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Original Research Article

Structural and colored disruption as camouflage strategies in two sympatric Asian box turtle species (*Cuora* spp.)

Rongping Bu [a,1], Fanrong Xiao [a,1], P. George Lovell [b], Zihao Ye [a], Haitao Shi [a,*]

[a] Ministry of Education Key Laboratory for Ecology of Tropical Islands, Key Laboratory of Tropical Animal and Plant Ecology of Hainan Province, College of Life Sciences, Hainan Normal University, Haikou, 571158, PR China
[b] Division of Psychology and Forensic Sciences, School of Applied Sciences, Abertay University, 1, Bell Street, Dundee, DD1 1HG, UK

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A B S T R A C T

Disruptive coloration is a common camouflage strategy that breaks body outlines and ostensibly blends organisms into complex backgrounds. However, contrasting false edges caused by an animal's structure can also break body outlines, although there is no empirical evidence to support this strategy. Here, we examined the Gabor edge disruption ratio (GabRat) of two species, the keeled box turtle (*Cuora mouhotii*) and the Indochinese box turtle (*C. galbinifrons*), on preferred (e.g., deciduous leaves) and non-preferred (i.e., grass) substrates. We quantified edge disruption in different substrates to compare interspecific differences in the GabRat values of disruptive coloration among the turtles' preferred and non-preferred (control) substrates. We found that both species exhibited higher GabRat values on preferred substrates, but interestingly, the keeled box turtle, with a uniformly colored carapace containing flat scutes and two keels, had a higher GabRat value than the Indochinese box turtle, characterized by two yellow stripes on its carapace. Our results indicated that the strong brightness gradients caused by the directional illumination of the flattened and keeled carapaces created disruptive coloration in the keeled box turtles, whereas a high chroma contrast created disruptive coloration in the Indochinese box turtles. For these turtles, the structural modifications resulted in variations in lightness that led to higher levels of disruption than the chromatic disruption of the Indochinese box turtle. Our study provides, to our knowledge, the first evidence of disruptive camouflage in turtles and the first comprehensive test of structural and colored disruption in vertebrates.

1. Introduction

Disruptive coloration is an important camouflage strategy. High-contrast markings near edges break up the body's outline, increasing the difficulty of detection or recognition (Thayer 1909; Stevens and Merilaita 2009; Webster et al., 2013; Sharman et al., 2018). Empirical investigations on disruptive coloration include analyzing natural animal markings and demonstrating a

* Corresponding author.
E-mail addresses: 18778395529@163.com (R. Bu), xiao71815@163.com (F. Xiao), p.g.lovell@abertay.ac.uk (P.G. Lovell), 2439199319@qq.com (Z. Ye), haitao-shi@263.net (H. Shi).
[1] Co-first author.

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survival advantage over background matching in artificial prey presented to wild avian predators (Cuthill et al., 2005; Merilaita and Lind 2005).

Disruptive coloration can be achieved in multiple ways, such as the aforementioned highly effective edge disruption (Cuthill et al., 2005; Schaefer and Stobbe 2006; Seymoure and Aiello 2015). Another strategy is surface disruption, in which high-contrast patterns on the body are perceived as distinct objects and, therefore, not as part of a whole animal (Stevens et al., 2009). This second form of disruptive coloration creates false edges on the animal that are more prominent than real edges (Stevens et al., 2009; Troscianko et al., 2009). For example, high-contrast coloring patterns give artificial prey a camouflage advantage against avian predators (Stevens et al., 2009; Seymoure and Aiello 2015). The third strategy is surface disruption with edge enhancement, in which boundaries of light and dark patches are optically enhanced by tones becoming lighter on the light side and darker on the dark side (Cott 1940; Osorio and Srinivasan 1991; Cuthill 2019). Experiments with humans searching indicate that edge enhancement hampers both object recognition and detection (Egan et al., 2016; Sharman et al., 2018; Adams et al., 2019).

