Prehatch sounds and coordinated birth in turtles

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Abstract

Hatching synchronisation is widespread in oviparous taxa. It has been demonstrated that many species use sounds to coordinate synchronous hatching, being widespread among archosaurs (birds and crocodilians). Recent studies have shown that some turtle species produce sounds from within the egg, but the role of this behaviour in synchronising hatch is untested. The reduced amount of information about sound production by turtle embryos, limited to a handful of species, mostly close related, precludes any inferences based on differences in their ecology, reproductive behaviour and phylogenetic context. With the goal to investigate if coordinated synchronous behaviour is mediated by within-egg vocalisations in turtles, we recorded clutches from six different turtle species. The selected animals present different ecological and reproductive niches and belong to distinct phylogenetic lineages at the family level. We aimed to understand: 1. what is the phylogenetic distribution of within-egg vocal behaviour among turtles; 2. if asynchronous-hatching turtle species vocalise from within the egg; 3. If clutch size influences synchronous behaviour; and 4. If within-egg turtle sounds follow any phylogenetic signal. Our results expand our understanding of the association of hatching emergence and pre-emergence sound production in chelonians and challenge previous hypothesis that within-egg sounds are accidentally produced as side-effects of other behaviours.

Keywords: Nest emergence, Vocalization, Acoustic repertoire, Synchrony

Introduction

Hatching synchronisation is widespread in oviparous taxa, being found in insects (Endo and Numata, 2020), fish (Majoris et al., 2022), amphibians (Warkentin, 2011), turtles (Spencer and Janzen, 2011), archosaurians (Ferguson, 1985; Vergne and Mathevon, 2008; Mariette et al., 2021), and squamates (Aubret et al. 2016); it may have evolved recurrently in oviparous lineages. It acts in different forms and intensities (Colbert et al., 2010), that can vary up to the population level (McGlashan et al., 2018). Although seemingly widespread, the evolutionary drivers for the selection of synchronous hatching are not well understood, and seem to vary among animals in different ecological contexts (Riley et al., 2020).

Most of the knowledge about synchronous hatching behaviour comes from archosaurians (birds and crocodilians; *e.g.*, Ferguson, 1985; Vergne and Mathevon, 2008; Mariette et al., 2021), which are some of the most studied animals due to the high number of social behaviours they display. In fact, synchronisation has been hypothesized to be linked to highly social behaviours such as parental care and vocal communication: prehatch vocalisations are used by birds (Brua, 2002; Mariette and Buchanan, 2016; Noguera and Velando, 2019) and crocodilians (Magnusson, 1980; Vergne and Mathevon, 2008) to mediate synchronous hatching. Furthermore, synchronised hatching facilitates parental care, as incubation and feeding/protection of hatchlings do not happen concurrently (Vergne and Mathevon, 2008; Mariette and Buchanan, 2016; but see Węgrzyn et al., 2023). Birds may also synchronise hatching in order to avoid less-favourable conditions after hatching of the first eggs (Mariette and Buchanan, 2016), and both birds and crocodilians communicate with their parents from within the egg (Brua et al., 1996; Vergne et al., 2007) – which may even be involved in vocal learning in some birds (Katsis et al., 2018; Colombelli-Négrel et al., 2021).

Differently from archosaurs, turtles mostly lack parental care, limited to temporary nest protection in a handful of species (Barrent & Humphery, 1986; Iverson, 1990; Kuchling, 1999). The South American river turtle (*Podocnemis expansa*) is currently the only turtle species thought to display post-hatch parental care (Ferrara et al., 2012). Many researchers advocate that synchrony in hatching behaviour is associated to the lack of parental care (*e.g.*, Jannet et al., 2018; Pearson and Warner 2018). Hatchlings can benefit from synchronous hatching by sharing the burden of digging out of the nest (Rusli et al., 2016), and decrease individual chances of being predated by swamping predators (Arnold and Wassersug, 1978; Ims 1990; Santos et al., 2016). Predation pressure might also have had a role in the selection of synchronous hatching, as eggs that hatch late would get exposed once the first individuals leave the nest (McGlashan et al., 2018).

Furthermore, in the last decade, turtles have been recognized as vocal animals, with all studied species – around one third of the clade – being recorded producing sounds (Ferrara et al., 2013; Jorgewich-Cohen et al., 2022b). Likewise, sound production from within the eggs and nests has been reported in some species such as all sea turtles (Ferrara et al., 2014a, 2014b, 2019; Monteiro et al., 2019; McKenna et al., 2019; Field, 2020; Nishizawa et al., 2021; Jorgewich-Cohen et al., 2022b), three river turtles (*Podocnemis spp*.; Ferrara et al., 2012; Del Río, 2022), one map turtle (*Graptemys ouachitensis*; Geller and Casper, 2019a), one softshell turtle (*Apalone spinifera*; Geller and Casper 2023), and the common snapping turtle (*Chelydra serpentina*, Geller and Casper, 2019b; Lacroix et al., 2022).

Considering that turtles likely represent the sister clade to birds and crocodilians (Joyce et al., 2021), it is reasonable to anticipate similar ecological value to the within-egg vocalisations produced by these animals. The discovery of within-nest acoustically mediated interaction in turtles has opened the discussion about the role of such signals, and the possibility that sounds are used to synchronise hatch (Ferrara et al., 2012, 2014a, 2014b, 2019; Geller and Casper, 2019a; Doody et al., 2021 – but see McKenna et al., 2019 and Lacroix et al., 2022). Furthermore, the distinct absence of parental care and the diversity of ecological niches occupied by turtles make them a great model to study prehatch vocalisations and its potential links to synchronous hatching.

Synchronised hatching behaviour has only been studied in half dozen turtle species (Spencer et al., 2001; Colbert et al., 2010; Spencer, 2012; Doody et al., 2012; McGlashan et al., 2012, 2015, 2017; Riley et al., 2020; Field et al., 2021; Bock et al., 2022; Lacroix et al., 2022), and the strategies used to achieve it have been shown to be diverse. Synchronous behaviours can be divided into four not necessarily mutually excluding categories: 1. *temporal synchrony* is induced by maternal effects that impose constrained incubation periods (Ims 1990; Aubret et al. 2016). Although it influences the time of egg incubation, it is not mediated by embryos coordination. Synchronicity can also be achieved through 2. *environmental synchrony*, where ecological cues induce hatching (Doody, 2011). This can be observed in the pig-nose turtle (*Carettochelys insculpta*), where embryos emerge after being subjected to hypoxia caused by nest flooding (Doody et al., 2012). This strategy also does not necessarily require any sort of embryo-embryo communication. The necessity of coordination among hatchlings and embryos has been reported in synchronised digging behaviour (Houghton and Hays, 2001, Rusli and Booth, 2016), which may represent a case of 3. *apparent synchrony* (or emergence synchrony), where hatching does not happen at the same time, but the “first-born” waits in the nest for their siblings to hatch (McGlashan et al., 2018), and only nest emergence is synchronised.

True hatch synchrony, or 4. *coordinated synchrony*, happens when hatchlings communicate their developmental status to their siblings, which alter the time periods of incubation through physiological mechanisms in order to hatch at a similar time, despite potential thermal differences in the nest (Ims 1990; McGlashan et al., 2012; Aubret et al. 2016). Hypothetically, there are three ways in which coordinated hatching synchrony can happen: a. "*catch up*", where embryos subjected to lower temperatures – *i.e.*, less developed – increase their developmental rates so that they can hatch at a synchronised time with more developed clutch mates (*e.g., Emydura*, *Chelodina* and *Apalone*; Spencer et al. 2001; McGlashan et al. 2011; Riley et al., 2020); b. *delayed hatch*, in which embryos aestivate and eggs do not hatch although they are completely developed or they stop developing at certain stage to wait for their siblings or better weather condition (Doody, 2011); and c. *early hatch*, where not yet fully developed eggs simply hatch following their siblings (*e.g., Chelydra* and *Chrysemys*; Spencer and Janzen 2011; McGlashan et al. 2018; Riley et al., 2020; Lacroix et al., 2022).

The physiological costs associated to synchronised hatching indicates that this behaviour has adaptative value (McGlashan et al. 2018; Riley et al., 2020). Together with the fact that vocalisations are widely used by archosaurs in within-nest communication (Brua et al., 1996; Vergne et al., 2007), it is parsimonious to infer communicative meaning to similar vocal behaviours in turtles. Yet, the limited information about turtle within-nest vocalisations makes it hard to understand patterns based on the phylogenetic distribution of this behaviour. Moreover, the species so far reported to vocalise prior hatching have similar reproductive strategies (Jorgewich-Cohen et al., 2022a), with large clutches and synchronised hatch – which can be expected to shape vocal behaviour. Information on species that lay one or few eggs that do not synchronise hatch would bring light to the discussion about the adaptative value and use of within-egg vocalisations by turtles.

