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Cover: Common Keeled Skink *Eutropis carinata* in oil pastels, colour pencils, & micron pen adapted from photograph by H. Byju © Pooja Ramdas Patil.



First confirmed reproduction by a translocated female Siamese Crocodile *Crocodylus siamensis* (Crocodylidae: Crocodilia) with observations of nest attendance and nest-associated fauna

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Abstract: The Siamese Crocodile *Crocodylus siamensis* is considered one of the most imperiled and poorly-studied crocodilians in the world. Translocations (reintroductions) - often in conjunction with head-starting of juveniles - are a critical component of efforts to restore viable wild populations of *C. siamensis*. We here report the first confirmed nesting by a known-age, head-started, and translocated female *C. siamensis* together with observations of nest attendance and nest-associated fauna based on camera trap imagery. Our observations occurred in the Greater Xe Champhone Wetland Complex (GXCWC) in Savannakhet Province, Lao PDR. GXCWC encompasses 45,000 ha of seasonally inundated natural and anthropogenic wetlands, agricultural ecosystems, scrubland, and forest. While collecting eggs for incubation in May 2022, we were able to identify a unique series of notched tail scutes on a female *C. siamensis* as she aggressively defended a nest. From these markings we determined the female was hatched on 11 August 2012 (age = 9.75 years) and released in March 2014, approximately 3.5 km from the nest site. A game camera placed at the nest on 11 May 2022 and recovered on 5 July 2022 (34 trap nights) recorded 1724 images. These images indicated the female remained in attendance at the nest throughout the monitoring period. Camera trap imagery captured eight nest repair events and two nest defense events; during the latter the female defended the nest from village dogs. Eleven species of nest-associated fauna were recorded by the game camera, including eight and three species of birds and mammals, respectively. Our observations are the first confirmed nesting by a head-started, translocated female *C. siamensis* indicating these are effective conservation strategies for restoring wild populations. We also unequivocally established that head-started female *C. siamensis* are capable of reproducing when nine-years-old.

Keywords: Behavior, camera trap, commensal fauna, conservation, head-starting, Lao PDR, nest defense, nest predation, reintroduction, Xe Champhone.

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Translocations (defined as the human mediated movement of organisms from one area with release into another area; IUCN 2013) – often undertaken in combination with captive-breeding and head-starting of juveniles – are playing an increasingly important role in the conservation of reptiles, including crocodilians (Germano & Bishop 2008; Ewen et al. 2014; Burke 2015). In many cases, translocation may be the only remaining option for reestablishing depleted or extirpated populations (Marsh & Trenham 2001; Stofer 1999). Among crocodilians, translocation of both head-started juveniles and adults is a strategy being used to successfully restore ecologically functional and demographically viable populations of several threatened species (e.g., Munoz & Thorbjarnarson 2000; Daltry & Starr 2010; Xing 2010; Manalo & Alcala 2015; Sam et al. 2015; Kar 2022).

There is no standardized definition of success regarding wildlife translocation because of varying time scales and differences in life history traits among target organisms (Seddon 1999; Germano et al. 2014; Miller et al. 2014; Burke 2015). However, a translocation can ultimately be considered successful only when a viable, self-sustaining population becomes established in the wild (Griffith et al. 1989; Dodd & Seigel 1991). As a first step towards achieving this objective, translocated individuals must demonstrate competency in the wild, such that they survive, grow, and reproduce (Alberts 2007; Roe et al. 2015). Common demographic indicators of near-term success include positive survival rates and reproduction by founder females (Armstrong & Seddon 2008; Ewen et al. 2014; Miller et al. 2014; Elsey et al. 2015; Platt et al. 2022b).

