REPTILES & AMPHIBIANS

Flooding-induced Failure of an Invasive Burmese Python Nest in Southern Florida

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Invasive species remain a threat to global biodiversity (Duenas et al. 2021). The ability of a given species to successfully invade and become established in a novel location is a complex process involving ecological traits of both the invader and the native community (Mack et al. 2000). Invaders typically encounter novel climatic conditions and selection pressures (Facon et al. 2006). Adaptive plasticity in invasive species has been suggested as an important mechanism in facilitating colonization and persistence in new environments because it improves the fitness of individuals to novel conditions (Ghalambor et al. 2007). However, populations rarely track environments optimally, thus introduced populations might be expected to be initially maladapted to novel environmental conditions (Ghalambor et al. 2015; Velotta et al. 2018). Maladaptation can be said to occur when individual fitness is lower than some relevant point of comparison (e.g., between individuals in their home versus away environment) (Brady et al. 2019a, 2019b). Successful invaders may have fitness levels high enough to increase population size, but that does not necessarily mean that their fitness is at a theoretical optimum (e.g., Jardeleza et al. 2022).

Burmese Pythons (*Python bivittatus*) are non-venomous constrictors native to southeastern Asia (Barker and Barker 2008) that have become established in much of southern Florida (Snow et al. 2007). Understanding the factors affecting the reproductive success of an invasive species can help to estimate population size and develop management plans. We still do not understand much about the reproductive biology of Burmese Pythons in both their native and invasive ranges (Guzy et al. 2023). Burmese Pythons are oviparous, are known to produce as many as 96 eggs per clutch in the wild (Currylow et al. 2023), and oviposition occurs in southern Florida during late April through May. The species has a long history in the pet trade (e.g., Coborn 1994) but nesting behavior in the wild is not well understood. Oviposition site selection is an important factor in determining reproductive success. For example, incubation conditions can directly affect offspring phenotype and consequently fitness (Qualls and Andrews 1999; Brana and Ji 2000; Janzen and Morjan 2002; Brown and Shine 2004). Therefore, females of egg-laying species should select nest sites that maximize the fitness of offspring and thus their own fitness.

Nesting is a vulnerable period in the life of reptiles and potential threats to eggs during incubation include predation, desiccation, flooding, and temperature fluctuations (see summary in Mazzotti 1989). Flooding can be particularly influential for nesting outcomes and success of developing embryos in habitats that experience periods of heavy rainfall or seasonal flooding (Kraemer and Bell 1980; Limpus et al. 2020). The

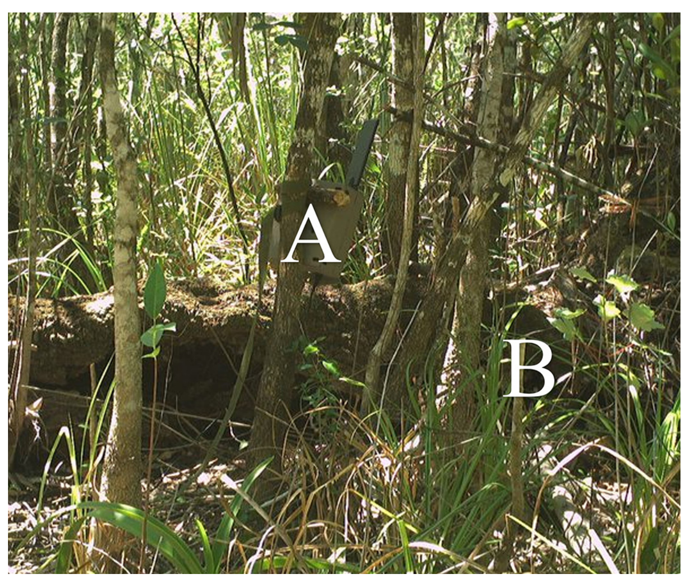

Figure 1. An oviposition site selected by a female Burmese Python (*Python bivittatus*) in Big Cypress National Preserve, Ochopee, Florida, USA, at 1512 h on 17 May 2023. A trail camera (A) is pointed toward the nest inside the hollow log (B). Note the dry conditions.