In order to investigate if coordinated synchronous behaviour is mediated by within-egg vocalisations in turtles, we recorded clutches from different turtle species. The selected animals present different ecological and reproductive niches and belong to distinct phylogenetic lineages at the family level. We aimed to examine: 1. what is the phylogenetic distribution of within-egg vocal behaviour among turtles; 2. if asynchronous turtle species vocalise from within the egg; 3. if clutch size influences prehatch sounds and synchronous behaviour, and 4. If within-egg turtle sounds follow any phylogenetic signal. The new evidence provides light to the current knowledge about synchronous behaviour and the sounds made by turtle hatchlings before hatching.

Methods

Nests from six different turtle species were recorded from the final 6 days of incubation to hatching day. We conducted experiments in the field and in captivity.

Species

Species selection was subjected to the availability of nests, but aimed to include representatives of all major turtle clades (Tab. 1). We also selected species with different reproductive strategies regarding clutch size (Jorgewich-Cohen et al., 2022a) that are expected to present different patterns of synchronous hatching behaviour: from 1 to 4 eggs, from 5 to 29 eggs, and 30 or more eggs. We included the South American river turtle (*Podocnemis expansa*) as a control species, since it is already known to vocalise from within the egg (Ferrara et al., 2012).

Species	**Family**	**Clutch size**	**Source**
Podocnemis expansa	Podocnemididae	Up to 130	In situ
Chitra indica	Trionychidae	up to 200	captive
Pseudemydura umbrina	Chelidae	3 to 5	mixed
Kinosternon subrubrum	Kinosternidae	2 to 5	captive
Batagur baska	Geoemydidae	15 to 30	captive
Deirochelys reticularia	Emydidae	4 to 10	captive

Table 1. Species selected for the present study.

Recordings

A professional recorder Tascam (dr-100 mk iii) with 192kHz/24-bit resolution was used in combination with an omnidirectional microphone (Rode Lavalier Go) for egg recording. The microphone was positioned among the eggs in both *in situ* and captive settings (detailed information and photos can be found in Supplementary material 1).

Estimated hatching dates were calculated based on the known incubation period of each species. Clutches were recorded every day, averaging between 7 and 8 hours a day, starting 2 weeks prior expected hatch date in order to ensure that the last days of development – where sound production is known in other species (Brua, 2002; Vergne and Mathevon, 2008) – would be included in our sampled periods. We analysed the recordings starting from 6 days prior hatching date until a day after hatching.

Recordings in captivity

Most recordings were conducted on captive turtles at Turtle Island, Styria, Austria. *Pseudemydura umbrina* eggs were recorded at Perth Zoo, Australia. We had access to one clutch from each species, except for *P. umbrina,* of which we analysed five clutches. Eggs from the same clutch were incubated together and placed 1cm from each other in all trials.

Recordings in situ

Field recordings were conducted at the Trombetas River Biological Reserve, Pará, Brazil, where ten nests of *Podocnemis expansa* were recorded for an average of 40 minutes each. Nests were oviposited approximately at the same date, and hatched a few days after recordings were conducted. Additionally, approximately 8 hrs of recordings were conducted in one wild nest of *P. umbrina* at Ellen Brook Nature Reserve, Perth, Australia. This nest was oviposited on 14 November 2020, and the recording was conducted on 28 April 2021 – approximately one week before nest emergence. The microphone was inserted in the nest, where eggs were positioned as laid. In comparison to recordings in captivity, wild nests were not exhaustively analysed due to time constraints.

Analyses of acoustic repertoires

We used Raven Pro 1.6 (Cornell Lab of Ornithology, Ithaca, NY) to analyse the recordings and search for sounds produced by embryos. The software R version 4.2.3 (R Core Team, 2022) was used to cut and measure sound parameters based on their aural and spectral characteristics. Sounds were categorized following traits used in previous research describing turtle acoustic repertoires (Ferrara et al., 2013; LaCroix et al., 2022): dominant frequency, maximum and minimum frequency, sound duration, mean variations of the intensity contour and number of pulses.

We chose for a conservative description of the vocal repertoire in order to assure we are only including sounds produced by the species. Therefore, we excluded any sounds that had an ambiguous source (*i.e.*, not obviously produced by the turtles). Sounds were sorted into different categories based on human perception, using acoustic and visual cues based on the aural and spectral characteristics of the vocalisations.

Phylogenetic distribution of prehatch sounds and synchronous birth in turtles

We compiled information about turtle species that have had their nests recorded in search of acoustic behaviour and species that have been studied regarding synchronous hatch. This information was then plotted in a phylogenetic tree with character states that represent absence and presence of these behaviours: 1. Within-egg sounds (0. absent, 1. present, 2. not recorded), and 2. Synchronous behaviour (0. absent, 1. present, 2. apparently absent, 3. apparently present). Character states assigned to each turtle species can be found in Supplementary Material 2. Additionally, we performed an ancestral-state reconstruction analysis for the presence or absence of both synchronous behaviour and prehatch call, which was inferred for each ancestral node in the tree using maximum-likelihood reconstruction.

We used an edited version of the phylogeny proposed by Pereira et al. (2017). The tree was pruned using the function drop.tip from the Ape package (Paradis and Schliep, 2019) in R platform (R core team, 2022). We created a tree containing only the taxa to which some information about vocal and/or synchronous behaviours were available, and used it to analyse the distribution of this traits among turtles.

Correlations among prehatch sounds, synchronous birth, and ecological traits

In order to understand if there are any correlations between prehatch sounds and synchronous behaviour and if they correlate to clutch size in a phylogenetic context, we performed a phylogenetic principal component analysis (phyPCA). Additionally, we included information from previous studies about other ecological traits that may influence vocal and synchronous behaviours: eggshell structure (hard or soft shelled), mean incubation time, nest depth (Field et al., 2021), presence or absence of diapause during incubation (Ewert, 1991; Horne, 2007), and type of sex determination (genetic or temperature determined; Bista and Valenzuela, 2020). We used the function phyl.pca (package phytools; Revell, 2012) in R platform.

Test phylogenetic signal of within-egg turtle sounds

To test if there is any phylogenetic signal in within-egg turtle sounds, we used sounds from all species recorded in this study and in previous studies that were available to us. These include *Podocnemis expansa* and *Batagur baska* (present work), *Chelydra serpentina*, *Graptemys ouachitensis,* and *Apalone spinifera* (Geller and Casper, 2019a, 2019b, 2023, respectively), all sea turtles (Ferrara et al., 2014a; Field, 2020; Jorgewich-Cohen et al., 2022b) except for *Eretmochelys imbricata* and *Lepidochelys olivacea* as we were unable to access samples.

We used one sound sample of each kind from each species. Sounds were resampled to the same sampling rate and bit depth using Audacity, and their characters were extracted using the spectro_analysis function of the package warbleR (Araya-Salas and Smith-Vidaurre, 2017). We ran a PCA using the extracted parameters and plotted the information from the first two PCs in order to visualize the similarity among sounds. Those that were plotted closer were considered more similar than those plotted far apart.

Results

In total, we analysed 147.8 hours of sound recordings from 19 nests. Audio files containing each sound type can be found in Supplemental material 3 and 4, respectively.

Among the six species recorded in the present work, only two of them produced vocalisations: *Podocnemis expansa*, confirming the findings from Ferrara et al. (2012); and *Batagur baska*. Results from each species are as follows:

Pseudemydura umbrina SIEBENROCK, 1901 (Chelidae)

We analysed 37.5 hours of recordings from 6 nests containing 2–4 eggs each, being 1 in the wild and 5 in captivity. No sounds were detected over the duration of the recordings, including those in which hatchlings were already out of the eggs but still in the nest.

Podocnemis expansa (SCHWEIGGER, 1812) (Podocnemididae)

