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# Factors Influencing Egg Predation of Two Sympatric Crocodilians in Mexico

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***Abstract*.—The rates of eggs predation in crocodilians can be influenced by the abundance of predators, their activity time, the crocodilian size, and parental care. We evaluated the relationship between crocodilian eggs predation and characteristics of the predatory species (egg search intensity and activity hours), of the nesting females (nest defense), and of the nesting site (habitat characteristics and climatic variables). We evaluated nests with camera traps during the 2014 nesting seasons of Spectacled Caimans (*Caiman crocodilus*) and American Crocodiles (*Crocodylus acutus*) in the Biosphere Reserve La Encrucijada, Mexico. We identified a relationship between the defense of the nest and the search for eggs by predators. The number of photographic records of females on the nest increased with the number of photographic records of the egg predators. We observed overlap of activity hours between crocodilian females and egg predators. Females were recorded on the nest only when their predator species was present. In addition, some climatic variables (air temperature and rainfall) and nests characteristics (depth to the first egg and distance to the closest tree) were positively associated with the success of egg predation, depending on the predator species.**

*Key Words*.—*Caiman crocodilus*; *Crocodylus acutus*; camera-traps; ecological interactions; hatchling attendance; wild nest protection

***Resumen*.—Las tasas de depredación de huevos de cocodrilianos pueden verse influenciadas por la abundancia de depredadores, su tiempo de actividad, el tamaño de los cocodrilianos y el cuidado parental. Evaluamos la relación entre la depredación de huevos de cocodrilianos y las características de la especie depredadora (intensidad de búsqueda de huevos y horas de actividad), de las hembras anidadoras (defensa del nido) y del sitio de anidación (características del hábitat y variables climáticas). Evaluamos nidos con cámaras trampa durante las temporadas de anidación de 2014 de caiman de anteojos (*Caiman crocodilus*) y cocodrilo americano (*Crocodylus acutus*) en la Reserva de la Biosfera La Encrucijada, México. Identificamos una relación entre la defensa del nido y la búsqueda de huevos por los depredadores. El número de registros fotográficos de hembras en el nido aumentó con el número de registros fotográficos de los depredadores de huevos. Observamos superposición de horas de actividad entre las hembras de cocodrilianos y los depredadores de huevos. Las hembras se registraron en el nido solo cuando su especie depredadora estaba presente. Además, algunas variables climáticas (temperatura del aire y lluvia) y características de los nidos (profundidad al primer huevo y distancia al árbol más cercano) se asociaron positivamente con el éxito de la depredación de huevos, dependiendo de la especie depredadora.**

*Palabras clave*.—asistencia de crías; cámaras trampa; *Caiman crocodilus; Crocodylus acutus*; interacciones ecológicas; protección de nidos silvestres.

## Introduction

Nesting success of crocodilians is influenced by biological processes (Thorbjarnarson 1996), environmental factors (Platt et al. 1995; Charruau et al. 2010), ecological interactions (Somaweera et al. 2013; González-Desales et al. 2020), and anthropogenic disturbances (González-Desales et al. 2016a). Many bird, mammal, and reptile species (n = 184) have been identified as nest predators of 19 species of crocodilians (Somaweera et al. 2013). The rates of nest predation can increase with predator abundance (Campos and Mourão

2015) and its activity time (Campos et al. 2016); however, rates decrease with increasing crocodilian size (González-Desales et al. 2020) and parental care (Charruau and Hénaut 2012). The extent of parental care of the mother can be influenced by body condition, climatic conditions, and the presence of predator and/or antagonistic species (Lang 1987; Charruau and Hénaut 2012; Campos et al. 2016; Barão-Nóbrega et al. 2018). Despite the advances in the monitoring of crocodilian nests with camera traps (Da Silveira et al. 2010; Platt et al. 2014; Merchant et al. 2014; Campos and Mourão 2015), there is still little information on crocodilian nest defense behavior and activity pattern of nest predators.

