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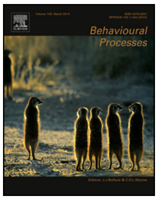

Background matching and camouflage efficiency predict population density in four-eyed turtle (*Sacalia quadriocellata*)

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ABSTRACT

Background matching is an important way to camouflage and is widespread among animals. In the field, however, few studies have addressed background matching, and there has been no reported camouflage efficiency in freshwater turtles. Background matching and camouflage efficiency of the four-eyed turtle, *Sacalia quadriocellata*, among three microhabitat sections of Hezonggou stream were investigated by measuring carapace components of CIE $L^*a^*b^*$ (International Commission on Illumination; lightness, red/green and yellow/blue) color space, and scoring camouflage efficiency through the use of humans as predators. The results showed that the color difference (ΔE), lightness difference (ΔL^*), and chroma difference (Δa^*b^*) between carapace and the substrate background in midstream were significantly lower than that upstream and downstream, indicating that the four-eyed turtle carapace color most closely matched the substrate of midstream. In line with these findings, the camouflage efficiency was the best for the turtles that inhabit midstream. These results suggest that the four-eyed turtles may enhance camouflage efficiency by selecting microhabitat that best match their carapace color. This finding may explain the high population density of the four-eyed turtle in the midstream section of Hezonggou stream. To the best of our knowledge, this study is among the first to quantify camouflage of freshwater turtles in the wild, laying the groundwork to further study the function and mechanisms of turtle camouflage.

1. Introduction

Camouflage is widespread among animals and includes crypsis, masquerade, motion dazzle, and motion camouflage (Thayer, 1896; Cott, 1940; Stevens and Merilaita, 2009). Among these, crypsis constitutes a complex subject and may aid in reducing detection by predators (Stevens and Merilaita, 2011). Background matching is an important type of crypsis that involves animal coloration generally resembling the color, lightness, and pattern of one background or several backgrounds (Stevens and Merilaita, 2009). Many animals' body color closely matches natural substrates. For example, Krupa and Gelusa (2000) found that the color of the pocket gopher's (*Geomys bursarius*) heads and backs closely matches the color of moist soil. Additionally, Mäthger et al. (2008) demonstrated that the reflectance spectra of cuttlefish (*Sepia officinalis*) skin patterns highly correlate with the spectra of natural substrates. In fact, some animals may actively select microhabitat with color similar to their body color. For instance, Japanese quail (*Coturnix japonica*) females choose a substrate that best matches their egg background coloration in order to provide the most effective camouflage (Lovell et al., 2013). In recent years, some studies have suggested that background matching is associated with reduced risk of predator detection (Lee et al., 2010).

With regard to quantification of color, Stevens et al. (2007) suggested that digital photography has many advantages over spectrometry. Digital photography can analyze whole spatial patterns of an animal, dispensing with reconstruction topography from point samples. It can also possibly provide means for quantifying the entire background color of the substrate inhabited by the animals. In addition, digital photography enables rapid data acquisition. All the aforementioned advantages of digital photography are important to study background matching, especially when the experiments are conducted in the field. Some recent studies of background matching have adopted digital photography and computer systems to quantify the color of animals (or avian eggs) and their habitat substrate (or avian nest) (Lee et al., 2010; Lovell et al., 2013). However, some authors have suggested that the best method for studying background matching is to test its camouflage efficiency by building a natural predator–prey system (Cuthill

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et al., 2005). This method, however, is difficult to carry out because of the improbability of witnessing predation events in the wild (Karpestam et al., 2013). One controllable method to study camouflage efficiency is to conduct detection experiments by presenting photographs of prey on paper to human predators (Gendron and Staddon, 1984; Todd, 2009). This allows for several iterations which are very difficult to conduct in the field, and it has been successfully used to study camouflage (Todd, 2009; Stevens et al., 2013), mimicry (Beatty et al., 2005), and aposematism (Summers and Clough, 2001).