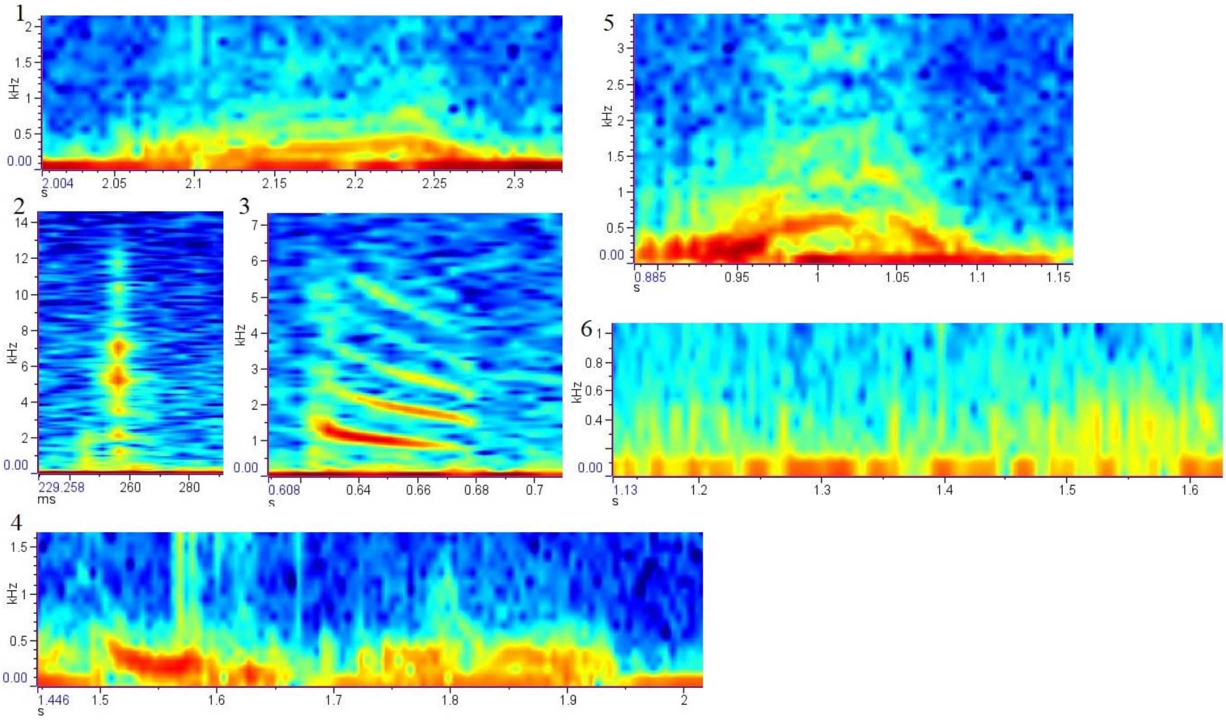


Figure 1 prehatch acoustic repertoire of *Podocnemis expansa*. Warmer colours represent higher amounts of energy

In total, from 7 hrs of recordings of 10 different nests, we were able to identify six different call types (Fig. 1). All sounds were produced by both embryos and hatchlings within the nest, often in association to digging.

Chitra indica (GRAY, 1831) (Trionychidae)

Over 32 hours of recordings were analysed from a subset of the original clutch (42) containing 12 eggs, from which 4 died. We detected cracking sounds, which got more frequent close to hatching date, but no vocalisations were captured. Hatchlings emerged from their eggs within a clutch on different dates, with a total difference of 4 days from the first to the last egg. Two of the hatchlings hatched alone with over 24hrs difference. The other six were hatched in two groups of three each, also with a day difference.

Batagur baska (GRAY, 1831) (Geoemydidae)

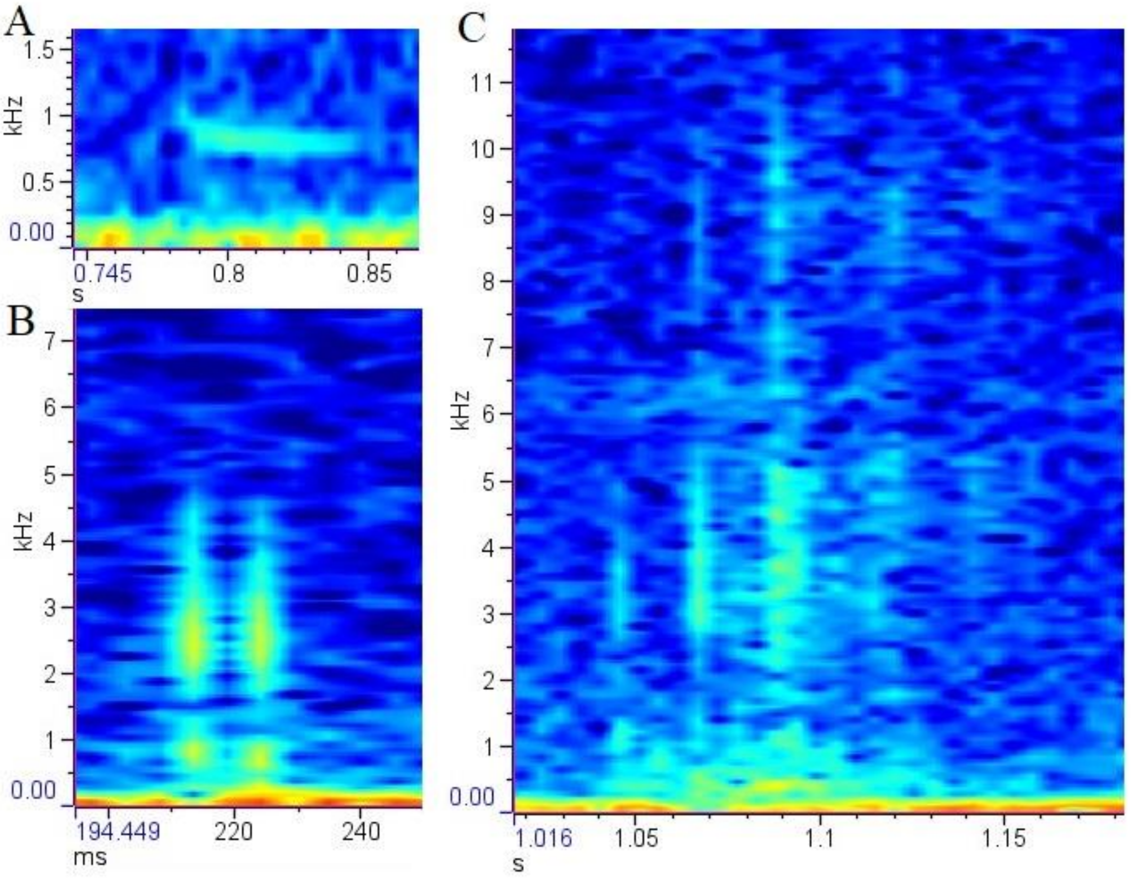


Figure 2 Prehatch acoustic repertoire of *Batagur baska*. Warmer colours represent higher amounts of energy

In total, we analysed 21.8 hours of recordings from one nest originally containing 29 eggs of which 7 hatched. Successful eggs hatched asynchronously, with a total difference of 21 days between the first and the last. We found, in total 22 sounds that were categorized into 3 groups (Fig. 2).

Deirochelys reticularia (LATREILLE, 1801) (Emydidae)

We analysed 9.5 hrs of sound recordings from a nest containing 6 eggs from which all survived. Eggs hatched in a relative asynchronous fashion, with a pair of hatchlings hatching every day, with a total difference of 3 days between the first and the last hatched egg. No sounds were found in the recordings except from sparce sounds which appeared associated with eggshell cracking.

Kinosternon subrubrum BONNATERRE, 1789 (Kinosternidae)

No vocalisations were detected during the 40 hrs of recordings from one nest containing two eggs. The hatchlings were unable to get out of the egg, so the zoo personnel freed them manually at the same day. Sounds from eggshells cracking got more frequent closer to hatching date.