The Spectacled Caiman (*Caiman crocodilus*) and American Crocodile (*Crocodylus acutus*) are the most widely distributed crocodilians in Central and South America (Pooley et al. 2021; Velasco and Ayarzagüena 2010; Rainwater et al. 2019). Both species exhibit a large variety of social, reproductive, and nest maintenance behaviors (Lang 1987). The nature and extent of female nest defense in crocodilians differs widely among and within species. The behavior can range from simple presence at the nest to aggressive behavior toward potential predators (Webb and Manolis 1998; Charruau and Hénaut 2012; Murray et al. 2020). Charruau and Hénaut (2012) observed the presence of female *C. acutus* at the nest led to a decrease in the presence other wildlife species; however, egg predation and a specific response to predators in this species were not reported. A similar pattern was observed in studies of *C. crocodilus* (Gorzula and Sejias 1989; Staton and Dixon 1977). Mesocarnivores are the major predators of crocodilian eggs in North and South America (Joanen and McNease 1989; Larriera and Piña 2000; Campos et al. 2016; Murray et al. 2016; Villegas et al. 2017). In Mexico, camera traps have identified three mammals as the primary predators of *C. crocodilus* and *C. acutus* nests (González-Desales et al. 2020): White-nosed Coati (*Nasua narica*), Northern Raccoon (*Procyon lotor*), and Lowland Paca (*Cuniculus paca*). *Nasua narica* is a diurnal species lives and forages in social groups of 6–65 individuals comprised of philopatric adult females and their offspring (Di Blanco and Hirsh 2006). *Procyon lotor* is a nocturnal species exhibiting both solitary (Greenwood 1982) and group foraging patterns (Whitney and Underwood 1952; Waser and Jones 1983; Chamberlain and Leopold 2002; Ladine 2017). Groups can be of males, females, or occasional groups of juveniles and adults of both sexes. *Cuniculus paca* is also a nocturnal (Michalski and Norris 2011) and commonly a solitary species (Meritt 1989). In other taxonomic groups, spatiotemporal patterns of predator and prey have been examined in detail using camera traps, contributing to understanding of how prey detect, recognize, and respond to their predators (Smith et al. 2020). The Species Occurrence Probability Index (derived from the Relative Abundance Index) is widely used to examine spatial and temporal relationships between individuals, species, or events (Monroy-Vilchis et al. 2009; 2011; Carrera-Treviño et al. 2018).

In Mexico, *C. crocodilus* and *C. acutus* are sympatric only in Chiapas, and nest loss due to predation has been documented in this region (González-Desales et al. 2020). This situation may be of conservation concern, particularly for *C. crocodilus*, which has a restricted distribution in Mexico. Therefore, we examined the following questions: (1) Is the search for eggs by predatory species the same in both nesting seasons?; (2) Do crocodilians defend the nest of the presence of predatory species?; (3) Do some climatic variables and external characteristics of the nest influence egg predation?; and (4) Is the detection probability of crocodilian egg predation by camera traps a viable method for measuring predation success?

## Materials and Methods

***Study area***.—We studied crocodilians on Isla La Concepción (15.067721°, -92.754368°), which is an islet within the La Encrucijada Biosphere Reserve of Mexico. The predominant vegetation is Red Mangrove (*Rizophora mangle*), Silver-leaved Buttonwood (*Conocarpus erectus*), Guiana Chestnut (*Pachira aquatica*), and tropical semi-evergreen forest. The islet is located on the margin of El Hueyate estuary and is surrounded by swamps (fresh and brackish). This site, to date, is the only area where scientific data are available on the nests of *Caiman crocodilus* in Mexico (González-Desales et al. 2016b). In the El Hueyate estuary, the American Crocodile and Spectacled Caiman are sympatric (González-Desales et al. 2021).

***Camera trap photographs***.—We placed camera traps with passive temperature and motion sensor: (1) Moultrie model MCG-M990i (Moultrie Products, Birmingham, Alabama, USA); (2) HCO ScoutGuard model SG550 (HCO Outdoor Products, Duluth, Georgia, USA); (3) HCO ScoutGuard model SG860C (HCO Outdoor Products). We placed these camera traps at 16 crocodilian nest sites (five *C. crocodilus* and 11 *C. acutus*), one per nest, during the 2014 nesting season (González-Desales et al. 2016a,b). We programmed the cameras to obtain three photographic records per activation, with 24-h operation during the months of nesting (March to September). We changed batteries and memory cards every week, and we placed each camera trap on a tree close to the nest (2–4 m for *C. crocodilus*; 2–11 m for *C. acutus*). To document nest defense behavior, we further positioned cameras to include in the field of view the likely route of approach by a maternal female to her nest.

***Activity patterns of crocodilians and nest predators***.—The egg predators in our study area were *Cuniculus paca* and *Nasua narica* for *C. crocodilus* and *Procyon lotor* for both *C. acutus* and *C. crocodilus* (González-Desales et al. 2020). These mammals are the most abundant in the study area (Hernández-Hernández et al. 2018). We used Spearman's Rank Correlation to determine if there was a significant relationship between the presence frequency of female crocodilians (*C. crocodilus* and *C. acutus*) and egg predators at the nests (RStudio software, version 1.3.959; RStudio Team, 2020). We grouped the photographic records accumulated each week from oviposition of eggs until hatching or predation (Torralvo et al. 2017). We evaluated the overlap of the activity time between crocodilians and egg predators using the Overlap Coefficient (Dhat1) in the R data analysis software camtrapR, based on Niedballa et al. (2016). This coefficient ranges from 0 to 1, where 0 indicates the hours of activity do not overlap, and 1 indicates to identical activity patterns (total overlap).

