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Editorial: Nesting in reptiles: Natural and anthropogenic threats and evolutionary responses

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Editorial on the Research Topic
Nesting in reptiles: Natural and anthropogenic threats and evolutionary responses

Reptiles, like other animals, are facing the sixth mass extinction event and are challenged with habitat loss, overexploitation, species invasions, pollution and climate change. Although many reptile species have survived past extinction events, others have not. We are at a critical juncture in which we must determine which species require our intervention vs. which species can persist on their own *via* evolutionary rescue. Perhaps the most vulnerable life stage of reptiles is the set of developing embryos in nature, which are rarely attended by the mother. The success of this strategy focuses attention on nest site choice behavior – the last time the mother can influence offspring, and thus, her own evolutionary fitness. Our Research Topic involved a collection of 17 papers on the science of nesting in reptiles within the context of anthropogenic threats and potential evolutionary responses. Although our papers form a somewhat eclectic aggregation, they help funnel us toward a better understanding of reptile populations by providing valuable empirical data and relevant reviews.

Introduction

The vast majority of the world's animals lay eggs and leave them unattended, a strategy that has persisted across two major extinction events spanning hundreds of millions of years. The success of this strategy focuses attention on nest site choice behavior–the last time the mother can influence offspring, and thus, her own evolutionary fitness (e.g., Refsnider and Janzen, 2010). It is likely that nest site choice played some role in getting oviparous animals without parental care through extinction events, large and small.

Reptiles are a prime example of oviparous animals without parental care; more than 80% are oviparous and less than 3% engage in parental care (Shine, 1988; Somma, 1990; Pyron and Burbrink, 2014). Some extinction events, including mass extinctions, involved changing climates, and reptiles and their ancestors may have used nest site choice to offset increasing developmental temperatures (e.g., by shifting the openness of nest sites across generations). Alternatively, but not mutually exclusively, embryonic thermal tolerances may have evolved, or thirdly, reptile ranges may have shifted toward and away from the poles as the climate warmed and cooled, respectively.

We are now on the verge of the sixth mass extinction event (Barnosky et al., 2011) and the climate continues to warm at an unprecedented rate (Allen et al., 2018). Moreover, in addition to climate change, reptiles, like other animals, are under threat from habitat loss and alteration, overexploitation, invasive species and pollution. We are at a critical juncture in which we must determine which species can use evolutionary rescue vs. which species need human intervention. If nesting is the most vulnerable stage for reptiles we need more knowledge about how nest site choice evolves or can evolve, consequences of developmental temperatures for offspring traits and survival, and factors affecting females' nesting decisions in order to predict effects of, and potential responses to, threats in vulnerable species.

The study of behaviors associated with (maternal) nest site choice in reptiles has lagged behind those on birds. For example, there are field guides to the nests and eggs of birds for most continents and many countries but no such field guides exist for reptiles (Doody et al., 2009). Our poor relative knowledge of nesting in reptiles is at least in part due to their secretive lives (Doody et al., 2009), but also to less relative research attention (Doody et al., 2013, 2021). Within reptiles we know more about nesting in turtles and crocodilians than we do for lizards and snakes partly due to nesting turtles of many species leaving tracks in the sand (Doody et al., 2021).

Our Research Topic intends to inch the science behind nesting in reptiles forward within the context of anthropogenic threats and potential evolutionary responses. Although our papers form a somewhat eclectic aggregation, they help funnel us toward a better understanding of reptile populations by providing valuable empirical data and relevant reviews. Herein we summarize these papers by examining common threads in concepts, disciplines, taxa, problems and proposed solutions.

Results

Our Research Topic included 17 papers; 15 of which addressed conservation directly or indirectly with nine considering evolutionary processes. Conceptually, most papers were ecological ($N = 16$), followed by behavioral ($N = 15$), developmental ($N = 14$), physiological ($N = 6$) and morphological ($N = 6$). Taxonomically, most papers focused on turtles ($N = 12$), followed by lizards ($N = 2$), crocodilians ($N = 2$) and snakes ($N = 1$). Geographically, most papers focused on species or populations in U.S. ($N = 7$), followed by Australia ($N = 3$), Africa ($N = 2$) and Mexico ($N = 1$), with four papers explicitly considering reptiles globally. Five of the 18 papers would be considered reviews. Most ($N = 15$) of the papers directly considered nest site choice or nesting biology.