Reptiles such as lizards (Stuart-Fox et al., 2004, 2006, 2008; Hamilton et al., 2008) and snakes (Jackson et al., 1976; Pough, 1976; Lindell and Forsman, 1996) are some of the most preferred model animals for studying vertebrate camouflage. However, because Chelonia has been traditionally considered to be the only order of Reptilia that exhibits no color change (Parker, 1948), until recently, the research of camouflage in turtles had progressed slowly. Little had changed in our understanding of how camouflage works in turtles since the landmark study of body color in *Chelodina longicollis* (Woolley, 1957). Since then, several research groups have indirectly suggested that the body color of turtles matches with their different backgrounds (Bartley, 1971; Rowe et al., 2006a,b, 2009; McGaugh, 2008). McGaugh (2008) showed that black softshell turtle (*Apalone spinifera atra*) carapaces have a tendency to gradually lighten in turtles from lagoons to rivers, and from rivers to lakes. These experiments indicate a positive association of turtle carapace and habitat substrate color component. However, with the exception of McGaugh (2008), other studies only measured individual color and did not quantify the substrate color of the turtles' habitat. Furthermore, camouflage efficiency in freshwater turtles has not been reported yet.

The four-eyed turtle (*Sacalia quadriocellata*) is an endemic Asian species (Zhang et al., 1998; Shi et al., 2011). Although it experiences the same pressures of over-hunting and habitat destruction as other turtle species in China (Zhao, 1998; Gong et al., 2004), its population densities have been maintained at higher levels than those of other species (Gong, 2006; Wang et al., 2010, 2011; Ge et al., 2012), suggesting that the four-eyed turtle possesses a high level of fitness and adaptation. To date, several studies have demonstrated such adaptability, including habitat selection (Gong et al., 2005), feeding behavior (Shi et al., 2011), and reproduction (He et al., 2010a,b), but the camouflage of this species has not been investigated.

Through field surveys, the population density of the four-eyed turtle in Hezonggou stream on Hainan Island was determined to be significantly different among stream sections (upstream, midstream, and downstream). The midstream possesses the highest density, whereas the upstream has the lowest (Xiao, 2014). Some turtle predators such as wild boars (e.g., *Sus scrofa*) exist in this stream ecosystem. Moreover, archeological records indicate that freshwater turtles were an important resource to early peoples of China for thousands of years (Fan and Zhang, 2008), and they continue to be hunted from this stream owing to their use as Chinese medicines and sources of foods (Shi et al., 2002; Dharmananda, 2005). Additionally, Nafus et al. (2015) suggested that humans depend on their vision to detect turtles. Therefore, the four-eyed turtle is thought to be faced with predation pressure of visual predators, especially humans, in Hezonggou stream. Considering that camouflage can reduce predation risk (Cooper and Greenberg, 1992; Lee et al., 2010), we hypothesized that the density difference among stream sections of Hezonggou stream may be correlated to turtle camouflage. Here we conducted comparative studies on background matching among stream sections with different densities in the four-eyed turtle by using digital photography and investigated their camouflage efficiency by considering humans as predators. We predict that the background matching and camouflage efficiency would be the best in midstream with the highest density and the worst in upstream with the lowest density.

2. Materials and methods

2.1. Study site and species

Fieldwork was conducted in a stream called Hezonggou (19°06′40″–19°08′83″ N, 109°55′82″–109°57′70″ E) in Wanling town of Qiongzhong county, Hainan province of China, from April to October 2013. A number of four-eyed turtles inhabit this stream and their population densities differ among different 1 km stream sections. The highest and lowest densities were found in midstream (21.5/km) and upstream (0.91/km), respectively, whereas downstream had 3.5 individuals per km (Xiao, 2014). Stream characteristics differed among the three stream sections. The mean stream elevation, water velocity, and stream width and depth were 325 m, 0.134 m/s, 3.2 m, and 0.3 m in the upstream; 291 m, 0.118 m/s, 3.8 m, and 0.57 m in the midstream; and 282 m, 0.09m/s, 5.34 m, and 0.41 m in the downstream. The stream gradient was 1.3% in the upstream, 1.6% in midstream, and 0.9% in downstream. Furthermore, the substrate component differed among stream sections as well. In the upstream, the substrate was composed of boulders and sand (ca.50%, respectively). In contrast, the substrate mainly consisted of many cobbles and pebbles (75%) in the midstream, whereas the downstream consisted of a large amount of sand and silt (90%). There are 241 species of vascular plants in the habitat of the four-eyed turtle, including pteridophytes, dicotyledons, and monocotyledons (Zhong et al., 2006). There are also wild boars (seen by L.S.) and snakes (e.g., *Rhabdophis adleri*, *Boiga multomaculata*, *Bungarus multicinctus*, Shi et al., 2011) in the area that could potentially prey on turtles. Additionally, there is illegal hunting pressure in Hezonggou stream (Shi et al., 2002).

