

Turtle Vocalizations as the First Evidence of Posthatching Parental Care in Chelonians

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Until recently, freshwater turtles were thought to be silent reptiles, neither vocalizing nor hearing very well. We recorded individuals in nature, captivity, and during interactions between adults and hatchlings and show that hatchlings and adult turtles, *Podocnemis expansa*, produce sounds in and out of the water. Sounds were emitted by hatchlings inside the egg, in open nests, in the river, and in captive conditions. Adult females were recorded producing sounds in the river, while basking, while nesting, and in captivity. Females were recorded in the river approaching and responding to hatchling sounds. We detected 2,122 sounds, classified in 11 different types. These data suggest that there is sound communication between adults and hatchlings and that these sounds may be used to congregate hatchlings with adults for mass migration. Hatchlings and females with transmitters were found migrating together. We consider these findings as the first evidence of acoustic communication mediating posthatching parental care in chelonians. We anticipate that our findings will influence the way turtle behavior is studied and interpreted, and add communication and sound pollution to turtle conservation concerns.

Keywords: turtles, sound, parental care, giant South American river turtle, *Podocnemis expansa*

Many tortoise species (38) are known to emit sounds during courtship and mating (Auffenberg, 1977; Campbell & Evans, 1967; Campbell, 1973; Frazier & Peters, 1981; Sacchi, Galeotti, & Fasola, 2003; Galeotti, Sacchi, Fasola, & Ballasina, 2005; Galeotti et al., 2005). Most of these published reports of tortoise vocaliza-

tions were serendipitous encounters. Some recordings were made during courtship and nesting of *Gopherus agassizii*, *Chelonoidis carbonaria* (Campbell & Evans, 1967), *Astrochelys radiata* (Auffenberg, 1978), *Chelonoidis elephantopus* (Jackson & Awbrey, 1972), *Testudo hermani*, and *Testudo marginata* (Galeotti, Sacchi, Fasola, & Ballasina, 2005; Sacchi et al., 2003). There is a lack of information regarding how these sounds are produced or how they function (Berry & Shine, 1980; Olsson & Madsen, 1998).

There are fewer studies documenting sound production in aquatic turtles. The marine leatherback turtle *Dermochelys coriacea* has been reported to be producing sounds (Mrosovsky, 1972). Cook and Forrest (2005) noted that this species produces three types of sound when it is out of the water.

The lack of information about sound production in freshwater turtles may be derived from early assumptions that turtles had poor hearing sensitivity, “deaf as a post” (Pope, 1955). However it has long been known that turtles have good sound sensitivity under 1 kHz (Campbell & Evans, 1967; Wever, 1978). Another misleading assumption about turtles is that aquatic species are silent. *Platysternon megacephalum* young have been reported to “squeal” and (Campbell & Evans, 1972), but no studies followed up on this report. Giles (2005) conducted the first detailed and comprehensive study of underwater sound production of a freshwater turtle species, *Chelodina oblonga*. Adults of this species were shown to have 17 categories of sound, including pulses of complex sounds with harmonic elements and frequency bands with or without modulation. (Giles, McCauley, & Kuchling, 2009).

There is no published information about turtle hatchlings producing sounds. However, it is well known that hatchling crocodilians are quite vocal, even vocalizing in the egg before they hatch. Lee (1968) observed communication among crocodilians inside eggs within a nest. He suggested that the prehatching grunting

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served to coordinate and synchronize hatching, protecting young crocodiles from missing the period when the mother opens the nest. Hatching too early may cause individuals to suffocate, and too late, to be subject to predation. Hatchlings might also emit sounds to solicit parental care. The behavior of offspring soliciting parental care using sounds has been described in elegant detail by Herzog and Burghardt (1977) and Vergne and Mathevon (2008). Young birds and crocodiles vocalize before and after hatching (Campbell, 1973; Magnusson, 1980; Vince, 1968). These vocalizations are thought to synchronize the timing of hatching (Vergne & Mathevon, 2008; Vince, 1968) and, in some crocodile species, sounds are emitted to elicit female approach to help open the nest (Vergne & Mathevon, 2008). Sound emission is considered critical to the survival of the young in some species (Magnusson, 1980), because females respond to these sounds during the first few days after hatching, their presence possibly diminishing predation (Stanton, 1978), which can be considered posthatching parental care.

