

## Protective coloration of European vipers throughout the predation sequence

Janne K. Valkonen<sup>a,\*</sup>, Annu Vakkila<sup>b</sup>, Susanna Pesari<sup>a</sup>, Laura Tuominen<sup>a</sup>,  
Johanna Mappes<sup>a</sup>

<sup>a</sup> University of Jyväskylä, Department of Biological and Environmental Science, Jyväskylä, Finland

<sup>b</sup> University of Oulu, Department of Biology, Oulu, Finland

### ARTICLE INFO

#### Article history:

Received 12 September 2019

Initial acceptance 1 November 2019

Final acceptance 5 March 2020

MS number 19-00621R

#### Keywords:

animal coloration  
conspicuousness  
crypsis  
dazzle coloration  
detection  
flicker–fusion  
predation  
vision  
warning signal  
zigzag pattern

Antipredator adaptations in the form of animal coloration are common and often multifunctional. European vipers (genus *Vipera*) have a characteristic dorsal zigzag pattern, which has been shown to serve as a warning signal to potential predators. At the same time, it has been suggested to decrease detection risk, and to cause a motion dazzle or flicker–fusion effect during movement. We tested these hypotheses by asking whether (1) the zigzag pattern decreases detection risk and (2) the detection is dependent on the base coloration (grey or brown) or the snake's posture (coiled, basking form or S-shaped, active form). Additionally, (3) we measured the fleeing speed of adders, *Vipera berus*, and calculated the flicker rate of the zigzag pattern, to see whether it is fast enough to cause a flicker–fusion effect against predators. Our results show that the zigzag pattern reduced detectability regardless of base coloration or posture of the snake. The brown zigzag morph was detected less often than the grey zigzag morph. The fleeing speed of adders appeared to be fast enough to induce a flicker–fusion effect for mammalian predators. However, it is unlikely to be fast enough to induce the flicker–fusion effect for raptors. Our findings highlight that the colour pattern of animals can be multifunctional. The same colour pattern that can decrease detection by predators can also serve as a warning function once detected, and potentially hinder capture during an attack.

© 2020 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Predation is a sequential process that begins with detection, recognition and capture and ends with handling and consumption (Endler, 1991). Various forms of coloration have evolved to protect prey during these separate steps; two of the best-studied functions of protective coloration are crypsis and aposematism, which protect individuals during the first two steps of the predation sequence. Cryptic prey gain protection by avoiding detection and recognition, whereas aposematic prey advertise their secondary defences so that predators avoid them after they have been detected (Cott, 1940; Poulton, 1890). Warning signal size, symmetry and conspicuousness have been found to enhance prey recognition and signal learning (Forsman & Merilaita, 1999; Gittleman & Harvey, 1980; Lindström, Alatalo, Mappes, Riipi, & Vertainen, 1999; Roper & Redston, 1987). Thus, at first these two strategies may appear to operate in opposition: cryptic prey are expected to be inconspicuous, whereas aposematic prey are expected to evolve conspicuousness (Ruxton, Allen, Sherratt, & Speed, 2018).

Even the most toxic prey, however, are preyed upon at least occasionally by predators. For example, poison frogs are consumed by birds, snakes, crabs and spiders (Rojas, 2017) and some toxic salamanders fall victim to snakes that have evolved immunity to their defences (Brodie, Ridenhour & Brodie, 2002). Thus, under some conditions, it could be beneficial even for aposematic prey to reduce detection through crypsis, so long as their warning signals can still be identified once detected (Wüster et al., 2004). Indeed, not all aposematic species appear overtly conspicuous, and some of them are difficult to detect despite their contrasting colour patterns (reviewed in Endler & Mappes, 2004; Tullberg, Merilaita, & Wiklund, 2005; Bohlin, Tullberg, & Merilaita, 2008). Warning signals can be designed so that at longer viewing distances, contrasting and easily recognizable colour markings exceed the visual resolution of the perceiver, thus blending together and appearing as a uniform colour that matches the background more closely (Barnett et al., 2017; Barnett et al., 2016).

In addition, colour patterns that hinder capture after a predator has decided to attack could provide extra protection. Two distinct mechanisms have been proposed to have this effect. The first is dazzle camouflage, which can impede the accurate estimation of

\* Correspondence: J. K. Valkonen, Department of Biological and Environmental Science, University of Jyväskylä, PO Box 35, FI-40014, Finland.