The Siamese Crocodile *Crocodylus siamensis* (Schneider, 1801) is a large (total length [TL] to ca. 4.0 m) mound-nesting crocodilian that occurs or formerly occurred in freshwater habitats of mainland Southeast Asia (Thailand, Laos, Vietnam, Cambodia) and the Sundaic Islands of Java and Borneo (Platt et al. 2019). Populations throughout this geographic range are now greatly diminished as a result of habitat destruction, commercial hunting for skins, direct persecution because of perceived danger to humans and livestock, and illegal collection to stock crocodile farms (Platt et al. 2019). Consequently, *C. siamensis* is ranked as Critically Endangered on the IUCN Red List of Threatened Species and considered one of the most imperiled crocodilians in the world (Platt et al. 2019). Despite this parlous conservation status, very little is known about the ecology of wild *C. siamensis*, including many aspects of reproduction (Platt et al. 2019). This dearth of

information is lamentable because such basic natural history data are a necessary prerequisite for designing and implementing effective conservation strategies for endangered species (Dayton 2003).

In Lao PDR (hereafter Laos), the conservation status of *C. siamensis* is particularly tenuous with small, fragmented populations that show little or no evidence of recruitment, restricted to Attapu, Khammouane, Salavan, and Savannakhet provinces (Platt et al. 2022a). In the early 2000s, surveys conducted by the Wildlife Conservation Society-Lao Program (WCS), working in collaboration with the Government of Laos, identified several small populations of *C. siamensis* in the Xe Champhone wetlands of Savannakhet Province that would likely benefit from conservation efforts (Bezuijen et al. 2013). Importantly, most of these populations already received some degree of *de facto* protection from the widespread local belief that crocodiles embody the spirits of dead ancestors and to harass, harm, or kill a crocodile could bring divine retribution in the form of misfortune, illness, or even death to the individual and community (Baird 2001; Platt et al. 2018a). Local proscriptions protecting crocodiles notwithstanding, numbers were low and population recruitment was lacking because of poor nesting success.

In 2010, we launched a community-based crocodile conservation project in Savannakhet Province with the ultimate objective of restoring a demographically viable population of *C. siamensis* in the Greater Xe Champhone Wetland Complex (GXCWC; Platt et al. 2014, 2022a), which encompasses 45,000 ha of seasonally inundated natural and anthropogenic wetlands, agricultural ecosystems, scrubland, and forest (for detailed site description see IUCN 2011; Platt et al. 2018b). As part of our project, local Village Conservation Teams (VCTs) search for crocodile nests and assist us with egg collection, incubation, and head-starting of juvenile crocodiles (Platt et al. 2022a). To briefly summarize, we search for crocodile nests during May-August, collect the eggs, and transport these to a village facility for incubation. Upon hatching, we permanently mark each hatchling by notching a unique series of double and single caudal scutes (Rainwater et al. 2007). We then head-start juveniles for approximately 32 months (TL ca. 70–100 cm) before releasing them into a densely vegetated reservoir near Tan Soum Village (Platt et al. 2014, 2022a). In 2014, we were forced to terminate our efforts after donor funding was unexpectedly cancelled; however, the project resumed in 2019 (Platt et al. 2022a). To date (September 2023), we have translocated 143 head-started *C. siamensis* into GXCWC, including 65 and

78 crocodiles released in 2013–2014 and 2022–2023, respectively.

We here report the first confirmed nesting by a known-aged, head-started, and translocated female *C. siamensis* together with observations of nest attendance and nest-associated fauna based on camera trap imagery. We broadly define nest attendance as a suite of parental behaviors that includes females maintaining and defending the nest, remaining near the nest, opening the nest when eggs hatch, and transporting hatchlings to water (Merchant et al. 2018; Murray et al. 2019). We follow Merchant et al. (2014) and characterize nest-associated fauna as wild and domestic vertebrates present on or in close proximity to the nest mound. We then categorize these associations according to Rainwater et al. (2024) as 1) feeding/foraging – the animal probed the nesting substrate, pursued prey or actively consumed food items on or near the nest; 2) loafing – the animal slept, sat, stood, rested, or preened (birds only) on or adjacent to the nest; 3) traveling – the animal moved across or close to the nest; 4) predation – an animal removed or attempted to remove crocodile eggs from the mound for consumption. We classified photorecords of crocodile behavior and nest-associated fauna as independent detections when the time interval between sequential photographs was \geq 30 minutes (e.g., O'Brien et al. 2003; Ngoprasert et al. 2019).

