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Egg predation and vertebrates associated with wild crocodilian nests in Mexico determined using camera-traps

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ABSTRACT

Interactions between species and individuals can determine their survival in the wild. Most of the time these relationships are difficult to study in situ by direct observation. However, technology can help collect these data with minimal impact on animals' behaviour. Egg stage is certainly the most vulnerable life stage in crocodilians, but few studies have focused on animal species visiting crocodilian nests and associated egg predation. Herein, we use camera-traps in four Mexican states (Chiapas, Oaxaca, Jalisco, Tabasco) to determine vertebrate species and egg predators associated with wild nests of *Caiman crocodilus chiapasius, Crocodylus acutus* and *Crocodylus moreletii*. We recorded 72 species of vertebrates at nesting sites and obtained the first photographic evidence of crocodilian egg predation by *Caracara cheriway, Cuniculus paca, Didelphis virginiana* and *Procyon lotor*. We also identified commensalism, cooperation, and predation as types of interactions within observed nesting areas, which indicates the importance of crocodilian nesting areas for other wild vertebrates. Finally, we found that crocodilian egg predation depends on species richness present in the area of study, as well as crocodilian size.

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Introduction

Predation is one of the interactions that occurs between at least two organisms of one or more species, where predators themselves can be prey at some stage of their life (Smith and Smith 2007; Del Val and Boege 2012). Adult crocodilians (Order Crocodylia) are opportunistic apex predators (Ritchie and Johnson 2009) which consume a diversity of vertebrate and invertebrate species (Casas-Andreu and Barrios 2003; Platt et al. 2006; Cupul-Magaña et al. 2015). However, at early life stages (i.e., eggs and neonates) they are

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preyed upon by diverse vertebrate species (Cintra 1988; Campos 1993; Villamarín-Jurado and Suárez 2007; Somaweera et al. 2013; Campos and Mourão 2014, Campos et al. 2016; González-Desales et al. 2016a). The importance of crocodilians as a food source for wildlife has been extensively documented by Somaweera et al. (2013), who identified the trend that small crocodilians are more vulnerable to predators.

Little is known about the predators of crocodilians and their effect on populations at a local scale, and these types of antagonistic relationships are difficult to monitor directly in the wild. Camera-traps are frequently used to monitor fauna with minimal disturbance to the species, allowing researchers to record their presence and observe aspects of their behaviour and habitat use (Rowcliffe and Carbone 2008; Monroy-Vilchis et al. 2009; Rovero et al. 2010; Meek et al. 2014). Nevertheless, camera-traps have been used little to study Mexican crocodilians. The few studies that have been done have examined species richness at nesting sites, nest protection and maintenance by females, and egg scavenging in *Crocodylus acutus* Cuvier, 1807(Charruau and Hénaut 2012; Platt et al. 2014), and no previous studies have used camera-traps to study *Crocodylus moreletti* Duméril and Bibron, 1851 or *Caiman crocodilus chiapasius* Bocourt 1876.

In Mexico, additional interactions between crocodilians and wildlife or humans should be considered for evaluation in species' monitoring manuals (Sánchez-Herrera et al. 2011) and ranching protocols (Barrios and Cremieux 2018) for wild populations of *Crocodylus moreletii*, due to the implications that result from the modification of ecological interactions. For example, crocodiles develop strategies to adapt to anthropogenically modified environments (nests built with human waste material; López-Luna et al. 2011) and also to avoid human presence (abandonment of nesting areas; Casas-Andreu 2003). As such, a negative effect would be expected in the loss of nests by predation in more anthropogenically modified environments, or by exotic or domestic fauna, as has been reported in other crocodilians (Merchant et al. 2014; Campos and Mourão 2014). Additionally, as in other taxonomic groups, the loss and fragmentation of habitat has led to negative interactions between wildlife and humans (Zarco-González et al. 2013; Carrera-Treviño et al. 2018).

Considering a few information on vertebrate interactions at nesting sites of Mexican crocodilians, in this study we monitored wild nests of the three crocodilians present in Mexico using camera-traps to identify vertebrate species and their interactions associated with crocodile nests. Specifically, we examined egg predation and analysed if the number of egg predators increase with the number of species recorded at nests. In addition, we reviewed the scientific literature on the use of trap cameras in the monitoring of crocodilian nests worldwide to identify known vertebrate crocodilian egg predators, and to determine if the size of crocodilians has an effect on the number of nests predated.