E-mail address: [janne.valkonen@jyu.fi](mailto:janne.valkonen@jyu.fi) (J. K. Valkonen).

prey speed and trajectory, without changing its appearance (Thayer, 1909). Certain colour patterns (e.g. stripes, zigzags and check squares) can produce this effect for human subjects (e.g. Scott-Samuel, Baddeley, Palmer, & Cuthill, 2011; Stevens, Yule, & Ruxton, 2008). In the second mechanism, the flicker–fusion effect, adjacent colour patterns blur together because of the physiological limitations of receiver vision and can change prey appearance during rapid movement (Pough, 1976; Umeton, Tarawneh, Fezza, Read, & Rowe, 2019). For example, black and white stripes can instead appear grey and blurry. The significance of the flicker–fusion effect in the protective coloration of animals is vastly understudied and poorly understood (Umeton, Read, & Rowe, 2017).

European vipers (genus *Vipera*) are venomous and exhibit a characteristic dorsal zigzag pattern (Arnold, Burton, & Ovenden, 1978). These snakes do not appear overtly conspicuous, but the zigzag pattern acts as a warning signal that is avoided by avian predators (Niskanen & Mappes, 2005; Valkonen, Niskanen, Björklund, & Mappes, 2011; Wüster et al., 2004). The zigzag pattern of vipers is also suggested to function as cryptic coloration because the attack rate on the black form of the adder, *Vipera berus*, which have been suggested to be more conspicuous, is higher than that on the zigzag form (Andrén & Nilson, 1981). The cryptic function of the zigzag pattern is also supported by studies where variation in coloration and zigzag pattern of a European viper, *Vipera latastei*, and a mimetic viperine snake, *Natrix maura*, were found to be associated with different habitat types (Santos et al., 2014). Neither Andrén and Nilson (1981) nor Santos et al. (2014) studied how predators find differently coloured snakes in their natural habitats; indeed, the detectability of snakes has never been addressed. Interestingly, Santos et al. (2018) found that the zigzag morph of *N. maura*, which mimics adders, is found in a wide range of habitat types; the striped morph, in contrast, is found almost exclusively in open habitats. This observation fits with the theory of aposematism, which predicts that aposematic species are capable of occupying a wider variety of habitats than cryptic species (Speed, Brockhurst, & Ruxton, 2010). Thus, there is support for both a cryptic and an aposematic function of the zigzag pattern.

Zigzag colour patterns can also have movement-dependent functions (Scott-Samuel et al., 2011; Stevens et al., 2008). While both striped and zigzag patterns have been shown to produce a dazzle effect (Hämäläinen, Valkonen, Mappes, & Rojas, 2015; Scott-Samuel et al., 2011; Stevens et al., 2008), the zigzag pattern of adders has also been suggested to cause a flicker–fusion effect (Lindell & Forsman, 1996; Shine & Madsen, 1994). We suggest that the function of the zigzag pattern of snakes is context dependent, allowing them to be cryptic when they are basking in a coiled posture and acting as a warning signal that facilitates recognition when they are on the move or detected.

To assess whether the zigzag pattern of vipers plays a role in crypsis, we tested its effect on their detectability. Likewise, we tested whether the detectability is associated with the base coloration (grey or brown) or posture (active or basking) of snakes. To evaluate the movement-dependent protective function of the zigzag pattern, we tested whether the fleeing speed of adders is high enough for mammalian and avian predators to experience a flicker–fusion effect.

## METHODS

### *Study Species*

Adders are a widely distributed, common and mostly diurnal species in the genus *Vipera* (Arnold et al., 1978). Males are



**Figure 1.** Colour morphs of snake replicas used to test the effect of coloration, posture and zigzag pattern on the detectability of snakes.

typically greyish with a dark dorsal zigzag pattern, whereas females are typically brownish with a less contrasting dark zigzag pattern. Juveniles are typically light brown. This colour difference suggests the possibility of different antipredator strategies between the sexes and age classes. Less contrasting brownish females and young juveniles may rely more on crypsis than higher contrast males (Lindell & Forsman, 1996; Shine & Madsen, 1994). Many populations also have a proportion of black melanistic individuals, and in some populations striped and nearly uniform grey individuals are present (Arnold et al., 1978; Nikolić & Simović, 2017).