***Egg predation success***.—We obtained data on the climatic variables air temperature (°C), relative humidity (%), and rainfall (mm) from the La Encrucijada automatic meteorological station of Servicio Meteorológico Nacional of the Comisión Nacional del Agua (CONAGUA), Mexico. We used data from March to September 2014 (nesting season for both *C. crocodilus* and *C. acutus*) and we calculated means for each variable per week and hour (coinciding with the activity patterns; see previous section). We also used data collected during previous studies (González-Desales et al. 2016a,b) on nest characteristics, including depth from the top of the nest to the first egg (cm), distance from the nest to the nearest body of water (cm), and distance from the nest to the closest tree (cm). Spectacled Caiman nests were located on small islets (diameter generally < 300 cm) surrounded by water, so predators had to reach nests through the interconnected tree branches from the shore to these islets.

Because the photographic records of predators are counts per unit of time (Roback and Legler 2021), to evaluate the relationship between the records of egg predators at nests, climatic variables, and nest characteristics, we performed a Poisson Regression. We used the Species Occurrence Probability Index (SOPI) to assesses egg predation success. An assumption of this index is that the egg predator species have the same probability of being registered at a site (Monroy-Vilchis et al. 2009). We created an egg predation success index (EPSi) to measure the success of egg searching by predators during the crocodilian nesting season, based on the following criteria: (1) only photographic records of animals predating eggs were included; the records of animals moving freely through the nesting site without approaching the nest were excluded; (2) nesting season was the standardization unit (100 or 1,000 trap-days; Monroy-Vilchis et al. 2011); and (3) we included only records of activities related to predation (e.g., sniffing, removal of nest substrate, eggs extraction, and consumption). To avoid overestimation of the EPSi by consecutive records of the same predator, and because it was not possible to identify the individuals, we followed Monroy-Vilchis et al. (2011) and considered independent photographs to be those with a difference of 24 h between each record of the same species. The EPSi was obtained with the formula:

$$\mathrm{EPSi} = [(\mathrm{PR}_{\mathrm{ind}} / \mathrm{SE}_{\mathrm{ns}})\ (\mathrm{NS}_{\mathrm{croc}})]$$

where $\mathrm{PR}_{\mathrm{ind}}$ = number of independent records of each predatory species (*Cuniculus paca*, *Nasua narica*, and *Procyon lotor*), $\mathrm{SE}_{\mathrm{ns}}$ = days of operation of the cameras trap in the nesting season (sampling effort), and $\mathrm{NS}_{\mathrm{croc}}$ = incubation time of each crocodilian species (*C. crocodilus* = 80.4 d and *C. acutus* = 74.6 d; González-Desales et al. 2016a, b). Subsequently, we evaluated the relationship between the EPSi and the number of predated nests with a Polynomial Regression because the relationship between these variables is not linear (Faraway 2009). The number of predated nests was the dependent variable. For this analysis, we used the RStudio software (version 1.3.959; RStudio Team, 2020) and considered differences significant with $P < 0.05$.

## Results

***Activity patterns of crocodilians and nest predators***.—Of the 11 and 20 vertebrates species identified in nests of *C. crocodilus* and *C. acutus*, respectively (González-Desales et al. 2020), only three species were egg predators. We obtained 3,317 photographs of crocodilian egg predators during this study (69 *Cuniculus paca*, 1,079 *Nasua narica*, and 2,169 *Procyon lotor*). We observed predator activities of sniffing and substrate removal at 54.5% of nests of *C. acutus*, and egg extraction and consumption in 18.2% of nests. Comparatively, each of these behaviors (sniffing, substrate removal, egg extraction and consumption) was observed at 100% nests of *C. crocodilus*, and all nests we monitored were predated (Table 1). We also acquired 1,710 photographs of the nest defense by presumed maternal females (372 *C. crocodilus* and 1,338 *C. acutus*). The sampling effort ($\mathrm{SE}_{\mathrm{ns}}$) for the *C. acutus* and *C. crocodilus* nesting seasons were 630 and 410 trap-days, respectively. The highest activity (most photographic records of nest defense) for female *C. acutus* occurred during weeks 2 and 13 on incubation, corresponding to the beginning (oviposition) and end (hatching) of the nesting season. For female *C. crocodilus* the highest nest defense activity was

**Table 1**. Total (PR) and independent ($PR_{ind}$) photographs of Lowland Paca (*Cuniculus paca*), White-nosed Coati (*Nasua narica*), and Northern Raccoon (*Procyon lotor*) during the American Crocodile (*Crocodylus acutus*) and Spectacled Caiman (*Caiman crocodilus*) nesting seasons in La Encrucijada Biosphere Reserve, Mexico. An asterisk (*) indicates nests that were predated.