2.2. Quadrats and photography

We selected 90 substrate quadrats measuring 1 × 1 m by systematic sampling in the upstream, midstream, and downstream sections of the stream. At each of the 3 stream sections, 30 quadrats were sampled at regular intervals of 30 m from the lower reach to the upper reach. Therefore, the first quadrat for each section was its lower boundary. Nine adult four-eyed turtles (including five females and four males), which were formerly captured from this study area by using nondestructive cage trapping and kept for 11 months in the laboratory, were used in this experiment. The turtles were maintained in a 130 × 80 cm indoor cement pool with water depth of 20–25 cm. Air temperature was 12–32 °C whilst water temperature was 12–30 °C during the period of breeding. They were fed a diet of shrimp, chopped pork, liver, banana, and vegetables. The photoperiod in the laboratory was the same as outside. All turtles during the experiments were respectively placed in each quadrat and photographed using a Canon EOS 20D camera with Canon lens (EF-S24–70 mm f/2.8, 8.2 megapixels) between 11:00 a.m. to 5:00 p.m., when natural light allowed for good visualization of turtles. We put the camera on a tripod and positioned it almost perpendicular to the water surface. In total, we collected 810 (90 quadrats × 9 turtles) digital photographs that were all saved in the non-compression RAW format (Stevens et al., 2007) for subsequent color measurements and analyses.

Calibration of lighting needed to be performed for each session/lighting for calculating reflection in digital photographs, as the light set-up changes the ratio between different wavelengths (Stevens et al., 2007). However, we did not conduct such calibration during our fieldwork since any distortion resulting from a particular wavelength maybe compensated when calculating the color differ-

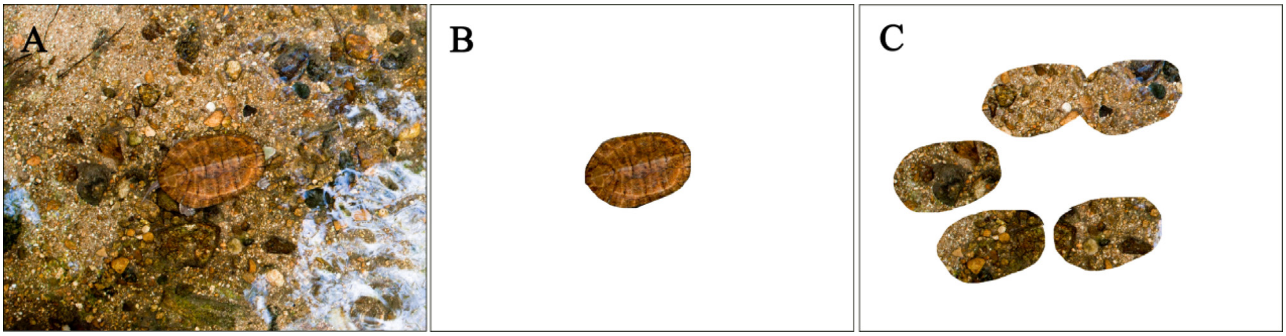

Fig. 1. Pictures of *S. quadriocellata* showing an example of turtle position (A) and color samples of carapace (B) and substrate (C). The carapace length is 125.58 mm.

ences between the turtle and its background, as any distortion in the wavelengths would be same for the turtle and its background (Eterovick et al., 2010).