### Detectability

To test whether the zigzag pattern of snakes reduces their detectability we exposed artificial snakes with five different colour morphs (black, brown, brown with zigzag, grey, and grey with zigzag) to humans as surrogate predators (Fig. 1). The use of humans as surrogate predators allowed us to test the detectability of snakes without the possible biases in foraging decisions that can affect natural predators (e.g. preference for some prey types; Penney, Hassall, Skevington, Abbott, & Sherratt, 2012; Barnett et al., 2016). To mimic subadult/adult size we made 40 cm long and ca. 2 cm thick snake replicas with precoloured plasticine (Caran D'ache Model'art, black 496, brown 497, grey 808), and hand-painted a zigzag pattern on them with satin black acrylic paint (Amsterdam Standard series, Lamp black). We placed 10 snake replicas of each colour morph, half of them in a coiled and half in an S-shaped posture (representing a basking snake or a mobile snake, respectively), along transect trails. The order of the snake replicas was rotated to avoid having adjacent snake replicas of the same colour morph. The distance between snake replicas was ca. 10 m (10–12 steps). The trail followed the terrain around three Biological Research Stations (Oulanka, Konnevesi and Lammi) in Finland. We asked 129 participants from different biology field courses to walk along the trails at normal walking speed and inform a guide following them when they detected a snake replica. The person guiding the participants through the trails recorded the time it took for each participant to finish the trail and the accuracy of snake replica detection. One snake replica (grey zigzag) disappeared during the trials at Konnevesi research station and was thus missing for 17 participants, most likely because of a predation attempt by a natural predator. Therefore, our data sets consist of 6443 detection/nondetection events with 129 participants in three locations.

To analyse the effect of the snake replicas' coloration on their detectability, we used a generalized linear mixed-effect model with binomial distribution and logit link function. The binary response

**Table 1**

Significance of terms included in binomial generalized linear mixed-effect model explaining detection probabilities of artificial snakes

Term in the model	df	LRT	$P \chi^2$
Duration of trial	1	20.66	0.025
Colour*Pattern*Posture	1	5.00	< 0.001

LRT: likelihood ratio test.

variable (detected or not) was explained by the colour (brown or grey) and the posture (coiled or S-shaped) of the snake replica, the presence of a zigzag pattern, and their two and three-way interactions. To control for the fact that participants walked at different speeds, the time that it took for them to finish the trail was included as a covariate. Because of our sampling structure, we included participant ID nested within location as a random effect in our model. The analysis was conducted using the lme4 package in R (Bates, Mächler, Bolker, & Walker, 2014).

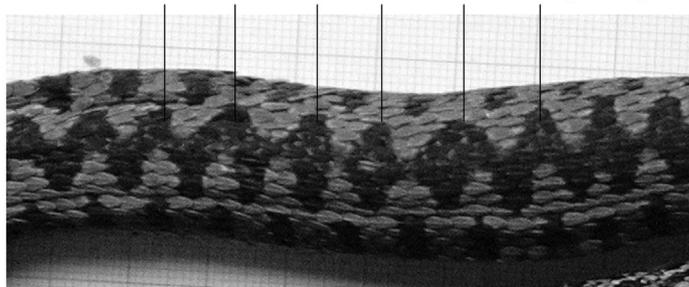
### Fleeing Speed

To evaluate the possibility of a flicker–fusion effect we measured the fleeing speed of adders. We captured 18 individuals (five females, 13 males), from four populations in the Jyväskylä area of Central Finland. They were housed in individual terraria (30 x 20 cm and 15 cm high) within a climate chamber. Snakes were kept in captivity only a few days and returned to the place of capture after the experiment. They were not fed during captivity, but water was offered ad libitum. Snakes were kept on a 12:12 h day:night cycle at 23.5–35 °C/10 °C. These temperatures were chosen because they are within the range of natural conditions for adders. The preferred body temperature of the adder is between 31.7 °C and 33.8 °C (Herczeg et al., 2007). Thus, to avoid overheating them, they were never exposed to the experimental maximum temperature for more than 2 h.

The fleeing performance of adders was measured by placing them at the end of a 190 cm long and 56 cm wide arena with pine bark as substrate. Snake body temperature was measured with a laser thermometer (Prego P–8380B) at the beginning of each fleeing trial. During the trials the snakes were provoked to flee by gently tapping them on the tail, and their fleeing speed was recorded with a video camera (Canon Legria HF R37) placed on top of the arena. The fleeing performance of each snake was measured seven to eight times. Snakes were allowed to recover between trials in their housing terraria (minimum 0.5 h), and they were tested a maximum of four times per day.

After completing the fleeing trials, we weighed and measured the full body length of each snake and then photographed them.

## Adjacent colour patches in the zigzag pattern



**Figure 2.** To determine the spatial frequency of the zigzag pattern we counted adjacent patches in the pattern within 10 cm and extrapolated that to the body length.