| | | *Cuniculus paca* | | *Nasua narica* | | *Procyon lotor* | |
|---|---|---|---|---|---|---|---|
| Species | Nest | PR | $PR_{ind}$ | PR | $PR_{ind}$ | PR | $PR_{ind}$ |
| *Crocodylus acutus* | 1 | 3 | 1 | 0 | 0 | 339 | 21 |
| | 2 | 0 | 0 | 0 | 0 | 218 | 15 |
| | 3 | 0 | 0 | 10 | 4 | 136 | 16 |
| | 4 | 0 | 0 | 0 | 0 | 599 | 23* |
| | 5 | 0 | 0 | 0 | 0 | 12 | 3 |
| | 6 | 3 | 1 | 0 | 0 | 826 | 35* |
| *Caiman crocodilus* | 1 | 0 | 0 | 165 | 7* | 3 | 1 |
| | 2 | 3 | 1 | 216 | 23* | 3 | 1 |
| | 3 | 12 | 2* | 259 | 4* | 0 | 0 |
| | 4 | 48 | 5* | 283 | 6* | 33 | 2* |
| | 5 | 0 | 0 | 146 | 8* | 0 | 0 |

observed during week 2, corresponding to the beginning of the nesting season (Fig. 1). Nest defense continued to a lesser extent throughout the nesting season for both crocodilian species. For *C.crocodilus* it was not possible to monitor activity at the end of the nesting season because all nests had been predated.

We found significant correlations between *C. acutus* and *P. lotor* ($r_s$ = 0.6; $P < 0.05$; Fig. 2) and between *C. crocodilus* and *N. narica* ($r_s$ = 0.73; $P < 0.05$; Fig. 2). At *C. acutus* nests, *P. lotor* exhibited nocturnal activity between 1800–0600 but at *C. crocodilus* nests exhibited diurnal activity from 0600–1800 (Fig. 3). *Nasua narica* had greater diurnal activity (0600–1900) at *C. crocodilus* nests. We observed an overlap coefficient close to 1 (Fig. 3) in activity hours of *C. acutus* and *P. lotor* (Dhat1 = 0.82) and *C. crocodilus* and *N. narica* (Dhat1 = 0.8).

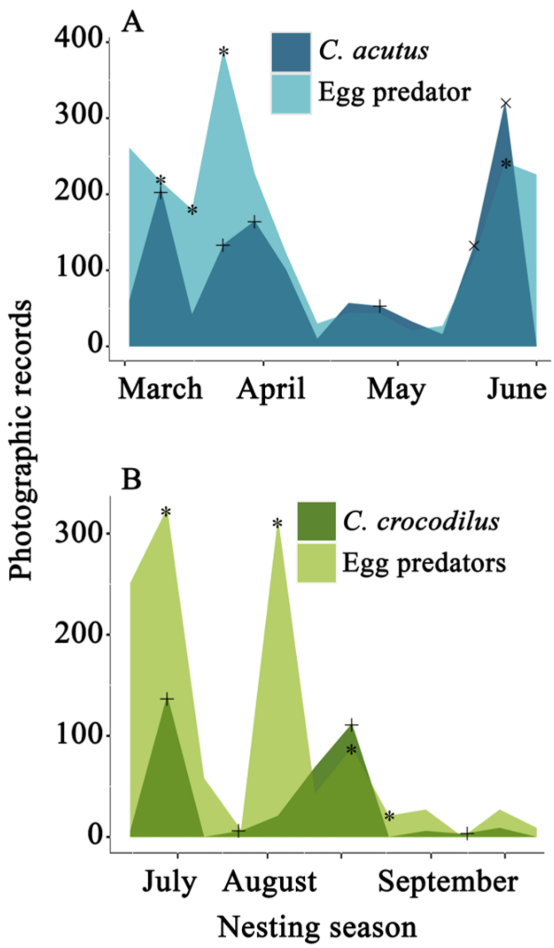


**Figure 1**. Activity patterns during the nesting season of (A) American Crocodile (*Crocodylus acutus*) and (B) Spectacled Caiman (*Caiman crocodilus*) in La Encrucijada Biosphere Reserve, Mexico. Increasing activity at nests by predators (*) resulted in increased nest defense by maternal females (+). The nests predated at the beginning of the nesting season correspond to the nests where no defense was observed, and the last to be depredated correspond to those where the female defended nests (×).