2.3. Color measurement and calculation

A blind experiment was conducted for color measurement. Color in the pictures of turtles and their substrates was quantified in Adobe Photoshop CS5 (Adobe Photoshop 1990–2010, Adobe Systems Incorporated) using CIE $L^*a^*b^*$(International Commission on Illumination) color spaces (Robertson, 2007) by a third party (M. Li), who was not otherwise involved in the field work and was unaware of the intention of this study. The color components within CIE $L^*a^*b^*$ color spaces are represented as three numbers, with 'L^*' representing lightness and the 'a^*' and 'b^*' representing color changes through the red-green and the yellow-blue spectra, respectively. The L^*, $a^*$and b^*components in the carapace of turtles were quantified by choosing them as a separate layer in Photoshop (Fig. 1). In order to quantify background components, five elliptical shapes were randomly selected throughout the background next to the turtle, and thus were merged into a separate layer and proceeded to a component measurement of the whole set of five elliptical shapes, to achieve a general background measurement (Eterovick et al., 2010; Fig. 1). These elliptical shapes were similar to turtle carapace shape and size (Fig. 1).

Color difference between turtles and their substrates was obtained by calculating Euclidean distance (ΔE). The lightness component (L^*) must be analyzed separately from the chroma component (a^*b^*) for an accurate colorimetric test (McCormick-Goodhart and Wilhelm, 2003). Therefore, besides calculating color difference (ΔE), we also calculated lightness difference (ΔL^*) and chroma difference (Δa^*b^*), as follows:

$$\Delta \mathrm{E} = \sqrt{\left(L_t^* - L_s^*\right)^2 + \left(a_t^* - a_s^*\right)^2 + \left(b_t^* - b_s^*\right)^2} \quad (1)$$

$$\Delta L^* = |L_t^* - L_s^*| \quad (2)$$

$$\Delta a^*b^* = \sqrt{\left(a_t^* - a_s^*\right)^2 + \left(b_t^* - b_s^*\right)^2} \quad (3)$$

Where t indicates turtle and s is substrate.

2.4. Detection experiment of camouflage efficiency by human predators

The camouflage efficiency index is a mean of scores by humans as predators. The detection experiment was also blind. Prior to the detection task, a third party (H. Wen, C. Lin, and Q. Wang) randomly chose 30 electronic photographs from the above 810 photographs from the fieldwork, with 10 photographs each for the upstream, midstream, and downstream. These 30 photographs were randomly arrayed and printed on a photographic paper (92cm × 65 cm). The third party then presented this paper to 129 participants (65 males and 64 females) consisting of 9–29 years old from two randomly selected secondary schools and one university in Haikou of Hainan province, China. No participant was colorblind, and most had normal visual condition. Only seven university students (2 males, 5 females) used lenses. The participants needed to skim each image and then rate the camouflage efficiency on a 5-point scale from 1 (the worst camouflage efficiency) to 5 (the best camouflage efficiency). Scoring time of each photo was standardized to 20 s to control the effect of time. In addition, the age and gender of the participants were recorded.

2.5. Statistical analysis

All statistical procedures were performed in SPSS 16.0 (SPSS, Inc., Chicago, IL), but graphed in Graph Pad Prism 5, with all data expressed as mean ± SE. Prior to running the analysis, a Kolmogorov-Smirnov test was used to test the normality of data of color and camouflage efficiency. For color data, we compared color difference (ΔE), lightness difference (ΔL^*), and chroma difference (Δa^*b^*) among three sections of the stream using Friedman tests, followed by Wilcoxon signed-rank tests to compare the results of different groups. For detection experiments, however, an analysis of variance (ANOVA) was used to compare camouflage efficiency. Stream section (upstream, midstream, or downstream), participant gender (male or female), and age (secondary school student or university student) were defined as fixed factors. The turtle individual was defined as a random factor. The mean score of camouflage efficiency was defined as a dependent variable. Multiple comparisons among means of stream section were performed by a Tukey post hoc test. A value of P less than 0.05 was considered statistically significant.