**Table 2**  
Estimates of binomial generalized linear mixed-effect model estimating the detection probability of differently coloured artificial snakes

Fixed effects	Estimate	SE	Z	P
(Intercept) Black coiled	-1.830	0.476	-3.841	<0.001
Duration of trial	0.198	0.042	4.760	<0.001
Grey	0.249	0.118	2.116	0.034
Brown	0.109	0.117	0.936	0.349
S-shaped	-0.202	0.116	-1.740	0.082
Zigzag	-1.027	0.119	-8.640	<0.001
Grey *S-shaped	-0.356	0.165	-2.158	0.031
Brown *S-shaped	0.209	0.165	1.265	0.206
Grey*Zigzag	0.157	0.168	0.933	0.351
Zigzag *S-shaped	-0.021	0.168	-0.127	0.899
Grey*Zigzag pattern*S-shaped	0.528	0.236	2.237	0.025

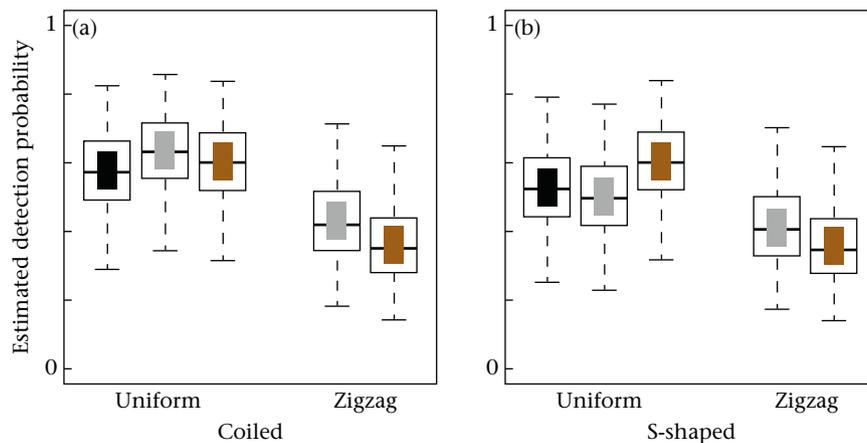
Variances of the random effects: participant ID: 0.2409; location: 0.0441.

We used photographs to determine the spatial frequency of adjacent colour patches (i.e. number of zigzags within body length) by counting the transitions in the pattern within a 10 cm length at the middle of the body and extrapolating that to total body length (Fig. 2). The maximum sprinting speed of snakes was determined from video recordings by measuring the longest distance that snakes reached within a 0.4 s time window in each trial. To obtain the maximum flicker frequency that snakes can achieve, we converted the maximum fleeing speed to body lengths/s, and multiplied the speed by the number of zigzags within the body length. This yielded our response variable, the number of adjacent colour patches of the zigzag pattern passing by a fixed point within 1 s during fleeing (flicker rate in Hz).

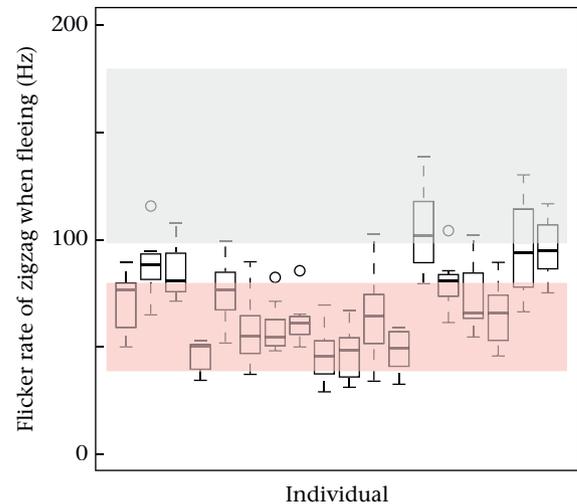
To test the effects of sex, size and body temperature on maximum flicker rate we used a general linear mixed model with a Gaussian distribution. The response variable, flicker rate, was explained by including weight, sex and body temperature as explanatory variables, and individual ID as a random factor to account for repeated measures within individuals.

#### Ethical Note

We followed the ASAB/ABS Guidelines for the Use of Animals in Research, the guidelines of the University of Jyväskylä and Finnish legislation. The experiment was permitted by the National Animal Experiment Board (ESAVI/9114/04.10.07/2014).



**Figure 3.** Estimated detection probabilities of uniformly coloured and zigzag patterned artificial snakes in (a) a coiled posture (basking) and (b) an S-shaped posture (active). Coloured rectangles indicate the base coloration of the snake replicas. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range.