Discussion

Here we summarize how this set of papers inches science forward within the context of our Research Topic. Our Research Topic was dominated by research with turtles. An age-old observation is the apparent link between rainfall and both the propensity to nest and nest survival in turtles. In a study of map turtles by Geller et al., although predation rate was lower when rain fell 24 h after nesting, turtles were more likely to nest on, or after, dry days than wet days. These findings were similar to those from their literature review; of 42 studies on 23 species of freshwater turtles, 29 studies (69%) demonstrated or suggested that rainfall increased the propensity to nest, while 13 (31%) did not. It is expected that future studies will reveal less of an association between rainfall and both propensity to nest and nest survival, because this review will loosen the grip that bias has on turtle researchers in this area. In another review, Geller and Parker used data and a literature review to determine that the main cue used by raccoons to locate turtle nests is soil disturbance. This will come as a surprise to many, as the traditional view is that the cues are the scent of the mother's cloacal fluids and/or the eggs. Recognizing the bias of studies in North America, the authors call for more studies of nest location cues by predators for turtles in other parts of the world where the predators are not raccoons. Keeping with nest survival, Duchak and Burke used natural and laboratory incubation experiments to show that 60% of low hatching success in wood turtles in New Jersey (USA) was linked to maternal identity (maternal effects), compared to 40% attributable to predation, flooding, and other environmental effects. The maternally-linked hatching failure in their population could be due to inbreeding, infertility, senescence, inadequate diet or environmental contamination, and this highlights the fact that the presence of many nests and low nest predation does not ensure sustainable reproductive rates. In contrast to low nest survival, Gravelle and Wyneken found high nest success in loggerhead sea turtle nests under a variety of incubation environments in both warm-temperate and subtropical climates in Florida (USA); nests in both bioclimatic zones differed in location, temperature, moisture levels, and clutch dimensions as well as the subtle genetic differences. There were highly successful hotspots, however, and the authors noted the potential for a simple and effective method for identifying high-priority conservation areas that would facilitate the maintenance of these hotspots for the recovery of imperiled loggerhead sea turtles through the management of essential habitats.

Focusing more on nest site choice within a climate change context, Sullivan et al. showed that mother Florida softshell turtles could offset climate effects on developing eggs by 2–3°C through nesting in more shaded areas. They also showed that canopy openness did not change considerably throughout incubation, giving nesting mothers some scope for predicting incubation temperatures. Finally, they showed that metabolic heating was ecologically negligible for a moderate-sized clutch of small eggs in this hot environment. In an overview paper, Topping and Valenzuela remind us that nest site choice behavior (along with maternal provisioning of the eggs) may be under strong selection because turtles typically lack parental care. To this end they offered three ideas not typically considered in the literature: (1) how water temperature impacts basking behavior, an abiotic factor that influences female physiology, which in turn may alter the timing of nesting and resource allocation to the eggs; (2) how biotic factors such as social facilitation influences nest-site choice; and (3) how water and not just air and soil temperature may affect the conditions experienced by developing embryos in the nest. Finally, they remind us that we lack solid evidence that nest site choice behavior is heritable, a critical trait for forecasting climate change responses. Fukuda et al. showed that while forecasted changes in rainfall and temperatures associated with climate warming could affect the nest success of saltwater crocodiles, sea level rise may be more of an imminent threat: their models predicted a loss of 49% of nesting habitat between 2013 and 2100, compared to mixed effects forecasted for temperature and moisture. The authors, however, underscored the need to determine the expansion of new nesting habitat which could offset those losses. For American crocodiles, Mazzotti et al., after finding a dramatic increase in the number of nests during 1970–2020 and mixed anthropogenic effects on nesting success, noted that the bet-hedging nesting strategy of the species provides a potential evolutionary advantage in climate warming scenarios. However, the authors were careful to suggest that there was likely a limit to the adaptive capacity of the species to face climate change. Anoles have been a model system for studying ectotherm ecology and evolution, including behavioral plasticity, but much less attention has been given to their nest site choice behavior according to Pruett et al., who review nesting behavior and developmental plasticity in the group. In addition to identifying the need for more nesting studies, the authors call for more field-relevant studies of behavioral plasticity using natural nests; most experiments to date poorly reflect natural nest environments but have served as a foundation for our current understanding and future work. Finally, the authors noted that anoles provide a good system for examining the effects of global change due to the marked effects of temperature on their very shallow nests and the wide variety of habitats and microhabitats (including anthropogenic ones) that create temperature- and moisture-related challenges for developing embryos.

