Protective coloration of European vipers throughout the predation sequence

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Protective coloration of European vipers throughout the predation sequence

Abstract

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 1) whether the zigzag pattern decreases detection risk and 2) whether the detection is dependent on the base coloration (grey or brown) or the snake's posture (coiled, to represent basking, or S-shaped, to represent an active snake). Additionally, 3) we measured the fleeing speed of adders (*Vipera berus*) and calculated the flicker rate of the zigzag pattern, to see if it is fast enough to cause a flicker-fusion effect against predators. Our results show that the zigzag pattern reduces detectability regardless of base colouration 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. Altogether our findings highlight that the colour pattern of animals can be multifunctional, serving differential protection during predation events. 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.

Keywords: animal coloration; conspicuousness; crypsis; dazzle coloration; detection; flicker-fusion; predation; zigzag pattern; warning signal; vision

Introduction

Predation is a sequential process (Endler 1991). First, a prey needs to be detected. After detection it needs to be recognized, and then a decision of whether or not to attack must be made; finally, the prey needs to be captured, handled and consumed. 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 act 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 (Poulton 1890; Cott 1940). Warning signal size, symmetry and conspicuousness have been found to enhance prey recognition and signal learning (Gittleman and Harvey 1980; Roper and Redston 1987; Lindström et al. 1999; Forsman and Merilaita 1999). 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 et al. 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 et al. 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 Ender and Mappes 2004; Tullberg et al 2005; Bohlin et al. 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. 2016; 2017).

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 one is dazzle camouflage, which can impede the accurate estimation of prey speed and trajectory, without changing its appearance (Thayer 1909). Certain colour patterns (e.g. stripes, zigzag and check squares) can produce this effect for human subjects (e.g. Stevens et al. 2008; Scott-Samuel et al. 2011). In the second mechanism, the flicker-fusion effect, adjacent colour patterns blur together because of the physiological limitations of receiver vision, and can actually change prey appearance during rapid movement (Pough 1976; reviewed in Umeton et al. 2017). 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 et al. 2017).

European vipers (genus *Vipera*) are venomous and exhibit a characteristic dorsal zigzag pattern (Arnold et al. 1978). These snakes do not appear overtly conspicuous, but the zigzag pattern acts as a warning signal that is avoided by avian predators (Wüster et al. 2004; Niskanen and Mappes 2005; Valkonen et al. 2011a). The zigzag pattern of vipers is also suggested to function as cryptic colouration because the attack rate on black adders, which have been suggested to be more conspicuous, is higher than the attack rate on the zigzag form (Andrén and 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 the detectability, in other words, how predators can find differently coloured snakes in their natural habitats. Interestingly, Santos et al. (2018) found that the zigzag morph of *Natrix maura*, which mimics adders, is found in all types of habitats; 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 using a wider variety of habitats than cryptic species (Speed et al. 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 (Stevens et al. 2008; Scott-Samuel et al. 2011). While both striped and zigzag patterns have been shown to produce a dazzle effect (Stevens et al. 2008; Scott-Samuel et al. 2011; Hämäläinen et al. 2015), the zigzag pattern of adders (*Vipera berus*) has also been suggested to cause a flicker-fusion effect (Shine and Madsen 1994; Lindell and Forsman 1996). 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 warning signal that facilitates recognition when they are on the move or detected.

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

Methods

Vipera berus is widely distributed, common and mostly diurnal species in the genus *Vipera* (Arnold et al. 1978). Male adders are 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 sexes and age classes. Less contrasting brownish females and young juveniles may rely more on crypsis than more contrasting males (Shine and Madsen 1994; Lindell and Forsman 1996). 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 and 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 towards some prey type; Penney et a. 2012; Barnett et al. 2016). To mimic subadult / adult size we fabricated 40 cm long and c.a. 2 cm thick snake replicas with pre-coloured 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 a total of 10 snake replicas of each colour morph, half of them in coiled and half in s-shaped posture (representing a basking snake and snake on the move, 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 c.a. 10m (10 to 12 steps). The trail followed the terrain around three Biological Research Stations (Oulanka, Konnevesi and Lammi) in Finland. 129 participants from different biology field courses were directed through trails at normal walking speed and asked to 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 whether or not each individual snake replica was detected. 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/non-detection events with 129 participants in three locations.

