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Putting eggs in one big basket: communal egg-laying between long-lived reptiles

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Abstract. Understanding communal nesting has provided a deeper insight into reptile social behavior. Conspecific communal nesting has been reported frequently, while interspecific communal nesting has remained somewhat opaque. Here, we report communal egg-laying involving long-lived reptiles (American Crocodile and Ornate Slider Turtle). Our results from both field observations and literature reviewed indicate this is the first known case of communal nesting between these two species, and could suggest that crocodilians provide secondary nest attendance for nesting turtles. In addition, we present a brief review of commensal egg-laying between crocodilians and other reptiles.

Key words: Crocodilian, *Crocodylus acutus*, nest attendance, nesting ecology, reptiles, testudines, *Trachemys ornata*.

Communal egg-laying is common in most reptile lineages (all sphenodontians, many lizards, and some snakes, turtles and crocodilians; reviewed by Doody et al. 2009), and this event could be defined as the egg oviposition by at least two gravid females sharing the same nest area or nest cavity throughout the nesting season (Espinoza & Lobo 1996). Available information suggests that communal egg-laying in reptiles mainly involves conspecific gravid females (Graves & Duvall 1995). Few cases involve clutches of different species within the same family (Chou 1979, Vitt 1986, Krysko et al. 2003); while records of communal egg-laying by species from different families are limited (Enge et al. 2000, Alfonso et al. 2012, Elsey et al. 2013). Here, we report a case of interspecific egg-laying involving the American Crocodile *Crocodylus acutus* and the Ornate Slider Turtle *Trachemys ornata* (for taxonomic status see Parham et al. 2015). We also present a brief review of communal oviposition between crocodilians and other reptiles. Our studies were motivated to enhance the little information about communal egg-laying between long-lived reptiles, and on the other hand, to explore the secondary nest attendance as an adaptive hypothesis for communal egg-laying between long-lived reptiles.

We conducted daily surveys to evaluate nesting activity of American Crocodiles at a golf course located in Puerto Vallarta, Mexico (20º39′59″N, 150º15′48″W; elev. < 1 m a.s.l.). We used digiscoping to obtain digital photographs of different maternal behaviors of American Crocodiles (e.g., Leary 2004, Larson & Craig 2006, Cupul-Magaña et al. 2015). Field observations were conducted during the morning (08:00 to 12:00 h) of each third day from March to July in 2014 and 2015, and only in March 2016.

For information on records and/or quantitative data of communal oviposition between crocodilians and other reptiles, we searched in the following databases: ISI Web of Science, SciELO Citation Index, BioOne, Science Direct, Scopus and Redalyc. In each of the databases, all records containing the words: crocodilian, nesting ecology, reproductive ecology, communal oviposition or communal egg-laying, in the title, abstract, and/or keywords fields were reviewed. In addition, we reviewed exhaustively herpetological journals on ecological and natural history studies on crocodilians. We also considered anecdotal observations from both non peer-reviewed papers and personal communications by members of the International Union for the Conservation of Nature Crocodile Specialist Group. We considered a record of commensal egg-laying when a non-crocodilian female lays eggs in an active crocodilian nest.

In March 2014, we observed the nesting activity of four American Crocodiles. The activities recorded varied from nest construction to guarding hatchlings and forming crèches (see Charruau & Henaut 2012 for description of nesting activities of American Crocodiles). We did not approach the nests to avoid altering the crocodiles' behavior. Four days after nest construction (April 2014), we observed an Ornate Slider Turtle, hereafter, turtle as it left the water and went directly to one of the crocodile nests. After digging with the hind legs into the crocodile egg cavity, the turtle began egg deposition, while the crocodile approached the nest (Fig. 1). No physical interactions between the two reptiles were observed. In late April 2015, we observed the same crocodile female reusing the nest hole from the prior year for egg laying. During oviposition by the crocodile, a turtle was observed under the crocodile's body (Fig. 2). We were not able to determine if it was interspecific egg-laying occurring in synchrony or the turtle was merely protecting its nest, which happened to be the same nest hole (Fig. 2). In March 2016, we observed for a third time the crocodile female nesting in the same site. About one hour later, we observed a turtle come out of the water body and begin egg laying close to the crocodile egg cavity.