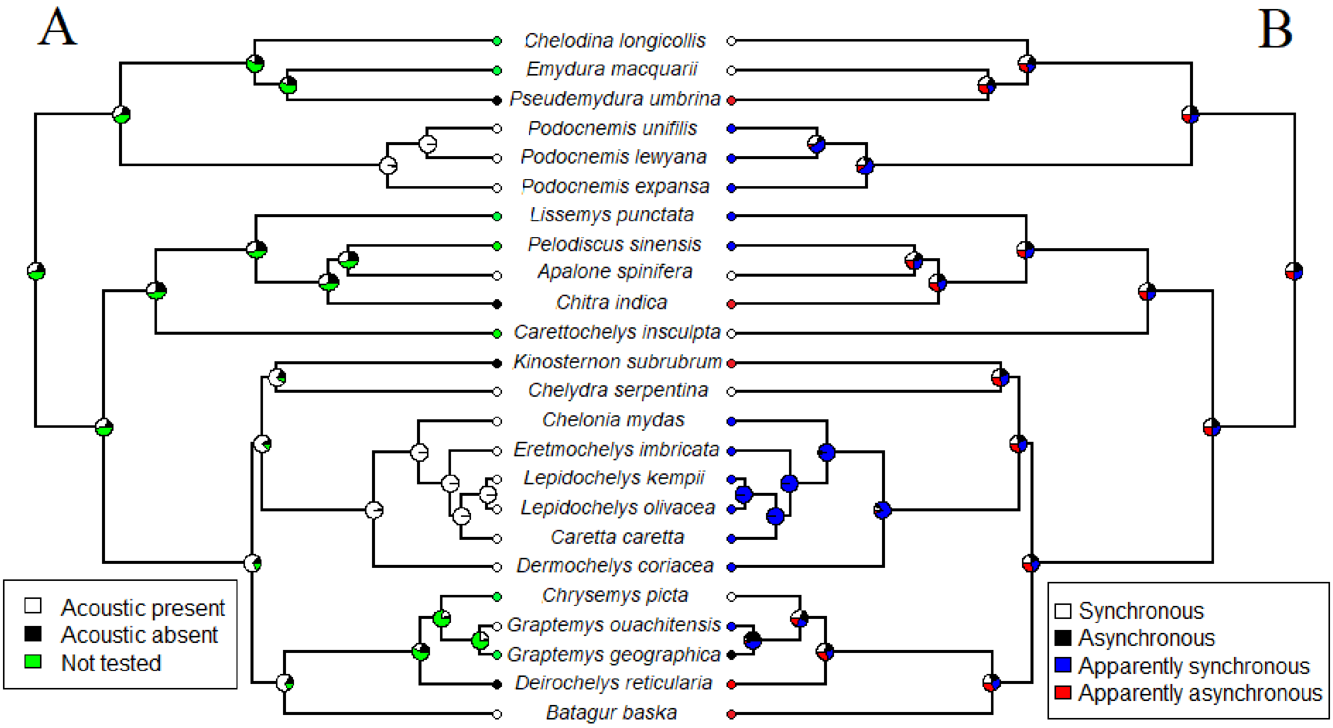
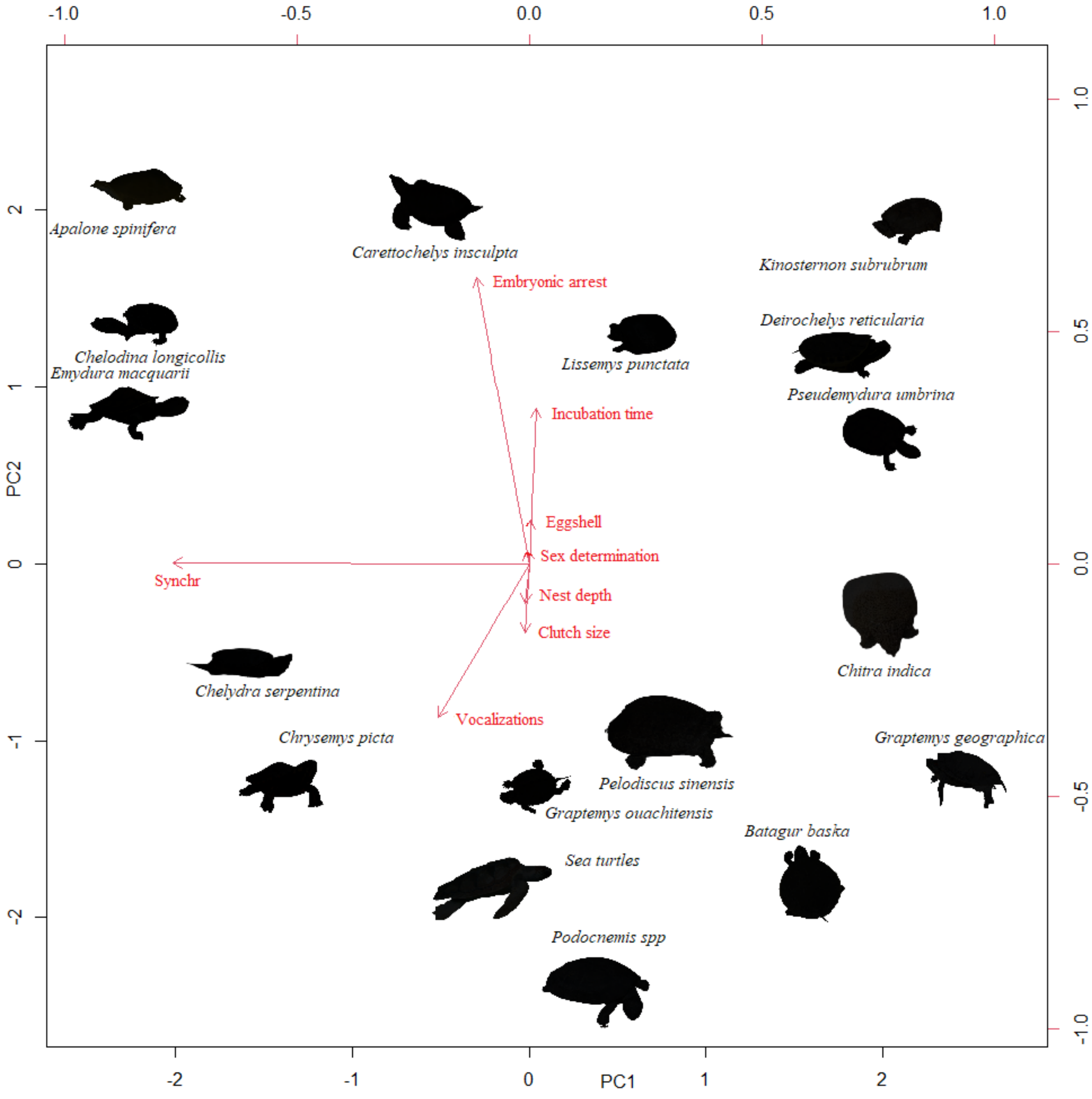


Figure 3 Phylogenetic tree with species of turtles that have been studied regarding within-nest sound production and/or synchronous behaviour. A. Information about acoustic behaviour and B. Information about synchronous behaviour. Both trees include reconstructions of inferred ancestral states (pie charts) in every node.

The character plotting and the ancestral state reconstruction show at least three evolutionary events that culminated in the innovation of within-egg acoustic behaviour – in podocnemidids, in *Apalone*, and potentially in Durocryptodira (Cryptodira excluding tryonichids). All tree tips reporting presence of vocalisations (12 species representing 6 out 14 turtle families, Fig. 3A) match with presence or apparent presence (not formally tested) of synchronous behaviour – except for *Batagur Baska*, apparently asynchronous.

The phylogenetic PCA (Fig. 4) plotted the vocalisation axis in a nearly direct correlation with the clutch size axis. Much greater angles were established between the vocalisations and the embryonic arrest and incubation time axes, indicating negative correlations.



synchronous and vocal behaviour in embryos and hatchlings of a selection of turtle species studied in the present and previous works

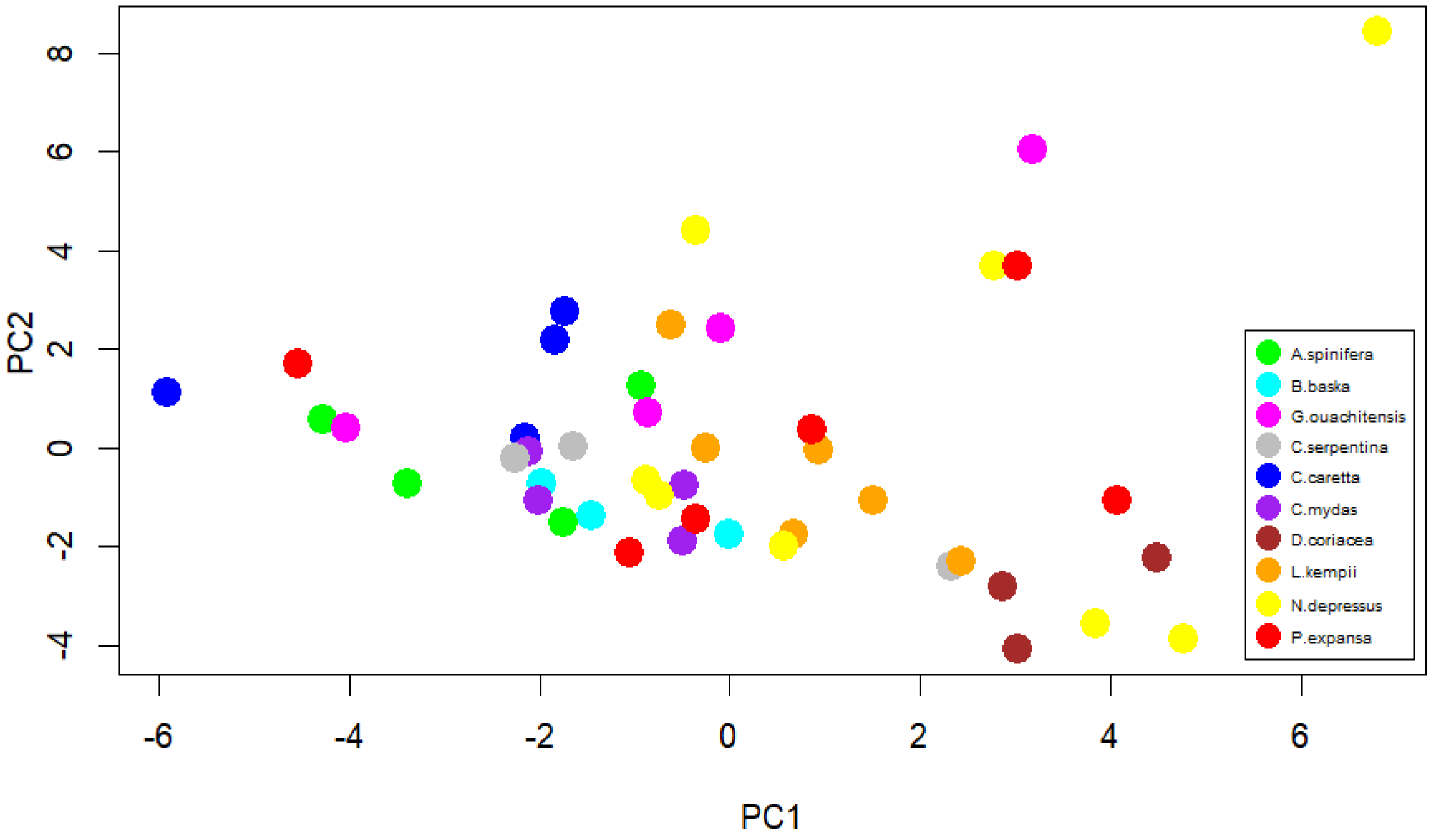


Figure 5 Similarities among within-egg turtle calls. Dots represent unique call types and colours represent different species.