Chelonian posthatching parental care has never been described, but prehatching parental care includes nest-site choice by females (Bernardo, 1996; St. Justin, Bowden, & Janzen, 2004; Roosenburg, 1996), since the nest-site location has a direct influence on the incubation characteristics for the eggs, which subsequently has a direct relationship to the survivorship and quality of the offspring produced, and in many species, their sex. The females of two terrestrial species of tortoises have been noticed to defend their nests against intruders *Monouria emys* (Kuchling, 1998), and in *Gopherus agassizii*, against a potential known egg predator, the Gila monster (*Heloderma suspectum*; Barrent & Humphery, 1986). Additionally, Iverson (1990) suggested that since female mud turtles (*Kinostemon flavescens*) bury into sand hills to deposit their eggs and remain near the eggs for up to 38 days, this could be called parental care, though it is unclear what care the turtle would be giving other than its presence. However, a more plausible instance of parental care was described for the chopotil (*Claudius angustatus*) in Mexico, where three gravid females were found aestivating in hard packed soil, with their eggs beneath them. Because this species has a sharp beak and pugnacious demeanor, it could, in fact, ward off small predators such as snakes and rodents (Espejel Gonzáles, Vogt, & Lopez Luna, 1998). The variable amount of energy invested in the embryo by the female in the form of lipids and size of the egg has also been suggested by some authors to be a form of prehatching parental investment or parental care (Congdon, 1989).

Our goal in this study was to report the first evidence of sound production in adult and hatchling giant South American river turtles (*Podocnemis expansa*), and to describe the acoustic characteristics and contexts of sound production to support our speculative hypotheses that sounds may mediate coordination of hatching as well as posthatching parental care. Our study differs from previous investigations (Giles, 2005; Giles et al., 2009) in that we recorded adult and hatchling turtles in both nature and in captivity, followed the movements of individuals, and know in what behavioral contexts sounds were produced so that we could verify the possible social interaction of adult females and recently hatched turtles. Recording contexts included: hatchlings inside open nests, in the river, and in captive conditions, adults in the river, and in captivity, and also interactions between adult and hatchlings, both in captivity and in the wild. We anticipate that our findings will greatly influence the way turtle behavior is studied and interpreted,

and add vocal communication and sound pollution to turtle conservation concerns.

Nesting Behavior of the Giant South American River Turtle

Podocnemis expansa occurs in most of the Amazon River Basin (Smith, 1974; Vogt, 2008), where, during the dry season, they migrate to specific areas of high beaches with coarse sand in which to nest (Alho & Pádua, 1982; Ojasti, 1967; Vogt, 2008). The nesting period depends on local river cycles; for example, in the Araguaya River, it happens between August and September (Vogt, 2008), in the Trombetas River, between September and October (Alho & Pádua, 1982; Pádua, 1981; Vogt, 2008), in the Guapore River, in August, and in the Rio Branco, in December–January (Vogt, 2008).

A few weeks before nesting, females group in front of the nesting beaches and come out of the water to bask communally (Alho & Pádua, 1982; Pádua, 1981), increasing their body temperature to accelerate ovulation (Vogt, 1980). At the time of egg laying, females come out of the water in cohesive groups, often hundreds at the same time, crawling the beach looking for a suitable nesting site. After females have nested, they return to the water and remain in groups in front of the beach in deep parts of the river for up to two months (which coincides with the rising of the waters and the hatching of their eggs) (Alho & Pádua, 1982; Pádua, 1981. Vogt, 2008). Females lay approximately 100 eggs once each year (Vanzolini, 1967, 2003). The incubation period varies from 36 to 75 days, depending on nest temperature (Ferreira, Jr., & Castro, 2003), and the sex of the hatchlings is determined by incubation temperature (Valenzuela, 1997, 2001; Vogt, 2008), males at low temperatures and females at high temperatures.

Method

We divided the recordings of the turtles according to age classes (adults and hatchlings) and to the location and context where they were recorded: both age classes isolated in captivity or in the wild, and during interactions between adults and hatchlings. We classified turtles as hatchlings up to one month after emergence from the nest.

Sound Recordings in Captivity

We recorded turtles in captivity to obtain a baseline of the sounds they were emitting, to help us adjust the recording equipment to be able to detect turtles vocalizing in nature. All sound recordings in captivity were made using a Fostex FR-2 digital recorder (Tokyo, Japan) initially set to a sampling frequency of 96 kHz, and a sample size of 24 bits. The underwater recordings were made with a Reson (TC4043; Goleta, CA) omnidirectional hydrophone with sensitivity of 2 Hz–100 kHz \pm 3 dB. Airborne sounds were recorded using a Sennheiser K6 unidirectional microphone with a Sennheiser ME-66 wind screen (Hanover, Germany). The system had a sensitivity of 40 Hz–20 kHz \pm 2.5 dB.