A few studies of nest site choice examined issues other than global climate change. For example, Patino-Martinez et al. tackled the complex relationship that can occur among substrate type and color, temperature, moisture, hatchling size, hatchling performance, hatching success and predator abundance in loggerhead sea turtles. In their hatchery experiments, egg incubation in light-colored sand led to higher hatching success and larger and physically fitter hatchlings. However, this was not the case for field data, and mothers chose to nest at similar densities in beaches with light vs. dark sand. They concluded that the population may be exhibiting a bet-hedging strategy in which different clutches might perform better on different substrates. Nesting strategies may also result in different outcomes depending on the life stage considered. Refsnider et al. measured the impacts of nest site characteristics on both hatching success and survival of neonates in eastern box turtles, a declining species. They found that hatching success was highest in nests that were deep and farthest from habitat edges, but survival of neonates was highest from shallow nests under minimal shade cover, which demonstrates that nesting females face a tradeoff between maximizing hatching success vs. neonate survival when constructing a nest cavity. The diamondback terrapin is another turtle species in decline, prompting Butler et al. to locate evidence of terrapins including nesting areas in four counties in Florida. Nests, which were mainly found by finding eggshells from raccoon depredation, were more likely to occur among Christmas Berry bushes but less likely to occur among oaks and wax myrtles. The authors explain the former is usually the first woody vegetation encountered as terrapins proceed inland from the water's edge and provides cover that may provide desirable thermal conditions for terrapin egg development. In contrast, oak and wax myrtle, when present in coastal regions, are typically found further inland; their thicker canopies may lead to lower nest temperatures which could reduce nest survival and lead to the overproduction of male hatchlings. Moreover, this cover may provide cover for mammalian nest predators. Shifting from predators to abiotic factors, Cassill et al., after recording that hatching success of loggerhead sea turtles was 65% in the face of several hurricanes in south Florida, found that hatching success was significantly influenced by distance from the high water line, distance from the vegetation line, and location along the beach axis.

It is typical for some papers in a Research Topic to cover conceptual areas linked to the main subject area rather than the subject area itself. In perhaps the most novel and exciting paper in this issue, Kuchling and Hofmeyr reveal evidence for viviparity – specifically egg retention to the hatching stage by a mother, in an elongated tortoise. This is the first reported case of viviparity in a turtle. The authors proposed that this facultative viviparity may have evolved to buffer embryos from excessively hot temperatures that would have been experienced in a natural nest. This mechanism of thermoregulating the eggs has been offered for the evolution of viviparity in lizards and snakes evolved in cold climates. Brown and Shine tested the possibility that embryogenesis may be affected by shifts in soil microbiota caused by anthropogenic disturbance, translocation of eggs for conservation purposes, or laboratory incubation in sterile media, by incubating the eggs of keelback snakes in untreated vs. autoclaved soil and by injecting lipopolysaccharide (LPS) into the egg to induce an immune response in the embryo. Neither autoclaved soil nor LPS-injected eggs affected hatching success, water uptake, incubation period, or white-blood-cell profiles, but both treatments reduced hatchling size. They concluded that microbiota in the incubation medium can affect viability-relevant phenotypic traits of hatchling reptiles and called for more studies to explore the complex mechanisms and impacts of environmental conditions on reptilian embryogenesis. Unda-Díaz et al. examined side effects of sea turtle egg relocation and hatchery incubation by comparing development and performance between hatchlings of olive ridley sea turtles incubated *ex situ* vs. *in situ*. Turtles from *ex-situ* clutches showed fewer proliferating cells in the dorsal and medial ventricular zones, less mature neurons in the dorsomedial and medial cortices, ovaries with a lesser number of proliferating cells, lower body mass and length at emergence and lower self-righting time. The authors called for future studies to disentangle the differential contribution of egg movement, reburial, nesting environment and parental origin to development. This information, they argue, would likely result in better conservation strategies for sea turtles. Abayarathna and Webb found that incubation temperatures did not influence the thermal preferences of hatchling velvet geckos; however, diet did. They concluded that predicting how future changes in nest temperatures will affect reptiles will require a better understanding of how incubation and post-hatchling environments shape hatchling phenotypes. These three papers, although not directly addressing nest site choice, have real implications for climate change responses in reptile populations.

We anticipate that these 17 papers, taken together, will advance the science of nesting in reptiles within the context of evolutionary and anthropogenic change. Importantly, many of these papers challenge assumptions about nesting ecology of reptiles, and thus have generated many important questions that can be pursued in future endeavors to better understand the likely impacts of anthropogenic impacts on reptiles and their capacity to respond.

Author contributions

JD wrote the first draft. JR contributed to and edited the draft. Both authors contributed to the article and approved the submitted version.

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Conflict of interest

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