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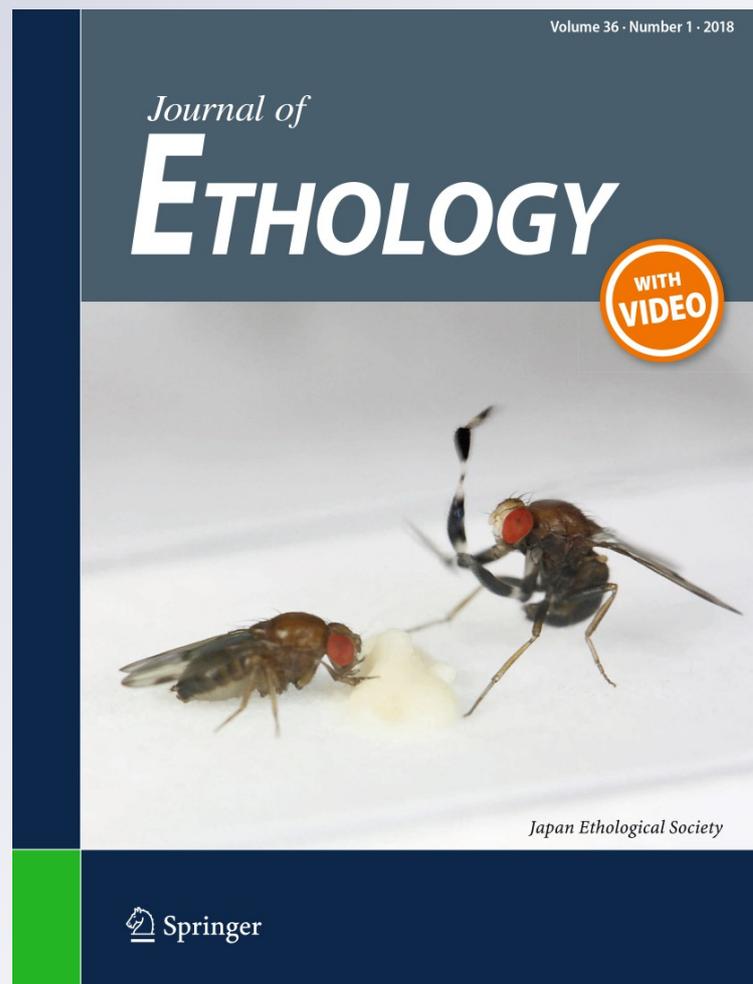
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Aposematic colouration does not explain fear of snakes in humans

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Abstract Snakes elicit a higher level of fear than other vertebrate animals, yet specific cues responsible for fear of snakes are equivocal. The bright colouration hypothesis suggests that fear responses to snakes are triggered by aposematic colouration, not by snakes per se. We investigated the role of aposematic colouration in fear of snakes in a sample of 10- to 15-year-old Slovak children. Both aposematically and cryptically coloured snakes presented as both colour and black-and-white pictures received higher perceived fear scores than other vertebrates. This suggests that aposematic colouration does not play a crucial role in eliciting fear of snakes. Our results support the snake detection theory suggesting that the human visual system has been influenced by long coexistence between predatory snakes and mammals. As a result, humans have evolved an attentional bias ultimately focused on the correct and rapid detection of these threats.

Keywords Snake detection theory · Bright colouration hypothesis · Predator · Perceptual bias

Introduction

Snakes rank among the most successful reptiles, evidenced by the high number of snake species (> 3,000) inhabiting all continents except Antarctica (Vidal and Hedges 2009). Molecular evidence suggests that snakes originated in the Jurassic (~ 150 million years ago) (Head 2015). Since this time, snakes have hunted for small placental mammals, from which the order Primates originated around 85 million years later (Zhang et al. 2008). Humans today are still targets of snake predation (Headland and Greene 2011). As a result, humans, similarly to non-human primates, manifest a superior acquired fear of snakes and a visual bias toward detection of snakes (LoBue and Rakison 2013; Öhman and Mineka 2001, 2003).

