SYMPOSIUM

Hatching Behavior in Turtles

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Synopsis

Incubation temperature plays a prominent role in shaping the phenotypes and fitness of embryos, including affecting developmental rates. In many taxa, including turtles, eggs are deposited in layers such that thermal gradients alter developmental rates within a nest. Despite this thermal effect, a nascent body of experimental work on environmentally cued hatching in turtles has revealed unexpected synchronicity in hatching behavior. This review discusses environmental cues for hatching, physiological mechanisms behind synchronous hatching, proximate and ultimate causes for this behavior, and future directions for research. Four freshwater turtle species have been investigated experimentally, with hatching in each species elicited by different environmental cues and responding via various physiological mechanisms. Hatching of groups of eggs in turtles apparently involves some level of embryo–embryo communication and thus is not a purely passive activity. Although turtles are not icons of complex social behavior, life-history theory predicts that the group environment of the nest can drive the evolution of environmentally cued hatching.

Introduction

Developing embryos are exposed to numerous environmental factors that elicit a diversity of phenotypic and fitness effects that are manifested both before and after birth (e.g., Deeming and Ferguson 1991). In oviparous species, perhaps the most influential environmental factor during embryonic development is temperature. Within the nonlethal range, for example, higher incubation temperatures notably accelerate embryonic development and thereby reduce time until hatching from eggs (e.g., Andrews 2004).

This timing of birth has enormous implications for both immediate and future survival. In animals that produce more than one offspring, assessing environmental cues is important to synchronize birth with siblings, thus it is not surprising that synchrony in the timing of births has evolved in many species (O’Donoghue and Boutin 1995). However, many factors promote intra clutch variation in incubation period in oviparous species, including differences in egg size, order of ovulation, and disparate thermal microenvironments of eggs (Andrews 2004). Despite these sources of developmental asynchrony, synchronous hatching through alteration of incubation period occurs in many oviparous taxa, including invertebrates (Frechette and Codere 2000), fishes (Bradbury et al. 2005), amphibians (Sih and Moore 1993; Warkentin 1995, 2000), crocodilians (Ferguson 1985), squamates (Vitt 1991), turtles (Doody et al. 2001; Spencer et al. 2001), and birds (Lack 1968; Vince 1969; Davies and Cooke 1983).

Data from studies of reptiles do not feature prominently in our understanding of environmentally cued hatching. However, turtles comprise one group where elements of this concept have been the subject of experimentation (Doody et al. 2001; Spencer et al. 2001; Colbert et al. 2010). Turtles ovulate clutches of eggs simultaneously, and embryonic development is arrested within the oviducts at the gastrula stage until oviposition (Ewert 1985). However, as the eggs are generally deposited in several layers within a nest, environmental gradients...
Hatching behavior in turtles

alter developmental rates among clutchmates (Maloney et al. 1990; Gyuris 1993; Thompson 1997). In particular, eggs near the top of a nest experience higher temperatures (up to 6°C higher in nests of the Murray River turtle, *Emydura macquarii*), which increases developmental rates and shortens incubation relative to eggs near the bottom of the chamber (Thompson 1988, 1989; Booth and Thompson 1991). Thus, hatching synchrony presumably should not occur within a turtle nest because incubation times should differ between eggs at the top and bottom of the nest.

Arguably, the best-known example of environmentally cued hatching is the image of hatchling sea turtles emerging from the nest *en masse*. However, this scenario confounds hatching from eggs with emergence from the nest and does not clarify mechanism in either case. For example, embryos might hatch synchronously because temperatures are relatively similar between the top and bottom of the nest (Fig. 1) or because they are responding to other cues. Similarly, hatchlings dig upwards from the nest chamber (Bustard 1967), but if they approach the surface during daylight, hatchlings will wait until dusk to emerge from the nest (Bustard 1967; Mrkosovsky 1968, 1980). Mass emergence from the nest by sea turtles thus may result from delayed emergence rather than environmentally cued synchronous hatching. Hence, freshwater turtles have been used as nascent models to experimentally assess hatching behavior because variability of temperatures within their nests (Fig. 1) conveniently disconnects temperature, embryonic development, and the timing of hatching.