Materials and methods

For direct observation of vertebrates associated with nests, camera-traps were set up at crocodilian nesting locations in three sites along the Mexican Pacific coast and in the Gulf of Mexico (Figure 1): Reserva de la Biosfera La Encrucijada (REBIEN) in Chiapas state, Estero La Ventanilla (EVEN) in Oaxaca state, Estero Majahuas (EMAJ) in Jalisco state, and Reserva Ecológica Estatal Laguna de las Ilusiones (LILUS) in Tabasco state. For additional details of these study sites see García (1988), González-Desales et al. (2016a), López-Luna et al.

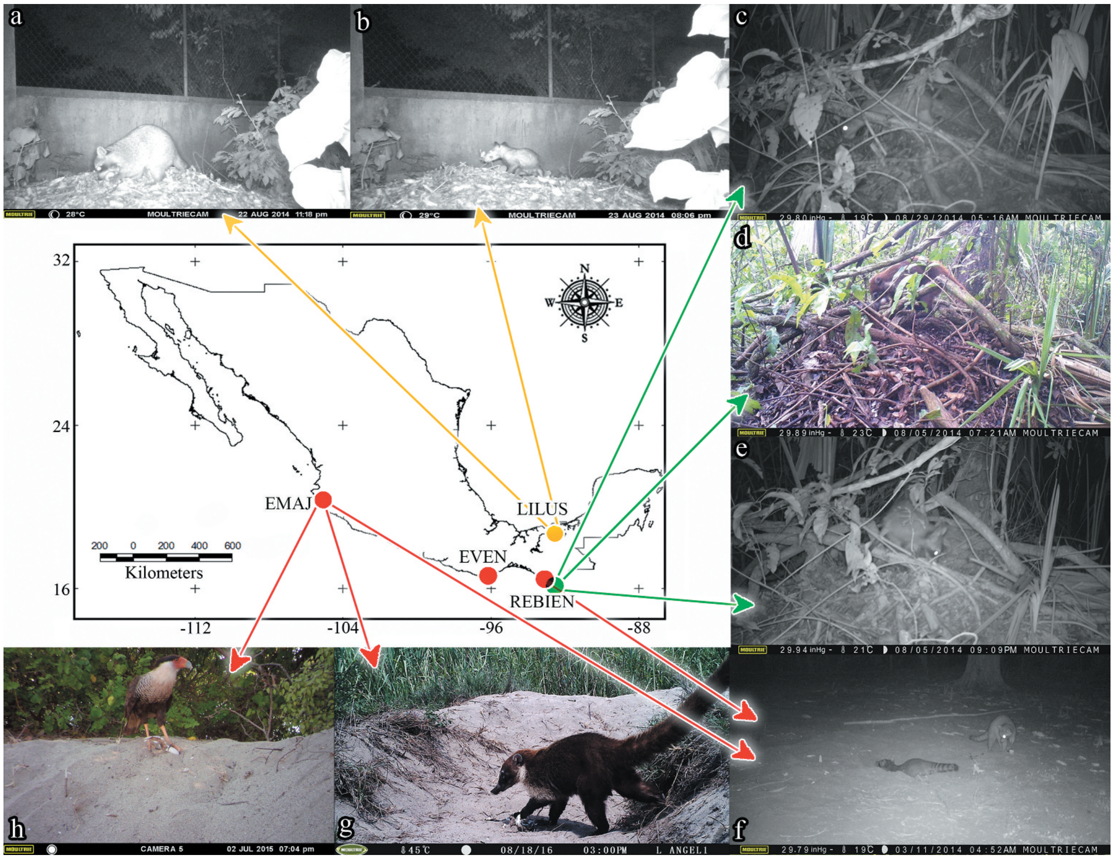

Figure 1. Geographical location of the study areas and photographic records of eggs predation. *Procyon lotor* (a, e, f), *Didelphis virginiana* (b), *Cuniculus paca* (c), *Nasua narica* (d, g), and *Caracara cheriway* (h).

(2011), SEMARNAT-CONANP (s/f). Table 1 shows the distribution, model and programming of camera-traps, the studied species, number observed nests and the duration of observation among the study areas.

