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Seasonal Variation of Hearing Sensitivity in the Red-eared Slider (*Trachemys scripta elegans*)

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Abstract Seasonal variation of hearing sensitivity has been observed in many vertebrate groups with obvious vocal behaviors. Circulating hormones, conspecific calling signals, and temperature are potential factors that drive these plasticity patterns. Turtles have a hearing range that appears to be limited to under 1.5 kHz and are often thought to be non-vocal; thus, they are commonly neglected in vocal communication research. In this study, we aimed to determine whether the auditory phenotype exhibits seasonal variation in sensitivity and to analyze the potential factors driving such variation patterns in turtles. We measured hearing sensitivity and sex hormone levels in female (estradiol) and male (testosterone and dihydrotestosterone) Red-eared sliders (*Trachemys scripta elegans*) during spring and winter. The results showed that auditory brainstem response (ABR) thresholds were significantly lower in spring than in winter at a frequency range of 0.5–0.9 kHz. The hearing-sensitivity bandwidth was wider, and the ABR latency was significantly shorter in spring than in winter. No significant differences were found in estradiol, testosterone, and dihydrotestosterone levels in *T. scripta elegans* between spring and winter. This study is the first to reveal the seasonal variation of peripheral hearing sensitivity in turtles, a special animal group with limited hearing range and less vocalization. Temperature variations may be used to explain these seasonal effects, but further research is required to confirm our findings.

Keywords auditory plasticity, seasonal variation, temperature, turtles

1. Introduction

As an indispensable part of acoustic communication, an animal's auditory system plays an important role in many social behaviors (Gerhardt and Huber, 2002; Narins *et al*., 2006). The physiological state of an animal can affect the response of the peripheral and/or central auditory systems (Lucas *et al*., 2007; Arch and Narins, 2009; Miranda and Wilczynski, 2009; Zeyl *et al*., 2013). The seasonal variation of hearing sensitivity has been reported in many vertebrate groups with obvious vocal behaviors and a hearing range of at least > 1.0 kHz, such as fishes (Sisneros and Bass, 2003), frogs (Zhang *et al*., 2012; Yang *et al*., 2018), and birds (Lucas *et al*., 2002; Gall *et al*., 2013; Vélez *et al*., 2015). However, this change of auditory phenotype remains unclear in the animals with a hearing range < 1.5 kHz.

Several possible mechanisms have been used to explain seasonal auditory variation. Firstly, circulating hormones can alter the reception and processing of acoustic signals (Elkind-Hirsch *et al*., 1992; Sisneros *et al*., 2004; Al-Mana *et al*., 2008; Lynch and Wilczynski, 2008; Zeyl *et al*., 2013). Exogenous steroid hormones lead to plasticity in the amplitude of the auditory brainstem response (ABR) (Caras *et al*., 2010), and changes in auditory function are associated with sex steroid fluctuations and the reproductive stage (Maruska *et al*., 2012). Estradiol can affect the number and dynamics of hair cell ion channels (Zakon, 1998), thereby affecting the frequency-filtering properties of the auditory system because the rate of

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activation and deactivation of ion channels is a major determinant of hair cell resonance (Fettiplace and Fuchs, 1999). Changes in hormone levels also influence the electrical tuning of hair cells to modulate seasonal hearing plasticity (Henry *et al*., 2017). In addition, for some species, conspecific vocal calling signals can increase hearing sensitivity during the breeding season (Gall and Wilczynski, 2015). Finally, temperature affects the auditory system in several animal groups, and an increase in body temperature typically results in improved hearing sensitivity (Wysocki *et al*., 2009; Sun *et al*., 2019; Wang *et al*., 2022). Therefore, by exploring the relationship among circulating hormones, conspecific calling signals, temperature, and the auditory system of animals, the association between the external social environment and the internal physiological state can be revealed, providing insights into the most basic processes that underlie vertebrate social behavior.