On 21 May 2022, a VCT found an active crocodile nest in dense vegetation along the shore of Kout Jek (16.3730°N; 105.2221°E; elevation = 132 m), an oxbow lake in the Champhone River floodplain. Accompanied by the VCT, we returned to the nest on 24 May 2022 to collect the clutch. The nest (approximate dimensions = 100 cm wide \times 60–70 cm high) was constructed in a dense thicket (vegetative canopy cover = 100%) at the base of a bamboo clump and on top of a nest mound built during the previous nesting season (2021), and consisted of leaves, woody debris, and soil. At the time of our visit the nest was located ca. 5.0 m from the edge of the lake. We previously visited this nest earlier in the year (15 February 2022) and recovered a clutch of 12 badly decomposed eggs from the 2021 nesting season. According to the VCT, the nest was inundated by seasonal floodwaters in July 2021, resulting in the loss of the complete clutch (see Joanen et al. 1977).

When we arrived at the nest (ca. 1500 h; 24 May 2023), the female crocodile (TL ca. 2.1 m) was lying in a well-defined “form” beneath a tangled mass of vines about 2.0 m away from the mound. As we drew closer to the nest, she crawled on top of the mound and exhibited aggressive behavior (loud hissing, forward lunges, and

jaw claps) directed at ourselves (Image 1a–b). When the female ascended the mound, we could clearly discern the three notched double and single caudal scutes allowing us to determine the identification number of this individual. A subsequent search of our database indicated the female crocodile was hatched on 11 August 2012 (age = 9.75 years) and released near Tan Soum Village in March 2014. The straight-line distance from the release site to Kout Jek is 3.5 km.

Using long bamboo poles, we were able to direct the female away from the nest, allowing us to open the mound and collect the eggs. The clutch consisted of 30 eggs with a mean (\pm 1SD) length, width, and mass of 74.1 ± 1.9 mm, 45.3 ± 1.0 mm, and 90.9 ± 4.1 g, respectively. At the request of the VCT and in accordance with local religious practices (Platt et al. 2018a), we left three non-viable eggs in the nest to appease the female crocodile. We transported the remaining eggs to our facility in Tan Soum Village for processing and incubation. Based on the presence/absence of opaque bands on the eggshells (Ferguson 1985), we determined the clutch contained only 2 (6.6%) viable eggs. The extent of opaque banding on the viable eggs suggested the clutch was deposited between 15–17 May. Prior to departing the nest site, we restored the physical structure of the mound and mounted a Moultrie Series A game camera on a post approximately 3.0 m from the nest. This game camera uses motion and passive infrared sensors to detect wildlife. The Moultrie Series A game camera has a trigger speed of 0.5 second, a flash and detection range of 21 m, and captures 26 megapixel images. The camera trap was aimed at the nest and programmed to take three photographs at 1-minute intervals when activated. In response to rapidly rising seasonal floodwaters that threatened to inundate the area, we returned and recovered the game camera on 5 July 2022. As during our initial visit, the female aggressively defended the nest when we approached. During 34 trap-nights of operation, the game camera recorded 1724 images.

Our camera trap imagery indicated the female remained in attendance at the nest at least intermittently throughout the 34-day monitoring period. When present, the female was concealed beneath the vine tangle where we encountered her on 24 May 2023. Because our camera was aimed at the nest rather than at the vine thicket, the female usually escaped detection, but was occasionally photographed when moving. In some images only the tail or tip of her snout is visible. Between 28 May and 16 June (1223 to 2113 h), our camera recorded eight nest repair events during which the female climbed onto the nest and employed