3. Results

3.1. Background matching

The results showed that background matching between shell color of the four-eyed turtle and habitat substrates was significantly different among sections of the stream (ΔE: $\chi^2 = 260.94$; ΔL^*: $\chi^2 = 245.92$; Δa^*b^*: $\chi^2 = 445.56$, in all variables $P < 0.0001$). The color difference (ΔE) in midstream (12.24 ± 0.17) was significantly lower than that of upstream (26.60 ± 0.87; $Z = -11.22$, $P < 0.0001$) and downstream (38.57 ± 1.14; $Z = -13.94$, $P < 0.0001$); the lightness difference (ΔL^*) was also significantly lower in midstream (9.75 ± 0.17) than in upstream (22.07 ± 0.90; $Z = -13.36$, $P < 0.0001$) and downstream (37.08 ± 1.18; $Z = -8.97$, $P < 0.0001$). In accordance, the chroma difference (Δa^*b^*) in midstream (7.02 ± 0.14) was also significantly lower than that of upstream (13.45 ± 0.32; $Z = -14.24$, $P < 0.0001$) and downstream (8.96 ± 0.17; $Z = -10.31$, $P < 0.0001$; Fig. 2). These results indicate that the background

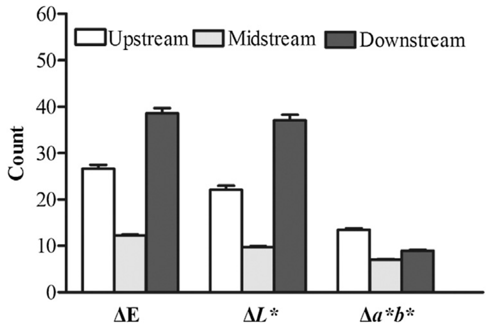

Fig. 2. Color difference between substrate and carapace of *S. quadriocellata* in each section of stream. ΔE: Color difference; ΔL^*: Lightness difference; Δa^*b^*: Chroma difference (all $P<0.0001$).

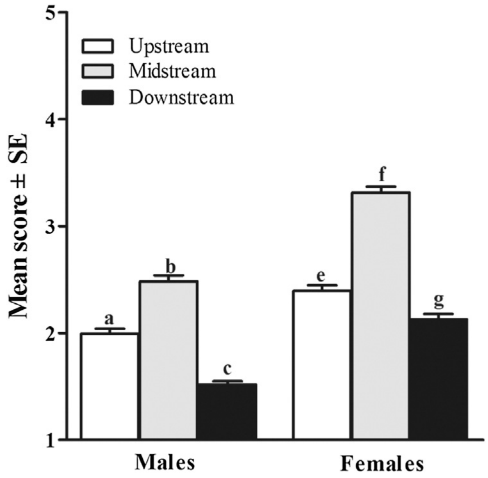

Fig. 3. Differences of camouflage efficiency in stream sections for male and female participants. Letters a to g denote differences based on Tukey post-hoc tests (all $P<0.001$).

matching of four-eyed turtles in midstream was significantly higher than that of upstream and downstream. Furthermore, both color and lightness differences in upstream were significantly lower than in downstream ($Z=-7.95$, $P<0.0001$ and $Z=-10.63$, $P<0.0001$, respectively; Fig. 2). In contrast, the chroma difference was significantly higher in upstream than in downstream ($Z=-14.24$, $P<0.0001$; Fig. 2).

3.2. *Camouflage efficiency*

The three stream sections differed significantly in camouflage efficiency, and there was an interaction effect between stream section and participant gender (Table 1). The turtles exhibited higher camouflage efficiency for all stream sections for female participants than males (Fig. 3). However, the camouflage efficiency in midstream was significantly higher than that of upstream and downstream in both genders of the participants (Tukey post hoc test, all $P<0.001$; Fig. 3). Moreover, the camouflage efficiency of the four-eyed turtle was significantly higher in upstream than in downstream for both genders of the participants (Tukey post hoc test, all $P<0.001$; Fig. 3). There was no interaction between stream section and participant age effects (Table 1).

4. Discussion

Our results are broadly in line with our expectations above. They illustrated that the substrate of the midstream section best matches the body color of the turtle, and the camouflage efficiency of the turtle is optimal when inhabiting this section. This study indicated that color, lightness, and chroma differences are lower in midstream than upstream or downstream, and showed that the score of camouflage efficiency is higher in midstream than in upstream or downstream.