Some species of the turtles have been reported to emit sounds for communication (Ferrara *et al*., 2014; Ferrara *et al*., 2017; Charrier *et al*., 2022; Zhou *et al*., 2022; Zhou *et al*., 2023), but their hearing sensitivity as well as the seasonal variation of hearing sensitivity and the potential underlying mechanisms remains poorly understood. The Red-eared slider (*Trachemys scripta elegans*) is a common and widely distributed seasonally breeding species (Ernst and Lovich, 2009). Generally, their mating occurs in spring temperatures of approximately 28.7 °C, when male turtles are more active and move greater distances than females, most likely in search of mating opportunities (Gibbons, 1990; Ma and Shi, 2017). Female *T. scripta elegans* dig nests and lay eggs predominantly from mid-April to mid-June, with the peak occurring from late April to late May in China when the temperature is over 30 °C (Li, 2013; Yang, 2014; Ma and Shi, 2017). Auditory research on *T. scripta elegans* revealed that their peripheral auditory sensitivity limits a range of sensitivity < 1.4 kHz, and is sexually dimorphic (Wang *et al*., 2019), more sensitive to sound underwater than in air (Christensen-Dalsgaard *et al*., 2012), develops earlier for low-frequency signals than for high-frequency signals during ontogenetic development (Wang *et al*., 2021), and is affected by temperature (Wang *et al*., 2022). Therefore, *T. scripta elegans* is an ideal model for studies on the seasonal variation of hearing sensitivity in animals with a limited hearing range and the potential factors driving these variation patterns.

In this study, we aimed to investigate whether seasonal variation affects the neurophysiological response properties of the auditory system of turtles and determine the potential factors driving these variation patterns. We used the ABR, a non-invasive and rapid method for measuring hearing sensitivity to obtain data on hearing range, ABR threshold, and ABR latency. Air temperature and plasma sex hormone levels (estradiol in females; testosterone and dihydrotestosterone in males) were also determined. We hypothesized that the hearing was more sensitive in spring than that in winter; the hormone levels or temperature variations may be used to explain these seasonal effects.

2. Materials and Methods

2.1. Animals collection and experimental design To investigate the seasonal variation of peripheral auditory sensitivity of *T. scripta elegans*, this study included females collected during spring at the end of May 2019 (body mass: 1 645.5 ± 93.0 g; carapace length: 224.43 ± 3.11 mm; n = 9) and winter in early January 2019 (body mass: 1 534.4 ± 181.3 g; carapace length: 220.42 ± 7.50 mm; n = 11) and males during the spring at the end of March 2019 (body mass: 986.5 ± 148.6 g; carapace length: 195.00 ± 16.20 mm; n = 10) and winter in early January 2019 (body mass: 1 056.5 ± 113.9 g; carapace length: 193.32 ± 7.57 mm; n = 10). Forty-four *T. scripta elegans* individuals were purchased from the same farm in the Hainan Province and were maintained in aquaria (length × width × height: 2.0 m × 1.0 m × 0.25 m; water depth: 0.15 m) prior to the experiments. All turtles were fed an artificial diet (5#; Dolphin Aquarium Co., Ltd., Guangdong, China) with ad libitum access. Eleven individuals of the same sex were maintained in each aquarium. The temperature under natural conditions was approximately 25–32 °C and 14–22 °C in spring and winter, respectively. The temperature during the electrophysiological tests was 32.5 ± 0.9 °C (female) and 28.9 ± 1.6 °C (male), and 19.3 ± 0.6 °C (female) and 19.4 ± 0.3 °C (male) of spring and winter, respectively. These temperatures were similar to that in previous studies during the same reproductive season of *T. scripta elegans* (Li, 2013; Yang, 2014; Ma and Shi, 2017).

2.2. Measurement of morphological data The body mass of the turtle was recorded using an electronic balance (0.1 g; SE-3001FZH; Ohaus Instrument Co., Ltd., Shanghai, China). Carapace length was measured using a Mitutoyo digital caliper (0.01 mm; 500-153; Mitutoyo Corp., Kawasaki-shi, Japan).

2.3. Animal anesthesia Before electrode placement, each turtle was deeply anesthetized to prevent movement and minimize adverse results during recording, as described by Wang *et al*. (2019, 2022). Briefly, a solution of 0.5% Pelltobarbitalum Natricum (CAS No.57-33-0, Xiya Reagents, Shandong, China) dissolved in 0.9% sodium chloride was administered via hindlimb intramuscular injection at an initial dose of 0.003 mL g^{-1}. Additional doses (20% of the initial

dose) were administered if the subject was not deeply anesthetized. Turtles remained relatively motionless for up to 150 min under anesthesia. Electrophysiological experiments were performed when the subjects showed no reflexive response to stimulation of the hind leg muscles with a pair of forceps.