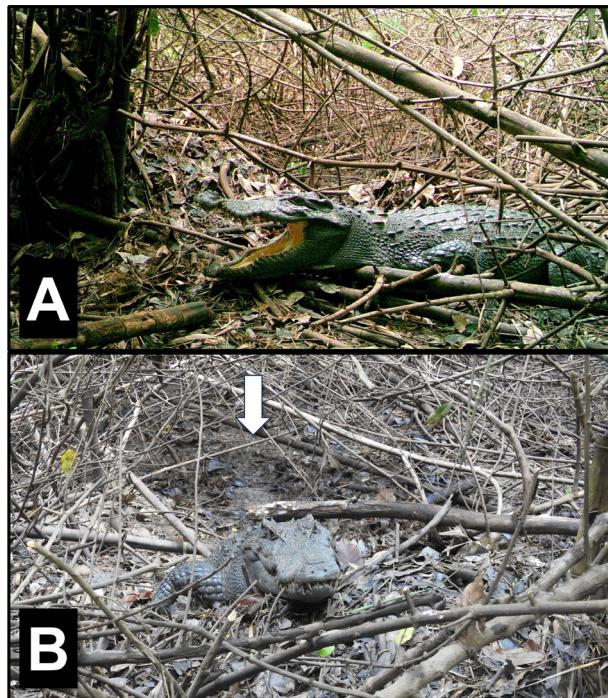


Image 1a–b. Female Siamese Crocodile defending the nest from approaching researchers. Nest mound at the base of bamboo clump at left: a—Female climbing atop nest mound to deter researchers attempting to extract the clutch | b—The white arrow denotes the well-defined “form” beneath the vine tangle where the female remained in attendance at the nest throughout much of the monitoring period.

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her rear legs to scrape leaf litter, woody debris, and soil onto the flanks of the mound (Image 2a–c). We assume the nest repair behavior was triggered by our opening the mound to remove the clutch. Notably, nest repair occurred despite our careful efforts to restore the physical integrity of the mound after removing the clutch. We also recorded six instances (1323 to 1826 h; 10 June to 3 July 2023) where the female was atop or beside the mound without effecting repairs. Finally, our camera recorded two nest defense events (1519 to 1520 h on 22 June 2023 and 1245 to 1250 h on 4 July 2023) directed towards village dogs (*Canis familiaris* [Linnaeus, 1758]) (Image 3). In both events the dogs approached to within ca. 2 m of the female and nest and then hastily withdrew without attempting to open the mound. In the second event the female left the nest and pursued the dog for a short distance (< 2m). Our game camera also recorded eleven species of nest-associated fauna, including eight and three species of birds and mammals, respectively (Table 1; Image 4a–h). With the exception of the village dogs, in no cases was the female observed reacting to the presence of nest-associated fauna.

To our knowledge, these observations represent the

Table 1. Nest-associated fauna (wild and domestic vertebrates) recorded by a camera trap deployed at a Siamese Crocodile *Crocodylus siamensis* nest in the Xe Champhone Wetlands (Savannakhet Province, Laos) during 34 trap nights of monitoring (24 May–5 July 2022). Each detection represents one or more sequential photographs separated by a time interval of ≥30 minutes (see text).

Species	Number of detections	Type of association
Birds		
Black-headed Bulbul <i>Brachypodius melanocephalus</i>	1	Traveling
Blue-winged Pitta <i>Pitta moluccensis</i>	2	Loafing
Hill Blue Flycatcher <i>Cyornis whitei</i>	1	Loafing
Pied Fantail <i>Rhipidura javanica</i>	1	Foraging and Loafing
Red Junglefowl <i>Gallus gallus</i>	5	Foraging
Verditer Flycatcher <i>Eumyias thalassinus</i>	1	Loafing
White-breasted Waterhen <i>Amaurornis phoenicurus</i>	8	Foraging and Traveling
White-rumped Shama <i>Copsychus malabaricus</i>	1	Foraging
Mammals		
Unidentified Rat Rodentia	9	Traveling
Domestic Dog <i>Canis familiaris</i>	2	Predation (attempted)
Domestic Cattle <i>Bos taurus × indicus</i>	8	Loafing

first confirmed nesting by a head-started *C. siamensis* released into the wild. Head-starting and translocation are the cornerstones of *C. siamensis* restoration efforts throughout Southeast Asia (Polet 2002; Temsiripong 2007; Daltry & Starr 2010; Sam et al. 2015), and while reproduction by translocated females is generally assumed (Platt et al. 2019), confirmation has not been forthcoming until now. Successful recruitment of captive-reared females into wild breeding populations has likewise been verified for other species of translocated crocodilians (Elsey et al. 2000; Larriera et al. 2006; Elsey 2007; Elsey et al. 2015; Platt et al. 2016; Leiva et al. 2019). Collectively, this growing body of evidence indicates that captive-reared, head-started crocodilians are not only able to survive and forage in the wild but also reproduce, suggesting these are effective conservation strategies for restoring wild populations.