Incubation temperature is the primary determinant of incubation times in reptiles (Dmi’el 1967; Sexton and Marion 1974; Mrkosovsky and Yntema 1980; Miller 1985; Gutzke and Packard 1987; Packard et al. 1987), but its influence on hatching from eggs *per se* is not known. The timing of hatching may be phenotypically plastic within certain boundaries set by incubation temperature, but the actual cues for hatching derive from a range of biotic and abiotic factors. Factors such as predation, hypoxia, dehydration, and flooding occur commonly in a range of ectothermic vertebrates (fish: Martin and Swiderski 2001; Speer-Blank and Martin 2004; amphibians: Warkentin 1995, 2000; reptiles: Doody et al. 2001; Spencer et al. 2001). With many of these taxa, hatching is spontaneous because embryonic development throughout a clutch is complete and the species can enter embryonic aestivation until conditions for hatching are optimal (Georges et al. 2008). Less common in nature is early hatching. Red-eyed treefrogs, *Agalychnis callidryas*, hatch early in response to egg-eating snakes and wasps (Warkentin 1995, 2000), as do the frogs *Hyla regilla* and *Rana cascadae* in response to egg-eating leeches (Chivers et al. 2001). The frog *Hyperolius cinnamomeoventris* hatches at a smaller size when exposed to egg-eating fly larvae (Vonesh 2000). Synchronous or spontaneous hatching is less likely to occur when eggs are developing at different rates and hatching cues occur well before the entire clutch has completed development. In such cases, there are likely consequences for both short- and long-term fitness, which provide opportunities to test ecological and evolutionary trade-off theories of optimality in the emerging field of embryonic behavior. This review focuses on the behavior of synchronous hatching in turtles and incorporates unpublished findings because of the nascentne of this research area. We discuss the environmental cues for hatching, the physiological mechanisms behind synchronous hatching, the proximate and ultimate causes for this behavior in the context of optimality theory, and future directions for research.

**Defining synchronous hatching**

Synchronous emergence of neonatal turtles from the nest is well documented (De Pari 1996; Tucker 1997, 1999; Nagle et al. 2004), although it is not ubiquitous (e.g., Kolbe and Janzen 2002), with many marine turtles hatching throughout the day but delaying emergence until dusk or night (Bustard 1967; Mrkosovsky 1968, 1980). Indeed, social facilitation behavior of hatchling green turtles (*Chelonia mydas*) occurs during emergence from the nest (Carr and Hirth 1961). But such emergence behavior should not be confused with synchronous hatching, which refers to coordinated departure from eggs of fully formed embryos (i.e., hatchlings). Experimental evidence of environmentally cued hatching in turtles has focused on three freshwater species, where thermal variability in the shallow nests is well established (Thompson 1988). Pig-nose turtles (*Carettochelys insculpta*) can hatch spontaneously, embodying the traditional view of synchronous hatching as described above for various anurans. Two other species of freshwater turtle have displayed some capabilities to hatch synchronously by responding to developmental and hatching cues of clutch mates: *E. macquarii* can hatch synchronously under warmer incubation temperature regimes (Spencer et al. 2001), and the painted turtle, *Chrysemys picta*, was unable to hatch synchronously in experimental protocols, despite clearly adjusting hatching
times (Colbert et al. 2010). Spontaneous or synchronous hatching in species that hatch early or accelerate development (as opposed to delaying hatching) is difficult to achieve, thus for the remainder of this review the term “synchronous hatching” should be understood to include any response of an embryo to the developmental stage or hatching behavior of clutch mates, which may not necessarily result in spontaneous hatching, but does result in the adjustment of incubation times. Such synchronous hatching occurs in precocial birds (Vince and Chinn 1971) and turtles (Spencer et al. 2001, Colbert et al. 2010).

Synchronous hatching and turtles

There has long been suspicion that hatching in sea turtles is somewhat coordinated, similar to their emergence from the nest. However, given that these large animals construct deep nests where both the thermal gradient and variance between the top and bottom of the nest is low (Packard and Packard 1988), there is no conclusive evidence that embryos respond to anything other than temperature. Much research into sea turtle biology has focused on cues for emergence (Bustard 1967; Mrosovsky 1968, 1980; Gyuris 1993) and hatching orientation postnest emergence (Mrosovsky 1978; Salmon and Lohmann 1989; Lohmann 1991), thus, these turtles now need experimental study of hatching synchrony.