However, our understanding of disruptive camouflage lack structural disruption, that is, a special physical structure that creates strong internal monochromatic edges. Many animals with binocular vision can perceive depth information from left—right disparities (Nityananda and Read 2017). Previous work suggests that binocular depth information can facilitate detection, but only when the target depth is known in advance, because observers direct their attention to the relevant depth plane (Nakayama and Silverman 1986; Finlayson et al., 2013). Depth difference may highlight part of the target's surface, while other part match the background, this may make it difficult for an observer to visually segment the target's real edges from its background (Adams et al., 2019).

The background also affects disruptive camouflage because disruptive coloration is contingent on background matching (Cott 1940; Schaefer and Stobbe 2006; Xiao and Cuthill 2016). Specifically, a disruptive pattern's effectiveness is greatly strengthened when some of its components closely match the background, while others differ strongly from it (Cott 1940). If all the components contrast with the background, then the body outline can be easily detected, but if only part of the pattern is indistinguishable from the background, then body-edge detection becomes much more difficult (Merilaita and Lind 2005; Stevens and Cuthill 2006). However, organisms that use edge disruption are freed from background matching (Schaefer and Stobbe 2006); species that employ this camouflage strategy can take advantage of more habitats because they are not restricted to areas where they are the most cryptic (Ruxton et al., 2004; Sherratt et al., 2005). Disruptive coloration may, thus, be linked to the evolution of generalist prey that exploit multiple regions and require patterns suitable as camouflage in different environments (Endler 2006). Several studies have suggested that disruptive coloration is possibly more advantageous than background matching for habitat generalists (Cuthill et al., 2005; Merilaita and Lind 2005; Endler 2006; Schaefer and Stobbe 2006).

Turtle camouflage has not received widespread attention, with no research on disruptive camouflage, and only a few studies on other camouflage strategies (see Nafus et al., 2015; Xiao et al., 2016). The sympatric keeled box turtle (*Cuora mouhotii*) and the Indochinese box turtle (*C. galbinifrons*) have distinct coloration that reflects background matching and disruptive coloration, respectively. The former exhibits uniform coloring and flat scutes (Fig. 1A; 2A), while the latter's body is divided by two yellow stripes and curved scutes (Fig. 1B; 2B). Both species are active in forests, often partially burying their bodies in leaf litter. Xiao et al. (2017) have suggested that the color of the part exposed to the substrates is similar to the color of the leaves, thus, functioning to reduce predation risk. Considering that the illusory depth edges help conceal targets from predators (Adams et al., 2019), we hypothesized that the flat scutes of keeled box turtles would result in two planes with different depths between the top plane and the ground plane (see Fig. 1A), resulting in the top scutes being highlighted in the substrates. Thus, predators would most likely detect the top scutes, which could interfere with the ability of predators to visually segment the real edges of turtles from the background. Moreover, ridged keels run along the bridge where the top scute and aide scute join. (see Fig. 2A), enhancing the appearance of false internal edges. Therefore, we predicted that the flat top scutes of keeled box turtles would offer structural disruption, while the contrasting stripes of Indochinese box turtles

Fig. 1. Photographs of *Cuora mouhotii* on bare ground (A) and *C. galbinifrons* on broad-leaved substrate (B). The carapace lengths of *C. mouhotii* and *C. galbinifrons* are 157.42 mm and 182.84 mm, respectively.