Our observations also unequivocally establish that head-started and translocated female *C. siamensis* are capable of reproducing at the age of nine-years-old. Moreover, if the clutch of decomposing eggs we recovered from the mound in February 2022 (from the 2021 nesting season) was deposited by the same female defending the nest in May 2022, she reproduced when only eight-years-old. Although captive-reared female *C. siamensis* on commercial farms in Cambodia

and Thailand occasionally begin reproducing in as little as 6–7 years (Platt et al. 2011; Yosapong Temsiripong, pers. comm.), sexual maturity in the wild is probably attained between 10–15 years or perhaps later (Youngprapakorn et al. 1971). Accelerated growth and early reproduction by female crocodilians has been reported for several species that were reared in captivity before being translocated (e.g., *Alligator mississippiensis* [Daudin, 1801] and *Caiman latirostris* [Daudin, 1801]) and is probably commonplace among head-started crocodilians (Elsey et al. 2000; Larriera et al. 2006). Decreasing the time required for translocated females to begin producing offspring has the potential to increase population growth rates, thereby lessening the likelihood that stochastic demographic events will negatively impact translocation outcomes (Elsey et al. 2000; Larriera et al. 2006).

The aggressive nest defense exhibited by the female crocodile is only the second instance of this behavior

(see also Platt et al. 2020) we witnessed during visits to 31 *C. siamensis* nests to collect eggs for incubation (2011–13 and 2019–23). Although nest attendance and defense are probably universal among the Crocodylia (Grigg & Kirschner 2015), these behaviors are poorly documented in *C. siamensis*. Similar to our observations, the few previous reports of nest attendance behaviors involved female *C. siamensis* defending nests against researchers; Kanwatanakid-Savini et al. (2012) found a female concealed in dense grass beside a nest in Thailand, Bezuijen et al. (2013), stated that a nest in Laos was “fiercely guarded by a female”, and Platt et al. (2020) described an aggressive encounter with a large female at another nest in Laos. That said, aggressive nest defense directed towards humans is probably an unreliable index of attendance behavior because female crocodilians may selectively avoid humans, and yet still defend nests against smaller predators (Kushlan & Kushlan 1980; Hunt & Ogden 1991). Tellingly, in a recent aerial survey conducted in GXCWC using drones (Platt et al. 2023), we observed female crocodiles at 60% of the nests, suggesting nest attendance behavior is more commonplace among *C. siamensis* than hitherto recognized. Although our camera trap imagery appears to be the first showing a wild female *C. siamensis* undertaking nest repairs, attending female *A. mississippiensis* (Dietz & Hines 1980; Joosten & McNease 1989; Hunt & Ogden 1991) and Spectacled Caiman (*Caiman crocodilus* [Linnaeus, 1758]) (González-Desales et al. 2023) are reported to reshape and add material to nest mounds opened by predators.

The camera trap imagery we obtained during a relatively brief monitoring period (34 days) is the first to document fauna associated with *C. siamensis* nests. Our findings are consistent with other reports that describe a diversity of vertebrates using crocodilian nest mounds as