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

To analyse the effect of the snake replicas' coloration on their detectability, we used a generalized linear mixed model with binomial distribution and logit link function. The binary response variable (detected or not) was explained by the colour (brown or grey) and the posture (coiled or s-shape) 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 et al. 2014).

Fleeing speed

To evaluate the possibility of a flicker-fusion effect we measured the fleeing speed of adders (*Vipera berus*). We captured 18 individuals, five females and 13 males, from four populations in the Jyväskylä area of Central Finland. Individuals were housed in individual terraria (30 cm x 20 cm x 15 cm, L x W x H) 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. They were kept on a 12 h day:12 h night cycle where temperatures were kept between 23.5 - 35°C and at 10°C, respectively. These temperatures were chosen because they are within the range of natural conditions that *V. berus* experiences. The preferred body temperature of the adder is between 31.7°C and 33.8°C (Herczeg et al. 2007). Thus, to avoid over-heating them, they were exposed to the highest temperature for a maximum of two hours.

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 7 to 8 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. We used photographs to determine the spatial frequency of adjacent colour patches (i.e. number of zigzags within body length) by counting the number of 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 per second, and multiplied the speed by the number of zigzags within body length. This yields our response variable, the number of adjacent colour patches of the zigzag pattern passing by a fixed point within a second during the flee (flicker rate in Hz).

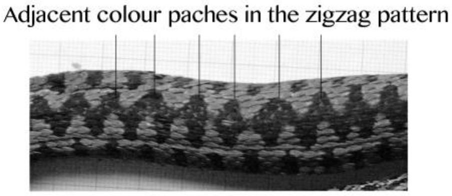

Figure 2. To determine the spatial frequency of the zigzag pattern we counted the number of adjacent patches in the pattern within ten cm and extrapolated that to whole body length.

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.

Results

Detectability

The probability of detecting snake replicas was best described by the three-way interaction of coloration, presence of zigzag pattern and posture (Table 1; Table 2; Fig3). The detectability of black and grey snake replicas without the zigzag pattern appeared to be lower in s-shaped or movement posture compared to the coiled basking posture, whereas the detectability of brown snake replicas without the pattern 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 (Fig3), suggesting a cryptic function of the zigzag pattern. The brown zigzag patterned (female adder morph) snake replicas were less likely to be detected compared to the grey zigzag patterned (male adder morph) ones, which indicates asymmetric benefits of zigzag pattern between the sexes of this species. Interestingly, the posture did not affect the detectability of neither brown or grey zigzag patterned snake replicas (Fig3). Thus, it seems that the crypsis provided by the zigzag pattern is not affected by the snake posture.