The PCA based on the spectro-analysis plotted the points in a seemingly random distribution, indicating lack of phylogenetic signal.

Discussion

Knowledge about within-egg and hatching sound production by turtles is limited to a small number of studied turtle species, and both behaviours are reported for just a few species. Studies that report within-egg sounds focused mostly on sea turtles (Ferrara et al., 2014a, 2014b, 2019; Monteiro et al., 2019; McKenna et al., 2019; Field, 2020; Nishizawa et al., 2021; Jorgewich-Cohen et al., 2022b), and species of the Podocnemididae (Ferrara et al., 2012; Del Río, 2022), but also on the Ouachita map turtle (*Graptemys ouachitensis*, Geller and Casper, 2019), the common snapping turtle

(*Chelydra serpentina*, Lacroix et al., 2021), and the Spiny Softshell Turtle (*Apalone spinifera*, Geller and Casper, 2023).

Studies on synchronous hatching behaviour have focused on eight species representing six different families (Spencer et al., 2001; Colbert et al., 2010; Spencer, 2012; Doody et al., 2012; McGlashan et al., 2012, 2015, 2017; Riley et al., 2020; Field et al., 2021; Bock et al., 2022; Lacroix et al., 2022), all of which synchronise hatching except for the Northern map turtle (*Graptemys geographica*, Riley et al., 2020). The only species that have been empirically demonstrated to display both behaviours are the loggerhead turtle (*Caretta caretta*, Field et al., 2021) and the common snapping turtle (Lacroix et al., 2021).

The cues used by embryos to alter the incubation time and synchronise hatching are currently unknown; various mechanisms may play a role either in isolation or in combination. Since the first cases of within-egg vocalisations were reported for turtles in the early 2010's, the hypothesis that these sounds are associated to synchronous hatching has been under discussion (Ferrara et al., 2012; Mckenna et al., 2019; Lacroix et al., 2022) – especially because embryo vocal communication is widespread among birds and crocodilians (Mariette et al., 2021), and has been shown to mediate synchronous behaviour (Vergne and Mathevon, 2008). Nevertheless, the limited number of empirical studies and the lack of data with broad phylogenetic and ecological coverage prevents any interpretations.

In this study, we recorded the clutches of six turtle species that occupy diverse ecological niches and phylogenetic distribution – increasing the knowledge about vocal behaviour to nine families of which seven have at least one representative known to vocalise (Podocnemididae, Trionychidae, Chelydridae, Cheloniidae, Dermochelyidae, Emydidae and Geoemydidae). Most of the species we recorded (4/6), however, did not produce any sounds. The concatenated trees show that the presence of vocal behaviour is associated to the presence (or apparent presence) of synchronous hatching behaviour. This is supported by the phylogenetic PCA, that implies some degree of correlation between the synchronous and vocal behaviour axes.

Our data does not empirically prove that vocalisations mediate social behaviours in embryos and/or hatchlings, but the lack of vocalisations in some species may be insightful. Although it is not possible to prove a negative assumption (*i.e.*, they *do not* vocalise), as it may only reflect the absence of data – Del Río (2022) reported sounds produced by embryos of the Magdalena River turtle (*Podocnemis lewyana*), while Bock et al. (2022) reported not registering any sounds in another study on the same species – our standardized protocol is expected to yield comparable results. That is, if no sounds were produced by most of the recorded species, this indicates, at least, that they are less vocal than the species with positive results.

Interestingly, the existence of seemingly silent embryos challenges the recently proposed idea that within-nest sounds are no more than accidental byproducts of other behaviours (McKenna et al., 2019; Field et al., 2021). The hypothesis that within-egg vocalisations mediate social behaviour is supported by the apparent absence of vocalisations in species with small and/or asynchronous hatching, while present in synchronously hatching species with similar ecological niches but different evolutionary histories (*i.e.*, podocnemidids and sea turtles – see more below). Furthermore, the idea that acoustic repertoires comprised of several types of sounds play an ecological role is the most parsimonious alternative. Considering that archosaurians are known to mediate synchronous behaviour through within-egg sounds (Vergne and Mathevon, 2008; Mariette et al., 2021), and that vocalisations are generally used in social interactions by adult archelosaurians (turtles + archosaurians; Jorgewich-Cohen et al., 2022), the role of within-nest vocalisations should not be prematurely dismissed.

Lacroix et al. (2021) got no response in a playback experiment designed to test if sounds induce pipping in eggs of the common snapping turtle. They proposed that either sounds do not mediate synchronous hatching behaviour or that they do so in much more specific and refined manner. In fact, these possibilities are not mutually exclusive if considered in a broad phylogenetic perspective (see below). Whereas focusing on the matter of the potentially higher complexity of sounds mediating within-nest behaviours, there are several stages from an embryonic stage to the life out of the nest that should be considered.

The relevance of acoustic signals potentially starts during the second phase of the embryological development (linked to maturation of the neuromuscular system, whereas the primary is linked to organ/tissue development), a few days before hatching, when neuromuscular activity increases (Spencer et al., 2001; Colbert et al., 2010; McGlashan et al., 2012). At this phase, acoustic signals would possibly play an important role in species that display "catch up" (*i.e.*, *Chelodina longicollis, Emydura mcquarii, Apalone spinifera, Podocnemis lewyana*, and *Caretta caretta*; McGlashan et al.,2015, 2017; Riley et al., 2020; Field et al., 2021; Bock et al., 2022) or "delayed" (not reported in any species so far) synchrony. These types of synchronous behaviours could also be mediated by other channels such as heart rate, vibrations, and chemical cues (Spencer et al., 2001; Spencer, 2012; McGlashan et al., 2012; Mariette et al., 2021), in combination, excluding the use of sounds. The same or different sounds may stimulate the previously mentioned modalities of coordinated synchronous behaviour during pipping and hatching (potentially as two separate events). Additionally, species that present early hatch synchrony (*i.e.*, *Chrysemys picta* and *Chelydra serpentina*; Colbert et al., 2010; McGlashan et al., 2012) could also benefit from acoustic cues at this stage.

After hatching, sounds could be used to mediate several species-specific behaviours that can sometimes be classified as apparent or emergence synchrony: both sea turtles and podocnemidids emit sounds while digging (Mckenna et al., 2019; Field et al., 2021; present work), a behaviour known to decrease individual energy investment (Rusli et al., 2016a, 2016b) – especially in species with deep nests (Field et al., 2021). Species could be using sounds to mediate waiting periods in the nest, regardless of if they synchronize hatching or not (*i.e.*, sea turtles, *Chrysemys*, respectively; Hays et al., 1992; McGlashan et al., 2012).

Seemingly, several species that leave the nest *en masse* are known to produce – quite similar – sounds (*i.e.*, sea turtles, podocnemidids, *Dermatemys mawii*; Ferrara et al., 2012; McKenna et al., 2019; Field et al., 2021; Jorgewich-Cohen et al., 2022), hypothetically in an ecological strategy that decreases individual risks through predator swamping (Santos et al., 2016), where sounds coming from multiple locations could be helpful to confuse predators, as it is known in other animal groups (Goodale et al., 2019, although turtle predators seem to orientate mostly visually, making this hypothesis less likely, especially in loud environments such as close to ocean waves). Synchronous nest emergence could also help to avoid exposure in open nests after the exit of clutch mates (Tucker et al., 2008; McGlashan et al., 2012), a behaviour that differs from predator swamping, but can also be sound mediated.

When conducting empirical tests on the role of acoustic cues in embryo and hatchling behaviour, it is crucial that the experimental design takes into account the different phases of development and the different behaviours they may mediate. As much as this approach can lead to clearer correlations between embryos “words” and actions (e.g., Vergne and

Mathevon, 2008), the outcome can be hard to decipher. McKenna et al. (2019) reported not finding any differences in the sounds produced by embryos and hatchlings of the olive ridley turtles (*Lepidochelys olivacea*) during incubation, hatching, and emerging from the nest. They proposed that these sounds have no biological purpose as they would expect them to differ from each other in each phase – such sounds are, unfortunately, not available.

The lack of complex vocalisations or a more refined use of specific sounds in association to specific behaviours, emplace of a seemingly random use of an unelaborated repertoire may be a reflex of the developmental stage of hatchling's vocal abilities. Many species are known to babble in the first stages of life, and refine their acoustic repertoire later (*i.e.,* birds, bats, dolphins and humans; Ter Haar et al., 2021; Eggleston et al., 2022). Unfortunately, at present, no studies on the ontogenetic changes of the acoustic repertoire in turtles exist.