Snake detection theory (SDT) suggests that snake predation influenced the evolution of primates by means of favouring acute perceptual abilities ultimately minimizing the likelihood of being attacked (Isbell 2006, 2009; Van Le et al. 2013). For example, detection of a snake by adult humans among fear-irrelevant distractors (e.g. flowers, mushrooms) on a touchscreen was consistently faster than vice versa (LoBue and DeLoache 2008; Öhman et al. 2001; for reviews and replications see LoBue and Rakison 2013). Similar results were obtained by testing children, who have in all probability limited experience and knowledge about the dangerousness of snakes (LoBue and Rakison 2013; Penkunas and Coss 2013a, b). This supports the idea that humans have perceptual biases for the rapid detection of evolutionary threats (LoBue et al. 2010).

In current research, Van Le et al. (2013) implanted electrodes in individual neurons of the brains of three macaque monkeys (*Macaca fuscata*) and found that the macaque brain responds selectively to images of snakes, which provides neurobiological support for the SDT (see review by Soares

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et al. 2017). The specific features which cause perceptual biases towards snakes compared with other visual stimuli remain, however, unclear. Humans, as well as most primates, have trichromatic vision which evolved as a response to the chromatic signals produced by fruits (Regan et al. 2001) or leaves (Dominy and Lucas 2001). Experiments with captive tamarins corroborated an idea that trichromats took significantly more ripe fruits than did dichromats (Smith et al. 2003). Alternatively, however, trichromatic vision may be advantageous for detection of predators (Vogel et al. 2006). Physiological research showed that the primate visual system is most attuned to highly chromatic bright colours such as yellow (Yoshioka and Dow 1996; Yoshioka and Vautin 1996). At least in white-faced capuchin monkeys, bright, but multi-coloured snakes are more provocative in triggering alarm calls than bright, but unicoloured snakes (Meno et al. 2013). Bright, multi-coloured snake skin, may be perceived by potential predators as a warning (aposematic) signal (Humphrey 1976; Ruxton et al. 2004; Smith 1977; Smith and Mostrom 1985). It is therefore not surprising that warm colours and colours producing high contrast between a foreground and a background capture stronger human visual attention than cool/neutral or less contrasting colours (Choi and Suk 2015). Bright and highly saturated colours generate a decrease in visual proximity of the stimuli (Egusa 1983; Mount et al. 1956). This suggests that high visibility of bright colours could be adaptive, because these colours may signal both food availability and/or the presence of a predator.

According to the bright colour hypothesis (LoBue and DeLoache 2011; Ruxton et al. 2004), animals which survived an attack by a conspicuously coloured snake could associate its colour with danger and avoid the snake in the future (Brattstrom 1955). Indeed, children perceived aposematically coloured snakes less positively compared with inconspicuous animals (Souchet and Aubret 2016). Snake skin pictures account for larger early posterior negativity than lizard skin pictures or bird plumage pictures, which suggests that snake skins capture more automatic attention than lizard skins or bird plumage (Van Strien and Isbell 2017). In contrast, snakes were detected on a touchscreen more quickly than frogs or flowers by preschool children regardless of whether the snakes were presented as coloured or black-and-white pictures (Hayakawa et al. 2011; LoBue and DeLoache 2011; Masataka et al. 2010). Macaque monkeys (*Macaca fuscata*), reared in a laboratory and with no experience of snakes detected grayscale pictures of snakes more quickly than flowers or koalas (Kawai and Koda 2016; Shibasaki and Kawai 2009). This evidence suggests that snake colour does not play a prominent role in their detection.

In the present study, we investigated the bright colour hypothesis by examining perceived fear of aposematically

and cryptically coloured snakes in comparison with other vertebrates on a sample of Slovak children. We predicted that if negative responses to snakes evolved as generalized aversive responses to their bright colour not to snakes per se (Souchet and Aubret 2016), then (1) fear of aposematic snakes is similar to fear of other aposematic vertebrates, (2) fear of cryptic snakes is similar to fear of other cryptic vertebrates.