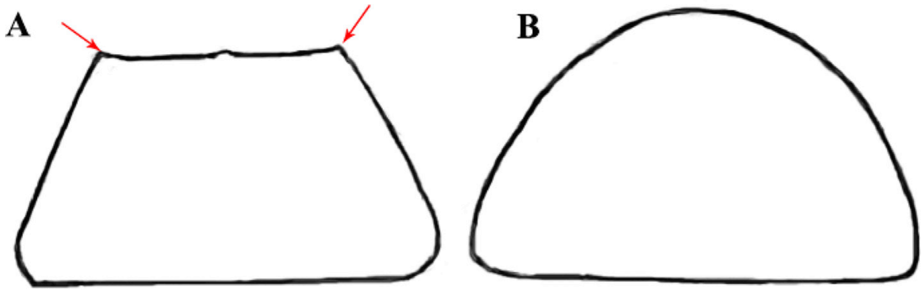

Fig. 2. Illustration of two carapace (upper shell) cross-sections. A: The keeled box turtle (*Cuora mouhotii*) has flatter scutes (the frontal view of the carapace resembles a trapezoid, forming two parallel planes above and below). The red arrows indicate the two keels at the edges of the top carapace. B: The Indochinese box turtle (*C. galbinifrons*) has a domed carapace (the frontal view of the carapace is semicircular). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

would act as disruptive coloration. We also predicted that these turtles would exhibit a higher disruptive degree on their preferred substrates.

2. Materials and methods

2.1. Animal and substrate selection

Field work was conducted at the Diaoluoshan Natural Reserve, a rainforest 860–914 m above sea level in Hainan Province, People's Republic of China (18°43′53″ N, 109°52′10″ E) from September to December 2019. We used 12 adult Indochinese box turtles (7 females and 5 males) and 12 adult keeled box turtles (8 females and 4 males) from the reserve. There is no obvious sexual dimorphism in body color between male and female individuals. We selected three substrate types (broad leaves, bamboo leaves, and bare ground) based on a previous long-term study of microhabitat selection in the two species, and used the same telemetry sites (for detailed data, see Xiao et al., 2017). Grass was selected as the control, because neither species preferred it (Xiao et al., 2017).

2.2. Photography

Turtles and substrates were photographed using a Canon EOS 550D camera with a Canon lens (EF-S24–70 mm f/2.8, 8.2 megapixels). The turtles were collected and photographed in the same substrate. Photography in the field took place between 11:00 a.m. and 2:00 p.m., when natural light allowed for good turtle visualization, and a black umbrella was used to counter the direction of light entry to ensure uniform illumination. The camera was placed on a tripod and positioned almost perpendicular to the substrates so that a constant image size could be maintained. Images were all saved in the uncompressed RAW format (Stevens et al., 2007) for subsequent color measurements and analyses. An 18% standard gray card was placed at the core of the images to avoid photographic bias (Mennon, China, 14.5 cm × 9.5 cm) and enable the normalization of estimated chromaticity while controlling for illumination variation. We collected 80 substrate images (20 images in each substrate) and 24 turtle images. Photographs were calibrated using the "Generate multispectral image" function in Image J (Troscianko et al., 2015). The images were aligned and linearized in terms of radiance and standardized to control for differing light conditions using the 18% standard gray card (Stevens et al., 2007; Troscianko et al., 2015).

2.3. Coloration measurement and calculation

The coloration in the middle and side stripes (or scutes; Fig. 3) of the carapaces were quantified in ImageJ using CIE$L^*a^*b^*$ (International Commission on Illumination) color spaces (Robertson 2007). Calibrated images were converted to $L^*a^*b^*$ stack, and the L^*, a^*, and b^* values of the middle and side stripes were measured respectively. The color components within CIE$L^*a^*b^*$ color spaces were represented as three numbers, with L^* indicating lightness, and a^* and b^* representing color changes through the red-green and yellow-blue color axes, respectively. Since direct visual searching is an important method for humans to catch turtles, and human eyesight has successfully been used to test the camouflage efficiency of turtles (Nafus et al., 2015; Xiao et al., 2016), so we used human eyesight to evaluate if color differences are distinguishable. Between-stripe chroma differences were calculated using Δa^*b^*; human eyes can identify chromaticity differences if Δa^*b^* is > 6 units (McCormick-Goodhart and Wilhelm 2003). In addition, we calculated the lightness difference (ΔL^*) between the middle and side stripes. The chroma differences (Δa^*b^*) and lightness difference (ΔL^*) were calculated as follows:

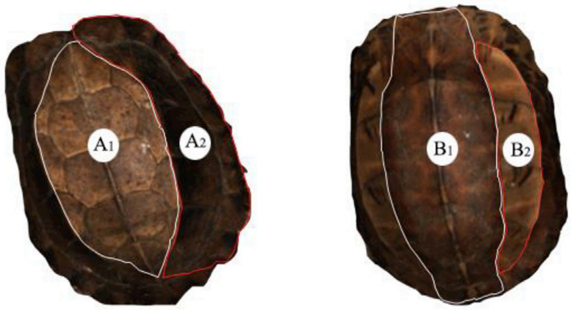

Fig. 3. Color or structure segmentation diagram. A_1 and A_2 are the middle and side scutes of *Cuora mouhotii*, respectively; B_1 and B_2 are the middle and side stripes of *C. galbinifrons*, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

$$\Delta a^* b^* = \sqrt{(a_m^* - a_s^*)^2 + (b_m^* - b_s^*)^2}$$

$$\Delta L^* = |L_m^* - L_s^*|$$

where “m” is the middle stripe on the carapace, and “s” is a side stripe on the carapace.

2.4. Disruption

We used the GabRat method, which uses angle sensitive filters to measure the ratio of false edges to coherent edges around the target outline in Image J (Troscianko et al., 2017; Price et al., 2019). This method takes into account the direction of perceived edges versus actual body outlines, enabling it to distinguish between false edges and coherent edges (Troscianko et al., 2017). Standardized photographs were exported as binary mask images in the TIFF format (white prey against a black background). A Gabor filter was applied to each pixel around the carapace edge using a sigma level (filter size) of 5, which is dependent on the px/mm of the carapace (Troscianko et al., 2017). Edge disruption per turtle was measured against a neutral background using the same sigma level. For each substrate image, the subject turtle was placed in five random positions that did not overlap with each other, allowing for the calculation of a general mean from five GabRats. This procedure was repeated on all 80 substrate images, resulting in 9600 edge-disruption measurements. GabRat values range from 0 to 1, with <0.2 being low edge disruption and >0.4 being high edge disruption (Troscianko et al., 2017; Price et al., 2019). GabRat calculations were performed by a third party unaware of study's intention.

2.5. Statistical analysis

All statistical procedures were performed in SPSS 18.0 (SPSS, Inc., Chicago, IL), and all data were expressed as means ± SE. A Kolmogorov–Smirnov test was used to test the normality of GabRat and lightness difference data before analysis. We compared interspecific GabRat differences in four kinds of substrates, and interspecific lightness difference using independent-sample t tests. Between-substrate GabRat differences between preferred and non-preferred substrates within each species were analyzed using Mann–Whitney U tests. The significance level was set at $P < 0.05$, and the Bonferroni method was used to correct the significance level when multiple comparisons were made.

3. Results

3.1. Color differences between middle and side stripes

The carapaces of keeled box turtles have uniform coloration because the chroma difference between the middle and side stripes was below the distinguishable threshold ($\Delta a^*b^* < 6$, Table 1). However, the middle and side stripes differed

Table 1
Color differences between the middle and side strips of two *Cuora* spp. carapaces. Δa^*b^*: chroma difference.

Name	Sample size	Δa^*b^*	ΔL^*	
			Mean ± SE	*t*-test
C. galbinifrons	12	6.34 ± 0.54	3.36 ± 0.52	$P < 0.001$
C. mouhotii	12	5.12 ± 0.34	10.26 ± 0.86	

significantly in the carapaces of Indochinese box turtles ($\Delta a^*b^* > 6$, Table 1). The lightness difference (ΔL^*) between middle stripe and side stripe of keeled box turtles were significantly greater than Indochinese box turtles ($t = -6.873$, $df = 22$, $P < 0.001$; Table 1).