We screened each photograph obtained by the camera-traps, and identified each individual to species using specialised literature (Howell and Webb 1995; National Geographic Society 2002; Ceballos and Oliva 2005) and personal experience of the authors. To identify the interactions in accordance with the activities carried out by the species in photographic records, we followed the proposal of Sutton and Harmon (2007), considering the benefit (+), effect (-) or no effect (0), towards crocodilians: 1- Cooperation (+/+), 2- Mutualism (+/+), 3- Commensalism (+/0), 4- Amensalism (-/0), 5- Competition (-/-), 6- Predation (±), and 7- Parasitism (±). We then obtained the percentage of the activity carried out by the species in each type of interaction. Additionally, we identified the presence or absence of fishermen, tourists, exotic or domestic fauna at each site.

We analysed the relationship between the number of egg predator species (dependent variable) and the richness of vertebrates identified per area (independent variable) using a nonlinear regression. For this analysis we included data from Parque Ecológico Punta Sur (PEPS) and Reserva de la Biósfera Banco Chinchorro (REBIBC) from Hénaut and Charruau (2012) and Platt et al. (2014). Those authors used camera-traps to study nesting

Table 1. Study areas, crocodilian species, season and number of nests monitored, and configuration of camera-traps in the present study.

Study areas	Observed species	Nesting season (year)	Camera-traps (number equipment's)	Number of observed nests	Programming of camera-traps
REBIEN	*Caiman crocodilus chiapasius*	Jul-Sep (2014)	Moultrie MCG-M990i (5) HCO ScoutGuard SG550 (2)	5	3 photographs per event
	Crocodylus acutus	Mar-May (2014)	Moultrie MCG-M990i (3) HCO ScoutGuard SG550 (2) HCO ScoutGuard SG860C (2)	13	3 photographs per event
EVEN	*Crocodylus acutus*	Mar-Jun (2011)	Moultrie 150 (6)	6	1 photograph per event
EMAJ	*Crocodylus acutus*	Jun-Ago (2012)	Moultrie DGS-I35 (2)	3	1 photograph per event
		Jun-Ago (2013)	Moultrie DGS-I35 (3)	5	1 photograph per event
		Jun-Ago (2014)	Moultrie DGS-I35 (3)	5	1 photograph per event
		Jun-Ago (2015)	Moultrie A-5 (2) Moultrie DGS-I35 (2)	5	1 photograph per event
		Jun-Ago (2016)	Moultrie DGS-I35 (5)	3	1 photograph per event
LILUS	*Crocodylus moreletii*	Jun-Ago (2015)	Moultrie MCG12590 (5) Bushnell TrophyCam 119,436 (6)	9	3 photographs and 10 seconds video per event

behaviour of *C. acutus* females and obtained data on species visiting their nests in a similar fashion to this study.

In addition, we obtained the number of nests lost by predation in other crocodilians from the scientific literature, searched in Google Scholar using the following keywords: camera-traps and crocodilians, eggs predation, nests predators, photographic records and nests, monitoring of the crocodilians with camera-traps, crocodilian predators. We only consider those scientific reports with egg predators identified by camera-traps. We evaluated the relationship between percentage of preyed upon nests and crocodilian maximum size, through a nonlinear regression analysis, considering the percentage of preyed upon nests as a dependent variable. The maximum size of these crocodilian species was obtained from the Crocodile Specialist Group website (http://www.iucncsg.org/pages/Crocodilian-Species.html). All statistical analyses were performed with Statgraphics Centurion 16.1 and results were considered significant at p-values < 0.05.

Results

Nests of *Caiman crocodilus chiapasius* were only recorded at REBIEN, where 1,882 photographic records were obtained in which 11 vertebrate species were identified: six mammalian, four avian, and one reptilian species (Table 2). Only three species were recorded preying on eggs: lowland paca (*Cuniculus paca*), white-nosed coati (*Nasua narica*) and northern raccoon (*Procyon lotor*) (Figure 1). No photographic records were obtained of exotic fauna or humans. All five monitored nests were preyed upon.

Nests of *Crocodylus acutus* were observed at REBIEN, EVEN, and EMAJ. For this species at REBIEN, 4,612 photographic records were obtained showing 20 vertebrate species: 11

Table 2. Vertebrates found associated with wild nests of the Crocodylia in Mexico in the present study and included in previous reports (* = Hénaut and Charruau 2012; + = Platt et al. 2014).