2.4. Auditory brainstem response measurements All recordings were performed in a soundproof booth lined with echo-attenuating acoustic foam. ABR was recorded for approximately 100 min, during which the turtles remained anesthetized. The turtles were positioned such that the speaker (frequency response range of 55–20 000 Hz; JBL GT7-6; Harman International Industries, Inc., Stamford, CT, USA) was 5 cm away from the jaw tip of the turtle. Standard platinum alloy subdermal needle electrodes (27 ga, 13 mm in length; Rochester Electro-Medical, Inc., Lutz, FL, USA) were inserted sub-dermally above the tympanum (recording electrode), on top of the head under the frontal scale (reference electrode), and in the front leg (ground electrode). The electrode impedance was less than 3 kΩ.

Stimulus presentation, ABR acquisition, equipment control, and data management were coordinated using a TDT RZ6 Multi-I/O processor, linked via fiber optic cables to a TDT RA4LI low-impedance digital headstage and RA4PA Medusa preamp, and linked to a laptop computer running BioSig software (Tucker-Davis Technologies, Alachua, FL, USA). One type of sound stimuli (tone burst) was generated using the TDT RZ6 Multi-I/O processor, which directly controlled the speaker and ran TDT SigGen software (Wang *et al.*, 2022). Each tone burst (9 ms duration, 2 ms rise time, and 2 ms fall time, with a sample rate of 24 414 Hz and an alternating polarity) was synthesized digitally from 200 Hz to 1 500 Hz in 100 Hz increments, attenuated in 5 dB steps from 85 dB to 30 dB sound pressure level (SPL), and presented at a rate of 4/s. Each ABR wave represented the average response to 200 stimulus presentations. Signals from the electrodes were amplified (20×) and filtered (high pass: 30 Hz; low pass: 3 000 Hz; notch filtered: 50 Hz). Sound stimuli were replicated once.

ABR stimulus levels were calibrated in the free field using a sensor signal conditioner (model 480C02; PCB Piezotronics, Inc., Depew, NY, USA) with a 1/4″ microphone (model 426B03, PCB Piezotronics). The distance between the speaker and the microphone was fixed at 5 cm and calibrated using the TDT RZ6 Multi-I/O Processor and BioSigRP (Tucker-Davis Technologies), which repeatedly played the signal at the same rate used while recording the ABRs, and simultaneously recorded the microphone signal at a sampling rate of 24 414 Hz.

ABR thresholds and latencies were determined by visual inspection, similar to the process described by Wang *et al.* (2019). Threshold measurements were defined as the lowest stimulus level at which no repeatable responses could be recognized (Scott *et al.*, 2017; Wang *et al.*, 2022; Zhu *et al.*, 2022). To reduce artificial errors, all turtle ABR thresholds were determined by the same experienced person. Usually, the ABR threshold was low, or the latency was short suggesting that the turtles' hearing was sensitive.

2.5. Measurement of sex steroids After the electrophysiological test, blood samples from the turtle were obtained by cardiac puncture at approximately the same time daily (evening, 19:00–20:30 h). The samples were centrifuged for 20 min at 4 000 r/min to separate the plasma. Plasma samples were transferred to separate Eppendorf tubes and stored at −80 °C until the estradiol, testosterone, and dihydrotestosterone levels were analyzed with ELISA kits (Nanjing Jiancheng Bioengineering Institute Co., Ltd., Nanjing, China). We assayed one replicate of each sample using whole plasma. The assay was run twice. Intra-assay and inter-assay variation was below 5.2% and 6.3%, respectively. The cross-reactivity of the hormone kits was low. All experimental steps were performed according to the manufacturer's instructions.

2.6. Ethics Statement This study was approved by the Animal Research Ethics Committee of the Hainan Provincial Education Centre for Ecology and Environment, Hainan Normal University (HNECEE-2018-001) and was performed in strict accordance with the institutional guidelines.