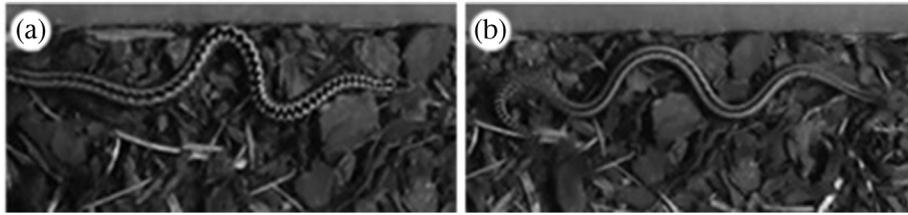


**Figure 4.** Flicker frequencies of adder zigzag pattern when fleeing. The grey shaded rectangle represents the critical flicker threshold range of avian vision (Coles, 207; Olsen, 2005; Boström et al., 2016) and the red one the flicker threshold range of mammalian predators (Loop & Berkley, 1975; Coile et al., 1989). The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.

## RESULTS

### Detectability

The probability of detecting snake replicas was best described by the three-way interaction of coloration, presence of zigzag pattern and posture (Tables 1, 2, Fig. 3). The detectability of black and grey snake replicas without the zigzag pattern appeared to be lower in the active (S-shaped) posture than in the basking (coiled) posture, whereas the detectability of uniform brown snake replicas was similar regardless of their posture. The detection probability of grey and brown zigzag patterned snake replicas was lower compared to the uniform ones in both postures (Fig. 3), suggesting a cryptic function of the zigzag pattern. The brown zigzag patterned (female adder morph) snake replicas were less likely to be detected than the grey zigzag patterned (male adder morph) ones, which indicates asymmetric benefits of the zigzag pattern between the sexes of this species. Interestingly, the posture did not affect the detectability of either brown or grey zigzag patterned snake



**Figure 5.** Illustration of the change in appearance of a male adder, *Vipera berus*, induced by the flicker–fusion effect. (a) At a slow speed the perceiver can separate adjacent colour patches of the zigzag pattern. (b) At a higher speed, adjacent colour patches form a more uniform striped colour pattern.

replicas (Fig. 3). Thus, it seems that the crypsis provided by the zigzag pattern is not affected by the snake posture.

#### Fleeing Speed

Of 18 adders, 14 achieved a fleeing speed fast enough to cause the flicker rate of their zigzag pattern to exceed 80 Hz (Fig. 4). The maximum detected fleeing speed was 89.7 cm/s (minimum 53.9 and mean 74.2), and the corresponding flicker rate of the zigzag pattern was 138.8 Hz (minimum 52.5 and mean 94.4). Not surprisingly, a drop in body temperature decreased the fleeing speed of adders, thus reducing the flicker rate of the zigzag pattern ( $t = 7.583$ ,  $P < 0.001$ ). We did not detect a significant effect of either weight or sex on the fleeing performance of adders (all  $t \leq \pm 1.080$ ,  $P \leq 0.295$ ).

#### DISCUSSION

In this study we tested whether the dorsal zigzag pattern typical of European vipers can offer protection against predation by reducing detectability and causing a flicker–fusion effect while the snakes flee. Our findings indicate that artificial snakes with a zigzag pattern were harder to detect than those without zigzags, which confirms that this pattern can also function as cryptic coloration, as suggested by circumstantial evidence (Andr n & Nilson, 1981; Santos et al., 2014, 2018). The fleeing speed of adders also suggests that the zigzag pattern could induce a flicker–fusion effect in some predators (see discussion below). Altogether, the findings reported here, combined with past results, suggest that the zigzag pattern of snakes can (1) provide protection from predation by initially being cryptic, (2) act as a warning signal if detected, and (3) hinder the risk of capture if attacked by using motion dazzle camouflage and the flicker–fusion effect.

The base coloration of male adders is typically greyer than in females, which are browner. Both sexes exhibit the dorsal zigzag pattern, but the pattern in females is often less contrasting against the base coloration (Arnold et al., 1978). During the mating season, which takes place at springtime, when the ground vegetation is low, male adders are more active than females and thus more likely to be detected by predators (Madsen, 2011). Our findings show that patterned grey viper replicas were more easily detected than brown ones, suggesting that the grey male adders may be more conspicuous to predators than their brown female counterparts. Increased conspicuousness in warning signals increases signal efficacy (Gittleman & Harvey, 1980; Lindstr m et al., 1999; Nokelainen, Hegna, Reudler, Lindstedt, & Mappes, 2012; Roper & Redston, 1987). This, together with our findings here, suggests asymmetric benefits of the zigzag pattern between the sexes: more conspicuous males may be more protected against predation than less conspicuous females via aposematism, whereas females may be better protected than males via crypsis. This asymmetric benefit

of the protective coloration may explain the existence of sexual dimorphism in the adder. However, based on evidence from previous studies (Niskanen & Mappes, 2005; Santos et al., 2014; Valkonen et al., 2011; W ster et al., 2004) and our present study, it is evident that both patterned colour morphs gain some degree of protection via the simultaneous effects of the aposematic and cryptic functions of the zigzag pattern.