Comparing putatively sound-mediated behaviours to (either analogous or homologous) behaviours displayed by potentially mute species can bring several insights on the processes that underlie synchrony. Considering that both hatching synchrony and vocal behaviour have costs (Deecke et al., 2005; Colbert et al., 2010), different ecological contexts are expected to yield different combinations of these behaviours. Some species, in theory, can be synchronous but silent: when behaviours are mediated by other channels of communication, or in cases where synchrony is not embryo-coordinated (*i.e.*, environmental and temporal synchrony). Vibro-acoustic environmental cues such as thunder and rain, and vibrations caused by translocation, can elicit synchronous hatch in the Indian flapshell turtle (*Lissemys punctata*, Vijaya, 1983) and the pig-nosed turtle (*Carettochelys insculpta*, Doody et al., 2012). Experiments at Perth Zoo (unpublished data) have demonstrated that eggs of the Western swamp tortoise (*Pseudemydura* *umbrina*) have higher chances of hatching when exposed to constant vibrations during incubation, although hatching is asynchronous. In a natural context, the pig-nosed turtle synchronises hatch when the nest gets flooded and embryos experience hypoxia (Doody et al., 2012). The embryos go through a developmental arrest until the rainy season, when conditions are more suitable (Doody et al., 2012). Although embryos of this species have never been sound recorded, our analysis indicates them to be most likely non-vocal, based on its distribution in the PCA.

We did not detect any sounds in the recordings from clutches of the chicken turtle (*Deirochelys reticularia*) or the Eastern mud turtle (*Kinosternon subrubrum*). Both species hatch asynchronously and go through diapause (embryological arrest) during incubation (Ewert, 1991; Horne, 2007. Observations from captive breeding suggests that species that go through diapause rarely synchronise hatching (P. Praschag, personal observation), which could at least partially explain the lack of vocalisations.

Shorter incubation time (2.5 months or less), with no diapause, is a characteristic in common to all species known to vocalise from within the egg. The Chinese softshell turtle (*Pelodiscus sinensis*), the turtle species with the shortest incubation period (Kuchling, 1999) and known to synchronize hatch (seemingly based on external temperatures, Zhu et al., 2023), was grouped within the known vocal species in our analysis. In contrast, the common Australian snake-necked turtle (*Chelodina longicollis*), that can have incubation periods of 2.5 years (Cann, 1998), was plotted in the opposite side of the graph. Curiously, studies focused on this species reached opposite conclusions regarding the presence of synchronous hatching (Spencer, 2012; McGlashan et al., 2015).

Some species of snake-necked turtles and mud turtles go through diapause and long incubation periods, although this occurs in the minority of the species in these distantly related genera (Kennett et al., 1993; Booth, 2002; Horne, 2007). A comparative study on synchronous and acoustic behaviour including species with different ecological traits can help elucidating this matter. Besides turtles, chameleons are the only reptile group in which post-laying true embryonic diapause is known to exist in some species (Ewert, 1991). Like turtles, chameleons display a great diversity of breeding strategies, sometimes exhibiting synchronous hatching and/or nest emergence. This, together with the recurrent discoveries of “mute” species vocalizing, makes chameleon eggs a potential valuable comparative model in which to study prehatch sounds and synchronous behavior in reptiles.

Interpreting results from species-specific studies in a phylogenetic perspective can be insightful, but the current widespread absence of data can only lead to preliminary conclusions. The presence of synchronous hatching in two distantly related species (*Chrysemys picta*, Cryptodira, and *Emydura mcquarii*, Pleurodira) has been used as an argument to propose the plesiomorphy of this trait (Colbert et al., 2010; Mcglasham et al., 2012). The same authors suggested that the potential ubiquity of synchronous behaviour could explain why the painted turtle (*Chysemys picta*) synchronises hatch although hatchlings overwinter in the nest. The same rationale can be applied to the apparent lack of influence that sounds have over synchronous pipping in the snapping turtle (Lacroix et al., 2022). However, our ancestral state reconstruction analysis had no resolution, recovering equal probabilities for all proposed states from both traits in most tree nodes. With the current state of knowledge about synchronous hatch and acoustic behaviour in turtles, it is not possible to infer their ancestral states and, therefore, the homology of these behaviours remains contentious.

Nevertheless, our findings bring new insights about the evolution of synchronous and acoustic behaviours. The production of sounds by embryos of *Batagur baska* can be interpreted as evidence of convergent evolution. Like in the case of sea turtles and podocnemidids, two distantly related groups with similar ecological traits, *B. baska* is a large bodied species that lays soft-shelled eggs in deep sand nests that incubate during a short period of time (~2 months). Differently from sea turtles and *Podocnemis*, *B. baska* did not synchronise hatch, with some of the eggs from our studied clutch hatching over 20 days apart from each other. We chose to be conservative and treat them as “apparently asynchronous” in our analysis, as there are no published accounts on their behaviour either in the wild or in captivity. Nevertheless, clutches incubated in captivity at the Project Batagur, ran by the Bangladesh Forest Department, hatch within one day (P. Praschag personal observation).

Based on studies that hypothesize that synchrony is an adaptative behaviour that promotes social facilitation by sharing the costs of digging (Rusli et al., 2016a, 2016b), Field et al. (2021) proposed that nest depth influences synchrony in nest emergence. Nest depth can potentially induce asynchronous hatching in species that most often show synchronous hatching (Field et al., 2021) as a consequence of a disparity in developmental stages caused by exposure to different temperatures during the incubation period and the time required to dig out of the nest (*e.g.*, *Chrysemys picta* and *Caretta carta*; Houghton and Hays, 2001; Field et al., 2021). The high degree of nest emergence synchrony observed in some podocnemidids opposed to *B. baska* and some sea turtles (Houghton and Hays, 2001; Rusli and Booth, 2016), may be associated to additional environment cues. Rain induces nest emergence in *Podocnemis expansa* (Simoncini et al., 2022) – which could additionally be classified as environmental synchrony (Doody, 2011).

Shallow or exposed nests and hard-shelled eggs of turtles like *Chitra indica, Pseudemydura umbrina* and *Kinosternon subrurbum*, recorded in the present study, may help explaining the absence of vocalisations. Temperature gradients do not change as much in shallow nests and hatching does not seem to be coordinated. Furthermore, these species do not need to invest as much effort in nest emergence as species with deep nests. Many species with small clutches hatch and emerge from nest individually (*e.g.*, *Terrapene ornata* and *Malaclemys terrapin*; Baker et al., 2013), making cooperative digging less important. Additionally, the costs associated to sound production would select for the disappearance of this behaviour in species that do not need to mediate any behaviour – especially in species with single-egged clutches like the twist-neck turtle (*Platemys platicephala*) or the pancake tortoise (*Malacochersus tornieri*). The presence of sounds and synchronous hatching in species such as *Graptemys ouachitensis* (Geller and Casper, 2019a) challenges this hypothesis. More species need to be recorded to clarify how much some of the traits selected in this study are correlated to sound production and hatching synchrony.

Traits associated to breeding in turtles, such as clutch size, nest depth, eggshell microstructures, egg arrested diapause and synchronous hatching behaviour seem to have evolved convergently and recurrently in the evolutionary history of the group (Ewert, 1991; Horne, 2007; Jorgewich-Cohen et al., 2022a). Some of these traits seem to be correlated, suggesting convergent evolution selected by similar ecological conditions (Jorgewich-Cohen et al., 2022a). Likewise, synchronous hatching behaviour seems to have evolved several times in association with species-specific ecological characteristics. Different types of synchronous behaviours probably have different selective pressures and evolutionary histories, with similar modalities potentially being convergent in different lineages.

Within-nest vocalisations could have a similar evolutionary pattern to the one observed in synchronous behaviour, potentially having evolved in association. Nevertheless, there is some evidence suggesting embryo sounds are most likely a plesiomorphic trait, as within-egg vocalisations being widespread in archosaurs and some squamates. Conversely, our phylogenetic distance analysis did not show any patterns based on the phylogenetic distribution of the studied species. This could be an artefact of the limited sample size, or it may indicate that there is no evolutionary pattern associated to such sounds. In the latter case, it can represent both a case of conservative behaviour or a case of strong convergence. Both scenarios rely on the assumption that strong selective pressures (e.g., predation) would maintain or develop similar behaviours in distant lineages. Considering our findings, it seems most parsimonious to interpret both within-egg and synchronous behaviours as traits that converged among lineages with similar ecologies. Understanding the mechanisms that mediate synchronous hatching behaviours may help elucidating this mystery.

Conclusions

Communication is central to group mediation and sociality. There are many social behaviours expressed by turtles during development, from embryo to nest emergence, that could be mediated by acoustic signals. Synchronous hatching behaviour might not necessarily be coordinated by sounds in every species – as seems to be the case in *Chelydra serpentina* (Lacroix et al., 2022) – but may be important for others. It is crucial that more experiments are conducted combining synchrony and acoustic tests, so we can have a clearer understanding of the patterns in which these behaviours are associated. Moreover, future work should aim to understand the behavioural patterns of synchronous embryonic development, hatching, dig, nest emergence, and dispersal as separate ecological events, as sounds might be used to mediate one of these behaviours but not the other.