Crocodilian	Site	Class	Species	Activity
Caiman crocodilus chiapasius	REBIEN	Reptilia	*Iguana iguana*	Transit
		Aves	*Amazilia rutila*	Transit
			Aramides cajaneus	Transit
			Cyanocorax yncas	Transit
			Tigrisoma mexicanum	Transit
		Mammalia	*Cuniculus paca*	Predation
			Dasypus novemcinctus	Transit
			Nasua narica	Predation/Transit
			Philander opossum	Transit
			Potos flavus	Transit
			Procyon lotor	Predation
Crocodylus acutus	EVEN	Reptilia	*Iguana iguana*	Basking/Nesting
		Aves	*Ardea alba*	Transit
			Bubulcus ibis	Transit
			Calocitta formosa	Transit
			Ortalis sp.	Transit
			Quiscalus mexicanus	Transit
			Tyrannus melancholicus	Transit
		Mammalia	*Nasua narica*	Transit
			Procyon lotor	Transit
	EMAJ	Amphibia	*Rhynella horribilis*	Basking/Transit
		Reptilia	*Aspidoscelis communis*	Basking/Transit
			Aspidoscelis lineatissima	Basking/Transit
			Ctenosaura pectinata	Basking/Transit
			Holcosus undulates	Transit
			Iguana iguana	Basking/Transit
			Loxocemus bicolour	Transit
		Aves	*Caracara cheriway*	Predation
			Columbina flavirostris	Sand Bath
			Egretta caurelea	Transit
			Eudocimus albus	Transit
			Megarynchus pitangua	Sand Bath
			Morococcyx erythropygus	Transit
			Myiarchus tuberculifer	Sand Bath
			Nyctanassa violacea	Basking/Transit
			Ortalis poliocephala	Sand Bath/Transit
			Plegadis chihi	Transit
			Tigrisoma mexicanum	Transit
			Tyrannus melancholicus	Transit
			Tyrannus vociferans	Sand Bath
			Zenaida asiatica	Transit
			Zenaida macroura	Transit
		Mammalia	*Baiomys taylori*	Transit
			Dasypus novemcinctus	Transit
			Didelphis virginiana	Transit
			Leopardus wiedii	Transit
			Nasua narica	Predation/transit
			Oryzomys melanotis	Transit
			Procyon lotor	Predation/transit
			Puma yagouaroundi	Transit
	PEPS*	Amphibia	Unidentified	
		Reptilia	*Aspidoscelis cozumela*	
			Ctenosaura similis	
			Iguana iguana	
		Aves	*Aramides cajanea*	
			Cathartes aura	Predation+
			Coragyps atratus	Predation+
			Leptotila jamaicensis	
			Mimus gilvus	
			Nyctanassa violacea	
			Quiscalus mexicanus	
		Mammalia	*Procyon pygmaeus*	

(*Continued*)

Table 2. (Continued).

Crocodilian	Site	Class	Species	Activity
	REBIBC*	Reptilia	*Anolis allisoni*	
			Aspidoscelis cozumela	
			Ctenosaura similis	
			Iguana iguana	
			Norops sagrei	
		Aves	*Columba leucocephata*	
			Myiarchus tyrannulus	
			Nyctanassa violacea	
			Quiscalus mexicanus	
			Seiurus aurocapilla	
	REBIEN	Reptilia	*Ctenosaura similis*	Basking/transit
			Iguana iguana	Basking/transit
		Aves	*Aramides cajanea*	Transit
			Buteogallus anthracinus	Transit
			Calocitta formosa	Feeding/transit
			Coragyps atratus	Transit
			Dryocopus lineatus	Transit
			Icteus sp.	Transit
			Leptotila verreauxi	Transit
			Nyctanassa violacea	Transit
			Ortalis leucogastra	Sand Bath/Transit
			Quiscalus mexicanus	Transit
			Tigrisoma mexicanum	Transit
		Mammalia	*Cuniculus paca*	Transit
			Didelphis virginiana	Transit
			Nasua narica	Transit
			Peromyscus mexicanus	Transit
			Philander opossum	Transit
			Procyon lotor	Predation
			Sciurus variegatoides	Transit
Crocodylus moreletii	LILUS	Amphibia	*Rhinella horribilis*	Transit
		Reptilia	*Basiliscus vittatus*	Basking/Vigilance/Transit
			Crocodylus moreletii	Transit
			Ctenosaura similis	Basking
			Iguana iguana	Transit/Basking
		Aves	*Ardea alba*	Transit/Feeding
			Bubulcus ibis	Transit/Feeding/Materials Extraction
			Butorides virescens	Transit
			Crotophaga surcirostris	Transit/Feeding
			Egretta thula	Transit/Feeding/Materials Extraction
			Icterus gularis	Transit
			Melanerpes aurifrons	Transit/Feeding
			Pitangus sulphuratus	Transit/Feeding
			Quiscalus mexicanus	Transit/Feeding
			Turdus grayi	Transit/Feeding
			Zenaida asiatica	Transit
		Mammalia	*Didelphis marsupialis*	Transit/Feeding
			Didelphis virginiana	Predation
			Procyon lotor	Transit/Feeding/Predation
			Sciurus melanogaster	Transit