3. Statistical Analyses

The data were sorted and analyzed using SPSS (version 22.0; IBM Corp., Chicago, IL, USA). Prior to statistical analysis, all data were examined for assumptions of normality and homogeneity of variance using the Shapiro-Wilk and Levene's tests, respectively. Differences in the ABR thresholds or latency at the same stimulus frequency between winter and spring in the same sex were analyzed using repeated-measures factorial analysis of variance (ANOVA) and one-way ANOVA followed by a least significant difference (LSD) pairwise post-hoc comparisons. Sex hormone levels (estradiol in females and testosterone and dihydrotestosterone in males) in the different seasons in turtles of the same sex were analyzed using an independent sample *t*-test. Results were expressed as the mean ± standard deviation (SD). $P < 0.05$ and $P < 0.01$ were considered statistically significant and highly statistically significant, respectively.

4. Results

4.1. ABR wave morphology The ABR waves in response to tone burst stimuli were characterized by valley-peak waveforms (Figure 1). Figure 1A–D shows a typical ABR response level series measured in female and male turtles in different seasons, for which thresholds of 40 (Figure 1A), 55 (Figure 1B), 45 (Figure 1C), and 60 dB SPL (Figure 1D) were obtained at 0.6 kHz.

4.2. Hearing-sensitivity bandwidth The hearing-sensitivity bandwidth of 77.8% of the females (0.2–1.4 kHz) and 100% of the males (0.2–1.2 kHz) was wider in spring than in winter (100% of the females, 0.2–1.0 kHz and 80% of the males, 0.2–0.9 kHz) (Figure 2).

4.3. ABR threshold The U-shaped ABR-derived audiograms and thresholds were above 30 dB at all stimulus frequencies (Figure 2). There were significant differences in ABR thresholds of the females and males between winter and spring ($F_{1,\ 18}$ = 78.01, P < 0.001 and $F_{1,\ 16}$ = 86.36, P < 0.001, respectively). The ABR thresholds of females (0.5 to 1.0 kHz; P < 0.01) and males (0.5 to 0.9 kHz; P < 0.01) were significantly lower in spring than in winter.

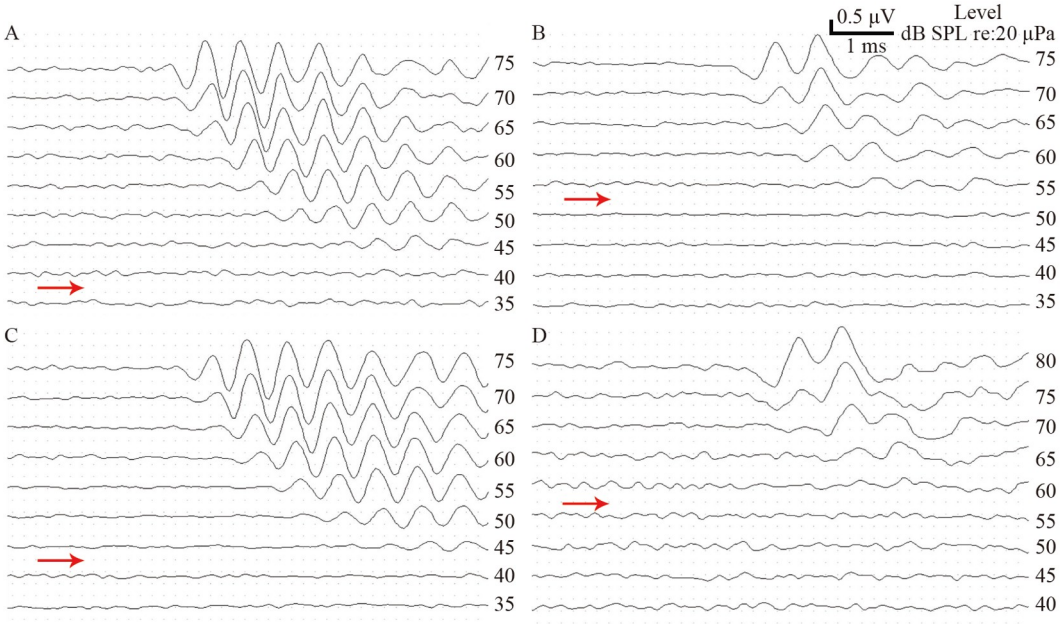

Figure 1 Auditory brainstem responses (ABRs) as a function of stimulus intensity in female (A and B) and male (C and D) *Trachemys scripta elegans* evoked by tone bursts of 0.6 kHz during spring and winter. The right-pointing arrowheads indicate the visually detected thresholds for the stimulus frequency.