References

Araya-Salas, M., & Smith-Vidaurre, G. (2017). warbleR: An R package to streamline analysis of animal acoustic signals. Methods in Ecology and Evolution, 8(2), 184-191.

Arnold, S.J. and Wassersug, R.J., 1978. Differential predation on metamorphic anurans by garter snakes (*Thamnophis*): social behavior as a possible defense. Ecology, 59(5), pp.1014-1022.

Aubret, F., Blanvillain, G., Bignon, F. and Kok, P.J., 2016. Heartbeat, embryo communication and hatching synchrony in snake eggs. Scientific Reports, 6(1), p.23519.

Baker, P.J., Costanzo, J.P., Iverson, J.B. and Lee Jr, R.E., 2013. Seasonality and interspecific and intraspecific asynchrony in emergence from the nest by hatchling freshwater turtles. Canadian Journal of Zoology, 91(7), pp.451-461.

Barrett, S.L. and Humphrey, J.A., 1986. Agonistic interactions between *Gopherus agassizii* (Testudinidae) and *Heloderma suspectum* (Helodermatidae). The Southwestern Naturalist, 31(2), pp.261-263.

Bista, B. and Valenzuela, N., 2020. Turtle insights into the evolution of the reptilian karyotype and the genomic architecture of sex determination. Genes, 11(4), p.416.

Bock, B.C., Cardona, A.J.R., María, M.A.S., and Páez, V.P., 2022. hatching synchrony in the Magdalena River turtle (*Podocnemis lewyana*). Annals of the 20th Annual Symposium on the Conservation & Biology of Tortoises & Freshwater Turtles, Tucson, Arizona.

Bonnaterre, P.J., 1789. Encyclopédie méthodique ou par ordre de matières: Tableau encyclopédique des trois règnes de la nature. Cetologie, erpétologie, ophiologie. chez Panckoucke.

Booth, D. T. 2002. The breaking of diapause in embryonic broad-shelled turtle, *Chelodina expansa* (Testudinata: Chelidae), at different temperatures: effects on pattern of oxygen consumption and hatchling morphology. Australian Journal of Zoology 48:369-378.

Brua, R.B., Nuechterlein, G.L. and Buitron, D., 1996. Vocal response of eared grebe embryos to egg cooling and egg turning. The Auk, 113(3), pp.525-533.

Brua, R.B., 2002. Parent-embryo interactions. Oxford Ornithology Series, 13, pp.88-99.

Cann, J., 1998. Australian freshwater turtles. Beaumont Pub..

Colbert, P.L., Spencer, R.J. and Janzen, F.J., 2010. Mechanism and cost of synchronous hatching. Functional Ecology, 24(1), pp.112-121.

Colombelli-Négrel, D., Hauber, M.E., Evans, C., Katsis, A.C., Brouwer, L., Adreani, N.M. and Kleindorfer, S., 2021. Prenatal auditory learning in avian vocal learners and non-learners. Philosophical Transactions of the Royal Society B, 376(1836), p.20200247.

Deecke, V.B., Ford, J.K. and Slater, P.J., 2005. The vocal behaviour of mammal-eating killer whales: communicating with costly calls. Animal Behaviour, 69(2), pp.395-405.

Del Río, J.S., 2022. Comunicación acústica em la prinera etapa de vida de la tortuga del río Magdalena: *Podocnemis lewyana*. Revista Latinoamericana de Herpetología, 5(2), pp.127-131.

Doody, J.S., 2011. Environmentally cued hatching in reptiles. Integrative and Comparative Biology, 51(1), pp.49-61.

Doody, J.S., Stewart, B., Camacho, C. and Christian, K., 2012. Good vibrations? Sibling embryos expedite hatching in a turtle. Animal Behaviour, 83(3), pp.645-651.

Doody, J.S., Dinets, V. and Burghardt, G.M., 2021. The secret social lives of reptiles. JHU Press.

Eggleston, R., Viloria, N., Delgado, S., Mata, A., Guerrero, H.Y., Kline, R.J., Beissinger, S.R. and Berg, K.S., 2022. Vocal babbling in a wild parrot shows life history and endocrine affinities with human infants. Proceedings of the Royal Society B, 289(1976), p.20220592.

Endo, J. and Numata, H., 2020. Synchronized hatching as a possible strategy to avoid sibling cannibalism in stink bugs. Behavioral Ecology and Sociobiology, 74, pp.1-10.

Ewert, M.A., 1991. Cold torpor, diapause, delayed hatching and aestivation in reptiles and birds. Egg incubation: its effects on embryonic development in birds and reptiles, pp.173-191.

Ferguson, M.W.J., 1985. In Biology of the Reptilia Vol. 14 (ed C. Gans) 329-491.

Ferrara, C. R., Vogt, R. C., and Sousa-Lima, R. S. 2012. Turtle vocalizations as the first evidence of posthatching parental care in Chelonians. J. Comp. Psychol. 127(1):24-32.

Ferrara, C.R., Vogt, R.C., Giles, J.C. and Kuchling, G., 2013. Chelonian vocal communication. In Biocommunication of animals (pp. 261-274). Dordrecht: Springer Netherlands.

Ferrara, C.R., Mortimer, J.A. and Vogt, R.C., 2014a. First evidence that hatchlings of *Chelonia mydas* emit sounds. Copeia, 2014(2), pp.245-247.

Ferrara, C. R., Vogt, R C., Harfush, M. R., Sousa-Lima, R. S., Albavera, E., and Tavera A. 2014b. First evidence of Leatherback Turtle (*Dermochelys coriacea*) embryos and hatchlings emitting sounds. Chelonian Conserv. Biol. 13(1):110- 114.

Ferrara, C.R., Vogt, R.C., Sousa-Lima, R.S., Lenz, A. and Morales-Mávil, J.E., 2019. Sound communication in embryos and hatchlings of *Lepidochelys kempii*. Chelonian Conservation and Biology: Celebrating 25 Years as the World's Turtle and Tortoise Journal, 18(2), pp.279-283.

Field, A., McGlashan, J.K. and Salmon, M., 2021. Evidence for synchronous hatching in marine turtle (*Caretta caretta*) embryos and its influence on the timing of nest emergence. Chelonian Conservation and Biology, 20(2), pp.173-183.

Geller, G.A. and Casper, G.S., 2019a. Late term embryos and hatchlings of Ouachita Map Turtles (*Graptemys ouachitensis*) make sounds within the nest. Herpetological Review, 50(3), pp.449-452.

Geller, G.A., Casper, G.S., 2019b. Chelydra serpentina (Snapping Turtle). Hatchling sounds. Herpetological Review 50: 768−769.

Geller, G.A. and Casper, G.S., 2023. Sound production by late-term embryos and hatchlings of the Spiny Softshell Turtle, *Apalone spinifera* (LeSueur, 1827), before nest exit. Herpetology Notes, 16, pp.483-491.

Goodale, E., Ruxton, G.D. and Beauchamp, G., 2019. Predator eavesdropping in a mixed-species environment: how prey species may use grouping, confusion, and the cocktail party effect to reduce predator detection. Frontiers in Ecology and Evolution, 7, p.141.

Gray, J.E., 1831. A synopsis of the species of the class Reptilia. Whittaker, Treacher, and Company.

Hays, G.C., Speakman, J.R. and Hayes, J.P., 1992. The pattern of emergence by loggerhead turtle (*Caretta caretta*) hatchlings on Cephalonia, Greece. Herpetologica, pp.396-401.

Horne, B.D., 2007. The ecology of developmental timing in a neotropical turtle, *Kinosternon leucostomum* (Doctoral dissertation, Ohio University).

Houghton, J.D.R. and Hays, G.C., 2001. Asynchronous emergence by loggerhead turtle (*Caretta caretta*) hatchlings. Naturwissenschaften, 88, pp.133-136.

Ims, R.A., 1990. On the adaptive value of reproductive synchrony as a predator-swamping strategy. The American Naturalist, 136(4), pp.485-498.

Iverson, J.B., 1990. Nesting and parental care in the mud turtle, *Kinosternon flavescens*. Canadian Journal of Zoology, 68(2), pp.230-233.

Jarrett, B.J., Rebar, D., Haynes, H.B., Leaf, M.R., Halliwell, C., Kemp, R. and Kilner, R.M., 2018. Adaptive evolution of synchronous egg-hatching in compensation for the loss of parental care. Proceedings of the Royal Society B, 285(1885), p.20181452.

Jorgewich-Cohen, G., Henrique, R.S., Dias, P.H. and Sánchez-Villagra, M.R., 2022a. The evolution of reproductive strategies in turtles. PeerJ, 10, p.e13014.

Jorgewich-Cohen, G., Townsend, S.W., Padovese, L.R., Klein, N., Praschag, P., Ferrara, C.R., Ettmar, S., Menezes, S., Varani, A.P., Serano, J. and Sánchez-Villagra, M.R., 2022b. Common evolutionary origin of acoustic communication in choanate vertebrates. Nature Communications, 13(1), p.6089.