3.2. Disruption

Disruption was effective in all substrates (GabRat > 0.2, Fig. 4). Keeled box turtles had GabRat values (broad-leaved, 0.404 ± 0.004; grass, 0.334 ± 0.004; bare ground, 0.388 ± 0.004; bamboo-leaved, 0.377 ± 0.003) that were higher than Indochinese box turtles in all substrates (broad-leaved,0.392 ± 0.002, $t = 2.757$, $P = 0.006$; grass, 0.320 ± 0.003, $t = 2.749$, $P = 0.006$; bare ground, 0.359 ± 0.003, $t = 5.540$, $P < 0.001$; bamboo-leaved, 0.369 ± 0.003, $t = 1.857$, $P = 0.064$). Broad-leaved substrates provided the best disruption for both species, with disruption for keeled box turtles being particularly high (GabRat > 0.4). The GabRat values of each species significantly differed among the four kinds of substrates ($P < 0.001$, lower than Bonferroni method adjusted the significance level of 0.0083). Indochinese box turtles had significantly higher edge disruption in broad leaves and bamboo leaves (preferred substrates, 0.381 ± 0.002) than on bare ground and grass (non-preferred substrates, 0.340 ± 0.002, $Z = -12.115$, $P < 0.001$). Keeled box turtles had higher edge disruption in broad leaves and on bare ground (preferred substrates, 0.396 ± 0.003) than in bamboo leaves and grass (non-preferred substrates, 0.356 ± 0.003, $Z = -9.904$, $P < 0.001$).

4. Discussion

We found that keeled box turtles have uniform coloration on their carapaces, while the side and middle stripes of Indochinese box turtles have a chroma difference, that can be distinguished. Furthermore, keeled box turtles have a significant greater than Indochinese box turtles in lightness difference (ΔL^*) between the middle and side stripe of the carapace. This difference highlighted the middle stripes of keeled box turtles and resulted in a false edge that generate structural disruption, while chroma difference of Indochinese box turtles may generate colored disruption.

The results showed that the GabRat values of keeled box turtles were significantly higher than those of Indochinese box turtles in four kinds of substrates, indicating that the former species exerted a stronger disruptive effect. The carapaces of keeled box turtles feature two prominent ridges on their otherwise flat scutes with directional illumination, which results in light and dark areas on either side of the ridges, creating a strong contrast along the ridge. Additionally, the flat scutes result in two planes of different depths between the top and ground planes (see Fig. 1A), resulting in the top carapace forming internal edges (see Fig. 3A_1). These edges were the "real" depth edges caused by the structural depth of the turtles and are completely different from the illusory depth edges caused by the coloration pattern of snakes (Adams et al., 2019). This is consistent with the structural disruption leading to a camouflage advantage against predators. This could be considered a structural analog of edge-enhanced disruption, which interferes with object detection and recognition (Egan et al., 2016; Sharman et al., 2018;