We recorded 10 2-hr sessions of three different groups of adult turtles, (2 groups of 3 ♀ and 1 ♂ and a group of 4 ♀ and 1 ♂) in fiberglass pools (2 × 1.5 × 0.5 m) between March and June, 2009 at the Instituto Nacional de Pesquisas da Amazônia (INPA;

Manaus, Brazil). Hatchlings isolated from adults were later recorded in November and December, 2009 and December, 2010 (with an adjusted sampling frequency of 48 kHz) in a concrete tank ($4 \times 2 \times 1$ m) at the facilities of the Trombetas River Biological Reserve (Pará, Brazil). Hatchlings were kept isolated for a month until released at the nesting beach where they hatched. The water and air temperatures varied from 27–32° C during 20 recording sessions. The number of hatchlings varied from 10 to 13,000 at any given 1-hr recording between 05:00 and 23:00 hours. During the recordings at the surface of the water, the microphone was positioned 15 cm above the water to capture the sounds as the heads of the hatchlings were breaking the surface.

Sound Recordings in Nature

Turtles in their natural habitat were recorded in the Trombetas River Biological Reserve, an area of 385,000 hectare (00°50′–01°50′ S; 56°17′–57°00′W) in northern Brazil. The Trombetas River is a clear-water tributary of the Amazon River in Oriximiná, State of Pará. This site was chosen because of the ongoing ecological study of this species being conducted there by one of us (RCV) since 1989, long enough that the movements and social activities of these turtles had been well documented in advance of this study to optimize the logistics of the collection of acoustic data.

Based on the preliminary recordings in captivity, the recorder was set to a sampling frequency of 48 kHz and a sample size of 24 bits for all recordings in the wild. We used the same microphones and hydrophones we used to record sounds in captivity, in addition to an Earthworks (M30) omnidirectional microphone (Milford, NH) of 5 Hz–30 kHz \pm 3 dB to record the hatchlings as they emerged from the nest and eggs.

Adult females were recorded in and out of the water. The underwater recordings were made in September and December, 2009 and between August, 2010 and January, 2011 in order to have recordings from the entire nesting period. During this period our underwater recording sessions lasted two hours and were accomplished by deploying the hydrophone 0.5 m from the bottom of the river (depths varied from 1.5 to 11 m) from a 6-m aluminum boat. During October and November, 2009, 12 adult females were recorded on the nesting beach. Each female was recorded for a maximum of 30 min during daytime hours, after being released on the nesting beach 200 m from the shoreline. The recording was accomplished by following the turtles on their way to the water from a distance of 5 m, with the microphone held at a height of 1 m.

Hatchling turtles were recorded in November and December, 2009 and December, 2010 on the nesting beaches, before hatching, and after hatching while still in the nest. We marked 48 natural nests on the beach with wooden stakes noting date of oviposition. After 36 days of incubation, the nests were opened for recording sessions. We recorded 7–101 eggs or hatchlings from each nest for 30 min.

Hatchlings kept in the tanks at the reserve were released periodically back into the wild. During three such releases, we also recorded vocalizations from 1,100 recently hatched turtles. Released hatchlings were recorded for two hours during two recording sessions in the lake, in areas where no adult females were noted to be present. Once we recorded hatchlings when adult females

were sighted in the water 4–5 m from the release site. (See the next section, “Sound recordings during interactions between adult females and hatchlings.”)

Sound Recordings During Interactions Between Adult Females and Hatchlings

We conducted experiments in nature, releasing over a thousand hatchlings in the river 4–5 m from adult females, and in captivity, recording an adult female in a plastic pool (1.8 m of diameter \times 0.5 m deep) with hatchlings. Three groups of 140 hatchlings with one adult female were recorded for one hour each as the adult was placed in the pool.

Monitoring Turtle Movements With Radio Telemetry

We attached VHF transmitters to three adult females and 10 hatchlings in December, 2009 and 2010. AVM MP2 transmitters (AVM Instrument Company, Colfax, CA) with a frequency of 165 MHz were attached to the carapaces of the turtles. Turtles were followed using a hand-held LA 12-Q receptor, with a 3-element Yagi antenna (AVM Instrument Company, Colfax, CA). When turtles with transmitters were located, the positions were registered with a Garmin GPSMAP 60Cx (Olathe, KS; for detailed description of telemetry methods, see Guillhon, Vogt, Schneider, & Ferrara, 2011).