We discovered that the difference of color matching might be associated with the components of substrate and the background color in different sections of the stream. In the midstream, the substrate is mainly made of a large number of cobbles and pebbles (Fig. 4B) of various colors. However, because sunlight can reach midstream at noon on a sunny day, these cobbles and pebbles basically appear brown-yellow, and this color is very similar to the body color of the four-eyed turtle. As for substrate in upstream, however, it consists of some boulders and some sand (Fig. 4A), and the color of these boulders is dark because of very high canopy density (90%) in this section. In contrast, in downstream the substrate consists of a large amount of sand and silt (Fig. 4C) with similar color, and is the brightest due to the lowest canopy density (30%). This could explain why the lightness difference (37.08 ± 1.18) between turtle and substrate was so high in downstream.

The carapace color of the four-eyed turtle more closely matched the substrate in midstream, which may increase camouflage efficiency and survival chances. For achieving better crypsis, the four-eyed turtle needs to choose the appropriate microhabitats. Chelonia species seem to possess tetrachromatic color vision (Liebman and Granda, 1971; Ammermüller et al., 1998; Honkavaara et al., 2002), including visible and UV spectrum, thus they can discriminate different colors (Young et al., 2012). Therefore, the four-eyed turtle may see the substrate color and succeed in selecting a better matching background. This is similar to the previous study on Japanese quail, which has been shown to seek out a substrate that best matches their egg coloration as a nest position to provide the most effective camouflage (Lovell et al., 2013). Furthermore, avian egg survival ratio is related to the color matching of eggs to nest background, as in eggs of Black-tailed Gulls (*Larus crassirostris*) (Lee et al., 2010). The population density (21.5/km) of four-eyed turtles was the highest in midstream of the stream (Xiao, 2014). In this regard, one may hypothesize that four-eyed turtles favor the midstream microhabitat because of the color matching of carapace to the substrate background in midstream.

Our results suggested that chroma differences between turtle and the substrate in midstream ($\Delta a^*b^*=7.02$) is lower than the chroma difference ($\Delta a^*b^*=7.39$) between *Bokermannohyla alvarengai* tadpoles and their background after disturbance (Eterovick et al., 2010). The low chroma difference and lightness difference relative to the substrate background achieved by a turtle may be enough to deceive its potential predators. The CIE $L^*a^*b^*$color space is designed to approximate human vision, spanning 400 nm to 700 nm wavelength, whereas other predators and the turtles themselves can detect ultraviolet, within wavelengths of 300–700 nm (Honkavaara et al., 2002). We should determine whether the ultraviolet affects turtle background matching in future studies.

Besides background matching, camouflage can be attained via disruptive coloration (Cott, 1940). Disruptive coloration shows that the appearance of false edge results from a contrasting pattern around the edge of an animal, reducing the edge detection or recognition capacity of a predator (Cott, 1940; Stevens and Merilaita, 2009). There is a contrasting ring pattern between the marginal and pleural scutes of adult four-eyed turtles, which seems to help hinder detection of the turtle body shape when on the substrate (Fig. 4D).

Camouflage efficiency is affected by the visual background, including the color, shape, and complexity of substrate background (Merilaita, 2003). Thus, it is reasonable to explain that camouflage efficiency of the four-eyed turtle is the highest in midstream,

Table 1
Results of analysis of variance (ANOVA) on camouflage efficiency. SS, sum of squares; d.f., degrees of freedom; MS, mean squares.

Source	SS	d.f.	MS	*F*	*P*
Intercept	10085.21	1	10085.21	883.52	<0.0001
Participant age	51.72	1	51.72	30.6	0.001
Participant gender	388.75	1	388.75	224.94	<0.0001
Turtle individual	71.97	6	11.99	0.925	0.521
Stream section	143.71	2	71.85	6.33	0.022
Participant age × stream section	10.12	2	5.06	3.22	0.558
Participant gender × stream section	13.45	2	6.73	15.9	<0.0001