mammalian, seven avian, and two reptilian species (Table 2). Photographic records of fishermen, tourists and domestic dog (*Canis lupus familiaris*) were also obtained (Table 3). Two of the thirteen monitored nests were preyed upon by *Procyon lotor* (Figure 1). With respect to EVEN, nine species of vertebrates were identified from 756 photographic records: two mammalian, six avian, and one reptilian (Table 2). We also recorded humans and domestic horse (*Equus caballus*) walking over some of the nests (Table 3). At EMAJ, 30 vertebrate species were identified from 12,949 photographic records: eight mammalian,

Table 3. Number of species identified, egg predators, domestic fauna and human presence at wild nests of Mexican crocodilians.

Site	Fauna	Predators	Domestic Fauna	Fishermen/ Tourists	Source
EMAJ	30	3		Present	Present study
REBIEN	25	3	*Canis lupus famliaris*	Present	Present study
PEPS	12	2		Present	Hénaut and Charruau (2012); Platt et al. (2014)
REBIBC	10		*Felis catus* *Rattus rattus*	Present	Hénaut and Charruau (2012)
EVEN	9	1	*Equus caballus*	Present	Present study; García-Grajales and Buenrostro-Silva (2015)
LILUS	20	2	*Felis catus* *Rattus norvegicus*	Present	Present study

15 avian, six reptilian, and one amphibian species (Table 2). Of these 30 identified species, *Nasua narica, Procyon lotor* and crested caracara (*Caracara cheriway*) preyed on crocodilian eggs (Figure 1).

Nests of *Crocodylus moreletii* were only recorded at LILUS, where 33,509 photographic records and 157 videos were obtained, from which 20 vertebrate species were identified: four mammalian, 11 avian, four reptilian, and one amphibian species (Table 2). Humans were also recorded in this area (Table 3). *Procyon lotor* and virginia opossum (*Didelphis virginiana*) preyed upon eggs of two monitored nests (Figure 1).

Overall, our study identified 72 vertebrate species at the monitored crocodilian nesting sites in Mexico, obtained from 53,865 photographic and video records. However, only five of these species preyed on eggs: *Caracara cheriway, Cuniculus paca, Didelphis virginiana, Nasua narica*, and *Procyon lotor* (Figure 1). The common green iguana (*Iguana iguana*) and *Procyon lotor* were the only two species recorded at all nesting sites (Table 2). From seven activities, we identify three types of interactions: a) Cooperation (free transit of the species = 65.8%), b) Commensalism (basking sites = 10%, feeding sites without predation of crocodilian eggs = 9.1%, dust bathing = 5%, extraction of plant matter = 1.6%, and vigilance sites = 0.8%), and c) Predation (predation of crocodilian eggs = 7.5%).

There was a relationship between the number of vertebrate species recorded at nests (Table 3) and the number of egg predators (r^2 = 86.74; $p < 0.05$), adjusting to the regression model: Y-square and square root-X (Figure 2(a)).

Our literature review identified 12 scientific publications that used camera-traps as a method of monitoring crocodilian nests published between 1982 and 2017, evaluating egg predation in 10 crocodilian species (Table 4). Predators corresponded with wildlife species in all crocodilian nests monitored. A relationship was also observed between the percentage of nests preyed upon (Table 4) and crocodilian size (r^2 = 75.04; $p < 0.05$), adjusting to the regression model: Y-square and X–inverse (Figure 2(b)).