Sound Analysis

We used the software Raven Pro 1.3 (Cornell Lab of Ornithology, Ithaca, NY) to generate spectrograms with a Hamming window type, and fast Fourier transform (FFT) window sizes, varying from 256 to 1024 samples, so we could identify the best spectrographic representation of each sound detection. Each sound detected in the recordings was analyzed (visual and aural inspections of spectrograms, waveforms, and frequency spectra) and categorized by two people independently. Detections with sufficiently high signal-to-noise ratio were then selected to characterize the sound repertoire by grouping them into categories for subsequent classification into sound types. Only those sounds that were not overlapping with other signals were selected for extraction of the acoustic parameters used to describe each type of sound in the repertoire. We measured six acoustic parameters: minimum and maximum frequencies (Hz), peak frequency (Hz), fundamental frequency (Hz), duration (s), and, number of inflection points.

Statistical Analysis

We used an analysis of variance (ANOVA) to test for differences in the peak frequency between the sounds emitted by different age classes, including all recording contexts and categories of sound. We used a contingency table to document the frequency of occurrence for each different type of sound recorded in each age class. A generalized linear model was used to fit the sound-detection counts (number of detections per minute) into a Poisson distribution to test for a correlation between number of detections and number of individuals recorded.

Results

Sound Repertoire

We detected 2,128 sounds in 380 h of recording, 468 emitted by adults and 1,660 by hatchlings. The lowest value recorded for peak frequency was 36.8 Hz and the highest was 4,500 Hz. The sounds were classified and categorized into 11 sound types, according to their aural and spectral characteristics (see Table 1 and Figure 1). The classification of sound types allows more detailed analyses of how each type of sound is used in different recording contexts.

Type I. Type I ($N = 47$) has harmonic but mostly nonharmonic frequency bands and is characterized by its high frequency (peak fundamental frequency ranged from 187.5 to 2,906.2 Hz). This sound was shorter (0.006 to 0.181 s) when compared with the other types.

Type II. Type II ($N = 404$) includes short (0.01 to 0.17 s), noisy sounds, with nonharmonic frequency bands (maybe formants) and a raspy aural quality. The peak fundamental frequency varied from 187.5 to 1,968.8 Hz.

Type III. Type III ($N = 1,361$) includes short sounds (0.006 to 0.54 s), with harmonic and nonharmonic frequency bands that may present little or no frequency modulation and a few inflection points (1 to 6). Aurally, this sound often has a tonal quality with some frequency modulation (ascending or descending). This sound is comprised of 1 to 4 notes (a continuous sound separated by a short silence) and 1 to 20 harmonics. Higher harmonics may be more intense than the fundamental frequency (peak values ranged from 93.8 to 2,531.2 Hz).

Type IV. Type IV ($N = 62$) includes very low-frequency sounds (peak frequency ranged from 93.8 to 281.2 Hz) with nonharmonic frequency bands having a mean duration of 0.16 s (0.05–0.37 s). This sound includes the lowest values for peak frequency among the signals recorded in the repertoire of hatchlings (36.8 to 284.2 Hz).

Type V. Type V ($N = 42$) is characterized by a series of short pulses lasting from 0.01 to 0.29 s and with mean peak frequency of 1,079.08 Hz. Some of these sounds have variable pulse-repetition rates, and when this rate increases along the signal, it may look like a harmonic series toward the end of the spectrogram,

with the harmonic interval equal to the pulse-repetition rate (Watkins, 1967).

Type VI. Type VI ($N = 86$) includes noisy sounds with harmonic and nonharmonic frequency-modulated bands with multiple inflection points ($0 - >20$). The peak frequency varied from 92 to 4,125 Hz and signal durations from 0.01 to 0.24 s. This sound may have up to 4 notes and up to 20 harmonics. Higher harmonics may be more intense than the fundamental frequency, which ranged from 89.6 to 2,295 Hz.

Type VII. Type VII ($N = 44$) includes more complex and longer sounds (0.02 to 0.6 s), with characteristics of both pulsed and complex sounds, and harmonic and nonharmonic frequency bands. This type of sound shows intermediate characteristics between sound Types V and VI. This hybrid sound in adults starts with frequency bands followed by pulses, and in hatchlings, pulses followed by frequency bands. The peak fundamental frequency of this sound varies between 187.5 and 1,406.2 Hz.