As mentioned earlier, three freshwater turtle species have a demonstrated capacity to hatch synchronously in the broad sense of the term (Spencer et al. 2001; Georges et al. 2008; Colbert et al. 2010). One other species (Chelodina longicollis) has conclusively demonstrated that it does not have the capacity to either delay or speed up hatching to ensure synchrony (R.-J. Spencer, unpublished data). Pig-nose turtle nesting and embryonic developmental behavior is primarily geared to predictable weather patterns of northern Australia (Georges et al. 2008). The response of C. insculpta embryos to rising water levels promotes synchronous hatching, but there is some evidence that biotic factors like vibration (see below) are also cues for hatching (Georges et al. 2008). Full-developed offspring only hatch from eggs when a nest is inundated with river water. There is also no evidence that pig-nose turtles hatch in a premature developmental state. On the other hand, the Australian turtle E. macquarii (Spencer et al. 2001) and the North American turtle C. picta (Colbert et al. 2010) adjust incubation period in response to some unknown factor(s) related to developmental stage of sibling embryos to ensure that hatching of eggs within a clutch occurs over a short time period. In contrast, the

![Temperature at various depths in freshwater turtle nesting areas at Albury, Australia.](image)
Mechanisms and cues of synchronous hatching in turtles

Pig-nose turtles nest late in the dry season from mid-July to early November in northern Australia (Georges and Kennett 1988, Doody et al. 2003). The incubation and hatching biology of *C. insculpta* is different in comparison to most turtles. Eggs require 64–74 days at 30°C to develop to a point where hatching is possible (i.e., until yolk internalization) after which they enter embryonic aestivation (Webb et al. 1986). The proximal cue for hatching is anoxia, which can be caused by immersing eggs in water or in a nitrogen-only atmosphere (Webb et al. 1986). In the field, torrential rain or flooding stimulates hatching (Georges 1992), an adaptation that synchronizes hatching with the onset of the wet season. Although a mature hatchling can remain in the egg for 59 days to yolk exhaustion, the anoxia stimulus to hatch in the field normally occurs within 20 days (Doody et al. 2001) after the eggs are developmentally mature (Georges et al. 2004, 2005, 2008). Hatching of *C. insculpta* is typically “explosive” (Webb et al. 1986; Doody et al. 2001): On immersion of eggs, the turtles hatch within minutes. Behavior of hatching clutch mates may also be important. In laboratory experiments, groups of eggs hatched faster than single eggs treated in the same way, indicating a function of sibling vibrations (Georges et al. 2008).

The ability of *C. insculpta* to hatch early prior to the aestivation period is limited. Nest mortality due to flooding was 20% when turtles nested late after a below average wet season (Doody et al. 2004). Most nests destroyed by floods were constructed at low elevations and had not completed development by the time flooding began (Doody et al. 2004). In contrast, *C. picta* and *E. macquarii* do not display developmental aestivation during incubation and have the capability of shortening the incubation period to hatch synchronously or early (Spencer et al. 2001; Colbert et al. 2010). Although the nesting cues may differ slightly between the species, the timing of nesting and incubation period is similar between *C. picta* and *E. macquarii* (Bowen et al. 2005). Nesting generally occurs in late spring-early summer in both species and nests are usually constructed close to water (Bowen et al. 2005). Clutch sizes vary depending on female size and location, but both species construct nests that are about 5–15 cm deep (Jackson et al. 2004). Incubation lasts 72–80 days in *C. picta* nests (Zweifel 1989) and 66–85 days in *E. macquarii* nests (Cann 1998). The major difference between the natural history of nests of *C. picta* and *E. macquarii* is that painted turtle hatchlings in the northern part of their range typically arrange themselves symmetrically in the nest and overwinter to emerge the following spring (Costanzo et al. 2008), whereas no delayed emergence occurs in *E. macquarii* (Cann 1998).

Both these freshwater turtle species do not delay hatching, unlike *C. insculpta*, and they can hatch prematurely (Colbert et al. 2010) or compensate by increasing developmental rates (J. McGlashan et al., submitted for publication) to synchronize hatching. Respiration rates in reptiles and precocial birds generally drop by up to 25% before hatching occurs (Birchard and Reiber 1995; Birchard 2000; Peterson and Kruegl 2005), but hatching can occur at any time after peak metabolism. The fall in metabolism prior to hatching is present in some species as resting, or the secondary developmental stage, which is variable in length (Fig. 2). If turtles like *C. picta* do not adjust their developmental rate, they may significantly shorten the secondary development stage (Fig. 2), which could reduce post-hatching fitness (Colbert et al. 2010).