***Egg predation success***.—There was a relationship between the predation of eggs by *P. lotor* with the climatic variables and the characteristics of the nests (D = 625.35; df = 6; P < 0.001); similarly for *N. narica* (D = 1148.5; df = 6; P < 0.001). We found that the mean air temperature (29.36° ± 0.42° [standard deviation] C) during the *C. acutus* nesting season was higher than that during the *C. crocodilus* nesting season (26.81° ± 0.57° C). Conversely, mean relative humidity (89.1 ± 1.87%) and rainfall (372.8 ± 963.25 mm) were higher during the *C. crocodilus* nesting season than during the *C. acutus* nesting season (74.61 ± 2.03% and 136.9 ± 283.66 mm, respectively). Regarding nest characteristics, the *C. acutus* nests exhibited higher values for the three variables measured compared to *C. crocodilus* nests: mean depth to first egg (*C. acutus*: 22.03 ± 3.37 cm; *C. crocodilus*: 10.52 ± 3.42 cm), mean distance from nest to nearest body of water (*C. acutus*: 836.4 ± 169.79 cm; *C. crocodilus*: 180.9 ± 106.13 cm), and mean distance from nest to closest tree (*C. acutus*: 415.3 ± 63.08 cm; *C. crocodilus*: 143.4 ± 150.61 cm).

Of the 3,317 camera trap records of crocodilian egg predators, we obtained 117 independent photographic records ($PR_{ind}$) of *P. lotor,* 52 of *N. narica*, and 10 of *C. paca* (Table 1), and considering the sampling effort ($SE_{ns}$; *C. acutus* = 630, *C. crocodilus* = 410); the calculated EPSi for each egg predator for the *C. acutus* nesting season was 13.38 records/trap-days for *P. lotor*, 0.47 records/trap-days for *C. paca*, and 0.23 records/trap-

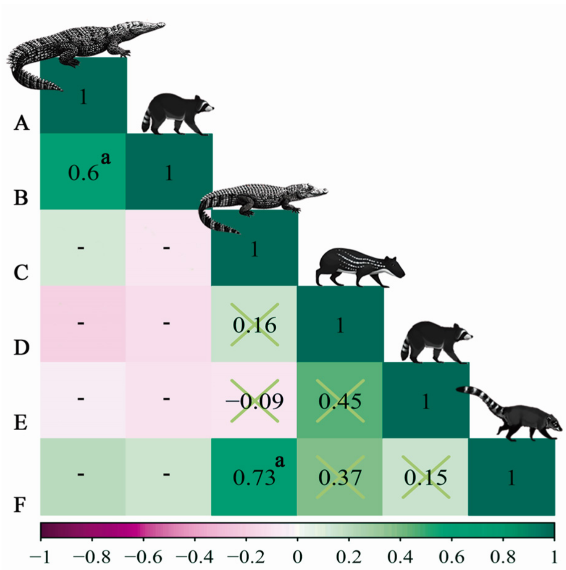


**Figure 2**. Spearman's Rank Correlations between (A) American Crocodiles (*Crocodylus acutus*) and (C) Spectacled Caimans (*Caiman crocodilus*) and egg predators. During the nesting season of *Crocodylus acutus*, only predation by (B) Northern Raccoon (*Procyon lotor*) was recorded. During the nesting season of *Caiman crocodilus*, predation by (D) Lowland Paca (*Cuniculus paca*), (E) *P. lotor*, and (F) White-nosed Coati (*Nasua narica*) was recorded. We do not include *C. paca* and *N. narica* registered in the nesting season of *C. acutus* due to the low number of records (see Table 1). Subscript a indicates a significant correlation ($P < 0.05$).

days for *N. narica*. For the *C. crocodilus* nesting season, EPSi was 9.41 for *N. narica*, 1.56 for *C. paca*, and 0.78 *P. lotor*. Finally, we observed a significant relationship between the number of nests lost to predation and the EPSi of the predatory species ($F_{2,3} = 119.89$; $P = 0.001$). This polynomial relationship (nests predated = -0.357 + 1.541×EPSi - 0.102×EPSi2) indicates that egg predation increases when the EPSi value increases and there is a maximum limit of predated nests is reached even though the EPSi value continues to increase, because of females actively defending nests.

## Discussion

Ours is the first study to analyze the activity patterns of the egg predators of *Caiman crocodilus* and *Crocodylus acutus* in Mexico. We observed a relationship between the presence of egg predators and female crocodilians of both species. Female crocodilians were present at nests when the egg predators visited it, not when other non-predatory vertebrate visited at nests, which has been previously described in *C. acutus* in Belize (Platt and Thorbjarnarson 2000) and other caiman species in South America (Bãrao-Nóbrega et al. 2016; Campos et al. 2016). In contrast, studies by Charruau and Hénaut (2012) and Combrink et al. (2016) observed female

**Table 2**. Relationships between search and predation of crocodilian nests by Northern Raccoon (*Procyon lotor*) and White-nosed Coati (*Nasua narica*), and nest characteristics and climatic variables during nesting seasons in La Encrucijada Biosphere Reserve, Mexico. The abbreviation SE = standard error.