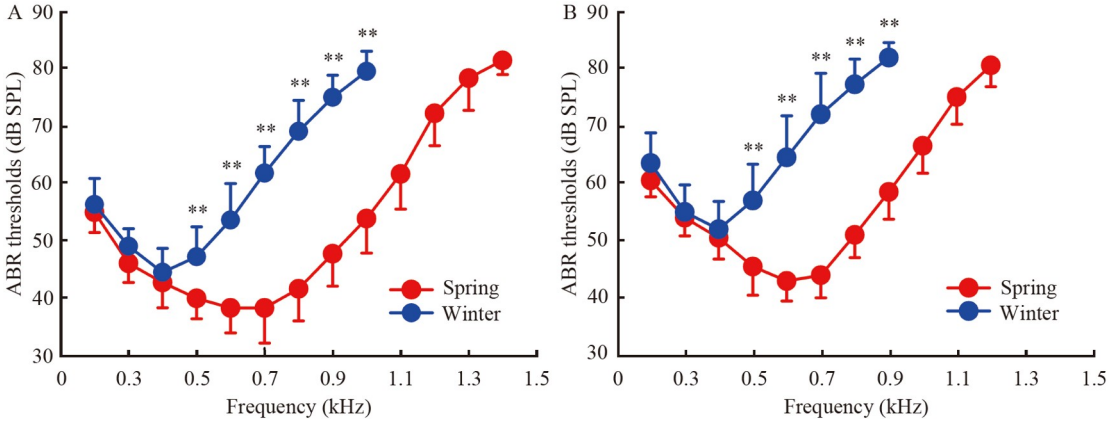

Figure 2 Auditory brainstem responses (ABRs) thresholds evoked by tone bursts in female (A) and male (B) *Trachemys scripta elegans* in different seasons. ** P<0.01

4.4. ABR latency Significant differences were observed in ABR latencies of females and males between winter and spring ($F_{1, 12}$ = 67.91, P < 0.001 and $F_{1, 14}$ = 201.36, P < 0.001, respectively) (Figure 3). The ABR latencies of females (0.2 to 0.9 kHz, P < 0.01) and males (0.2 to 0.9 kHz, P < 0.01) were significantly lower in spring than in winter.

4.5. Sex steroid concentrations There were no significant differences observed in estradiol levels in females between winter and spring (P = 0.73) (Figure 4A) and there were no significant differences in testosterone (Figure 4B) and dihydrotestosterone (Figure 4C) levels observed in males between spring and winter (P > 0.05).

5. Discussion

In this study we revealed the seasonal variation of peripheral hearing sensitivity in turtles, a special animal group with a limited hearing range and minimal vocalization (Popper and Hawkins, 2016; Wang *et al.*, 2019). Temperature variations likely explain these seasonal effects; but further research is required to confirm our findings.

5.1. Seasonal variation of peripheral hearing sensitivity in turtles Although studies have shown seasonal variation in hearing sensitivity in many animal groups, such as frogs and birds, they have focused on vocal species with a hearing range of at least 1.0 kHz (Lucas *et al.*, 2007; Caras *et al.*, 2010; Zhang *et al.*, 2012; Vélez *et al.*, 2015; Yang *et al.*, 2018). To the best of our knowledge, this is the first study to report a seasonal change of peripheral hearing sensitivity in an animal group with little to no vocalization and a limited hearing range. We found that ABR thresholds and latencies in turtles differed significantly between spring and winter, with improved hearing sensitivity in the spring. This indicates that turtles exhibit seasonal variation (winter vs. spring) of peripheral hearing sensitivity, which is consistent with previous studies on seasonal differences in the auditory sensitivity of fishes (Bhandiwad *et al.*, 2017), frogs (Zhang *et al.*, 2012), birds (Lucas *et al.*, 2002; Lucas *et al.*, 2007), and mammals (Hamill *et al.*, 1989).