Type VIII. Type VIII ($N = 69$) are short sounds (0.01 to 0.38 s), with nonharmonic frequency bands and small frequency modulation that can be ascending or descending. Mean peak-frequency values are low (526.5 to 2,812.5 Hz).

Type IX. Type IX ($N = 33$) includes frequency-modulated sounds with harmonically related frequency bands. The number of inflection points per sound varies from 0 to 5. The peak frequency varied from 750 to 1,875 Hz. Compared with the other types of sound, this one was relatively long (0.071 to 0.837 s).

Type X. Type X ($N = 8$) comprises single-frequency tonal sounds with mean duration of 0.13 s (0.04 to 0.24 s).

Type XI. Type XI ($N = 2$) is characterized by a long series (0.23 to 0.49 s) of short pulses.

The vocal repertoires of *P. expansa* adults and hatchlings were similar in regard to the types of sounds; the repertoires of both age classes include signals with pulses, tonal sounds, harmonic series, and hybrid sounds. The Sound Types II, III, V, and VII were present in both age classes. Sound Types I, IV, and VI were recorded only in hatchlings. The Sounds VIII, IX, X, and XI were recorded only in adults (see Table 2). In general, peak frequencies of the adult sounds were lower than that of the hatchlings ($N = 1649$, $F = 48.55$, $R = 0.169$, $p < .001$). There were also differences in the frequency of

Table 1

Descriptive Statistics for the Acoustic Parameters of Each Type of Sound Produced by Podocnemis Expansa Hatchlings: Fast Fourier Transform 512

Type	Age	Context	Frequency minimum (Hz) 95% CI	Frequency high (Hz) 95% CI	Time (s) 95% CI	Peak frequency (Hz) 95% CI	Number of harmonics	Number of inflection points
I (47)	H	E, N, Air	638.78, 891.17	1708.63, 1800.07	0.03, 0.06	846.24, 1246.47	1	0
II (404)	A, H	E, N, Air, W	532.5, 625.22	4676.6, 5626.25	0.04, 0.05	998.49, 1153.5		
III (1361)	A, H	E, N, Air, W	611.92, 652.54	1850.59, 2002.05	0.05, 0.06	863.31, 918.11	1->20	1-6
IV (62)	H	E, N, Air	83.59, 110.59	501.8, 616.55	0.12, 0.19	188.64, 217.62		
V (42)	A, H	E, N, Air, W	285.64, 476.26	3369.09, 5809.38	0.07, 0.1	779.15, 1379.72		
VI (86)	H	E, N, Air, W	520.63, 682.6	3685.98, 5731.34	0.05, 0.08	1116.5, 1447.16	1->20	0->20
VII (44)	A, H	E, N, Air, W	207.11, 439.67	6491.37, 13534.05	0.14, 0.24	610.22, 1269.97	2->20	2->20
VIII (69)	A	Air, W	487.41, 611.11	1935.43, 2994.53	0.07, 0.09	1152.6, 1459.47		
IX (33)	A	Air, W	193.03, 204.97	1327.73, 1996.55	0.24, 0.36	558.95, 760.76	0-10	0-5
X (8)	A	Air, W	33.53, 153.27	388.97, 464.37	0.08, 0.18	179.82, 248.72		
XI (2)	A	Air	0, 0	815.11, 1374.79	0.11, 0.61	49.7, 606.6		

Note CI = confidence interval; H = hatchling; A = adult; E = egg; N = nest; Air = Air; W = water.