Materials and methods

Participants

The study was conducted in January and August 2017. The participants (63 males and 93 females) consisted of children of secondary school age. The questionnaire was administered to all participants in selected classes irrespective of the participants' attitudes towards animals. The age of the participants ranged from 10 to 15 years (mean = 12.6, SE = 0.12). This age group was chosen intentionally, because we used Likert-scale ratings, which are more sensitive when compared to dichotomous instruments (Bowling 2005). Likert-scale data obtained from children < 10 years of age, however, may not be reliable (Mellor and Moore 2013). Age and sex of participants were noted. Experimental groups of participants ($n = 110$) were asked to rate colourful pictures while the control group ($n = 46$) rated black-and-white pictures.

Measures

We presented 32 colour pictures to experimental groups of children in lecture halls. Each picture depicted one animal (a frog, reptile, bird or mammal) and was presented individually. Each category of animal contained two aposematic and two cryptic species. There are suggestions that bright colouration of snakes might correlate with aggressive behaviour and venom potency, although no evidence has been found for this as yet [see Allen et al. (2013) for discussion]. In order to avoid these possible associations, the same pictures were manipulated in Adobe Photoshop in such a way that the aposematic animals were changed to cryptic ones and the cryptic to aposematic ones [for more details see Prokop and Fancovicová (2013)]. As a result, each participant was presented with images of eight aposematic species of vertebrate (frogs, snakes, birds and mammals; two species per taxon) and eight images of cryptic species of the same taxa. An additional eight pictures were manipulated pictures of aposematic vertebrates, which were presented as cryptic, and eight pictures of cryptic vertebrates, which were presented as aposematic. Each participant was shown all 32 pictures in random order. Each picture was presented for

1 min. Over this time, the participants rated their perceived fear ('Imagine you encounter the animal in the picture in the field. How afraid would you be of this animal?') and their willingness to protect the animal ('Do you think that this species should be protected by law?') on a 5-point ordinal scale (respectively, 1 = not at all, 5 = extremely dangerous; 1 = not necessary to protect, 5 = protection extremely important). The latter variable was used to examine whether fear of snakes is domain-specific, i.e. snake colour influences perceived fear, no fear-irrelevant ratings. The ratings of fear and willingness to protect the animals were reliable (Cronbach's $\alpha = 0.90$ and 0.81 , respectively). Control children rated fear ($\alpha = 0.78$) and willingness to protect ($\alpha = 0.6$) the same (unmanipulated pictures of eight aposematic species vertebrates and eight cryptic species of the same taxa). We calculated the individual scores for each subscale by averaging the responses to the constituent items.

Statistical analyses

Data were not normally distributed (Kolmogorov-Smirnov test), thus, the Friedman test, a non-parametric form of ANOVA, was used to analyse the data. Post hoc tests were performed with the Wilcoxon signed-ranks test. To reduce a type I error rate with multiple comparisons, p -values were Bonferroni corrected ($\alpha = 0.05/3 = 0.016$). All tests are two-tailed, and performed with SPSS (version 23).

Results

Colour pictures

Friedman ANOVA revealed significant differences in ratings of fear of aposematic as well as cryptic animals ($H_3 = 227.87$

and 233.78 , both $p < 0.001$, respectively). Contrary to predictions 1 and 2, the fear scores of snakes were significantly higher than the scores of other vertebrates regardless of whether the snakes were aposematic or cryptic (Figs. 1, 2). Almost identical results were obtained by comparing manipulated pictures of snakes and other vertebrates; both manipulated aposematic and cryptic snakes received higher fear scores compared to other vertebrates ($H_3 = 253.71$ and 212.29 , both $p < 0.001$, respectively) (Figs. 1, 2). These results provide no support for the bright colour hypothesis.

Willingness to protect aposematically coloured snakes, as well as snakes in manipulated pictures, did not differ from willingness to protect other vertebrates ($H_3 = 5.96$ and 2.75 , $p = 0.11$ and 0.43 , respectively) (Fig. 3).