We found records of fifteen turtles (62%), five lizards (21%) and four snakes (17%) using crocodilian nests as egg-laying sites (Table 1). Most secondary nesters have been reported in the family Alligatoridae. The majority of the reports referred to the American Alligator *Alligator mississippiensis* nests (14 commensal nesting), followed by the Broad-snouted Caiman *Caiman latirostris* (3 species) and Black Caiman *Melanosuchus niger* (one species). In the family Crocodylidae, the reports of secondary nesters are few, but three of the four Neotropical *Crocodylus* interact with other reptiles, mainly turtles of the genus *Trachemys* (Table 1). Striking observation were the reports of *Podocnemis unifilis* nests in different type crocodilian nests (hole and mound nests,

Table 1. Records of reptile nests in crocodilian nests. (a) The authors reported the occurrence of *Anolis carolinensis*, *Pseudemys nelsoni* and *Apalone ferox* in five alligator nests, but they did not quantify how many of each commensal species were found per alligator nest. (b) Each alligator nest contained five eggs of *Scincella lateralis*. (c) The authors found 7 turtle nests in 5 alligator nests.

Nesting species	Commensal species	Crocodilian nests	Reptile nests	Reference
Crocodylia	Squamata			
Alligatoridae	Larcetilia			
Alligator mississippiensis	*Anolis carolinensis*	103	2	Kushlan & Kushland (1980a)
		5	2 eggs	Brandt & Mazzotti (2000)[a]
		112	1	Deitz & Jackson (1979)
	Scincella lateralis	6	2	Elsey et al. (2013)[b]
		145	55	Elsey et al. (2016)
	Serpentes			
	Farancia abacura abacura	112	1	Deitz & Jackson (1979)
	Farancia abacura reinwardtii	2	4	Hall & Meier (1993)
	Lampropeltis getula holbrooki	-	2	Elsey et al. (2013)
		145	5 eggs	Elsey et al. (2016)
	Nerodia erythrogaster	66	-	Merchant et al. (2014)
	Testudines			
	Apalone ferox	111	-	Deitz & Hines (1980)
		21	-	Brandt & Mazzotti (2000)[a]
		112	3	Deitz & Jackson (1979)
		1586	4	Enge et al. (2000)
	Kinosternon sp.	1586	28	Enge et al. (2000)
	Kinosternon baurii	103	1	Kushlan & Kushland (1980a)
	Kinosternon subrubrum	112	1	Deitz & Jackson (1979)
	Pseudemys nelsoni	15	7	Goodwin & Marion (1978)[c]
		103	20	Kushlan & Kushland (1980a)
		100	5	Hunt (1987)
		129	16	Hunt & Odgen (1991)
		21	-	Brandt & Mazzotti (2000)[a]
		112	20	Deitz & Jackson (1979)
		1586	422	Enge et al. (2000)
		1	2	Cline et al. (2016)
	Pseudemys concinna	20	1	Elsey et al. (2013)
	Sternotherus odoratus	1586	1	Enge et al. (2000)
		66	-	Merchant et al. (2014)
	Trachemys scripta	66	-	Merchant et al. (2014)
Caiman latirostris	Squamata			
	Larcetilia			
	Salvator merianae	-	1	Carlos Piña (pers. comm.)
	Testudines			
	Phrynops hilari	-	-	Merchant et al. (2014)
	Trachemys dorbigni	-	-	Merchant et al. (2014)
Melanocushus niger	Testudines			
	Podocnemis unifilis	1	8	Maffei and Da Silveira (2013)
Crocodylidae	Squamata			
Crocodylus acutus	Larcetilia			
	Iguana iguana	1	-	Dugan et al. (1981)
	Testudines			
	Trachemys ornata	4	1	This study
Crocodylus intermedius	Squamata			
	Larcetilia			
	Iguana iguana	-	-	Ariel Espinosa-Blanco (pers. comm.)
	Tupinambis cryptus	1	1	Ariel Espinosa-Blanco (pers. comm.)
	Testudines			
	Podocnemis unifilis	-	-	Hernández et al. (2010)
		-	-	Espinosa-Blacno et al. (2013)
Crocodylus moreletii	Testudines			
	Trachemys venusta	-	-	M. González-Ramón (pers. comm.)
Crocodylus novaeguineae	Testudines			
	Unidentified turtle	-	-	Charlie Manolis (pers. Comm.)
Crocodylus rhombifer	Testudines			
	Trachemys decussata	14	8	Ramos-Targarona (2013)

Table 2. Available records of communal interspecific nesting among reptiles.