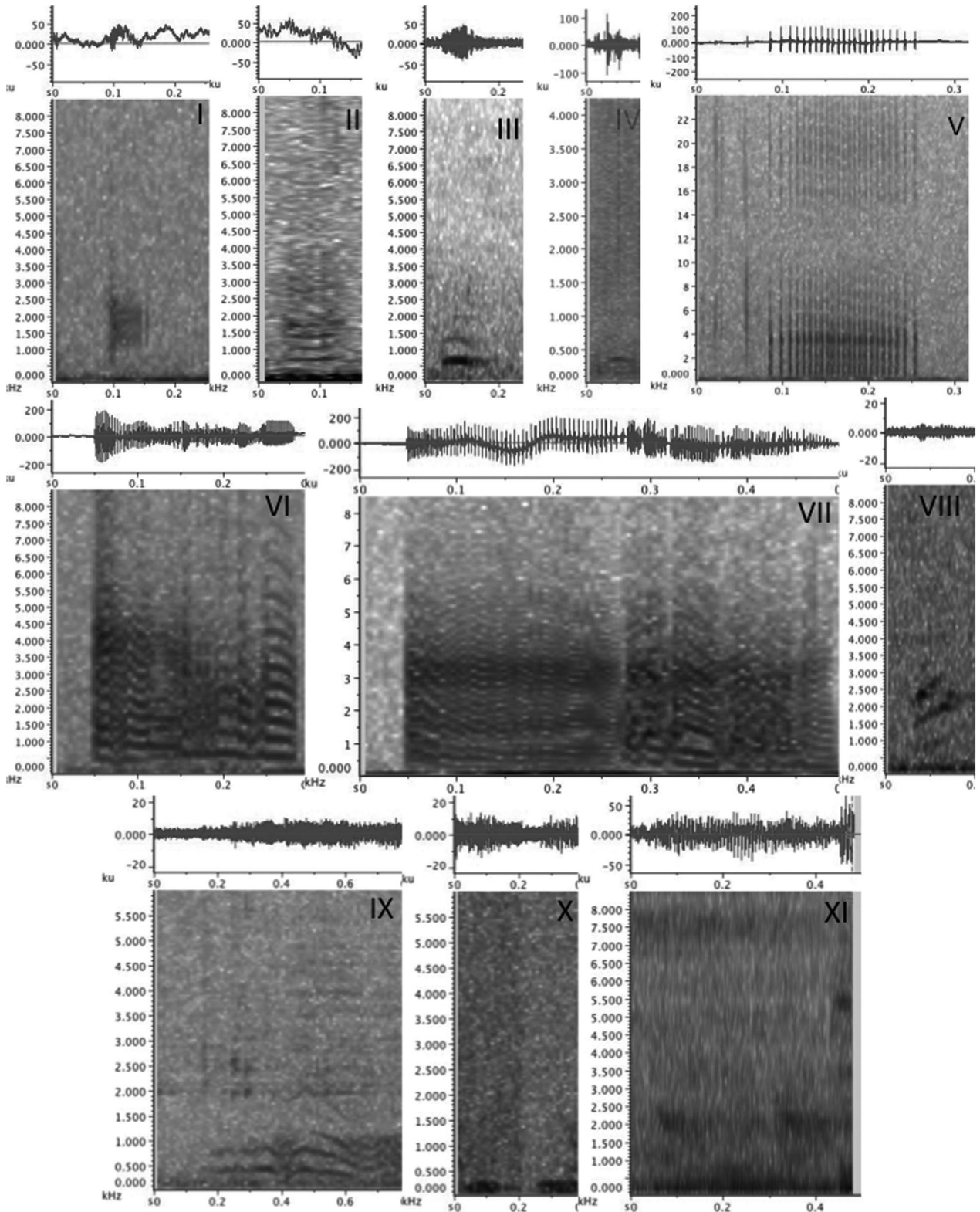


Figure 1. Waveform and spectrogram views of the sounds produced by *Podocnemis expansa*. We used different fast Fourier transform (FFT) window sizes to generate the spectrograms (512-pt FFT for Sound Types I, III, VI and VII; 1024-pt FFT for Sound Types II and IV, and 256-pt FFT for Type V). All spectrograms were done using Hamming windows. Note that IV.1 is an amplification of the frequency axis of Sound IV to improve signal visualization.

Table 2
Contingency Table of Occurrence of Each Type of Sound Recorded for Adult and Hatchling *Podocnemis Expansa*

Class/type	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	total
Adults	0	6	336	0	4	0	4	69	34	8	2	463
Hatchlings	47	394	987	64	37	90	20	0	0	0	0	1639
Total	47	400	1343	64	41	90	24	69	34	8	2	2122

occurrence of each type of sound between adults and hatchlings ($N = 2,122$, $df = 10$, $p < .0001$, Table 2).

Contexts of Sound Production

In captivity, upon introduction of an adult female into a tank with 140 hatchlings, most hatchlings moved toward the female, covering her and resting in her axial and inguinal cavities, on the neck, and all over the carapace while sounds were being recorded.

The late-term embryos recorded in the wild began to emit sounds 8 to 36 h before hatching. In captivity, we found a positive relationship between the number of sound detections per minute and the number of hatchlings ($N = 290$; $p < .0001$); that is, more sounds were emitted when more individuals were in a group. Hatchling sound-emission rate in captivity was low. The total number of detections divided by the total recording effort was equal to approximately 0.37 sounds/min.