Reptiles & Amphibians ISSN 2332-4961
https://doi.org/10.17161/randa.v31i1.21384

water level in the Greater Everglades Ecosystem (GEE) fluctuates seasonally because of variation in rainfall. Rates of rainfall are considerably reduced in the fall and winter leading to water levels being lowest in the spring (Kushlan 1986), which corresponds to nesting season for invasive pythons (Bartoszek et al. 2021; Currylow et al. 2023).

We do not know how seasonal flooding may affect oviposition site selection by females or hatchling survival of Burmese Pythons. In their native range, Burmese Pythons inhabit primarily aquatic environments (Smith et al. 2021) and nest in a variety of locations that include open-ground sites, tree holes, termite mounds, and fallen logs (Wall 1921). In a study of the spatial ecology of invasive pythons in southwestern Florida, Bartoszek et al. (2021) noted that females did not select oviposition sites based on any particular land cover type but did show a preference for habitats 1.5 m in elevation. In addition, invasive pythons have been observed using anthropogenic structures for nesting purposes (Hanslowe et al. 2016).

On 10 May 2023, a female python (423 cm SVL, 59.1 kg mass) fitted with a radio transmitter oviposited in a hollow log in a cypress swamp at Big Cypress Nature Preserve, Ochopee, Florida, USA. The elevation of the site was 0.85 m (University of Florida GeoPlan Center 2023) and no standing water was observed within several hundred meters at the time of laying (Fig. 1). The female coiled around the eggs (Fig. 2A)

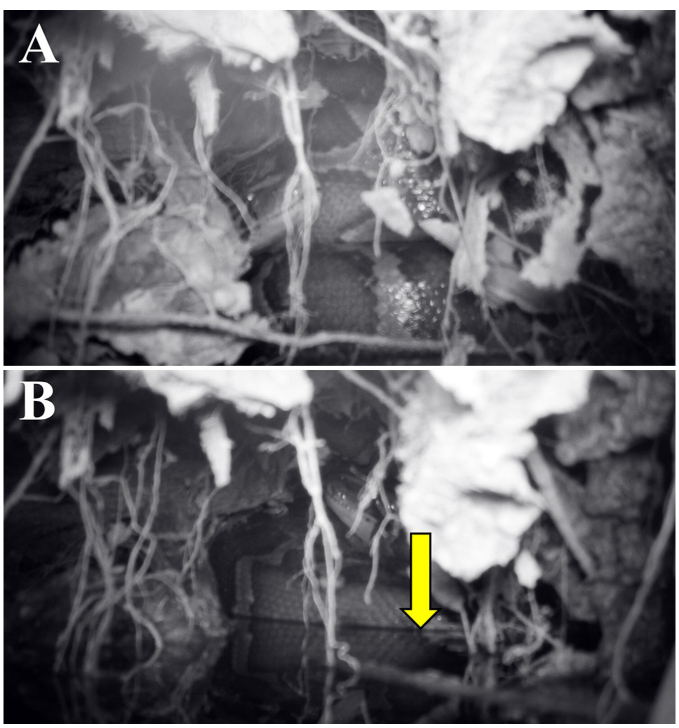

Figure 2. Trail-camera images of a female Burmese Python (*Python bivittatus*) tightly coiled around her clutch inside a log in Big Cypress National Preserve, Ochopee, Florida, USA, taken on 31 May 2023 at 1638 h (A) and on 30 June 2023 at 2323 h (B). The arrow in the latter photograph shows that the water level inside the log rose substantially when compared to the earlier image.

and engaged in shivering thermogenesis (Snow et al. 2010). We placed several cellular trail cameras (Spartan GOLIVE 4G LTE, Spartan Camera, Duluth, Georgia, USA) to monitor female behavior. On 24 June 2023, we first observed water on the trail cameras at the base of the log where the female was nesting. During incubation the water level continued to rise and submerged several coils of the snake and eggs (Fig. 2B). On 6 July 2023, the female was no longer tightly coiled around the eggs and instead was swimming within the log. When we arrived at the oviposition site on 7 July 2023, we observed the female in the log next to the egg cluster but not coiled around it.