Nesting species	Commensal species	Reference
Testudines		
Chelydra serpentina	*Chrysemys picta*	Robinson and Bider (1988)
Squamata		
Anolis argillaceus	*Tarentola combiei* *Sphaerodactylus armasi*	Alonso et al. (2012)
Hemidactylus frenatus	*Hemidactylus mabouia* *Sphaerodactylus elegans*	Krysko et al. (2003)
Hemidactylus mabouia	*Sphaerodactylus elegans* *Sphaerodactylus notatus*	Krysko et al. (2003)
Insecta		
Acromyrmex sp.	*Philodryas patagoniensis* *Psomophis obtusus* *Philodryas patagoniensis* *Micrurus frontalis altirostris* *Psomophis obtusus* *Philidryas agassizii* *Psomophis obtusus* *Phalotris bilineatus*	Vaz-Ferreira et al. (1970)

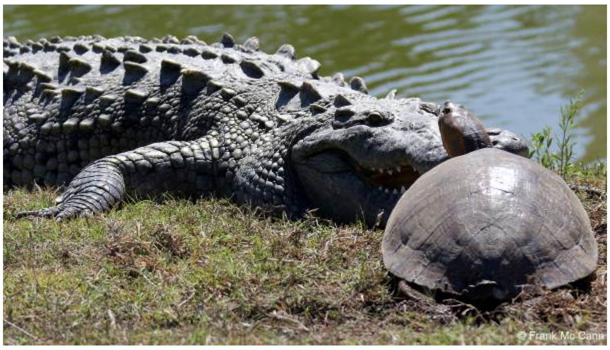

Figure 1. Ornate Slider Turtle *Trachemys ornata* laying eggs in an American Crocodile *Crocodylus acutus* nest. 4 April 2014, Marina Vallarta Golf Course, Puerto Vallarta, Jalisco, Mexico. Photo by F. Mc Cann.

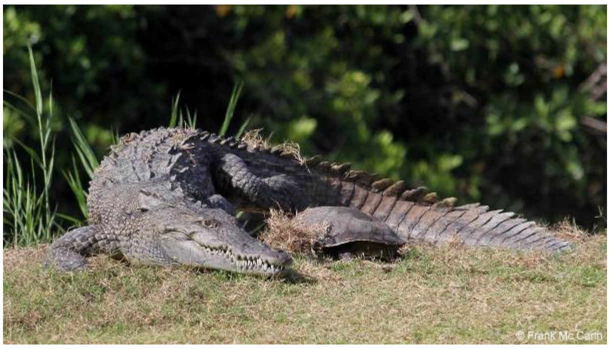

Figure 2. Nesting American Crocodile and Ornate Slider Turtle placing eggs inside the egg cavity of crocodile nest. 21 April 2015, Marina Vallarta Golf Course, Puerto Vallarta, Jalisco, Mexico. Photo by F. Mc Cann.

Crocodylus intermedius and *Melanosuchus niger*, respectively). Additionally, we found a record of interspecific communal oviposition involving turtles from different families, other involving different lizard species, and other involving different snake species nesting in ant nests (Table 2).

Our field observations are the first record of a freshwater turtle nesting in an American Crocodile nest. Our literature review reveals that interspecific communal egg-laying is more common than was previously thought. Some studies have evaluated the ecological and evolutionary implications of communal egg-laying in reptiles (Radder & Shine 2007, Mateo & Cuadrado 2012, Refsnider et al. 2013, Peñalver-Alcázar et al. 2015). Communal egg-laying could be beneficial when suitable oviposition sites are constrained by high population density and/or heterogeneous environment. Alternatively, some adaptive benefits could explain communal egg-laying when habitat restriction and environmental factors are unclear; both mechanisms can be working in some cases (Doody et al. 2009). The hypotheses explaining communal oviposition in reptiles are focused mainly on conspecifics with little or no parental care (reviewed by Doody et al. 2009), motivating speculation on interspecific communal egg-laying among reptiles. Unfortunately, the nesting success for egg-laying reptiles in crocodilian nests has not been recorded, and thereby the benefits of communal oviposition involving crocodilians and other reptiles are unknown (Goodwin & Marion 1977, Kushlan & Kushlan 1980a; Dugan et al. 1981, Hunt & Ogden 1991).