Premature hatching in *C. picta* was inferred from behavioral and morphological assessments of neonates (Colbert et al. 2010). That is, turtles that were known or suspected to have hatched prematurely exhibited reduced ability to turn themselves when overturned in performance trials and typically had substantial residual yolk extruding from the abdominal cavity. In contrast, a recent study monitored embryonic rates of development in *E. macquarii* throughout the entire incubation period and found that these turtles do not hatch in a premature developmental state because less developed embryos responded to the presence of more advanced eggs within a clutch by increasing metabolic and heart rates. The assumption is that turtles have limited capacity to regulate metabolic processes independent of temperature, because they are ectothermic and thermoconformers. Hence, increases in metabolic rates and embryonic development above temperature regimes are improbable and early, or synchronous hatching, should be achieved through incomplete development (Colbert et al. 2010). Both VCO₂ and heart rate of *E. macquarii* increased in response to
the developmental stage of neighboring eggs. This outcome supports the dashed-line scenario illustrated in the graphical model of the “catchup” hypothesis for synchronous hatching (Fig. 2). However, differences in \( V_{\text{CO}_2} \) and heart rate in stimulated *E. macquarii* embryos do not manifest until the last one-third of incubation, rather than throughout the incubation period as illustrated in Fig. 2.

How development is accelerated is unknown. Turtle embryonic development requires a fixed number of heart beats (Du et al. 2009); thus, faster heart rates induced by warmer temperatures should result in shorter incubation times. But heart rate is not fixed even at constant temperatures, hence incubation temperature may determine the upper and lower ranges, rather than a specific heart rate, for an individual. Heart rate in *E. macquarii* can vary by up to 15\% around the average rate throughout a day, with diurnal peaks and troughs throughout the entire incubation period (F. K. Loudon et al., unpublished data) (Fig. 3). It may be possible for embryonic turtles in the presence of more advanced eggs to maintain increased heart rates and thus develop faster than normal rates. However, diurnal patterns of heart rate have not been compared between more- and less-developed embryos within a clutch.

At a metabolic level, maturation of cardiovascular control mechanisms in late-term embryos may also be important. Slight physiological increases in metabolic (and thus, developmental) rate could provide a means to accelerate embryonic development and growth, given the inability of an embryo to thermoregulate behaviorally. However, mechanisms responsible for ontogenetic shifts in heart rates and metabolism are unknown, but may relate to matura-

![Fig. 2 Metabolic profile of turtle embryos (eggs) throughout the incubation period. Solid black line represents the stimulus eggs that have been incubated separately at warmer temperatures for the first week of development. The gray line represents eggs that are not stimulated to increase their developmental rates throughout incubation, but reduce their secondary developmental stage to hatch synchronously with the stimulus eggs. The dashed line represents eggs that are stimulated to increase their developmental rates and hatch at a similar developmental stage as the stimulus eggs. The gray regions represent the secondary developmental stage. The secondary developmental stage of eggs that simply hatch early is approximately half (dark gray region) of that of the other eggs (light gray + dark gray regions). Based on the metabolic profile of *E. macquarii* (Thompson 1989). From J. McGlashan et al. (unpublished data).](http://icb.oxfordjournals.org/)

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the incubation process of chickens and hypoxic conditions induce its production in embryos (Decuypere et al. 1991; Dewil et al. 1996; Buys et al. 1998; De Smit et al. 2006).

The cues for hatching in *C. picta* and *E. macquarii* are unknown and may differ between the species, as do the mechanisms for synchronous hatching. With *C. picta* hatching at a developmentally premature stage, the cues for hatching are likely to be localized toward the end of incubation when more advanced embryos begin to hatch. Avian and crocodilian embryos may communicate developmental stage by means of audible clicks (Driver 1965; Ferguson 1985). Additional cues might come from vibrations of eggs in close contact at hatching or other means of physical disturbance, such as a predator opening a nest or disturbing a clutch (Vitt 1991; Warkentin 1995, 2000). However, vocalization is not known in embryonic or hatching turtles, and there is no contact between eggs during incubation in these synchrony experiments (Spencer et al. 2001; Colbert et al. 2010; J. McGlashan et al., unpublished data; R.-J. Spencer, unpublished data). Spencer et al. (2001) note that sounds produced by pipping eggs could be a potential cue, as well as the changes in oxygen consumption, CO₂ production, and heart rate that are characteristic of the overall decrease in metabolic rate before hatching. The increase in metabolic rates during the last third of development in *E. macquarii* indicates that both elevated CO₂ levels and heart rates are plausible explanations for a potential hatching cue (Spencer et al. 2001). With eggs not incubated in contact with each other, differences in heart rate may only be detected during the last phase of incubation when the heartbeat strengthens. Similarly, CO₂ levels in a nest may only reach high concentrations during the last phases of incubation when embryonic development and metabolism accelerate. High CO₂ levels within a nest may indicate imminent hatching and may cue the production of thyroid hormone, as in chickens (Decuypere et al. 1991), and increased development of less advanced embryos. Audible cues from pipping eggs and gas exchange within a nest thus may be responsible for synchronous or early hatching in *E. macquarii* and other species. The close proximity of eggs and likely higher CO₂ concentrations in nests relative to the lab experiment accentuate the ecological probability of this scenario.