Discussion

Camera-traps have been shown as a useful tool for in situ observations of crocodilian nesting sites. For the south Pacific coast (Chiapas, Mexico), a previous study reported that 5.9% of *C. acutus* nests were lost by predation, but the predator was not mentioned (González-Desales et al. 2016a). Similarly, in the case of *C. c. chiapasius* in a region of the

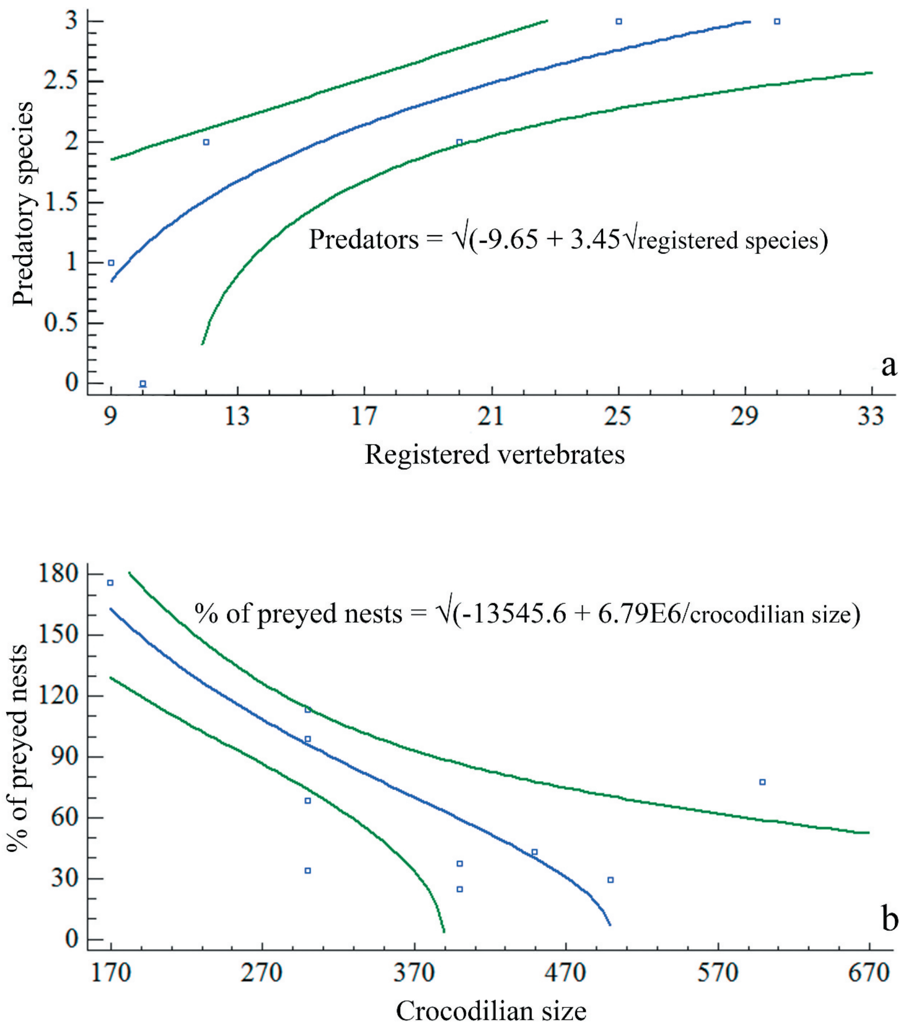

Figure 2. Non-linear regression models: (a)- Predator species increase with the number of vertebrates recorded in the areas of study. (b)- The number of nests lost decreases as crocodilian size increases.

Chiapas coast, it has been reported that egg predation occurs, with losses of 47.4% without identifying the predator (González-Desales et al. 2016b). While in another region of the same coast (Oaxaca, Mexico), it was identified that *Procyon lotor* preyed on *C. acutus* eggs (García-Grajales and Buenrostro-Silva 2015), prior to this study, there were only photographic records of egg scavenging by *Coragyps atratus* and *Cathartes aura* for Mexican crocodilians (Platt et al. 2014).

