Protective coloration of European vipers throughout the predation sequence

Valkonen, Janne K.

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1 **Protective coloration of European vipers throughout the predation**

2 **sequence**

3

4 **Abstract**

5 Antipredator adaptations in the form of animal coloration are common and often

6 multifunctional. European vipers (genus *Vipera*) have a characteristic dorsal

7 zigzag pattern, which has been shown to serve as a warning signal to potential

8 predators. At the same time, it has been suggested to decrease detection risk, and

9 to cause a motion dazzle or flicker-fusion effect during movement. We tested

10 these hypotheses by asking 1) whether the zigzag pattern decreases detection

11 risk and 2) whether the detection is dependent on the base coloration (grey or

12 brown) or the snake's posture (coiled, to represent basking, or S-shaped, to

13 represent an active snake). Additionally, 3) we measured the fleeing speed of

14 adders (*Vipera berus*) and calculated the flicker rate of the zigzag pattern, to see

15 if it is fast enough to cause a flicker-fusion effect against predators. Our results

16 show that the zigzag pattern reduces detectability regardless of base colouration

17 or posture of the snake. The brown zigzag morph was detected less often than

18 the grey zigzag morph. The fleeing speed of adders appeared to be fast enough to

19 induce a flicker-fusion effect for mammalian predators. However, it is unlikely to

20 be fast enough to induce the flicker-fusion effect for raptors. Altogether our

21 findings highlight that the colour pattern of animals can be multifunctional,

22 serving differential protection during predation events. The same colour pattern

23 that can decrease detection by predators can also serve as a warning function

24 once detected, and potentially hinder capture during an attack.

25

28

Introduction

30   Predation is a sequential process (Endler 1991). First, a prey needs to be

31   detected. After detection it needs to be recognized, and then a decision of

32   whether or not to attack must be made; finally, the prey needs to be captured,

33   handled and consumed. Various forms of coloration have evolved to protect prey

34   during these separate steps. Two of the best-studied functions of protective

35   coloration are crypsis and aposematism, which act during the first two steps of

36   the predation sequence. Cryptic prey gain protection by avoiding detection and

37   recognition, whereas aposematic prey advertise their secondary defences so that

38   predators avoid them after they have been detected (Poulton 1890; Cott 1940).

39   Warning signal size, symmetry and conspicuousness have been found to enhance

40   prey recognition and signal learning (Gittleman and Harvey 1980; Roper and

41   Redston 1987; Lindström et al. 1999; Forsman and Merilaita 1999). Thus, at first

42   these two strategies may appear to operate in opposition; cryptic prey are

43   expected to be inconspicuous, whereas aposematic prey are expected to evolve

44   conspicuousness (Ruxton et al. 2018).

45   Even the most toxic prey, however, are preyed upon at least occasionally

46   by predators. For example, poison frogs are consumed by birds, snakes, crabs

47   and spiders (Rojas 2017) and some toxic salamanders fall victim to snakes that

48   have evolved immunity to their defences (Brodie et al. 2002). Thus, under some

49   conditions, it could be beneficial even for aposematic prey to reduce detection

50   through crypsis, so long as their warning signals can still be identified once

51   detected (Wüster et al. 2004). Indeed, not all aposematic species appear overtly

52   conspicuous, and some of them are difficult to detect despite their contrasting

53   colour patterns (reviewed in Ender and Mappes 2004; Tullberg et al 2005;

54   Bohlin et al. 2008). Warning signals can be designed so that at longer viewing

55   distances, contrasting and easily recognizable colour markings exceed the visual

56   resolution of the perceiver, thus blending together and appearing as a uniform

57   colour that matches the background more closely (Barnett et al. 2016; 2017).

58   In addition, colour patterns that hinder capture after a predator has

59   decided to attack could provide extra protection. Two distinct mechanisms have

60   been proposed to have this effect. The first one is dazzle camouflage, which can

61   impede the accurate estimation of prey speed and trajectory, without changing

62   its appearance (Thayer 1909). Certain colour patterns (e.g. stripes, zigzag and

63   check squares) can produce this effect for human subjects (e.g. Stevens et al.

64   2008; Scott-Samuel et al. 2011). In the second mechanism, the flicker-fusion

65   effect, adjacent colour patterns blur together because of the physiological

66   limitations of receiver vision, and can actually change prey appearance during

67   rapid movement (Pough 1976; reviewed in Umeton et al. 2017). For example,

68   black and white stripes can instead appear grey and blurry. The significance of

69   the flicker-fusion effect in the protective coloration of animals is vastly

70   understudied and poorly understood (Umeton et al. 2017).

71   European vipers (genus *Vipera*) are venomous and exhibit a characteristic

72   dorsal zigzag pattern (Arnold et al. 1978). These snakes do not appear overtly

73   conspicuous, but the zigzag pattern acts as a warning signal that is avoided by

74   avian predators (Wüster et al. 2004; Niskanen and Mappes 2005; Valkonen et al.