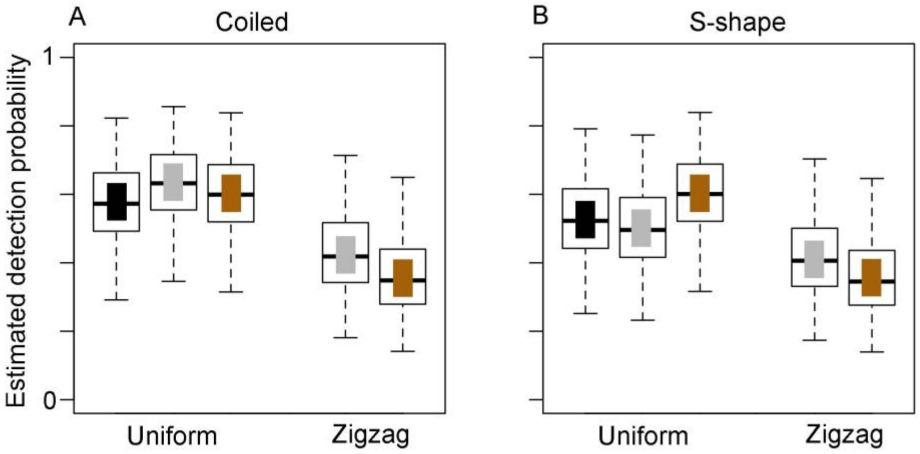

Figure 3. Estimated detection probabilities of zigzag patterned and uniformly coloured artificial snakes. Panel A presents snake replicas in coiled posture (basking) and panel B snakes at s-shape posture (on move). Coloured rectangles indicate base colouration of snake replicas.

Table 1. Significance of terms included in binomial generalized mixed effect model explaining detection probabilities of artificial snakes.

Term in the model	df	LRT	p χ^2
Duration of trial	1	20.66	0.025
Colour*Pattern*Posture	1	5.00	< 0.001

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

Random Effects	Variance			
Participant ID	0.2409			
Location	0.0441			
Fixed Effects	Estimate	SE	Z	p-value
(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-shape	-0.202	0.116	-1.740	0.082
Zigzag	-1.027	0.119	-8.640	<0.001
Grey *S-shape	-0.356	0.165	-2.158	0.031
Brown *S-shape	0.209	0.165	1.265	0.206
Grey*Zigzag	0.157	0.168	0.933	0.351
Zigzag *S-shape	-0.021	0.168	-0.127	0.899
Grey*Zigzag pattern*S-shape	0.528	0.236	2.237	0.025

Fleeing speed

Fourteen out of 18 adders achieved a fleeing speed fast enough to cause the flicker rate of their zigzag pattern to exceed 80 Hz. This speed is very likely to exceed the flicker threshold of most of their mammalian predators (Fig4.; Loop and Berkley 1975; Coile et al. 1995). The maximum detected fleeing speed was 89.7 cms^{-1} (min. 53.9 and mean 74.2), and the corresponding flicker rate of the zigzag pattern was 138.8 Hz (min. 52.5 and mean 94.4). This however indicates that the fleeing speed of adders is probably not fast enough to allow their zigzag pattern to cause a flicker-fusion effect in raptors, as predatory birds are suggested to detect the flicker above 100Hz and even up to 180Hz (Olsen 2005; Boström et al. 2016; Krautwald-Junghanns et al. 2008). 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<001). We did not detect a significant effect of neither weight or sex on the fleeing performance of adders (all t=< ±1.080, p=>0.295).