Remarkably, we found that the ABR thresholds were significantly lower in spring than in winter in both males and females at a hearing-sensitivity range of 0.5–0.9 kHz. The

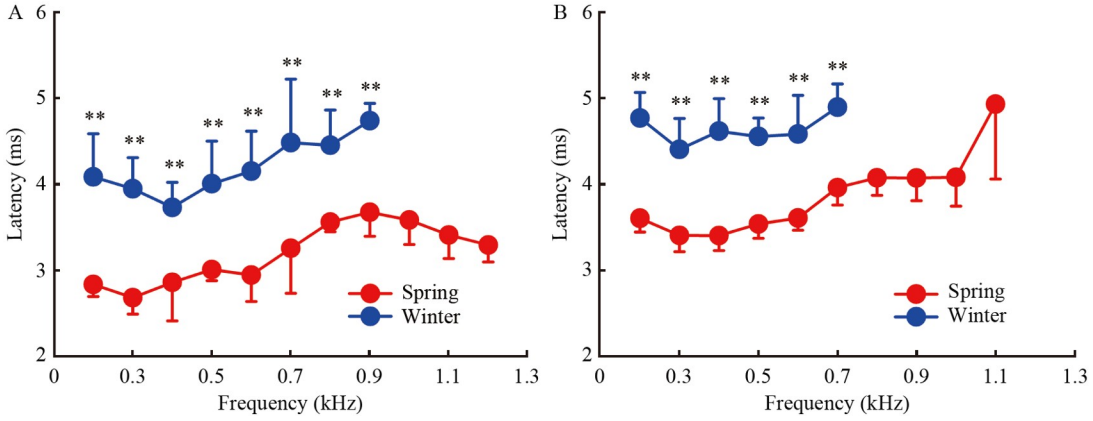

Figure 3 Auditory brainstem responses (ABRs) latency evoked by tone bursts in female (A) and male (B) *Trachemys scripta elegans* with different seasons. ** P<0.01

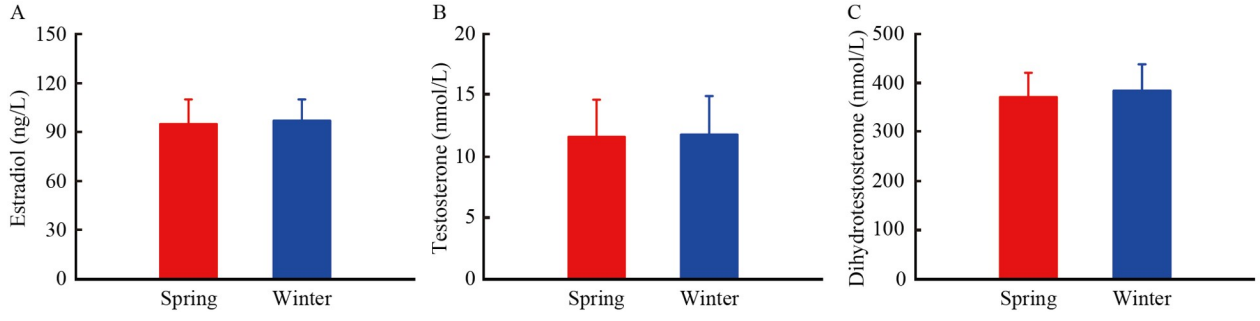

Figure 4 The levels of sex hormones in *Trachemys scripta elegans* in spring and winter. Females: estradiol; Males: testosterone and dihydrotestosterone.

lowest observed threshold also changed from 0.4 kHz in winter to 0.6–0.7 kHz and 0.6 kHz in female and male turtles in spring, respectively. Zhang *et al.* (2012) reported that although the ABR thresholds differed significantly between the reproductive and non-reproductive seasons of the Emei music frog (*Babina daunchina*), the lowest observed ABR threshold frequency was not significantly different. Therefore, our results suggest that the adaptation of the turtle's auditory system may be grossly underestimated compared with that of other vertebrate groups. Thus, our study may provide insights into the seasonal variation of hearing sensitivity in other vertebrate groups, especially those with minimal vocalization.