Upon our approach the female exited the flooded log and swam away. All eggs were swollen, wrinkled, and/or discolored and were completely submerged in various states of deterioration. We also noted a strong "rotten egg" odor when removing eggs from the log. All 78 eggs were collected, placed on perlite, and transported back to the laboratory at Big Cypress National Preserve headquarters. Eggs were dissected within 4 h of collection to confirm fertilization and assess the stage of embryonic development (Table 1). Two eggs were infertile but the fertile eggs contained embryos that had died at various stages of development (Fig. 3). None were viable.

Although embryos were not dissected to a degree that would allow us to identify the specific stage of development as outlined for several species of snake (*Thamnophis sirtalis*: Zehr et al. 1962; *Python sebae*: Branch et al. 1975; Boughner et al. 2007; *Naja kaouthia*: Jackson 2002; *Boaedon fuliginosus*: Boback et al. 2012), we grouped embryos into four categories based on gross evaluation of external morphology (Fig. 3). We then used the description of ten developmental stages provided for embryos of the closely related *P. sebae* (Boughner et al. 2007) to estimate the approximate stage of arrested development in our eggs.

The least developed embryos we observed had no pigmentation or visible scales while the heart was internalized within a closed body cavity (n = 3, Fig. 3). Based on the staging of Boughner et al. (2007), this would be analogous to

Table 1. Burmese Python (*Python bivittatus*) embryos (n = 78) separated into four groups based on stage of development identified by gross evaluation of anatomical features (see text and Fig. 3). Two eggs were infertile. Eggs were recovered on 7 July 2023 from a single python nest in Big Cypress National Preserve, Ochopee, Florida, USA.

Stage of Development	No. of Eggs
Infertile	2
Group 1	3
Group 2	32
Group 3	9
Group 4	32

Figure 3. Dissected Burmese Python (*Python bivittatus*) eggs collected from a flooded nest in Big Cypress National Preserve, Ochopee, Florida, USA, showing an infertile egg (extreme left) and four distinct stages of embryonic development. Photograph by Lisa McBride.

stage 6 in *P. sebae*. Next, we grouped the embryos that were of larger body size with fewer coils and well-developed cranial features but no pigmentation (n = 32, Fig. 3), corresponding most closely to stage 7 of *P. sebae*. Based on Boughner et al. (2007), the embryos we separated into groups three and four would both fall within the final developmental stage (stage 10) of *P. sebae*, as both groups had well-developed external anatomical features and pigmentation. However, the embryos we placed in the third group (n = 9) were considerably smaller and substantially less pigmented (Fig. 3) than those placed in the fourth group (n = 32, Fig. 3). We were unable to estimate the number of days post-oviposition at which development was arrested for each of our groups. Boughner et al. (2007) did provide timing data for *P. sebae*, but the total incubation period for that species is between 80 and 90 days, whereas the incubation period for Burmese Pythons is 57 to 63 days (De Vosjoli 1991). To our knowledge, no publications describe the stages of embryonic development in Burmese Pythons.

The rising water within the log during incubation and the complete inundation of eggs at the time of our arrival suggest that the death of all embryos was due to asphyxiation. Non-avian reptilian eggs have a single shell membrane involved in water and gas exchange (Packard et al. 1977). Gas exchange is required by the developing embryo to maintain respiration and submersion of eggs can disrupt development and cause drowning (Foley et al. 2006; Cheng et al. 2015). However, some species of egg-laying reptiles appear less sensitive to inundation. For example, eggs of sea turtles appear able to survive complete inundation, but this ability varies based on timing and duration of submersion (Limpus et al. 2020). The freshwater turtle, *Dermatemys mawii*, has been documented laying eggs that can successfully hatch following more than 30 days of nest inundation (Polisar 1996) and nesting of another freshwater turtle, *Chelodina rugosa*, is known to occur underwater (Kennett et al. 1998). At least one species of crocodilian appears to lay eggs with physical characteristics more adapted to withstand inundation (Cedillo-Leal et al. 2017). The American Alligator (*Alligator mississippiensis*) and American Crocodile (*Crocodylus acutus*) inhabit much of southern Florida and flooding has been identified as a major source of nest failure and hatchling mortality (Joanen 1969; Joanen et al. 1977; Joanen and McNease 1979). The incubation period for alligators, crocodiles, and pythons in southern Florida occurs during the transition between the dry and wet seasons when rising water levels can flood nests and asphyxiate embryos (Mazzotti 1989; Kushlan and Jacobsen 1990, Bartoszek et al. 2021).