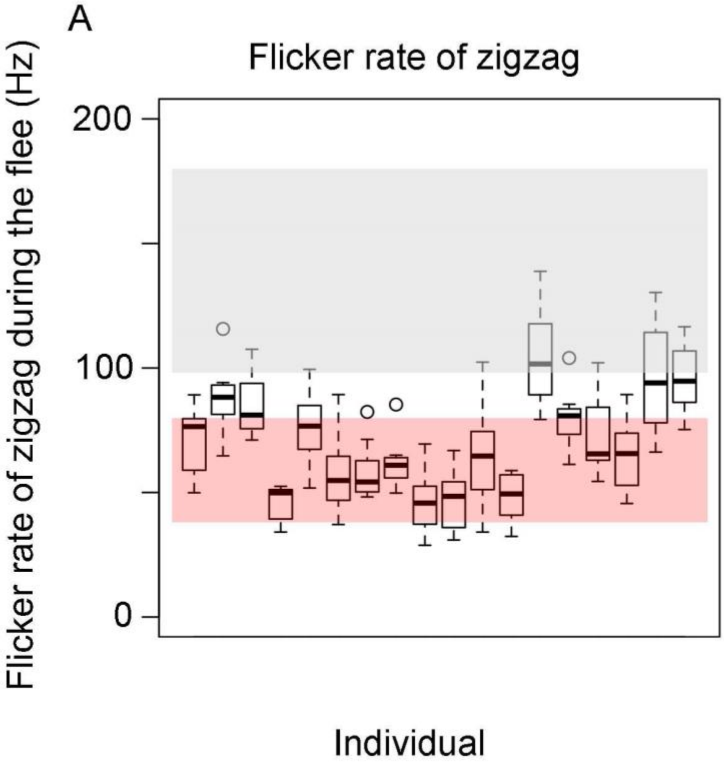

Figure 4. Flicker frequencies of adder zigzag pattern during the flee. The grey shaded rectangle represents the critical flicker threshold range of avian vision (Olsen 2005; Boström et al. 2016; Krautwald-Junghanns et al. 2008) and the red one the flicker threshold range of mammalian predators (Loop and Berkley 1975; Coile et al. 1995).

Discussion

Here, we tested if the dorsal zigzag pattern, typical of European vipers, can offer protection against predation by reducing detectability and also causing a flicker-fusion effect while the snakes flee. Our finding that artificial snakes with a zigzag pattern are harder to detect than those without zigzag confirms that this pattern can also function as cryptic coloration, as suggested earlier by circumstantial evidence (Andrén and Nilson 1981; Santos et al. 2014; 2017). By measuring the fleeing speed of the adders in relation to their coloration and the vision of ecologically relevant predators, we found that the zigzag pattern could indeed induce a flicker-fusion effect in mammals, but likely not in avian predators. 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 (*Vipera berus*) is typically greyish, whereas that of females is brownish. Both sexes exhibit the dorsal zigzag pattern, but the pattern in females is often less contrasting against the base colouration (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 finding that grey viper replicas (those with the zigzag pattern) were more easily detected than brown ones indicates that the grey male adders may be more conspicuous to predators than brownish females. Increased conspicuousness in warning signals, increases, in turn, the signal efficacy (Gittleman and Harvey

1980; Roper and Redston 1987; Lindström et al. 1999; Nokelainen et al. 2012). 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 can 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 (Wüster et al. 2004; Niskanen and Mappes 2005; Valkonen et al. 2011a; Santos et al. 2014) and our present study, it is evident that both zigzag patterned colour morphs, grey and brown, gain some degree of protection via the simultaneous effects of the aposematic and cryptic functions of the zigzag pattern.

Adders (*Vipera berus*) have been suggested to enhance their probability of escaping predator attacks through a flicker-fusion illusion made possible by their colour patterns (Shaine and Madsen 1994; Lindell and Forsman 1996). The flicker-fusion 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 form perception of 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 (Shaine and Madsen 1994; Lindell and Forsman 1996). Our measurements of fleeing speed show that most adders are capable of reaching a speed high enough to induce a flicker-fusion effect in mammalian predators (up to 80 Hz; Loop and Berkley 1975; Coile et al. 1995). However, it is very unlikely this would be efficient against avian predators because their critical flicker threshold can be as high as 180 Hz (Olsen 2005; Boström et al. 2016; Krautwald-

Junghanns et al. 2008). The critical flicker threshold of vision systems is expected to decrease in low light conditions and thus flicker fusion should happen in lower speed (reviewed in Titcomb et al. 2014; Umeton et al. 2017). Adders (*V. berus*), however, are diurnal and most active in good weather conditions. Thus they are most likely 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 (fig5). Striped patterns can hinder the estimation of speed and trajectory of movement and, thus, enhance the probability that a fleeing snake escapes from a predator’s attack (Jackson et al 1976; Pough 1976; Scott-Samuel et al. 2011; Hämäläinen et al. 2015; Murali & Kodandaramaiah 2016). The zigzag pattern has been found to cause a similar effect, but it is unclear if one of the patterns is more effective than the other (Stevens et al. 2008; Scott-Samuel et al. 2011). 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 a well-known phenomenon in vision science, its role in predator avoidance by prey is rarely 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 toward raptors but can be effective against other predator types.