5.2. The potential factor associated with seasonal variation of peripheral hearing sensitivity in turtles Studies on the endocrine based acoustic communication have provided insights into the broader applicability of hormonal modulation of vertebrae sensory physiology and behavior (Arch and Narins, 2009; Henry *et al.*, 2017). Currently, endocrine regulation is the most likely explanation for the auditory plasticity of vertebrates. For example, a study on Midshipman fish (*Porichthys notatus*) showed that seasonal changes in auditory sensitivity are correlated with plasma steroid hormone levels (Rohmann and Bass, 2011). In addition, the auditory system of the female Round goby (*Neogobius melanostomus*) is affected by estradiol levels (Zeyl *et al.*, 2013). However, in our study, although the sensitive response of the turtle's auditory system had clear differences in the different seasons, we found no significant differences in estradiol levels in females, and testosterone, and dihydrotestosterone levels in males. Hormones regulate the reception and processing of acoustic signals through a complex process. Some studies found that hormonal regulation of hearing sensitivity is strictly time-sensitive and changes according to specific reproductive behavior (Baugh *et al.*, 2019; Gall *et al.*, 2019). Therefore, sex hormones can not be used to explain the seasonal variation (winter vs. spring) of hearing sensitivity in turtles. Moreover, the relationship between the variation of hearing sensitivity and circulating sex hormones of turtles requires further research with a focus on pre- or post-specific reproductive behavior.

For species with seasonal calling behavior, the increase in hearing sensitivity during the reproductive season is largely related to conspecific vocal signals (Sisneros *et al.*, 2004; Henry and Lucas, 2009; Sisneros, 2009; Rohmann and Bass, 2011; Gall *et al.*, 2013; Gall and Wilczynski, 2015). These studies suggest that conspecific calling signals may be an important factor in the seasonal variation of hearing sensitivity. The underwater vocalizations of *T. scripta elegans* have been described (Zhou *et al.*, 2022); however, the behavioral significance of the calls remains unclear. Future research on the calling behavior of *T. scripta elegans* and its function may help explain the seasonal variation of hearing sensitivity. Therefore, our research may bring more attention to the acoustic communication of turtles.

Many previous studies have found that temperature affects hearing sensitivity (Doyle and Fria, 1985; Stiebler and Narins, 1990; Wysocki *et al.*, 2009; Sun *et al.*, 2019). In this study, the temperature under natural conditions during electrophysiological tests was 32.5 ± 0.9 °C and 19.3 ± 0.6 °C and 28.9 ± 1.6 °C and 19.4 ± 0.3 °C for spring and winter, respectively. These temperatures are similar to that in previous reports and studies conducted during the reproductive season of *T. scripta elegans* (Li, 2013; Yang, 2014; Ma and Shi, 2017). Interestingly, we found that the ABR thresholds at frequencies between 0.4 kHz and 1.1 kHz were significantly lower at 30 °C than at 18 °C, and the lowest ABR threshold was observed at 0.6–0.7 kHz at 30 °C; it was previously reported to be 0.3 kHz at 18 °C in the non-reproductive season of male *T. scripta elegans* by artificially controlling the temperature (Wang *et al.*, 2022). These findings are similar to those of the present study. Therefore, temperature variations may be used to explain the seasonal changes; however, further research is required.

5.3. The function of seasonal variation of peripheral hearing sensitivity in turtles Seasonal variation of hearing is assumed to enhance the ability of individuals to respond to vocal signals related to mating, food, or predation risk during the reproductive season (Zhang *et al.* 2012; Gall and Wilczynski, 2015; Henry *et al.*, 2017). In some bird species, increased social stability may be related to seasonal changes in hearing sensitivity (Lucas *et al.*, 2002). In the reproductive season (spring), male *T. scripta elegans* improve their chances of gaining successful mating opportunities by increasing their mate-searching activities (Gibbon and Lovich, 1990). Courtship behavior is highly ritualized and begins when a male finds a female (Jackson and Davis, 1972). Female *T. scripta elegans* have the highest number of follicles in March when they dig their nest; they begin laying eggs predominantly from mid-April to mid-June, with the peak occurring from late April to late May in China (Li, 2013; Yang, 2014; Ma and Shi, 2017). Therefore, the physiological state of turtles shapes their auditory response properties, possibly ensuring that behaviorally relevant signals are detected and encoded by the auditory system. In contrast, a reduction in hearing sensitivity of *T. scripta elegans* during winter may help save energy, because sensory tissue maintenance requires high energy (Niven and Laughlin, 2008).

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