. A possible reason why 2 of these species were not found in the Terminos-Centla wetlands is that *D. crassus* tends to avoid floodplains, such as in Amazonas (Bodmer 1990), and in Florida, *P. concolor* avoids open wetlands (Cox et al. 2006). However, nothing is known about whether the other 3 species avoid areas that flood for long periods; more studies are needed.

In Tabasco and Campeche 42 species of medium-sized and large mammals were reported (Hidalgo-Mihart et al. 2016, Vargas-Contreras et al. 2016). Except for the opossums (*Didelphis*) and the squirrels (S*ciurus*), whose precise identification is difficult to determine only by camera-traps, we did not record 7 of the species listed as potentially occurring in the region: *Caluromys derbianus, Chironectes minimus, Mustela frenata* Lichtenstein, 1831*, Potos flavus* (Schreber, 1774), *Bassariscus sumichrasti* (Saussure, 1860), *M. pandora, and D. mexicana* (Reid 2009). We likely did not record *M. pandora* and *D. mexicana* because our study sites are located at the edge of these species' distributions and population densities are likely quite low. This might also apply for *M. frenata*, which was recently recorded for the first time in nearby regions in the state of Campeche (Contreras-Moreno et al. 2015), and its presence in the Terminos-Centla wetlands is yet to be determined. *Potos flavus* and *B. sumichrastii* are rarely caught in camera-traps set on the ground because they are arboreal and nocturnal species (Srbek-Araujo and Chiarello 2005). Also, because the excursions to set the camera-traps were made by day, chances of direct observations were low. To determine the presence of these species, methods other than those employed in our study are needed. Finally, there are historical records of *Caluromys derbianus* and *Chironectes minimus* near our study area (Brown 2004), and even *C. derbianus*, which is mostly arboreal, has been recorded in camera-trap studies of terrestrial mammals (e.g. Lira-Torres and Briones-Salas 2011, 2012). However, both species are associated with habitats not found in the Terminos-Cenltla wetlands: *C. derbianus* has been associated with well-preserved evergreen forests (Medellín 1994, Lira-Torres and Briones-Salas 2012), and *C. minimus* has been associated with semi-aquatic environments of clear streams and fast currents (Galliez et al. 2009).

In all the sites in the NPAs of Laguna de Terminos and Pantanos de Centla (East and West Centla, Atasta and North Palizada) we observed species classified as endangered by Mexican legislation, which reinforces the importance of these NPAs. Nevertheless, unprotected sites of the Terminos-Centla wetlands such as Chenkan or South Palizada, or partially protected such as Sabancuy and Chekubul, also contained a considerable number of endangered species. Because of the increase of industrial agriculture (mostly oil palm) in coastal Campeche (Gobierno del Estado de Campeche 2014), and because of the developments for tourism in Sabancuy and Chenkan (Gobierno del Estado de Campeche 2012), enforcement of municipal- and state-level land management frameworks is important, where these wetlands have been set aside as conservation areas. It is also important to encourage the development of community-based protected areas as soon as possible.

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Authors' Contributions

MGHM, FCM, AJC, RJL, YBC, LPS, CHL, DF, DT and JKG collected the data, made the analysis and identified the specimens. MGHM, FCM, AJC, CHL, DF and DT wrote the text.

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