We are unaware of any studies of egg tolerance to inundation in snakes. However, the possibility for tolerance exists as some species of snakes lay eggs in or near aquatic environments, and at least one species of snake (Sea Krait, *Lauticauda semifasciata*) has been observed laying eggs in crevices of caves containing fresh water (Tu et al. 1990), but hatching success of those eggs was not reported Although most oviparous snakes do not attend nests after laying eggs, pythons provide parental care during the incubation period via shivering thermogenesis and protection via their presence, and pythons have been observed abandoning nests if incubation is disturbed (Lourdais et al. 2013). However, whether Burmese Pythons perceive flooding as a sufficient disturbance to elicit abandonment is not clear. In the case of this one nest, the female did not abandon the completely inundated eggs and the partial submersion of her body. Some birds are known to abandon flooded nests and can renest in a given reproductive season (e.g., Canada Geese, *Branta canadensis*; Beaumont et al. 2018), but this practice is not commonly associated with non-avian reptiles.

We did not find any other signs of disturbance of the nest from cameras or inspection of eggs that could have caused the mass mortality of embryos. The observed variation in embryonic development at which eggs drowned probably corresponded to the position of each individual egg as waters rose, with eggs at the bottom of the nest experiencing mortality earlier than those eggs at the top. The observed failure of this python nest was a direct result of oviposition-site selection by the female. The frequency at which females lay eggs in suboptimal locations in southern Florida is currently unknown. This maladaptive behavior would suggest Burmese Pythons have fitness levels below theoretical optima. Maladaptation is relatively common in wild populations (Hereford 2009) and can be present with no negative population outcome (Brady 2013). Identification of maladaptive traits and behaviors are informative for understanding the ecology of Burmese Pythons in the GEE and could be exploited for management.

Flooding has been considered a management tool for some invasive species within specific environmental contexts (Sher et al. 2000 Andersen and Shafroth 2010; Abbas et al. 2012). Water flow through the Everglades has been heavily influenced by human activities and water levels are controlled by water management practices at a broad landscape level. Anthropogenic control of regional hydrology has been shown to significantly affect alligator nest success in the Everglades (Ugarte et al. 2013). It is unclear whether flooding represents a feasible management tool for controlling invasive pythons and further investigation could provide important insights, particularly when considering the timing and duration of any prescribed flooding (Limpus et al. 2020).

A recently published synthesis (Guzy et al. 2023) detailing the knowledge accrued on invasive python biology in GEE revealed considerable gaps, including reproduction. Successful python control could benefit from an understanding of reproductive biology (e.g., reproductive cycles and oviposition sites) to help develop population estimates and evaluate control tools. While the nest failure we report here might indicate a mismatch between environmental conditions in the GEE and nesting behavior of Burmese Pythons, invasive pythons have shown the ability to rapidly adapt to novel selective pressures in their invasive range (Card et al. 2018). Further studies on oviposition site selection, tolerance of embryos to flooding, and overall nest success of invasive Burmese Pythons hold the potential to provide important insights into python biology and management.

Acknowledgements

We thank the National Park Service (NPS), University of Florida, and the U.S. Geological Survey (USGS) for facilitating this research. Funding and/or in-kind support was provided by the USGS Greater Everglades Priority Ecosystem Science Program, USGS Biothreats and Invasive Species Program, and USGS Fort Collins Science Center. We thank A. Currylow for prior project management of the USGS research team; F. Ridgley and veterinary staff at Zoo Miami and Steve Hanser of USGS for consultation and assistance with associated project activities; NPS staff; and research interns D. Rodas, C. Joye, G. McCargar, and G. Aponte-Santiago, who assisted with data collection. All data accumulated for this portion of the study are included in this manuscript. This study was performed under the auspices of USGS Fort Collins Science Center and IACUC protocol number 2020-06. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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