There were significant differences in willingness to protect cryptic animals ($H_3 = 11.05$, $p = 0.011$), although the Wilcoxon signed-ranks test revealed only a higher willingness to protect mammals compared with snakes (Fig. 4). No differences were found in willingness to protect manipulated cryptic vertebrates ($H_3 = 0.86$, $p = 0.84$) (Fig. 4). These results suggest that snakes are perceived more negatively than other vertebrates specifically in the fear domain, not in the individual's willingness to protect them.

Black-and-white pictures

Friedman ANOVA revealed significant differences in ratings of fear of aposematic as well as cryptic animals ($H_3 = 112.1$ and 118.29 , both $p < 0.001$, respectively). Again, the fear scores of snakes were significantly higher than the scores of other vertebrates regardless of whether the snakes were aposematic or cryptic (Fig. 5). Willingness to protect aposematic as well as cryptic animals was influenced by taxon ($H_3 = 19.9$ and 22.3 , both $p < 0.001$, respectively). Children were less willing to protect snakes compared with other,

Fig. 1 Ratings of fear between aposematically coloured snakes and other vertebrates. Box plots represent medians, 25th and 75th percentiles, minimum and maximum values. The differences between the variables are based on the Wilcoxon signed-ranks test ($***p < 0.001$)

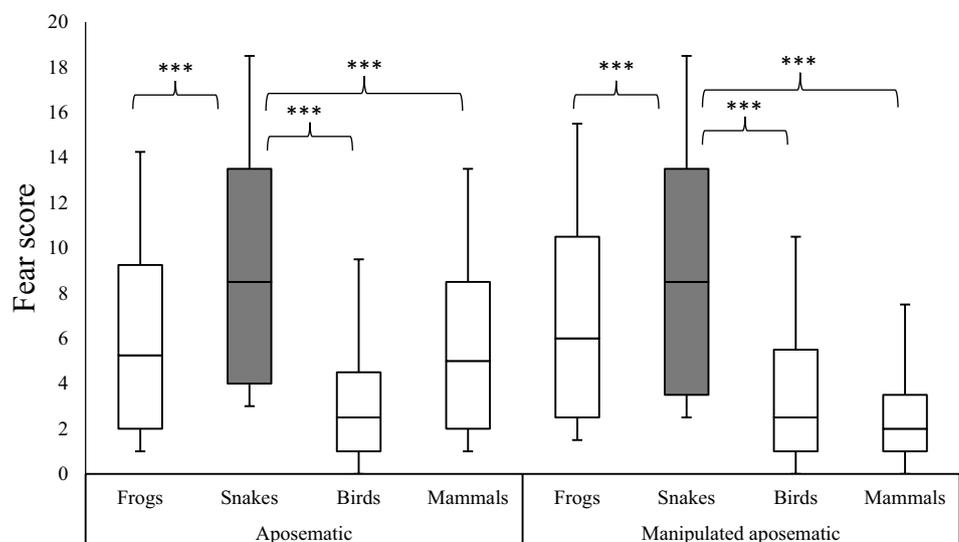


Fig. 2 Ratings of fear between cryptically coloured snakes and other vertebrates. *Box plots* represent medians, 25th and 75th percentiles, minimum and maximum values. The differences between the variables are based on the Wilcoxon signed-ranks test (** $p < 0.001$)