Adders have been suggested to increase their probability of escaping predator attacks through a flicker–fusion illusion made possible by their colour patterns (Shine & Madsen, 1994; Lindell & Forsman, 1996). This illusion requires movement of an object across the visual field of a perceiver at a speed fast enough to cause the object's adjacent colour patterns to blur together and appear to be a uniform average colour (Pough, 1976). So far, suggestions about the flicker–fusion effect of the zigzag pattern have been based on observations of antipredator behaviour and survival of differently coloured snakes (Shine & Madsen, 1994; Lindell & Forsman, 1996). Our measurements of fleeing speed show that most adders can reach a speed high enough to induce a flicker–fusion effect in mammalian predators (up to 80 Hz; Loop & Berkley, 1975; Coile et al., 1989; Fig. 4). However, it is very unlikely this would be efficient against avian predators because their critical flicker threshold can be as high as 180 Hz (Coles, 2007; Olsen, 2005; Bostr m et al., 2016; Fig. 4). The critical flicker threshold of vision systems is expected to decrease in low light conditions and thus flicker–fusion should happen at lower speeds (reviewed in Titcomb, Kikuchi, & Pfennig, 2014; Umeton et al., 2017). Adders, however, are diurnal and most active in good weather conditions. Thus, they are most likely to be exposed to predation when viewing conditions are optimal for visual predators.

Interestingly, when the dorsal zigzag pattern of a fleeing adder blurs together it appears as a uniform dorsal stripe (Fig. 5). Striped patterns can hinder the estimation of speed and trajectory of movement, thus increasing the probability that a fleeing snake escapes from a predator's attack (H m l inen et al., 2015; Jackson, Ingram, & Campbell, 1976; Murali & Kodandaramaiah, 2016; Pough, 1976; Scott-Samuel et al., 2011). The zigzag pattern has been found to cause a similar effect, but it is unclear whether one of the patterns is more effective than the other (Scott-Samuel et al., 2011; Stevens et al., 2008). The flicker–fusion effect was defined by Pough (1976) as an antipredator strategy where adjacent colours of prey blur together to form an 'average' coloration that changes the prey's background matching. This is also how the flicker–fusion effect is often considered in current literature, which has led to both the formulation of confusing hypotheses and equally confusing interpretation of results (reviewed in Umeton et al., 2017). Although the existence of the flicker–fusion effect is well known in vision science, its role in predator avoidance by prey has rarely been demonstrated (Umeton et al., 2019). Our results highlight again the importance of considering the adaptive value of each antipredator strategy

from the point of view of the receiver(s). As our results show, flicker–fusion may not work towards raptors but can be effective against other predator types. Furthermore, the flicker–fusion effect does not seem to change prey coloration to make it more ‘background matching’, as originally suggested by Pough (1976; see Fig. 5). Instead, it seems to change the snake’s patterning appearance such that it may more effectively induce motion dazzle camouflage. In line with Umeton et al. (2017), we suggest that the flicker–fusion effect should be viewed as a mechanism (not as an antipredator strategy) that can change the appearance of a moving prey if it moves fast enough. How prey appearance changes depends mainly on its colour patterning and the visual capabilities of the perceiver (i.e. the predator).

Understanding the conceptual differences between the mechanisms shaping animal protective coloration is undeniably important for recognizing the evolutionary forces behind antipredator strategies. We highlight that it is equally important to understand that these conceptually opposing strategies and mechanisms (e.g. aposematism, crypsis, motion dazzle camouflage and flicker–fusion effect) are not mutually exclusive, but can all work sequentially during a single predation event.

## Acknowledgments

We thank all the participants that attended the detectability experiment and research stations of Lammi (University of Helsinki), Konnevesi (University of Jyväskylä) and Oulanka (University of Oulu) for allowing us to conduct our experiments during the field courses. We also acknowledge Sebastiano De Bona, Katja Rönkä, Swanne Cordon, Bibiana Rojas, Anne Winters, Chloe Fouilloux, Ossi Nokelainen and the anonymous referees who provided valuable comments on the manuscript. This study was funded by Societas Biologica Fennica Vanamo, Oulun Luonnonystävään Yhdistys and The Academy of Finland (SA252411).