| Egg predator | Predictor variables | Estimate | SE | *Z* | *P*-value |
|---|---|---|---|---|---|
| *Procyon lotor* | Intercept | 104.93 | 6.60 | 15.88 | < 0.001 |
| | Air temperature | -1.45 | 0.09 | -14.71 | < 0.001 |
| | Relative humidity | -0.55 | 0.03 | -17.26 | < 0.001 |
| | Rainfall | 15.98 | 1.02 | 15.25 | < 0.001 |
| | Depth from the top of the nest to the first egg | -0.60 | 0.06 | -9.09 | < 0.001 |
| | Distance from the nest to the river | -0.004 | 0.001 | -3.98 | < 0.001 |
| | Distance from the nest to the closest tree | 0.003 | 0.0007 | 3.89 | < 0.001 |
| *Nasua narica* | Intercept | 4.46 | 8.90 | 0.50 | > 0.050 |
| | Air temperature | 0.60 | 0.14 | 4.12 | < 0.001 |
| | Relative humidity | -0.20 | 0.057 | -3.57 | < 0.001 |
| | Rainfall | -35.80 | 4.89 | -7.32 | < 0.001 |
| | Depth from the top of the nest to the first egg | 0.66 | 0.086 | 7.72 | < 0.001 |
| | Distance from the nest to the nearest body of water | -0.02 | 0.0028 | -10.52 | < 0.001 |
| | Distance from the nest to the closest tree | 0.0008 | 0.0003 | 2.32 | < 0.050 |

crocodile present at nests when other non-predatory species were also at nests. We speculate that female crocodilians in our study have learned to differentiate between egg predators and harmless species.

Some studies suggest that crocodilian nest attendance is greater at the beginning and end of the incubation period as a strategy to avoid predation (Charruau and Hénaut 2012; Combrink et al. 2016; but see Torralvo et al. 2017; Merchant et al. 2018) by predators attracted to olfactory cues following oviposition and the pre- and post-hatching vocalizations of neonates. Campos et al. (2016) reported that female Schneider´s Dwarf Caiman (*Paleosuchus trigonatus*) defend nests during the night, which results in an increase in diurnal predators. While Merchant et al. (2018) observed that nest defense by female American Alligators (*Alligator mississippiensis*) occurred during the hours of greatest predation (nocturnal activity by predators). We suggest that nest defense by female crocodilians is dictated by the presence of predators at the nest regardless of time of day.

The frequency of nest attendance by female crocodilians can be influenced by their physiological condition and the distance of the nest from water (Bãrao-Nóbrega et al. 2018) and the size and number of predators

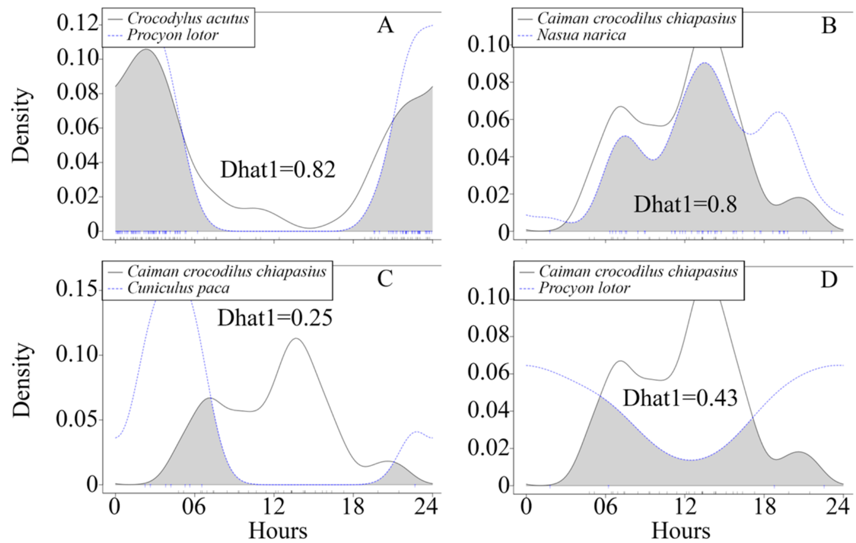


**Figure 3**. Comparison of diurnal and/or nocturnal activity pattern between crocodilians and egg predators in La Encrucijada Biosphere Reserve, Mexico. Egg predators of (A) American Crocodiles (*Crocodylus acutus*) and of (B-D) Spectacled Caimans (*Caiman crocodilus*) are Northern Raccoon (*Procyon lotor*), Lowland Paca (*Cuniculus paca*), and White-nosed Coati (*Nasua narica*).

at the nest (González-Desales et al. 2020). Studies on nest predation in Australian Freshwater Crocodile (*Crocodylus johnstoni*) found that the probability of egg predation increased when maternal female crocodiles were absent (Somaweera et al. 2011), similar to what we found. This pattern is reported in mammal predators (e.g., big cats); they are more active when their prey is more vulnerable due to the absence of parents (Harmsen et al. 2011). We found that females reacted defensively before predators removed nest material, in contrast with Campos et al. (2016), who reported females reacted defensively after the removal of nest material.