**Proximate and ultimate significance of synchronous hatching in turtles**

Life-history theory predicts that the timing of transitions between different life stages should vary with the costs and benefits accruing in current and succeeding stages (Werner and Gilliam 1984). Adaptive responses of posthatching animals to predators are
common and include morphological changes, life-history shifts, and behavioral responses (Lima and Dill 1989; Harvell 1990). With such a diverse range of mechanisms underpinning synchronous hatching in turtles, the ecological, physiological, and evolutionary causes are also likely to be diverse. Collectively, embryonic aestivation, explosive hatching, and sibling communication in Carettochelys are unique adaptations for matching timing of hatching with the onset of the wet season, especially important, given the high annual variation in timing of nesting (Doody et al. 2001, 2004). The proximal cue for hatching is anoxia and, as water levels increase, clarity of the aquatic environment declines and predation risk of hatchlings may further decrease. Timing emergence from the nest with the onset of the wet season may also maximize food availability for hatchlings (Webb et al. 1986; Doody et al. 2001). In Papua New Guinea, though, hatchlings may have to contend with osmoregulatory challenges because many nests are constructed on coastal beaches where salinity of the surrounding water can approach ocean water levels (Georges et al. 2008). Irrespective of any synchronized hatching, hatchling Chelonia insculpta emerge from the nest as nest temperatures are decreasing, at night (Doody et al. 2001).

The timing of hatching, the transition from egg to larval and juvenile stages, varies with risk of mortality to both embryos and hatchlings (Sih and Moore 1993, Warkentin 1995, 2000). The link between synchronous hatching and group emergence has been tied closely to the concept of predator swamping. Predator swamping is typically invoked, even if only implicitly, as an explanation for temporal and spatial synchrony in behavior among individuals in a population (Tucker et al. 2008). Among these instances where per capita predation is presumably diluted by synchrony are included the iconic arribada nesting of sea turtles (Pritchard 1969) and behavioral synchrony of hatching turtles in nests (Tucker et al. 2008). In the olive ridley sea turtle (Lepidochelys olivacea), first-night predation was higher for solitary nests compared with arribada nests (Eckrich and Owens 1995). Tucker (1997) suggested that synchronous nesting in the red-eared slider turtle (Trachemys scripta elegans) was a predator-swamping tactic (Tucker 1997; Tucker et al. 2008).

Most predators on hatchling turtles are generalists (e.g., Janzen et al. 2000), so the factors responsible for synchronization of hatching or emergence may involve prey switching rather than predator swamping (Ims 1990). Indeed, Tucker et al. (2008) released T. s. elegans neonates in different-sized groups and found no support for the predator-swamping hypothesis. Instead, neonates emerging from nests, and particularly those emerging early, had the highest survivorship. Prey that are first to perform a particular behavior may have better chances for survival due to the lag time before predators switch to new prey (Ims 1990; Testa 2002). The prey-switching hypothesis also supports selection for the “catchup” mechanisms of synchronous hatching in C. picta, E. macquarii, and, possibly, C. insculpta. This developmental pattern makes sense if selection favors early synchronous emergence from nests (in accordance with prey switching) rather than delayed synchronous emergence (in accordance with predator swamping) (Tucker et al. 2008).