## References

- Andrén, C., & Nilson, G. (1981). Reproductive success and risk of predation in normal and melanistic colour morphs of the adder, *Vipera berus*. *Biological Journal of the Linnean Society*, 15, 235–246.
- Arnold, E. N., Burton, J. A., & Ovenden, D. (1978). *Field guide to the reptiles and amphibians of Britain and Europe*. London, U.K.: Collins.
- Barnett, J. B., Cuthill, I. C., & Scott-Samuel, N. E. (2017). Distance-dependent pattern blending can camouflage salient aposematic signals. *Proceedings of the Royal Society of London B*, 284(1858), 20170128.
- Barnett, J. B., Redfern, A. S., Bhattacharyya-Dickson, R., Clifton, O., Courty, T., Ho, T., et al. (2016). Stripes for warning and stripes for hiding: Spatial frequency and detection distance. *Behavioral Ecology*, 28(2), 373–381.
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). *Fitting linear mixed-effects models using lme4*. arXiv preprint arXiv:1406.5823.
- Bohlin, T., Tullberg, B. S., & Merilaita, S. (2008). The effect of signal appearance and distance on detection risk in an aposematic butterfly larva (*Parnassius apollo*). *Animal Behaviour*, 76(3), 577–584.
- Boström, J. E., Dimitrova, M., Canton, C., Håstad, O., Qvarnström, A., & Ödeen, A. (2016). Ultra-rapid vision in birds. *PLoS One*, 11(3), e0151099.
- Brodie, E. D., Jr., Ridenhour, B. J., & Brodie, E. D., III (2002). The evolutionary response of predators to dangerous prey: Hotspots and coldspots in the geographic mosaic of coevolution between garter snakes and newts. *Evolution*, 56(10), 2067–2082.
- Coile, D. C., Pollitz, C. H., & Smith, J. C. (1989). Behavioral determination of critical flicker fusion in dogs. *Physiology & behaviour*, 45(6), 1087–1092.
- Coles, B. H. (2007). *Essentials of avian medicine and surgery*. Oxford, U.K.: Blackwell.
- Cott, H. B. (1940). *Adaptive coloration in animals*. London, U.K.: Methuen.
- Endler, J. A. (1991). Interactions between predators and prey. In J. R. Krebs, & N. B. Davies (Eds.), *Behavioural ecology. An evolutionary approach* (pp. 169–196). Cambridge, U.K.: Cambridge University Press.
- Endler, J. A., & Mappes, J. (2004). Predator mixes and the conspicuousness of aposematic signals. *American Naturalist*, 163, 532–547.
- Forsman, A., & Merilaita, J. (1999). Fearful symmetry: Pattern size and symmetry affects aposematic signal efficacy. *Evolutionary Ecology*, 13, 131–140.
- Gittleman, J. L., & Harvey, P. H. (1980). Why are distasteful prey not cryptic? *Nature*, 286(5769), 149–150.
- Hämäläinen, L., Valkonen, J., Mappes, J., & Rojas, B. (2015). Visual illusions in predator–prey interactions: Birds find moving patterned prey harder to catch. *Animal Cognition*, 18(5), 1059–1068.
- Herczeg, G., Saarikivi, J., Gonda, A., Perälä, J., Tuomola, A., & Merilä, J. (2007). Sub-optimal thermoregulation in male adders (*Vipera berus*) after hibernation imposed by spermiogenesis. *Biological Journal of the Linnean Society*, 92(1), 19–27.
- Jackson, J. F., Ingram, W., III, & Campbell, H. W. (1976). The dorsal pigmentation pattern of snakes as an antipredator strategy: A multivariate approach. *American Naturalist*, 110(976), 1029–1053.
- Lindell, L. E., & Forsman, A. (1996). Sexual dichromatism in snakes: Support for the flicker–fusion hypothesis. *Canadian Journal of Zoology*, 74(12), 2254–2256.
- Lindström, L., Alatalo, R. V., Mappes, J., Riipi, M., & Vertainen, L. (1999). Can aposematic signals evolve by gradual change? *Nature*, 397(6716), 249–251.
- Loop, M. S., & Berkley, M. A. (1975). Temporal modulation sensitivity of the cat I: Behavioral measures. *Vision Research*, 15(5), 555–561.
- Madsen, T. (2011). Cost of multiple matings in female adders (*Vipera berus*). *Evolution*, 65(6), 1823–1825.
- Murali, G., & Kodandaramaiah, U. (2016). Deceived by stripes: Conspicuous patterning on vital anterior body parts can redirect predatory strikes to expendable posterior organs. *Royal Society Open Science*, 3(6), 160057.
- Nikolić, S., & Simović, A. (2017). First report on a trichromatic lowland *Vipera berus bosniensis* population in Serbia. *Herpetological Conservation and Biology*, 12(2), 394–401.