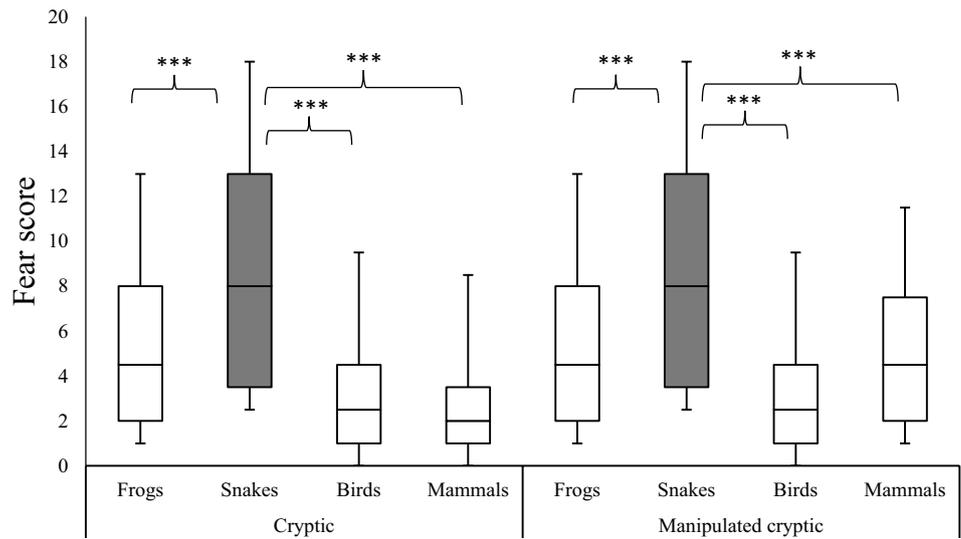


Fig. 3 Ratings of willingness to protect aposematically coloured snakes and other vertebrates. *Box plots* represent medians, 25th and 75th percentiles, minimum and maximum values. No significant differences were found between variables

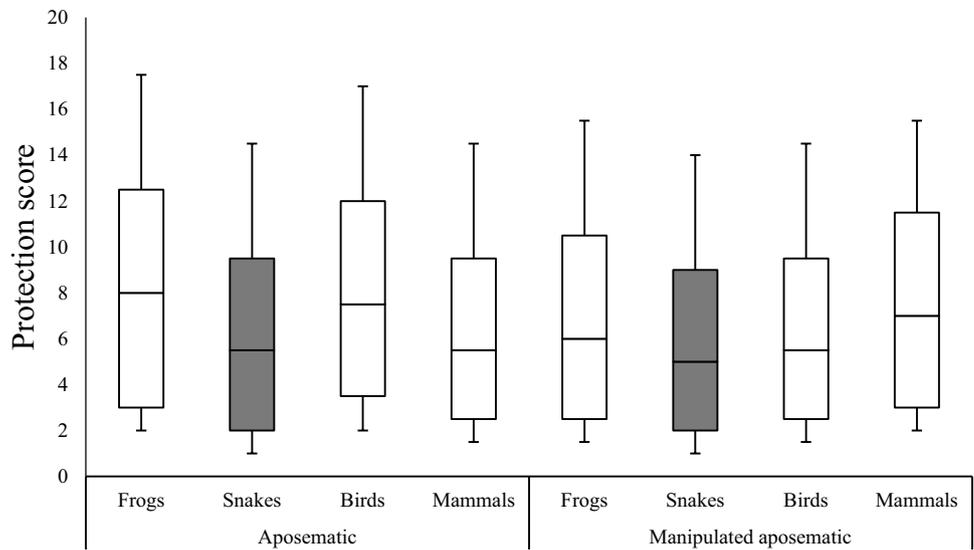


Fig. 4 Ratings of willingness to protect cryptically coloured snakes and other vertebrates. *Box plots* represent medians, 25th and 75th percentiles, minimum and maximum values. The differences between the variables are based on the Wilcoxon signed-ranks test (** $p < 0.01$)