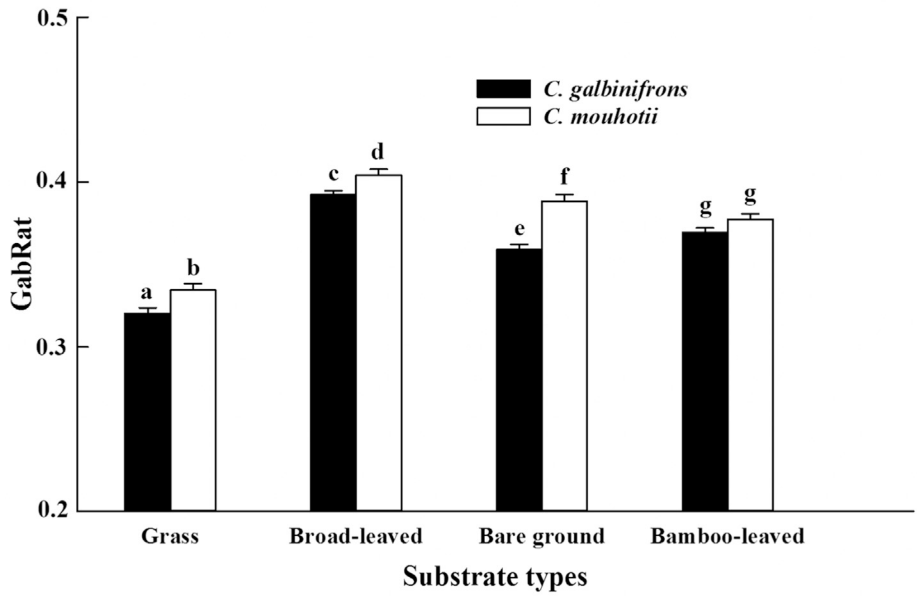

Fig. 4. GabRat values of two *Cuora* spp. on each substrate. *C. mouhotii* had higher values than *C. galbinifrons* on each substrate (independent-sample *t*-test). Different lowercase letters above the bars represent significant differences, while the same letters represent no significant difference (comparison of each species in different substrates or interspecies in the same substrate).

Adams et al., 2019). An alternative explanation of the high GabRat is that the trapezoidal shape of keeled box turtle (see Fig. 2A) results in an enhanced depth cue between the middle stripe and background, and the side scutes form an oblique plane travelling upward from a horizontal ground plane. The highlight of the middle stripe interferes with a predator's ability to segment the actual boundary of a turtle from its background. It is speculated that such shapes may result in binocular visual predator more likely to detect internal edge, but not real edges (Finlayson et al., 2013; Cammack and Harris 2015; Adams et al., 2019).

In contrast, the Indochinese box turtles had lower GabRat values, which may indicate that they are easier to be detected. Compared to keeled box turtles, they have an arched carapace. Although chroma differences cause disruptive coloration, a continuous smooth structure results in little difference in depth, and smaller differences in lightness may reduce the color differences between middle and side stripes (Nakayama and Silverman 1986). Thus, predators can overcome the effects of disruptive coloration (Nityananda and Read 2017; Adams et al., 2019). Several studies have supported the idea that lowering contrast reduces the effectiveness of disruptive camouflage (Cuthill et al., 2005; Merilaita and Lind 2005; Stevens et al., 2009). Moreover, this result corroborates the findings of previous studies showing that humans can better distinguish striped individuals (Stevens et al., 2011; Troscianko et al. 2013, 2018).

In addition, both species had some disruptive effects across the four kinds of substrates, indicating that the camouflage mechanism is likely inherent to turtles themselves. This is consistent with the fact that the disruptive effect is intrinsic to shore crabs (*Carcinus maenas*) (Price et al., 2019). These findings support the idea that disruptive coloration allows animals to use a wider range of substrates and is possibly advantageous for habitat generalists (Cuthill et al., 2005; Endler 2006; Schaefer and Stobbe 2006; Price et al., 2019). Moreover, as mentioned above, keeled box turtles exhibit greater disruption than Indochinese box turtles. This may correlate with the use of substrates. Keeled box turtles have a significantly larger home range and move more frequently than Indochinese box turtles (Wang 2010), increasing encounters with distinct substrates. Other studies have reported a positive correlation between disruptive coloration and survival in a range of heterogeneous substrates (Cuthill et al., 2005; Schaefer and Stobbe 2006; Tan et al., 2020). However, the keeled box turtles' flatter carapace is less resistant than that of Indochinese box turtles to mechanical pressure and more vulnerable to predator bites (unpublished data). Therefore, better disruptiveness is crucial to the survival of keeled box turtles (Ruxton et al., 2004; Sherratt et al., 2005; Ramirezdelgado and Castillo 2020). The potential threat of predation could exert a strong selective pressure for structural camouflage.

Additionally, the keeled box turtles were distributed more densely than the Indochinese box turtles in Diaoluoshan Natural Reserve (Wang et al., 2011; Lian 2009), suggesting that their higher disruptive effect may provide a survival advantage. Moreover, both species are known to be active and half-cover themselves in leaf litter (Xiao et al., 2017). This may reduce detectability through employing multiple camouflage strategies, such as background matching and masquerading (Hultgren and Stachowicz 2008; Mayani-Parás et al., 2015; Holveck et al., 2017; Hughes et al., 2019). However, we cannot exclude the influence of other factors on population density. For example, keeled box turtles can protect themselves from predators by hiding in rock crevices (Xiao et al., 2017).