Joyce, W.G., Anquetin, J., Cadena, E.A., Claude, J., Danilov, I.G., Evers, S.W., Ferreira, G.S., Gentry, A.D., Georgalis, G.L., Lyson, T.R. and Pérez-García, A., 2021.

A nomenclature for fossil and living turtles using phylogenetically defined clade names. Swiss Journal of Palaeontology, 140(1), pp.1-45.

Katsis, A.C., Davies, M.H., Buchanan, K.L., Kleindorfer, S., Hauber, M.E. and Mariette, M.M., 2018. Prenatal exposure to incubation calls affects song learning in the zebra finch. Scientific reports, 8(1), p.15232.

Kennett, R., A. Georges, and M. Palmer-Allen. 1993. Early developmental arrest during immersion of eggs of a tropical freshwater turtle, *Chelodina rugosa*. (Testudinata: Chelidae), from Northern Australia. Australian Journal of Zoology 41:37-45.

Kuchling, G., 1999. The reproductive biology of the Chelonia (Vol. 38). Springer Science & Business Media.

Lacroix, C., Davy, C.M. and Rollinson, N., 2022. Hatchling vocalizations and beneficial social interactions in subterranean nests of a widespread reptile. Animal Behaviour, 187, pp.233-244.

Latreille, P.A. 1802. In: C.N.S. Sonnini de Manoncourt and P.A. Latreille. Histoire Naturelle des Reptiles, avec Figures Déssinnées d'après Nature. Vol. 1. Détérville, Paris, xx + 280 p.

Magnusson, W.E., 1980. Hatching and creche formation by *Crocodylus porosus*. Copeia, 1980(2), pp.359-362.

Majoris, J.E., Francisco, F.A., Burns, C.M., Brandl, S.J., Warkentin, K.M. and Buston, P.M., 2022. Paternal care regulates the timing, synchrony and success of hatching in a coral reef fish. Proceedings of the Royal Society B, 289(1982), p.20221466.

Mariette, M. M. & Buchanan, K. L. (2016). Prenatal acoustic communication programs offspring for high posthatching temperatures in a songbird. Science 353, 812–814.

Mariette, M.M., Clayton, D.F. and Buchanan, K.L., 2021. Acoustic developmental programming: a mechanistic and evolutionary framework. Trends in Ecology & Evolution, 36(8), pp.722-736.

McGlashan, J.K., Spencer, R.J. and Old, J.M., 2012. Embryonic communication in the nest: metabolic responses of reptilian embryos to developmental rates of siblings. Proceedings of the Royal Society B: Biological Sciences, 279(1734), pp.1709-1715.

McGlashan, J.K., Loudon, F.K., Thompson, M.B. and Spencer, R.J., 2015. Hatching behavior of eastern long-necked turtles (*Chelodina longicollis*): The influence of asynchronous environments on embryonic heart rate and phenotype. Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology, 188, pp.58-64.

McGlashan, J.K., Thompson, M.B., Van Dyke, J.U. and Spencer, R.J., 2017. Thyroid hormones reduce incubation period without developmental or metabolic costs in Murray River short-necked turtles (*Emydura macquarii*). Physiological and Biochemical Zoology, 90(1), pp.34-46.

McGlashan, J.K., Thompson, M.B., Janzen, F.J. and Spencer, R.J., 2018. Environmentally induced phenotypic plasticity explains hatching synchrony in the freshwater turtle *Chrysemys picta*. Journal of Experimental Zoology Part A: Ecological and Integrative Physiology, 329(6-7), pp.362-372.

McKenna, L.N., Paladino, F.V., Tomillo, P.S. and Robinson, N.J., 2019. Do sea turtles vocalize to synchronize hatching or nest emergence?. Copeia, 107(1), pp.120-123.

Monteiro, C.C., Carmo, H.M., Santos, A.J., Corso, G. and Sousa-Lima, R.S., 2019. First record of bioacoustic emission in embryos and hatchlings of hawksbill sea turtles

(*Eretmochelys imbricata*). Chelonian Conservation and Biology: Celebrating 25 Years as the World's Turtle and Tortoise Journal, 18(2), pp.273-278.

Nishizawa, H., Hashimoto, Y., Rusli, M.U., Ichikawa, K. and Joseph, J., 2021. Sensing underground activity: diel digging activity pattern during nest escape by sea turtle hatchlings. Animal Behaviour, 177, pp.1-8.

Noguera, J.C. and Velando, A., 2019. Bird embryos perceive vibratory cues of predation risk from clutch mates. Nature ecology & evolution, 3(8), pp.1225-1232.

Paradis, E. and Schliep, K., 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, *35*(3), pp.526-528.

Pereira, A.G., Sterli, J., Moreira, F.R. and Schrago, C.G., 2017. Multilocus phylogeny and statistical biogeography clarify the evolutionary history of major lineages of turtles. Molecular Phylogenetics and Evolution, 113, pp.59-66.

R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Raven Pro 1.6. 4 (2023). Raven Pro: Interactive Sound Analysis Software (Version 1.6. 4) [Computer software]. Ithaca, NY: The Cornell Lab of Ornithology.

Revell, L.J., 2012. phytools: an R package for phylogenetic comparative biology (and other things). Methods in ecology and evolution, (2), pp.217-223.

Riley, J.L., Hudson, S., Frenette-Ling, C. and Davy, C.M., 2020. All together now! Hatching synchrony in freshwater turtles. Behavioral Ecology and Sociobiology, 74, pp.1-15.

Rusli, M.U. and Booth, D.T., 2016. Bigger clutch sizes save offspring energy during nest escapes. Behavioral Ecology and Sociobiology, 70, pp.607-616.

Rusli, M.U., Booth, D.T. and Joseph, J., 2016. Synchronous activity lowers the energetic cost of nest escape for sea turtle hatchlings. Journal of Experimental Biology, 219(10), pp.1505-1513.

Santos, R.G., Pinheiro, H.T., Martins, A.S., Riul, P., Bruno, S.C., Janzen, F.J. and Ioannou, C.C., 2016. The anti-predator role of within-nest emergence synchrony in sea turtle hatchlings. Proceedings of the Royal Society B: Biological Sciences, 283(1834), p.20160697.

Schweigger, A.F., 1812. Prodromns monographiae Cheloniorum auctore Schweigger. Regiomonti. Academia Albertina (KONIGSBERG, East Prussia).

Siebenrock, F., 1901. Beschreibung einer neuen Schildkrötengattung aus der Familie Chelydidae aus Australien: *Pseudemydura*. Anzeiger der Akademischen Wissenschaften Wien, 38, pp.248-251.

Simoncini, M.S., de Sousa, H.C., Gonçalves Portelinha, T.C., Falcon, G.B., Collicchio, E., Machado Balestra, R.A., Ferreira Luz, V.L., Colli, G.R. and Malvasio, A., 2022. Hydrological Effects on the Reproduction of the Giant South American River Turtle *Podocnemis expansa* (Testudines: Podocnemididae). Ichthyology & Herpetology, 110(3), pp.547-560.

Spencer, R.J., Thompson, M.B. and Banks, P.B., 2001. Hatch or wait? A dilemma in reptilian incubation. Oikos, 93(3), pp.401-406.

Spencer, R.J. and Janzen, F.J., 2011. Hatching behavior in turtles. Integrative and Comparative Biology, 51(1), pp.100-110.

Spencer, R.J., 2012. Embryonic heart rate and hatching behavior of a solitary nesting turtle. Journal of Zoology, 287(3), pp.169-174

Ter Haar, S.M., Fernandez, A.A., Gratier, M., Knörnschild, M., Levelt, C., Moore, R.K., Vellema, M., Wang, X. and Oller, D.K., 2021. Cross-species parallels in babbling: animals and algorithms. Philosophical Transactions of the Royal Society B, 376(1836), p.20200239.

Tucker, J.K., Paukstis, G.L. and Janzen, F.J., 2008. Does predator swamping promote synchronous emergence of turtle hatchlings among nests?. Behavioral Ecology, 19(1), pp.35-40.

Vergne, A.L., Avril, A., Martin, S. and Mathevon, N., 2007. Parent–offspring communication in the Nile crocodile *Crocodylus niloticus*: do newborns' calls show an individual signature?. Naturwissenschaften, 94, pp.49-54.

Vergne, A.L. and Mathevon, N., 2008. Crocodile egg sounds signal hatching time. Current Biology, 18(12), pp.R513-R514.

Vijaya, J., 1983. Auditory cues as possible stimuli for hatching eggs of the flap-shell turtle *Lissemys punctata granosa*. Hamadryad, 8(1), p.23.

Warkentin, K.M., 2011. Plasticity of hatching in amphibians: evolution, trade-offs, cues and mechanisms. Integrative and comparative biology, 51(1), pp.111-127.

Węgrzyn, E., Węgrzyn, W. and Leniowski, K., 2023. Hatching asynchrony as a parental reproductive strategy in birds: a review of causes and consequences. Journal of Ornithology, pp.1-21.