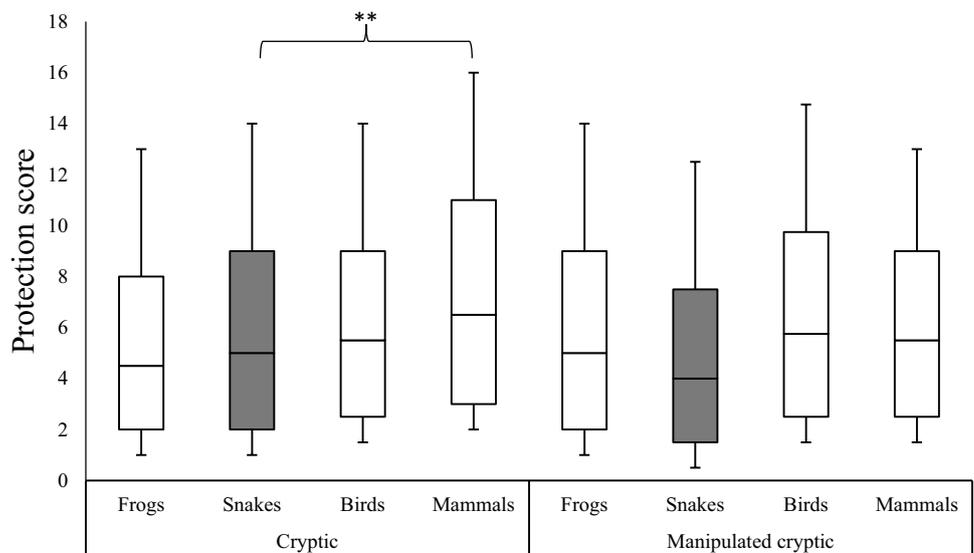
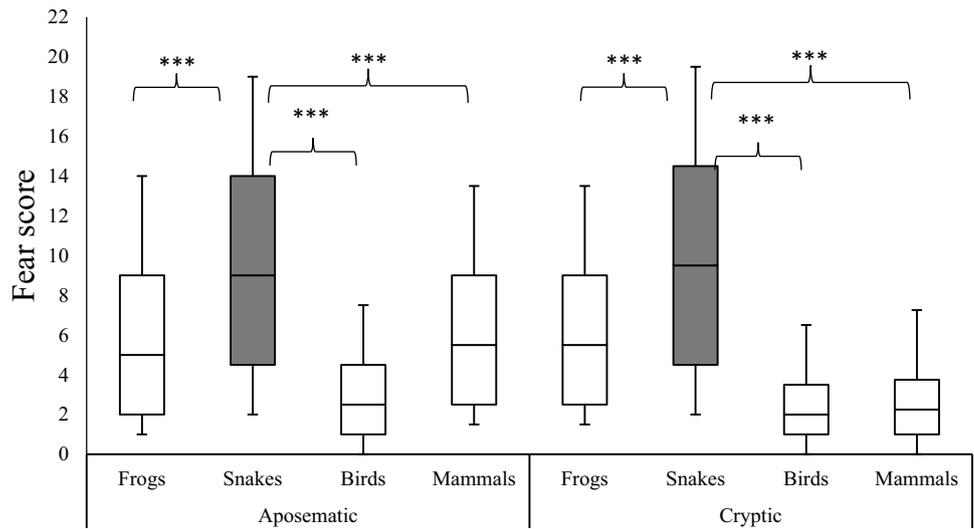


Fig. 5 Ratings of fear between snakes and other vertebrates presented as black-and-white pictures. *Box plots* represent medians, 25th and 75th percentiles, minimum and maximum values. The differences between the variables are based on the Wilcoxon signed-ranks test (***p* < 0.001)



particularly aposematically coloured, vertebrates (Fig. 6). These results suggest that snakes are perceived more negatively than other vertebrates specifically in the fear domain, although an individual's willingness to protect them was significantly lower for aposematic snakes presented as black-and-white pictures.