The results from examining Indochinese box turtles verified our hypothesis that the false edge caused by yellow stripes acts as camouflage for this species. Their disruptive effect in broad-leaved and bamboo-leaved substrates was significantly better than on bare ground and in grass. Broad-leaved and bamboo-leaved substrates, which appear to more closely match the background color of Indochinese box turtles, are more complex than bare ground or grass, and background complexity reduces detectability (Dimitrova and Merilaita 2014; Xiao and Cuthill 2016).

The disruptive effect of keeled box turtles was significantly better on broad leaves and bare ground than on bamboo leaves and grass, possibly because it does not match the latter two substrates but does seem to match the former two. These findings confirm that disruptive coloration is contingent on background matching (Cott 1940; Schaefer and Stobbe 2006; Adams et al., 2019). The keeled box turtles were often found on bare ground and in rock crevices beneath the high forest during our long-term ecological field study (Wang, 2010; Xiao et al., 2017), and their flat scutes heightened the disruptive effect on bare ground and broad-leaved areas around those crevices. Similarly, the dorsal coat color of the plains pocket gopher (*Geomys bursarius*) highly matches to their background surrounding, which is their burrow (Krupa and Geluso 2000). While this hypothesis is compelling, we would require further analyses to verify whether the carapace color of keeled box turtles actually matches the bare ground.

Relevant research on disruptive camouflage in vertebrates is rare. In amphibians, the dorsal patterns of leaf litter toads (*Rhinella alata*) provide disruptive coloration (Mcelroy 2016), and Australian frogs (*Limnodynastes tasmaniensis*) exhibit disruptive camouflage over a wide range of spatial scales (Osorio and Srinivasan 1991). A comparison of tadpoles with different colors and patterns showed that disruptively colored tadpoles gained an anti-predation advantage over uniformly colored tadpoles (Eterovick et al., 2018; Gontijo et al., 2018). Among reptiles, edge-enhancement patterns in snakes enhances the effect of disruptive camouflage (Egan et al., 2016; Adams et al., 2019). For example, water snake (*Natrix sipedon sipedon*) coloration changes from disruptive to uniform between the juvenile and adult stages (Beatson 1976). In birds, Japanese quails tended to choose dark substrates that disrupted egg outlines as nesting material (Lovell et al., 2013). Similarly, another study using avian cup-nests found that contrasting materials provided disruptive camouflage (Mulder et al., 2020). In mammals, the dark leg markings of even-toed ungulates serve as disruptive coloration (Stoner et al., 2003). Despite there being few studies, it seems that structural disruptive camouflage is rare, with most other vertebrates using disruptive coloration instead.

Overall, we are the first to demonstrate disruptive camouflage in turtles. We are also the first to test for structural disruption in vertebrates, and we demonstrated that it is even more disruptive than disruptive coloration in their preferred substrates. Whether such structures contribute significant advantages to a species' survival requires testing with actual predators. This study opens a new direction in vertebrate camouflage research that focuses on the influence of body shape and color on visual disruption. Furthermore, because many turtle species (e.g., *Notochelys platynota*, *Staurotypus triporcatus*, and *Staurotypus salvinii*) generate misleading internal edges through carapace structure, we recommend empirically verifying structural disruption as a camouflage strategy in turtles.

Authors' contributions

Fanrong Xiao, P. George Lovell, and Haitao Shi designed the study. Rongping Bu and Zihao Ye collected the samples. Rongping Bu and Zihao Ye performed the fieldwork. Rongping Bu, Fanrong Xiao, and Haitao Shi analyzed the data and wrote the manuscript. P. George Lovell edited the manuscript. All authors read and approved the final version of the manuscript.

Ethics approval

Fieldwork was conducted 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-2014-002), which conforms to the Law of People's Republic of China. No turtles were harvested for this study or incurred injury or death while in the traps, and all the turtles were released in the original capture area at the end of the experiment.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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