Mesocarnivores can modify their time of activity and habitat use to avoid interspecific competition (Carrera-Treviño et al. 2018). Our data suggests that *N. narica* and *P. lotor* have developed strategies (resource partitioning) to avoid competition for crocodilian eggs with different activity pattern. These differences can diminish interactions between egg predator species as has been observed with Grey Wolves (*Canis lupus*) and monitor lizards (*Varanus* spp.), both of which predate eggs of *C. johnstoni* (Somaweera et al. 2011). Combrink et al. (2016) also reported that egg predators of Nile Crocodiles (*Crocodylus niloticus*) adapted their activity patterns to avoid competition, with Marsh Mongooses (*Antilax paludiosus*) arriving to the nest first and Nile Monitors (*Varanus niloticus*) arriving second (Combrink et al. 2016). In Smooth-fronted Caimans (*Paleosuchus trigonatus*), the egg predators Southern Naked-Tailed Armadillos (*Cabassous unicinctus*), Nine-banded Armadillos (*Dasypus novemcinctus*), Tayras (*Eira barbara),* South American Coatis (*Nasua nasua*), Giant Armadillos (*Priodontes maximus*), and Black Tegus (*Tupinambis tegulxin*) visit nests at different times and most are nocturnal but did not coincide in visiting the same nest at the same time (Campos et al. 2016). Of these, *P. maximus* is the main egg predator (Campos et al. 2016).

We found that sometimes two to four *P. lotor* visited *C. acutus* nests at the same time, with some individuals facing the river (possibly watching for the maternal female crocodile to emerge from the water), while other individuals sniffed and removed nest substrate, and still others just standing to the side and waiting for the eggs to be exposed. *Procyon lotor* can form family groups of individuals and help each other to get some resource of interest (Monroy-Vilchis et al. 2011). It is possible that *P. lotor* engages in cooperative hunting/feeding at crocodilian nests, with different functions being performed by one or more individuals but with all individuals in the group receiving a nutritional reward (crocodilian eggs; Pitt et al. 2008). *Procyon lotor* individuals can shift their activity time with the aim of avoiding intraspecific competition (Ladine 2017), the individuals can benefit by forming coalition groups that jointly defend the resources to have a better access to them (Pitt et al. 2008). Additional studies in which nests are monitored with camera traps are necessary to further assess resource partitioning and associated behaviors among crocodilian egg predators.

We observed between 1–10 individual *N. narica* at nests of *C. crocodilus* at a given time. In three nests, we observed a solitary male exploring the nest but having no success in finding eggs. In contrast, adult female *N. narica* and juveniles opened all nests monitored. Di Blanco and Hirsh (2006) reported that adult females and


**Figure 4**. Trail camera photographs taken during the American Crocodile (*Crocodylus acutus*) nesting season in La Encrucijada Biosphere Reserve, Mexico. Egg predation by (A-B) Northern Raccoon (*Procyon lotor*), (C-D) nest defense, (E) hatchling defense towards Northern Raccoon, and (F) hatchling attendance.

the offspring of *N. narica* forage cooperatively, which affords them the advantage of easily locating most nests. It is important to mention that the family groups of *N. narica* are larger and more aggressive than the other species predator of this study, and that in our study, they had 100% predation success in *C. crocodilus* nests. The relatively small size of *C. crocodilus* facilitates predation of its nests by gregarious species such as *N. narica*.

Nest monitoring with camera traps captured aggressive behavior (nest and hatchling defense) by *C. acutus* (81.1%; Fig. 4) and *C. crocodilus* (40.0%). The lower percentage on the defense of the nests by *C. crocodilus* may be due to its smaller size with respect to nest predators. For both species the defensive behaviors included threatening mouth gaping and aggressive charging toward predators. These maternal behaviors have been also reported in *C. niloticus* while guarding nests (Combrink et al. 2016). We regularly observed nest maintenance, characterized by piling up substrate and leaf litter on the nest, in *C. crocodilus* (20%), possibly as a response to removal or disruption of nest material by predators. Additionally, *C. acutus* females often watched (monitored) nests from the edge of the water (Fig. 4). Previous studies have documented that *C. acutus* females remain near the nest during incubation (Charruau and Hénaut 2012). We recommend that in future studies using camera traps to monitor crocodilian nests, cameras should be positioned when possible so that the river (or other closest body of water) is included in the frame (e.g., behind or to one side of the nest), to potentially capture vigilance of maternal females watching the nest from the water.