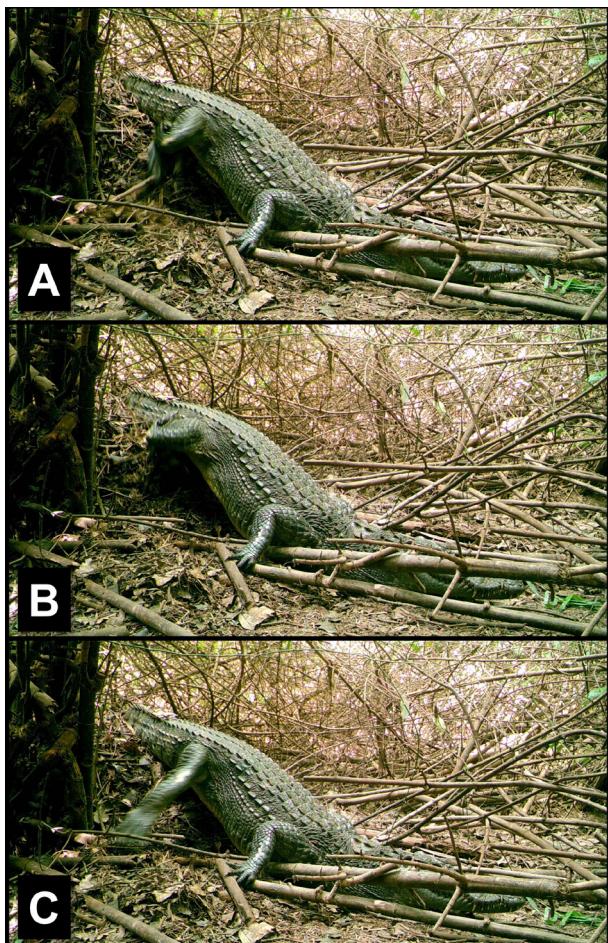


Image 2a–c. The sequence of images showing female Siamese Crocodile repairing nest after the mound was opened and clutch removed by researchers. © Wildlife Conservation Society.



Image 3. Female Siamese Crocodile defending nest from village dog. © Wildlife Conservation Society.