Furthermore, the flicker-fusion effect does not seem to change prey colouration to make it more ‘background-matching’, as originally suggested by Pough (1976) (see Fig 5). Instead, the flicker-fusion effect 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 mainly depends on its colour patterning and the visual capabilities of the receiver (i.e., the predator).

Figure 5. Illustration of flicker-fusion effect induced change in appearance of a male adder (Vipera berus). In panel A the snake is moving slow enough for the perceiver to separate adjacent colour patches of the zigzag pattern that blend together at a higher speed (B), forming a more uniform striped colour pattern.

Understanding the conceptual differences between the mechanisms shaping animal protective colouration is undeniably important for recognising the evolutionary forces behind antipredator strategies. We would like to 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 they can all work sequentially during a single predation event.

References

Andrén C, Nilson G. 1981. Reproductive success and risk of predation in normal and melanistic colour morphs of the adder, *Vipera berus*. Biol. J. Linn. Soc. 15:235–246.

Arnold EN, Burton JA, Ovenden D. 1978. *Field guide to the reptiles and amphibians of Britain and Europe*. Collins.

Barnett JB, Cuthill IC. 2014. Distance-dependent defensive coloration. *Current Biology*. *24*(24): R1157-R1158.

Barnett JB, Redfern AS, Bhattacharyya-Dickson R, Clifton O, Courty T, Ho T, Hopes, A, McPhee T, Merrison K, Owen R, Scott-Samuel NE, Cuthill IC. 2016. Stripes for warning and stripes for hiding: spatial frequency and detection distance. *Behavioral Ecology*. *28*(2): 373-381.

Barnett JB, Cuthill IC, Scott-Samuel NE. 2017. Distance-dependent pattern blending can camouflage salient aposematic signals. In *Proc. R. Soc. B.* (Vol. 284: No. 1858, p. 20170128).

Bates D, Mächler M, Bolker B, Walker S. 2014. Fitting linear mixed-effects models using lme4. *arXiv preprint arXiv:1406.5823*.

Boström JE, Dimitrova M, Canton C, Håstad O, Qvarnström A, Ödeen A. 2016. Ultra-rapid vision in birds. *PloS one*. 11(3): e0151099.

Bohlin T, Tullberg BS, 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.

Brodie ED. 1989. Genetic correlations between morphology and antipredator behaviour in natural populations of the garter snake Thamnophis ordinoides. *Nature*. 342(6249): 542-543.

Brodie Jr ED, Ridenhour BJ, Brodie III ED. 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 DC, Pollitz CH, Smith JC. 1989. Behavioral determination of critical flicker fusion in dogs. *Physiology & behaviour.* 45(6): 1087-1092.

Cott HB. 1940. *Adaptive coloration in animals*. -London, Methuen.

Dell'Aglio DD, Toma TSP, Muelbert AE, Sacco AG, Tozetti AM. 2012. Head triangulation as anti-predatory mechanism in snakes. *Biota Neotropica*. 12(3): 315-318.

Endler JA. 1991. Interactions between predator and prey. *Behavioural ecology*.

Forsman A, Merilaita J. 1999. Fearful symmetry: pattern size and symmetry affects aposematic signal efficacy. Evol. Ecol. 13:131–140

Gittleman JL, Harvey PH. 1980. Why are distasteful prey not cryptic? *Nature*. 286(5769): 149-150.

Herczeg G, Saarikivi J, Gonda A, Perälä J, Tuomola, A, Merilae J. 2007. Suboptimal thermoregulation in male adders (*Vipera berus*) after hibernation imposed by spermiogenesis. *Biological journal of the Linnean Society*. 92(1): 19-27.

How MJ, Zanker JM. 2014. Motion camouflage induced by zebra stripes. *Zoology*. 117(3): 163-170.

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.

Jackson JF, Ingram III W, Campbell HW. 1976. The dorsal pigmentation pattern of snakes as an antipredator strategy: a multivariate approach. *The American Naturalist*. 110(976): 1029-1053.