In reptiles, nest site selection is not random but it needs to be flexible to find suitable nesting conditions in response to changing environmental conditions and maximize offspring fitness (Refsnider & Janzen 2010, Somaweera & Shine 2013). Some long-lived reptiles display nest site fidelity (freshwater turtles, Valenzuela & Janzen 2001,; marine turtles, Tripathy & Pandav 2007; crocodilians, Elsey et al. 2008; tuataras, Refsnider et al. 2010). Specifically, crocodilians sometimes even exhibit fine-scale fidelity, reusing the same nest from previous years (Charruau et al. 2010, López-Luna et al. 2011, Somaweera & Shine 2013), which reduces the associated costs of finding and/or selecting the nest-sites by both nesting females.

The rare use of crocodilian nests by lizards, snakes, and some kinosternid turtles suggests a random communal oviposition, and it could be explained (mainly) by the unavailability of nesting habitat during water level fluctuations in the aquatic environment. However, the year-to-year variation of turtles nesting in crocodilian nests suggests that crocodilian nest construction coincides with the nesting season of other nesting reptiles (Enge et al. 2000). The nesting synchrony of both intra and inter-specific organisms could reduce nest predation (Robinson & Bider 1988, Mateo & Cuadrado 2012). On the other hand, crocodilian nests could provide resource requirements for nesting turtles such as nest-site characteristics, incubation conditions, and from predators' protection. Enge et al. (2000) observed that the incidence of turtle nests was related to water level fluctuations. Deitz & Jackson (1979) suggested that alligator nests could be easy to locate by nesting turtles and the nest material is easy to excavate, reducing the time of exposure to predators. Our results suggest that crocodilians provide secondary nest attendance for nesting turtles. Some scientists have suggested that the main benefit for turtle nests in the crocodilian nest is defense of their nests from predators, including reptiles of other species such as snakes, turtles, teiid and varanid lizards (Goodwin & Marion 1977, Kushlan & Kushlan 1980a, Hunt & Ogden 1991, Enge et al. 2000; and see crocodilian nest predation reviewed by Somaweera et al. 2013). Some early observations showed that the turtles can expose or crush alligator eggs; which suggested that the disturbance by turtles could increase the predation on alligator nests (Deitz & Hines 1980). A subsequent study rejected this hypothesis, because the predation rates in alligator nests with and without turtle nests were similar (Hunt & Ogden 1991). Our field observations provide additional data on the ability of nesting crocodiles to distinguish between harmless reptiles and potential predators (Kushlan & Kushlan 1980b). However, nest attendance of crocodilians includes a wide range of behaviors, such as nest-site selection, nest defense, nest maintenance, and nest thermoregulation (Lang 1987, Alonso-Tabet 2009, Charruau & Hénaut 2012), which might improve nesting success and offspring fitness in turtles (Kushlan & Kushlan 1980a). Mateo & Cuadrado (2012) experimented with Oudri´s fan-footed Gecko *Ptyodactylus oudrii*, their results showed that the hatching success was lower from solitary clutches than that of communal clutches under controlled conditions. Some studies have suggested the hatching success as an adaptive benefit of commensal nesting in crocodilian nests (Dietz & Jackson 1979, Enge et al. 2000), but this possibility should be explored in further studies.

There are some aspects that are not investigated here but deserve attention to provide new insights in the ecological and evolutionary consequences of interspecific communal oviposition among long-lived reptiles; for instance, what might be the advantages of putting eggs in a big basket for secondary nesters? Alternatively, what might be the adaptive implications of synchronous hatching in communal egg-laying between crocodilians and reptiles? The interplay between interspecific egg-layers occurs via complex pathways (not to mention species-specific physiological and behavioral characteristics), and thereby the intrinsic and/or extrinsic factors that promote interspecific communal oviposition are difficult to identify.

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