Nest guarding can have several costs to crocodilians, such as weight loss and reduced body condition to the maternal female (Barão-Nóbrega et al. 2018), because the frequency of feeding during the incubation period is reduced and the size of prey consumed is smaller than when not guarding nests (Barão-Nóbrega et al. 2016). Sometimes females abandon the nest (Joanen and McNease 1989; Webb et al. 1983), and nest abandonment is one of the main causes of nesting failure in some species (*A. mississippiensis* and the Saltwater Crocodile, *C. porosus*). This is a possible explanation for the loss of several nests of *C. crocodilus* by predation at La Encrucijada Biosphere Reserve. It is important to highlight that *C. crocodilus* may require double the effort to protect their nests compared to *C. acutus*, as they must avoid predation from both diurnal (*N. narica*) and nocturnal (*C. paca* and *P. lotor*) predators, and because of its smaller size. This is similar to what has been observed in Brazil, where the nesting strategy of *C. crocodilus* (smaller species) has a metabolic cost associated with nest attendance, but not in Black Caiman (*M. niger*, a larger species; Barão-Nóbrega et al. 2018).

We found that some female *C. crocodilus* (40%) and *C. acutus* (18.1%) did not defend their nests. Some of the possible causes of the lack of nest defense in these cases are deliberately nest abandonment or death of the female. Other reasons may be: (1) the difficult availability of resources for female crocodiles; (2) the low presence of nest predators; (3) ignorance of the presence of nest predators by females; and (4) nest defense behavior that is appearing evolving in crocodiles. The nest defense probably varies among females due to factors such as nesting experience and the frequency of predator visits (Huang et al. 2013). Additionally, nests defense incurs costs, such as time and energy invested in the active defense and that crocodilian presence at the nest can attract predators (McLean et al. 1986). Not defending a nest also allows females the opportunity to forage (Zhang et al. 2015).

We identified at least three nesting strategies that influence predation: (1) females that defend and open the nest (*C. crocodilus* and *C. acutus*) and protect their hatchlings (*C. acutus*); (2) females that defend but do not open the nest (*C. acutus*); and (3) females that lay eggs and then abandon the nest (*C. crocodilus* and *C. acutus*). Previous studies have reported that *C. acutus* females assist their hatchlings during the hatching process, and if this does not occur, hatching success declines (Charruau et al. 2010; Charruau and Hénaut 2012). We observed that upon egg hatching, *C. acutus* females opened the nest with their front and hind legs and transported (in their mouths) several hatchlings at the same time to water. This hatchling transport process sometimes took more than one day. In addition, female *C. acutus* aggressively defended against *P. lotor* when the latter approached during nest opening by the maternal female (Fig. 4). In the case of females *C. crocodilus* nest opening or hatchling assistance were not documented in this study, due to all nests monitored were predated. González-Desales et al. (2016b) also reported a high predation rate for *C. crocodilus* nests (nine predated of 19 evaluated) at La Encrucijada Biosphere Reserve, Mexico.

Few studies analyze environmental variables and their relationship with the predation of crocodilian eggs. Larriera and Piña (2000) reported that the number of predated nests of Broad-snouted Caiman (*Caiman latirostris*) increased during the dry season. Likewise, in *A. mississippiensis*, greater predation of eggs was observed in seasons with low water levels (Hunt and Ogden 1991). This indicates a relationship between climatic factors, nest characteristics, and egg predation in *C. acutus* and *C. crocodilus* at our study site. For example, for *C. acutus*, the risk of egg predation is greater when nests are closer to the river (nearest water), and the depth from the top of the nest to the first egg in the clutch is less, and nests are farther away from a tree. For *C. crocodilus* risk of nest predation is greater if nests are closer to bodies of water, and depth to the first egg is greater and nests are farther away from a tree. In both species, the proximity of the nests to trees is important; for *C. acutus*, the canopy cover offers conditions that favor the incubation of eggs (Charruau 2012). In *C. crocodilus* trees support and provides material for the construction of nests (Gonzalez-Desales et al. 2016b).

In conclusion, the results of our study suggest that the activity and success of nest predators of *C. acutus* and *C. crocodilus* at La Encrucijada Biosphere Reserve, Mexico, vary by season (corresponding to the beginning (oviposition) and end (hatching) of the nesting seasons), time of day, and a suite of climatic factors and nest characteristics. Nest predators also exhibited resource partitioning, presumably to avoid negative interactions with competitors at nest sites. Some maternal female crocodiles and caiman actively defended nests against predators, but this behavior varied among individuals. Finally, EPSi can be a useful tool for evaluating egg predation success at nests of different species.

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