- Niskanen, M., & Mappes, J. (2005). Significance of the dorsal zigzag pattern of *Vipera latastei gaditana* against avian predators. *Journal of Animal Ecology*, 74(6), 1091–1101.
- Nokelainen, O., Hegna, R. H., Reudler, J. H., Lindstedt, C., & Mappes, J. (2012). Trade-off between warning signal efficacy and mating success in the wood tiger moth. *Proceedings of the Royal Society B*, 279(1727), 257–265.
- Olsen, P. (2005). *Wedge-tailed eagle*. Melbourne, Australia: CSIRO.
- Penney, H. D., Hassall, C., Skevington, J. H., Abbott, K. R., & Sherratt, T. N. (2012). A comparative analysis of the evolution of imperfect mimicry. *Nature*, 483(7390), 461.
- Pough, F. H. (1976). Multiple cryptic effects of crossbanded and ringed patterns of snakes. *Copeia*, 1976(4), 834–836.
- Poulton, E. B. (1890). *The colours of animals: their meaning and use especially considered in the case of insects*. London, U.K.: Kegan Paul, Trench, Trübner & Co.
- Rojas, B. (2017). Behavioural, ecological, and evolutionary aspects of diversity in frog colour patterns. *Biological Reviews*, 92(2), 1059–1080.
- Roper, T. J., & Redston, S. (1987). Conspicuousness of distasteful prey affects the strength and durability of one-trial avoidance learning. *Animal Behaviour*, 35(3), 739–747.
- Ruxton, G. D., Allen, W. L., Sherratt, T. N., & Speed, M. P. (2018). *Avoiding attack: The evolutionary ecology of crypsis, aposematism and mimicry* (2nd ed.). New York, NY: Oxford University Press.
- Santos, X., Azor, J. S., Cortés, S., Rodríguez, E., Larios, J., & Pleguezuelos, J. M. (2018). Ecological significance of dorsal polymorphism in a Batesian mimic snake. *Current Zoology*, 64(6), 745–753.
- Santos, X., Vidal-García, M., Brito, J. C., Fahd, S., Llorente, G. A., Martínez-Freiria, F., et al. (2014). Phylogeographic and environmental correlates support the cryptic function of the zigzag pattern in a European viper. *Evolutionary Ecology*, 28(4), 611–626.
- Scott-Samuel, N. E., Baddeley, R., Palmer, C. E., & Cuthill, I. C. (2011). Dazzle camouflage affects speed perception. *PLoS One*, 6(6), e020233.
- Shine, R., & Madsen, T. (1994). Sexual dichromatism in snakes of the genus *Vipera*: A review and a new evolutionary hypothesis. *Journal of Herpetology*, 28(1), 114–117.
- Speed, M. P., Brockhurst, M. A., & Ruxton, G. D. (2010). The dual benefits of aposematism: Predator avoidance and enhanced resources collection. *Evolution*, 64(6), 1622–1633.
- Stevens, M., Yule, D. H., & Ruxton, G. D. (2008). Dazzle coloration and prey movement. *Proceedings of the Royal Society of London B*, 275(1651), 2639–2643.
- Thayer, G. H. (1909). *Concealing-colouration in the animal kingdom: an exposition of the laws of disguise through color and pattern: being a summary of Abbott H. Thayer's discoveries*. New York, NY: Macmillan.
- Titcomb, G. C., Kikuchi, D. W., & Pfennig, D. W. (2014). More than mimicry? Evaluating scope for flicker–fusion as a defensive strategy in coral snake mimics. *Current Zoology*, 60(1), 123–130.
- Tullberg, B. S., Merilaita, S., & Wiklund, C. (2005). Aposematism and crypsis combined as a result of distance dependence: Functional versatility of the colour pattern in the swallowtail butterfly larva. *Proceedings of the Royal Society of London B*, 272(1570), 1315–1321.
- Umeton, D., Read, J. C., & Rowe, C. (2017). Unravelling the illusion of flicker fusion. *Biology Letters*, 13(2), 20160831.
- Umeton, D., Tarawneh, G., Fezza, E., Read, J. C., & Rowe, C. (2019). Pattern and speed interact to hide moving prey. *Current Biology*, 29(18), 3109–3113.
- Valkonen, J., Niskanen, M., Björklund, M., & Mappes, J. (2011). Disruption or aposematism? Significance of dorsal zigzag pattern of European vipers. *Evolutionary Ecology*, 25(5), 1047–1063.
- Wüster, W., Allum, C. S., Bjargardóttir, I. B., Bailey, K. L., Dawson, K. J., Guenioui, J., et al. (2004). Do aposematism and batesian mimicry require bright colours? A test, using European viper markings. *Proceedings of the Royal Society of London B*, 271(1556), 2495–2499.