Using camera-traps, this study identified 72 vertebrate species that had some type of relationship with crocodilian nests in Mexico. Of these species, five preyed on nests: three on *C. c. chiapasius*, three on *C. acutus*, and two on *C. moreletii*. Eggs were mainly preyed upon by mammalian mesocarnivores, and *Procyon lotor* was recorded preying on eggs of all three Mexican crocodilians. Previously, this species had only been recorded with camera-traps preying on the eggs of *Alligator mississippiensis* (Hunt and Ogden 1991; Merchant et al. 2014). *Nasua narica* and *Cuniculus paca* were reported for the first time as predators of Mexican crocodilians through photographic records in the present study. The different egg predators between areas can be attributed to the fact that ecosystem

Table 4. Number of nests affected by predation (wild and exotic fauna, as well as by humans) of crocodilians on a global level identified through photographic records.

Crocodylia	Predator	Nests Affected	Authors
Alligator mississippiensis	*Oryzomys palustris*	1(15)	Hunt and Odgen (1991)
	Procyon lotor	-(62)	Merchant et al. (2014)
	Procyon lotor	3(15)	Hunt and Odgen (1991)
	Sus scrofa	-(62)	Merchant et al. (2014)
	Tupinambis merianae	1(1)	Mazzotti et al. (2015)
	Ursus americanus	11(15)	Hunt and Odgen (1991)
Caiman crocodilus chiapasius	*Cuniculus paca*	2(5)	Present study
	Nasua narica	5(5)	
	Procyon lotor	1(5)	
Caiman crocodilus crocodilus	*Cebus apella*	2(23)	Da Silveira et al. (2010)
	Homo sapiens	1(23)	
	Panthera onca	3(23)	
	Tupinambis teguixin	5(23)	
Caiman yacare	*Cerdocyon thous*	24(57)	Campos and Mourão (2014)
	Dasypus novemcintus	2(57)	
	Eira barbara	15(57)	
	Nasua nasua	19(57)	
	Salvator merianae	2(57)	
	Sus scrofa	2(57)	
Crocodylus acutus	*Caracara cheriway*	2(21)	Present study
	Cathartes aura	1(4)	Platt et al. (2014)
	Coragyps atratus	1(4)	
	Nasua narica	2(21)	Present study
	Procyon lotor	2(13)	
	Procyon lotor	1(21)	
Crocodylus johnstoni	Aves	-(111)	
	Canis lupus dingo	109(111)	
	Reptiles	-(111)	
Crocodylus moreletii	*Didelphis virginiana*	2(9)	Present study
	Procyon lotor	1(9)	
Crocodylus niloticus	*Varanus niloticus*	7(19)	Combrink et al. (2016)
Crocodylus porosus	*Varanus indicus*	2(14)	Magnusson (1982)
	Varanus indicus	38(38)	
Melanosuchus niger	*Didelphis marsupialis*	1(14)	Torralvo et al. (2017)
	Homo sapiens	7(111)	Da Silveira et al. (2010)
	Panthera onca	6(111)	
	Panthera onca	2(14)	Torralvo et al. (2017)
	Rodentia	1(7)	Villamarín-Jurado and Suárez (2007)
	Sapajus macrocephalus	6(14)	Torralvo et al. (2017)
	Tupinambis teguixin	10(111)	Da Silveira et al. (2010)
	Tupinambis teguixin	5(14)	Torralvo et al. (2017)
Paleosuchus trigonatus	*Cabassous unicinctus*	1(4)	Campos et al. (2016)
	Dasypus novemcintus	1(4)	
	Eira barbara	1(4)	
	Nasua nasua	1(4)	
	Priodontes maximus	1(4)	
	Tupinambis teguixin	2(4)	

interactions can vary as a function of the availability of habitat resources (Smith and Smith 2007), the composition of predator-prey communities (Ritchie and Johnson 2009), as well as the activity pattern of the predator (Harmsen et al. 2011).

Our literature survey showed that camera-trapping has been used as a method for monitoring crocodilian nests globally in recent years, with 30 species being identified as egg predators, in addition to humans stealing nests. For *C. acutus* and *C. moreletii* nests, the presence of domestic fauna as well as the presence of fishermen and tourists were recorded, but without predation or extraction of eggs. It is probable that nest robbing was not recorded due to the monitoring of the nests during this study. Specifically, in REBIEN it has been identified that the stealing of *C. acutus* nests occurs in regions where nesting areas are near human settlements (2.8 ± 1.19 km) and where nests are close to waterbodies (4.60 ± 2.5 m; González-Desales et al. 2016a).