During the experiments in which we released the hatchlings in the proximity of adult females, we identified sound types emitted by both hatchlings and adults (Sounds II, III, V, VII). Therefore, it is not possible to know which size class was recorded. However, because we recorded sounds at the same time, specific only to adults (VIII and IX), we presume that these were the sounds of females. In addition, we recorded Sound Type VI, which is specific to hatchlings, and some sounds recorded were louder near the hatchlings as they were released. The absence of adult recordings in the immediate vicinity suggests that these louder sounds were also emitted by hatchlings. After the release of the hatchlings, we recorded specific adult female sounds, suggesting that they may have been responding to the nearby hatchlings' sounds. Additionally, we observed females approaching the released hatchlings (the presumed sound source).

Turtle Movements

During the first three days after the release of the turtles with transmitters in 2009, we found three hatchlings with transmitters migrating with a group of *P. expansa* adults 2.5 km downstream from the release site. This was the last time these hatchlings were located; either they traveled out of range faster than expected, or transmitters stopped transmitting, or the turtles were consumed by a predator. In 2010, immediately after the release of the turtles we lost the signals of 11 hatchlings and one adult. One hatchling was located 3.8 km downstream with a pod of turtles, including the two females with transmitters.

Five days after the release of the turtles in 2010, one hatchling with a functioning transmitter was located with a mixed age group of *P. expansa*. This group was located 1.3 km downstream from the release site. The hatchling remained with this group of turtles

in the same area until the transmitter battery lost its charge 10 days after the release.

Discussion

We described a complex array of different vocalizations by the Amazon River turtle, which are clearly used to coordinate behavior among individuals. This is the first description of such behavior in chelonians. Our results also reveal that *P. expansa* vocalizes in all life-history stages, from the late stages of embryogenesis while still within the egg shell to adulthood, as is well-known in other vertebrates such as birds and crocodylians (Vince, 1968; Britton, 2001; Vergne, Avril, Martin, & Mathevon, 2007; Vergne, Pritz, & Mathevon, 2009). The peak frequencies of the sounds emitted by *P. expansa* varied from 36.8 to 4,500 Hz, which are consistent with the auditory sensitivity for the species (30 to 6,000 Hz, with peak sensitivity between 1,000 and 1,500 Hz; Wever, 1978).

We have used broad discrete categories (or sound types) to discriminate the vocalizations to show the variability of the repertoire and compare these data between adult and hatchling turtles. However, we have observed that the repertoire is not discrete and the sounds may have hybrid aural and spectral characteristics; that is, the sound types may merge into each other as part of a graded repertoire, which is a phenomenon that is also observed in other taxa (Fischer & Hammerschmidt, 2002; Hammerschmidt & Fischer, 1998; Mercado, Schneider, Pack, & Herman, 2010; Murray, Mercado, & Roitblat, 1998; Schott, 1975; Sousa-Lima, Paglia, & da Fonseca, 2008).

The vocal repertoire of *P. expansa* includes 11 different types of sound that vary from pulses and tonal sounds to more complex noisy signals with frequency-modulated harmonic and nonharmonic bands, and even "hybrid sounds." These types of sound have been observed in other species of aquatic and terrestrial turtles, such as *C. oblonga* (Giles, 2005; Giles, McCauley, & Kuchling, 2009), *Testudo marginata* (Sacchi, Galeotti, & Fasola, 2003), and *Platysternon megacephalum* (Campbell & Evans, 1972). Giles et al. (2009), described a polymorphic "chirp" of *C. oblonga* comprised of similar sounds, with some variation in the spectral nature within groupings. We have also observed this polymorphism in Sound Type III of *P. expansa*. The variability in the vocal behavior of *P. expansa* demonstrates that their acoustic repertoire is more extensive than that found in other reptiles in general (Britton, 2001; Frankenberg, 1982; Garrick & Garrick, 1978; Young, 2003), but not as extensive as that of other aquatic organisms that rely on acoustic communication, such as aquatic mammals (Serrano, 2001).

Differences in vocalizations between large and small individuals of the same species occur in many taxa (e.g., Sousa-Lima, Paglia, & da Fonseca, 2002, 2008), and turtles are no exception. Young A.

radiata produce vocalizations that are less distinct than those produced by adults (Auffenberg, 1978), and in *C. oblonga*, the vocalizations observed in a subadult were shorter than those in adult males (Giles, 2005). We noticed a difference in the types of vocalization and the structure of the sounds produced by *P. expansa* of different age classes. Adults produced eight types of sound and hatchlings seven. Sound Types I, IV, and VI were recorded exclusively in hatchlings, and Types VIII, IX, X, and XI, only in adults.