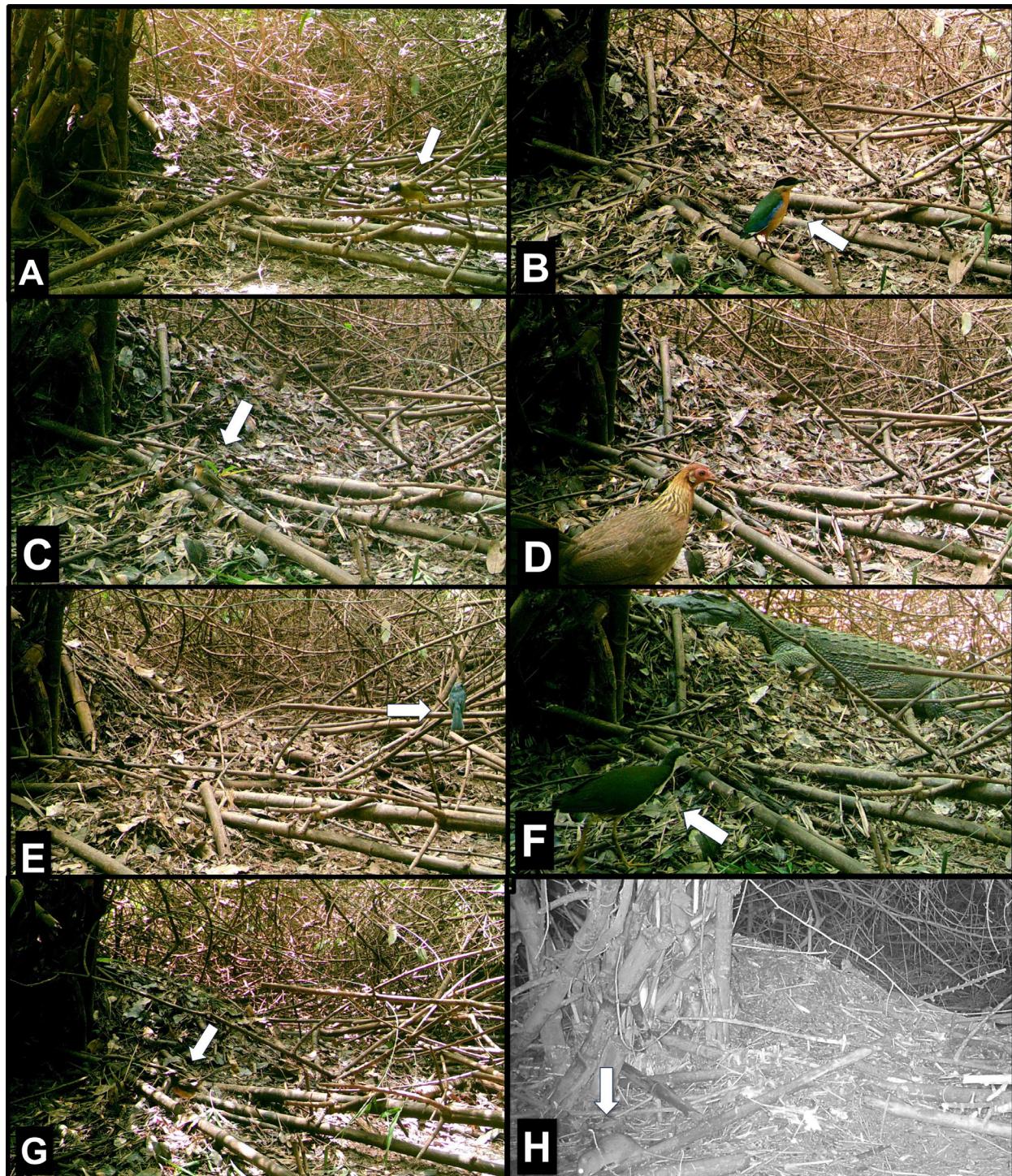


Image 4a-h. Examples of fauna associated with Siamese Crocodile nest during a 34-day monitoring period (24 May–5 July 2023): a—Black-headed Bulbul | b—Blue-winged Pitta | c—Hill Blue Flycatcher | d—Red Junglefowl | e—Verditer Flycatcher | f—White-breasted Waterhen | g—White-rumped Shama | h—Unidentified species of rat. © Wildlife Conservation Society.

feeding and loafing platforms, foraging substrates, and nesting sites (Merchant et al. 2014; Eversole & Henke 2018; Escobedo-Galván et al. 2019; Platt et al. 2021; González-Desales et al. 2020; Rainwater et al. 2024).

Characterizing the associations of the six species of passerines we recorded at the nest proved challenging owing to the limited number of images that we obtained; however, most birds appeared to be loafing or traveling.

In contrast, Red Junglefowl (*Gallus gallus* [Linnaeus, 1758]) and White-breasted Waterhen (*Amaurornis phoenicurus* [Pennant, 1769]) were foraging on and around the nest mound. While crocodilian nest mounds harbor an abundance of potential invertebrate prey for birds (Medem 1971; Staton & Dixon 1977; Merchant et al. 2014; Platt et al. 2021; Rainwater et al. 2024), foraging at the mound also entails some degree of risk because crocodilians (including *C. siamensis*; Sam et al. 2015) frequently prey on birds (Gabrey & Elsey 2017). An unidentified species of rat(s) was the nest associate most frequently recorded by our camera. Although some rodents are predators of crocodile eggs (Webb et al. 1977; Hunt & Ogden 1991; Platt et al. 2021), our images indicated the rats traveled across the nest and through the area without attempting to breach the mound and consume eggs. Free-ranging dogs are known predators of crocodile eggs (Vyas 2010; Somaweera et al. 2013), and we consider the two instances when village dogs approached the nest as attempted predation events thwarted by the aggressive response of the attending female. In contrast, the presence of domestic cattle at the nest on numerous occasions (in one series of images sleeping cattle remained at the nest for almost five hours) elicited no response from the female crocodile suggesting these large mammals were not perceived as a threat to the nest. Likewise, González-Desales et al. (2023) speculated that female *C. crocodilus* attending nests learned to differentiate between potential egg predators and harmless species.

In closing, we caution that our camera trap imagery almost certainly represents an incomplete record of events transpiring at the nest during the monitoring period. The passive infrared sensors in camera traps detect animals based on a combination of heat and motion, and the effectiveness of these sensors depends on multiple factors such as distance from the camera to the target individual, body size (i.e., larger individuals generate more heat), and ambient temperature. As such, passive infrared sensors are very effective at detecting large mammals, but less reliable for detecting small-bodied endotherms and ectotherms (Hobbs & Brehme 2017), including crocodilians (Merchant et al. 2012; Charruau & Henaut 2012; Combrink et al. 2016). Given the technical constraints associated with passive infrared sensors, our camera trap likely either failed to capture or incompletely captured instances of crocodilian behavior and nest-associated fauna, especially smaller species of birds and mammals.

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