With respect to the predators we Valenzuela (2005a, 2005b)) mentions that *Nasua narica* and *Procyon lotor* are omnivorous and feed mainly on fruits, seeds, invertebrates, and small vertebrates. It is also mentioned that *N. narica* occasionally feeds on turtle eggs and *P. lotor* feeds on turtle, bird, and caiman eggs. The consumption of turtle eggs by *N. narica* (Valenzuela 1998) was recorded in Cuixmala, which is an area where *Crocodylus acutus* nests have been found (Casas-Andreu 2003) and where recent predation of crocodile eggs by *N. narica* has been described (direct observations; Cuapio 2015). With respect to *Caracara cheriway*, it is considered to be an opportunist species (Morrison et al. 2008) that feeds on invertebrates, fish, amphibians, reptiles, and birds (Pérez-Estrada and Rodríguez-Estrella 2016). The consumption of reptile eggs by this species has not been recorded previously. The diet of *Cuniculus paca* consists of stalks, leaves, seeds, and fruits (Ortega and Arita 2005). *Didelphis virginiana* is an opportunist omnivore species that feeds on insects, vertebrates, carrion, fruits, and seeds (Zarza and Medellín 2005). The results obtained from the present study, in addition to identifying egg predators of Mexican crocodilians, also contribute to the knowledge of the dietary habits of these predators.

This is the first study in Mexico where the interactions between fauna and crocodilian nests have been identified, giving evidence that the construction of the nests generally favours the activities of other species without causing damage to the survival of the crocodilians (commensalism), except for predation. An example of commensalism would be sand baths as they help to clean skin, feathers, or fur, in addition to eliminating ectoparasites and aiding in thermoregulation (Barandongo et al. 2018). It has also been recorded in *A. mississippiensis* that commensalism is the most frequent interaction at nesting sites (Merchant et al. 2014). In other countries, parasitism has also been documented as a type of interaction between *Iguana iguana* and *C. acutus* nests (Dugan et al. 1981). This interaction was not documented during the present study. In other cases, commensalism favours the crocodilian, which is the case with nests that are constructed in termite mounds where their temperature assists in the incubation of *Paleosuchus trigonatus* eggs (Magnusson et al. 1985). With respect to the most frequent activity (free transit), while this is not necessarily an interaction that is specific to nests, we suggest that this is a result of the elements that make up the nesting sites which offer vertebrate species refuge sites (hollow logs, rocks, human structures), perching sites (tree branches), or food (fruit trees), as moving from one site to another would result in eventually crossing over a nest, making this an occasional interaction (cooperation).

The results suggest that anthropogenic disturbance does not appear to have an effect on the association between the crocodilian nesting sites and wild/exotic fauna in the areas of study. LILUS is the area with the most anthropogenic disturbance and yet no predation by exotic fauna, nor greater number of nests lost, was recorded in this or any other monitored area. It has been documented that human disturbance affects nesting sites (Casas-Andreu 2003), but it does not appear have an effect on ecological interactions with wild or exotic fauna. A low percentage of predation by exotic fauna has also been observed with other species of crocodilians previously.

Additionally, we identified a greater number of predator species at sites where there were more vertebrate species, supporting the prediction of Stephens et al. (2009), which states that an interaction between species can be attributed to the high coincidence of their spatial distributions. This is to say, the greater the co-occurrence, the greater the probability of an interaction taking place. The non-linear model of this analysis also indicated that there was a limit to the number of predators, even as more species were recorded. In addition, we found the number of nests preyed upon appears to be a function of the size of the crocodilian, indicating that the bigger the crocodilian is, the number of nests preyed upon will be less. We found this pattern is repeated on local and global levels. Considering the sympatric crocodilian species at REBIEN, the number of nests preyed upon (47.4%) was greater with the species of the smallest size (*C. c. chiapasius*) in comparison with the nests preyed upon (5.8%) of the species of the greatest size (*C. acutus*; González-Desales et al. 2016a, 2016b).

Overall, our results indicate that the predation of crocodilian eggs is dependent on: a) ecological factors, such as the richness of vertebrate species at the nesting sites, and b) biological characteristics, such as crocodilian size, the life stage in which they find themselves (Somaweera et al. 2013), and parental care (Ferguson 1985). Additionally, mammalian mesocarnivore species (*Didelphis virginiana, Procyon lotor* and *Nasua narica*) with large distributions and with generalist and opportunist diets are principally responsible for the predation of the eggs of Mexican crocodilians.

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