High-frequency sounds in birds and mammals have characteristics that influence receivers to approach the sender of the signal (Morton, 1977). In general, young individuals emit higher frequencies than adults of the same species (Morton, 1977). The peak frequency in adults was lower than in the hatchlings, and signal duration was longer for adults. Short repetitive sounds which have characteristics that begin and terminate abruptly, facilitate locating the producer of the sound by another individual (Gelfand & McCracken, 1986). Sound Types II, III and VIII of *P. expansa* have characteristics that would enable location of the sender and elicit approach of conspecifics. These types of sounds were the most common types recorded in the vocal repertoire of this species, appearing in almost all of the contexts and categories of behavior recorded. Sounds similar to these types of sound have also been found in the vocal repertoire of *C. oblonga*, birds, and crocodilians, and are recognized as “contact calls” (Vince, 1968; Britton, 2001; Marler & Slabbkoorn, 2004; Giles, 2005).

Sound detection was proportional to the number of hatchlings recorded; that is, bigger groups vocalize more often, which is consistent with our speculative hypothesis of predation dilution. Additionally, if we consider the maximum number of hatchlings recorded (13,000), the sound emission rate per individual is very low, suggesting that *P. expansa* hatchlings are not very vocal. Giles et al. (2009) also found a low rate of sound emission for *C. oblonga* adults. In light of this, we hypothesize that there might be conflicting selective pressures acting on the evolution of turtle hatchling acoustic behavior. Predation pressure would inhibit the evolution of frequent acoustic behavior, whereas increased survival of individuals soliciting parental care and/or migrating in acoustically synchronized groups may allow low levels of acoustic behavior to evolve.

Air- and water-borne sounds were emitted by hatchlings inside open nests, in the river, and in captive conditions. Adult females in the river were recorded responding to hatchling sounds and observed approaching the sound source. Individuals with transmitters (hatchlings and females) were found migrating together. Furthermore, postnesting migration of females was artificially induced in three different years by releasing 4,000 to 6,000 hatchlings into the water in the vicinity of the females (Vogt, 2008). The studies of the movements of *P. expansa* using VHF transmitters demonstrate that the females leave the area of the nesting beaches only after the eggs have hatched and the hatchlings enter the water, suggesting that the hatchlings migrate with a group of turtles, including females, males, and subadults, to the flooded forests.

We consider our findings to be the first evidence of acoustic communication mediating posthatching parental care in chelonians. We speculate that the turtle hatchling sounds may function to: (a) Synchronize hatching and induce communal digging

to help move the siblings toward the surface and out of the nest; (b) synchronize emergence from the nest to dilute the predation pressure during hatchling dispersion to water; and (c) solicit females to approach so that the hatchlings can be lead and accompanied by the females in their migration to the flooded forest.

Noise pollution from human activities, once thought to be irrelevant in turtle conservation, may now generate some concern. Noise produced by ships, boats, jet skis, and other motorized watercrafts may affect the reception of sound by turtles and potentially interfere with their communication, to such a degree that it has a negative effect on hatchling survivorship and adult communication. Concerns also arise in relation to current conservation strategies, which include maintenance of young individuals isolated in captivity after hatching (Andrade et al. (2005); Moreira et al. (2009); Noronha and Siveira (2009); Balestra et al. (2010). The lack of acoustic interaction between individuals might be jeopardizing important social interactions among females and hatchlings.

The fact that turtle vocalizations were not recognized until now is probably due to low emission rates, low pitch, and amplitude. Nonetheless, a quiet person can hear hatchling turtles vocalizing in an open nest without any amplification. We hope that our study will generate interest in the investigation of vocal communication in other taxa of turtles to better understand the occurrence and the evolutionary history of this behavioral trait. Knowing that turtles vocalize may help explain how hundreds of turtles are able to find communal hibernacula, migrate to nesting beaches or feeding areas, or form nesting arribadas. Turtles can no longer be classified within the silent majority of reptiles.

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Correction to Herrmann, Keupp, Hare, Vaish, and Tomasello (2012)

In the article “Direct and Indirect Reputation Formation in Nonhuman Great Apes and Human Children,” by Esther Herrmann, Stefanie Keupp, Brian Hare, Amrisha Vaish, and Michael Tomasello (*Journal of Comparative Psychology*, Advance online publication, July 2, 2012. doi:10.1037/a0028929), the title should have read “Direct and Indirect Reputation Formation in Nonhuman Great Apes (*Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, *Pongo pygmaeus*) and Human Children (*Homo sapiens*).” All versions of this article have been corrected.

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