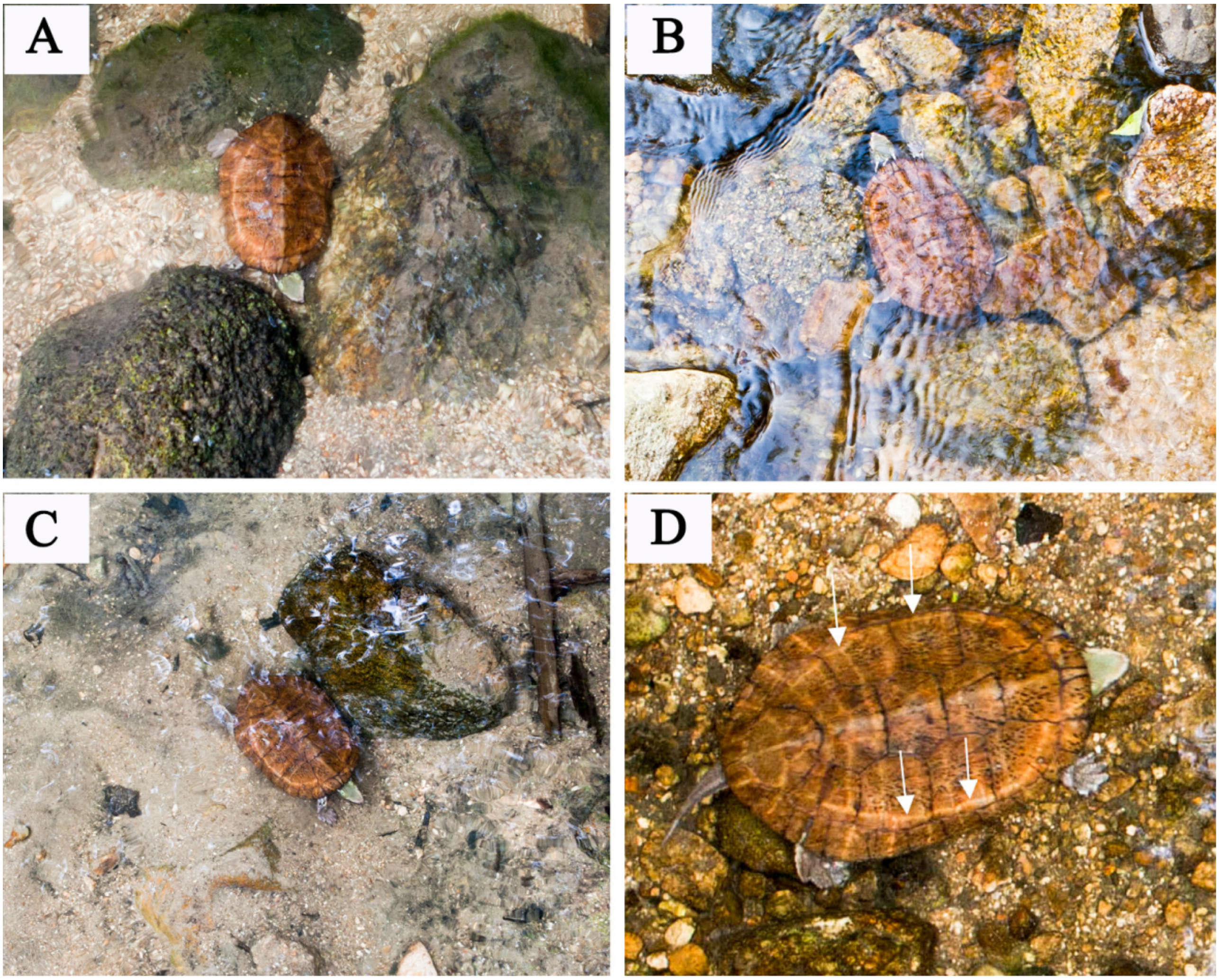

Fig. 4. *S. quadriocellata* (carapace length = 125.58 mm) and substrates of the stream. A: upstream, B: midstream, C: downstream, D: disruptive coloration (arrows).

because (1) the color matching (including chroma and lightness) is the best in midstream compared with other sections (this study), (2) the shape similarity between the turtles and the stones is significantly higher in midstream (0.784 ± 0.004) than in upstream (0.661 ± 0.009) (Xiao, 2014), and (3) the complexity of substrate is the highest in midstream which is composed of a large number of small stone pieces and a small amount of sand. However, camouflage efficiency is higher in upstream than in downstream, whereas the opposite trend is noted for chroma matching. One reason for the discordance is that the complexity of substrate in upstream is higher than in downstream, another possible reason is the lightness in upstream is lower than in downstream.