Substantial costs are associated with the “catchup” or early-hatching mechanisms for synchronous hatching. Increases in metabolic rate by E. macquarii translate directly into increases in rate of embryonic development and utilization of yolk reserves, which are vital for the initial few weeks of neonatal development and survival (J. McGlashan et al., unpublished data). However, the costs of hatching prematurely are likely to be more immediate. The trade-off between the benefits of premature hatching and the costs are primarily embedded in the secondary development period of incubation (Fig. 2). Varying the length of this stage may have both short- and long-term costs because secondary development is associated with the maturation of the neuromuscular system, whereas primary development (up to the peak metabolic rate) is associated with organ and tissue development. Examples of such costs are reflected by Japanese quail chicks (Coturnix coturnix japonica) with accelerated development, which take 1–2 h later to stand than normal chicks (Vince and Chinn 1971), and by early-hatching C. picta, whose neuromuscular function is reduced for at least 9 months after hatching (Colbert et al. 2010). However, a subsequent release experiment involving these C. picta neonates found that these performance disadvantages did not appear to translate into reduced survival early in life (P. L. Colbert et al., unpublished data). Selection for early hatching without reduced capabilities may be far stronger in E. macquarii compared with C. picta because the Australian turtle emerges from the nest much sooner than the North American turtle. Indeed, hatchlings in some populations of C. picta can spend more than 9 months overwintering within a nest (Costanzo et al. 2008) and selection may favor individuals that minimize the mobilization of yolk reserves during incubation because they are required to survive overwintering. Position within the nest...
also has profound implications for winter survival in C. picta (Costanzo et al. 2008), thus, individuals hatching first may have a distinct advantage in securing optimal overwintering sites within the nest (i.e., surrounded by clutch mates near the bottom of the nest). Winter conditions within nest chambers can present a serious challenge to survival, even for a cold-adapted species such as the painted turtle (Costanzo et al. 2008). Nest thermal gradients that differentially affect developmental rates of clutch mates in the summer may also have differential effects on freezing mortality in the winter (Weisrock and Janzen 1999). Hence, despite both species hatching earlier than expected, the ultimate and proximate (i.e., increased developmental rates vs. premature hatching) mechanisms for synchronous hatching in C. picta may be very different from those in E. macquarii. In contrast to C. picta, growth and performance of accelerated E. macquarii is not significantly different from normally incubated embryos, at hatching and even several months after hatching (J. McGlashan et al., unpublished data).

Even in species where synchronous or early hatching occurs, disparate proximate mechanisms probably underlie superficially similar phenotypic traits (Colbert et al. 2010; J. McGlashan et al., unpublished data). Colbert et al. (2010) suggested that phylogenetic inertia may be responsible for its presence in modern day turtles, but for a trait to remain common in many species, it must, at a minimum, offer no selective disadvantage to individuals displaying it. Clearly, less-developed embryos in C. picta are potentially disadvantaged, in terms of neuromuscular capabilities, by hatching early. Also in species that synchronize nesting and nest in high densities, the dilution or predator swamping effect in reducing the individual risk of predation may be a strong positive selective force, but with solitary nesters, the disadvantage of synchronous hatching (reduced coordination and resources) may far exceed any advantages of group emergence from a nest. Moreover, the trait must be conserved across taxa. In three species of freshwater turtles where hatching has been experimentally determined to be synchronous (or partially synchronous), the mechanisms by which it occurs are very different. A fourth species, C. longicollis, does not hatch synchronously or even show signs of developmental adjustment in response to more- or less-advanced siblings within a clutch (R.-J. Spencer, submitted for publication). Thus, the behavior of hatching in turtles in response to environmental cues currently has enigmatic evolutionary implications.

Conclusions and future research

This review highlights that hatching behavior in turtles is poorly understood. However, although temperature is the major factor controlling embryonic development in ectotherms, its effects on hatching times may be less substantial. The plasticity of hatching times in turtles may have upper and lower boundaries roughly set by developmental stage, within which specific biotic and abiotic factors serve as key cues for actual hatching. These cues, particularly in turtles that are hatching early, are poorly known and require further in-depth experimentation. For example, communication between siblings within nests is not a new phenomenon (e.g., chicks [Driver 1965] and crocodiles [Ferguson 1985]). However, less obvious cues drive synchronous hatching in some species, so much so that they induce accelerated developmental rates at certain stages of the incubation period (J. McGlashan et al., submitted for publication). The physiological mechanisms behind this plasticity of developmental rate are not known but could even have implications for understanding the evolution of endothermy in vertebrates.

This review identifies four different mechanisms of hatching behavior in turtles from the only four species that have been assessed experimentally (Spencer et al. 2001; Georges et al. 2008; Colbert et al. 2010; R.-J. Spencer, unpublished data). The breadth of behaviors involved in development and hatching of embryonic turtles is only just being revealed, and clearly more experimentation is required in species that have shown some propensity to exhibit environmentally cued hatching. Similarly, the proximate and ultimate causes for these behaviors are not known and require both physiological experimentation on embryonic development and hatching release experiments to assess longer-term implications for fitness. Hatching in turtles is not a passive activity and there is clear, but currently limited, evidence for embryo–embryo communication in turtles. Reptiles are not icons of complex social behavior, but in the group environment of the nest, optimality or trade-off theory predicts that behavior, such as environmentally cued hatching, can evolve.

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