Kauppinen J, Mappes J. 2003. Why are wasps so intimidating: field experiments on hunting dragonflies (Odonata: Aeshna grandis). *Animal Behaviour*. 66(3): 505-511.

Krautwald-Junghanns M, Orosz SE, Tully Jr T. 2008. *Essentials of avian medicine and surgery*. John Wiley & Sons.

Lindell LE, Forsman A. 1996. Sexual dichromatism in snakes: support for the flicker-fusion hypothesis. *Canadian Journal of Zoology*. 74(12): 2254-2256.

Lindström L, Alatalo RV, Mappes J, Riipi M, Vertainen L. 1999. Can aposematic signals evolve by gradual change? *Nature*. 397(6716): 249-251.

Loop MS, Berkley MA. 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 RH, Reudler JH, Lindstedt C, Mappes J. 2012. Trade-off between warning signal efficacy and mating success in the wood tiger moth. In *Proc. R. Soc. B.* 279(1727): 257-265.

Olsen P. 2005. *Wedge-tailed Eagle*. Csiro Publishing. Melbourne, Australia.

Penney HD, Hassall C, Skevington JH, Abbott KR, Sherratt TN. 2012. A comparative analysis of the evolution of imperfect mimicry. *Nature*, *483*(7390), 461.

Poulton EB. 1890. *The colours of animals: their meaning and use especially considered in the case of insects*. Kegan, Trennch, Trubnes & Co

Pough FH. 1976. Multiple cryptic effects of crossbanded and ringed patterns of snakes. *Copeia*. 1976(4): 834-836.

Rojas B. 2017. Behavioural, ecological, and evolutionary aspects of diversity in frog colour patterns. *Biological Reviews*. 92(2): 1059-1080.

Roper TJ, Redston S. 1987. Conspicuousness of distasteful prey affects the strength and durability of one-trial avoidance learning. *Animal Behaviour*. 35(3): 739-747.

Ruxton GD, Allen WL, Sherrat TN, Speed MP. 2018. *Avoiding Attack: The Evolutionary Ecology of Crypsis, Aposematism and Mimicry. Second Edition*. Oxford University Press.

Santos X, Vidal-García M, Brito JC, Fahd S, Llorente GA, Martínez-Freiría F, Parellada X, Plequezuelos JM, Sillero N. 2014. Phylogeographic and environmental correlates support the cryptic function of the zigzag pattern in a European viper. *Evolutionary ecology.* 28(4): 611-626.

Santos X, Azor JS, Cortés S, Rodríguez E, Larios J, Pleguezuelos JM. 2017. Ecological significance of dorsal polymorphism in a Batesian mimic snake. *Current Zoology*. 64(6):745-753.

Scott-Samuel NE, Baddeley R, Palmer CE, Cuthill IC. 2011. Dazzle camouflage affects speed perception. *PLoS One*. 6(6), e20233.

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 DH, Ruxton GD. 2008. Dazzle coloration and prey movement. *Proceedings of the Royal Society of London B*. 275(1651): 2639-2643.

Thayer GH. 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.* NY Macmillan, New York

Titcomb GC, Kikuchi DW, Pfennig DW. 2014. More than mimicry? Evaluating scope for flicker-fusion as a defensive strategy in coral snake mimics. *Current Zoology*. 60(1): 123-130.

Tullberg BS, 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 JC, 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. 2011a. Disruption or aposematism? Significance of dorsal zigzag pattern of European vipers. *Evolutionary Ecology*. 25(5): 1047-1063.

Valkonen JK, Nokelainen O, Mappes J. 2011b. Antipredatory function of head shape for vipers and their mimics. *PloS one*. 6(7): e22272.

Wüster W, Allum CS, Bjargardóttir IB, Bailey KL, Dawson KJ, Guenioui J, Lewis J, McGurk J, Moore AG, Niskanen M, Pollard CP. 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.