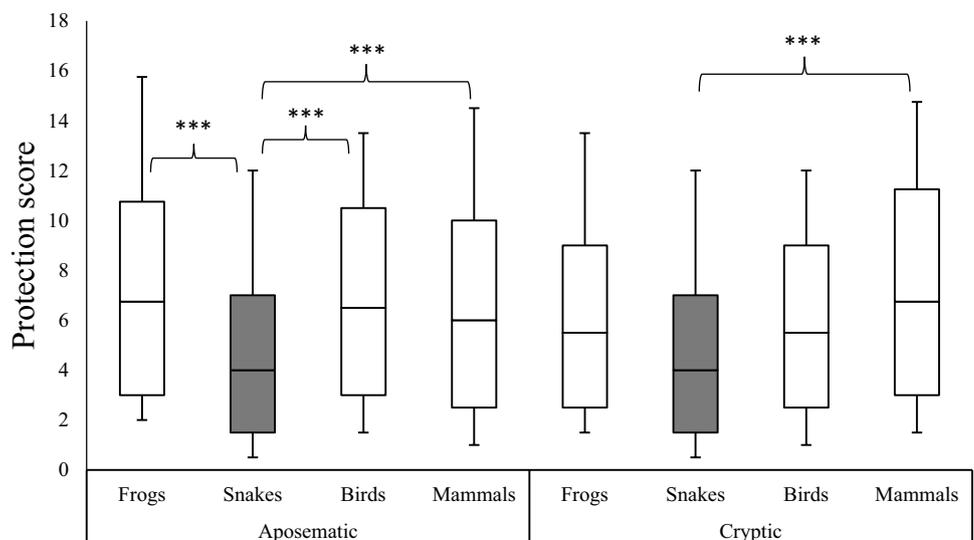
Discussion

This study investigated the role of bright colouration in human fear of snakes. Specifically, the bright colour hypothesis states that primates evolved aversive responses to colours that are frequently associated with danger (Ruxton et al. 2004). Consequently, snakes are perceived by primates with fear, because they are often brightly coloured (Souchet and Aubret 2016). Our results do not support the

bright colouration hypothesis, because humans manifested a higher level of fear towards snakes than to other vertebrates irrespective of their colour.

Previous research demonstrated that aposematically coloured animals are detected by humans faster than non-aposematic animals (Bohlin et al. 2012; Hayakawa et al. 2011), which may suggest that fear of aposematic animals is higher than fear of cryptic animals (Prokop and Fančovičová 2013). In the case of snakes, however, aposematic colouration significantly contributes to their perceived beauty (Marešová et al. 2009). It also seems that a snake's (coiled) shape (Kawai and He 2016; LoBue and DeLoache 2011), striking posture (Masataka et al. 2010) and/or snake skin scales (Kawai and He 2016; Van Strien and Isbell 2017), but not colouration per se play a crucial role in our rapid detection of snakes (LoBue and DeLoache 2011).

Fig. 6 Ratings of willingness to protect snakes and other vertebrates presented as black-and-white pictures. *Box plots* represent medians, 25th and 75th percentiles, minimum and maximum values. The differences between the variables are based on the Wilcoxon signed-ranks test (***p* < 0.001)



Our results are in sharp contrast to those of Souchet and Aubret (2016) who suggest that aposematic colours, along with snakes' dorsal zig-zag patterns, could influence negative perception of snakes. Pictures of cryptic snakes (both original and experimentally altered) in our study showed snakes without zig-zag patterns, indicating that colouration was not responsible for higher fear of snakes. Furthermore, the median scores for fear of aposematically (Fig. 1) and cryptically coloured snakes (Fig. 2), as well as for snakes presented as black-and-white pictures (Fig. 5), were almost identical, which provides additional support for the low importance of colour in eliciting fear of snakes. Souchet and Aubret (2016), however, used simple drawings of snakes (apart from snakes' heads which were photographed) instead of more realistic photographs. These drawings could be perceived by children differently than real snakes, because it is not clear how these are perceived subcortically (Baynes-Rock 2017). Further, in-depth study investigating neural activity of the superior colliculus as an early input area of the brain in snake detection (Almeida et al. 2015) in response to more and less realistic visual cues of snakes is required.

In conclusion, fear of snakes does not seem to be influenced by aposematic colouration. Colour variation showed little effect on the discomfort engendered by snake photographs. Aposematic colours undoubtedly increase human attention, but the specialized visual system of humans that evolved during a long predatory relationship between snakes and mammals allows for quick and accurate detection of snakes in all probability through the repetitive cross-hatched grid of snake scales, or snakes' body shape and movement. Finally, the larger repetitive blotches of the one confirmed suite of snake predators of humans, e.g., African, Indian, and Indonesian pythons, coupled with their large size might be important for quick identification of partially exposed pythons hidden in detritus and leaf litter on the forest floor.

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Compliance with ethical standards

Ethical approval Written parental consent was received before the research was carried out. All procedures performed in the studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committees and with the 1964 Helsinki Declaration and its later amendments or comparable ethical standards.

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