Both background matching and camouflage efficiency revealed more favorable results upstream than downstream, but the opposite trend was observed for the population density of four-eyed turtle. We considered four alternative explanations for this inconsistency. A common explanation is that there is a discrimination threshold for the color vision of a predator (Théry and Casas, 2002; Théry et al., 2005; Defrize et al., 2010) or human (McCormick-Goodhart and Wilhelm, 2003). The camouflage efficiency is the highest at midstream, which possibly limits the predators' prey distinction threshold. However, although the camouflage efficiency is higher upstream than downstream, owing to both sections being beyond the threshold of discrimination, it is possible that the inconsistent trends noted for camouflage and population density of the four-eyed turtle previously existed in these two sections. Another explanation is that interspecific competition between four-eyed turtle and other turtle species such as big-headed turtle (*Platysternon megacephalum*) may result in low population density in upstream for the former, since the aggressive big-headed turtles inhabit the upstream section (Shi et al., 2011). The third explanation is that the stream characteristics such as stream width and depth in the upstream may be related to the low density of four-eyed turtle. For example, Gong et al. (2005) found that this species preferred to inhabit deep-water microhabitats. However, the upstream section may be short of suitable microhabitat because its stream depth is the lowest when compared with other sections (Xiao, 2014). In addition, other factors, such as food resource richness, can also lead to different population density. In conclusion, these explanations were not mutually exclusive, and the inconsistency may result from various combinations of the reasons above.

Camouflage is an interface among anti-predation behavior, habitat suitability, and conservation (Nafus et al., 2015). Both color quantity and score of camouflage in this study were based on the vision of humans, who are potential predators to the turtles. Therefore, the results of this study would have major implications for turtle conservation. Our results may not completely apply to predators that have color vision differing from that of humans. However, archeological records suggest that people have used freshwater turtles for seven thousand years in China (Fan and Zhang, 2008). Furthermore, almost all freshwater turtles in Hainan province have been over-hunted by human beings in recent decades (Gong et al., 2004, 2006). Additionally, many people living near Hezonggou stream often engage in activities along this stream, including catching turtles whenever they sight them (Shi et al., 2002). Overall, there is no doubt that human beings have become a major predator for the four-eyed turtle. Therefore, we suggest further studies should focus on improving our understanding of how humans affect conservation of camouflage-dependent turtles, as illegal hunting becomes more and more serious in China (Zhao, 1998; Shi and Parham, 2000; Shi et al., 2007; Gong et al., 2009; Liang et al., 2013; Chow et al., 2014). In addition, habitat suitability assessments traditionally depend on landscape-scale habitat traits (Millar and Blouin-Demers, 2012). The landscape scale, however, can fail to capture subtle but important microhabitat traits. As anthropogenic habitat changes may alter the background (Gong, 2006) in a way that may make turtles more conspicuous, microhabitat-dependent camouflage may be less effective. Thus, our study implies that habitat management should focus on microhabitat traits for camouflage-dependent species.

In summary, our work reveals that four-eyed turtles' body color most closely matches the substrate of midstream, and the camouflage efficiency is best when inhabiting this section of Hezonggou stream. We suggest that four-eyed turtles could enhance camouflage efficiency by selecting microhabitat that best matches their body color and shape. To the best of our knowledge, this study is among the first to quantify camouflage of freshwater turtles in the wild. Not only can it lay the groundwork to study function and mechanisms of turtle camouflage, but it can also offer suggestions for turtle conservation in an environment with excessive hunting.

Conflict of interest

We declare that all authors have no conflict of interest.

Compliance with ethical standards

Fieldwork and the detection experiment of camouflage efficiency by human participants were carried out in strict accordance with the guidelines of the Animal Research Ethics Committee of Hainan Provincial Education Centre for Ecology and Environment, Hainan Normal University (HNECEE-2011-003), which conforms to the Law of People's Republic of China. Additionally, oral consent was obtained from each human participant (and parent for participants younger than 18 years) prior to the detection experiment.

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