75   2011a). The zigzag pattern of vipers is also suggested to function as cryptic

76 colouration because the attack rate on black adders, which have been suggested

77 to be more conspicuous, is higher than the attack rate on the zigzag form

78 (Andrén and Nilson 1981). The cryptic function of the zigzag pattern is also

79 supported by studies where variation in coloration and zigzag pattern of a

80 European viper (*Vipera latastei*) and a mimetic viperine snake (*Natrix maura*)

81 were found to be associated with different habitat types (Santos et al. 2014).

82 Neither Andrén and Nilson (1981) nor Santos et al. (2014) studied the

83 detectability, in other words, how predators can find differently coloured snakes

84 in their natural habitats. Interestingly, Santos et al. (2018) found that the zigzag

85 morph of *Natrix maura*, which mimics adders, is found in all types of habitats;

86 the striped morph, in contrast, is found almost exclusively in open habitats. This

87 observation fits with the theory of aposematism, which predicts that aposematic

88 species are capable of using a wider variety of habitats than cryptic species

89 (Speed et al. 2010). Thus, there is support for both a cryptic and an aposematic

90 function of the zigzag pattern.

91   Zigzag colour patterns can also have movement-dependent functions

92 (Stevens et al. 2008; Scott-Samuel et al. 2011). While both striped and zigzag

93 patterns have been shown to produce a dazzle effect (Stevens et al. 2008; Scott-

94 Samuel et al. 2011; Hämäläinen et al. 2015), the zigzag pattern of adders (*Vipera*

95 *berus*) has also been suggested to cause a flicker-fusion effect (Shine and Madsen

96 1994; Lindell and Forsman 1996). We suggest that the function of the zigzag

97 pattern of snakes is context-dependent, allowing them to be cryptic when they

98 are basking in a coiled posture and acting as warning signal that facilitates

99 recognition when they are on the move or detected.

100   To assess whether the viper zigzag pattern plays a role in crypsis, we

101   tested the effect of the viper zigzag pattern on their detectability. Likewise, we

102   tested whether the detectability is associated with the base colouration (grey or

103   brown) or posture (on the move or coiled) of snakes. To evaluate the movement-

104   dependent protective function of the zigzag pattern, we tested if the fleeing

105   speed of adders is high enough for mammalian and avian predators to

106   experience a flicker-fusion effect.

107 **Methods**

108 *Vipera berus* is widely distributed, common and mostly diurnal species in the

109 genus *Vipera* (Arnold et al. 1978). Male adders are typically greyish with a dark

110 dorsal zigzag pattern, whereas females are typically brownish with a less

111 contrasting dark zigzag pattern. Juveniles are typically light brown. This colour

112 difference suggests the possibility of different antipredator strategies between

113 sexes and age classes. Less contrasting brownish females and young juveniles

114 may rely more on crypsis than more contrasting males (Shine and Madsen 1994;

115 Lindell and Forsman 1996). Many populations also have a proportion of black

116 melanistic individuals, and in some populations striped and nearly uniform grey

117 individuals are present (Arnold et al. 1978; Nikolić and Simović 2017).

118 *Detectability*

119 To test whether the zigzag pattern of snakes reduces their detectability, we

120 exposed artificial snakes with five different colour morphs (black, brown, brown

121 with zigzag, grey, and grey with zigzag) to humans as surrogate predators (fig 1).

122 The use of humans as surrogate predators allowed us to test the detectability of

123 snakes without the possible biases in foraging decisions that can affect natural

124 predators (e.g. preference towards some prey type; Penney et a. 2012; Barnett et

125 al. 2016). To mimic subadult / adult size we fabricated 40 cm long and c.a. 2 cm

126 thick snake replicas with pre-coloured plasticine (Caran D'ache Model'art, black

127 496, brown 497, grey 808), and hand-painted a zigzag pattern on them with satin

128 black acrylic paint (Amsterdam Standard series, Lamp black). We placed a total

129 of 10 snake replicas of each colour morph, half of them in coiled and half in s-

130 shaped posture (representing a basking snake and snake on the move,

131 respectively), along transect trails. The order of the snake replicas was rotated to

132   avoid having adjacent snake replicas of the same colour morph. The distance

133   between snake replicas was c.a. 10m (10 to 12 steps). The trail followed the

134   terrain around three Biological Research Stations (Oulanka, Konnevesi and

135   Lammi) in Finland. 129 participants from different biology field courses were

136   directed through trails at normal walking speed and asked to inform a guide

137   following them when they detected a snake replica. The person guiding the

138   participants through the trails recorded the time it took for each participant to

139   finish the trail, and whether or not each individual snake replica was detected.

140   One snake replica (grey zigzag) disappeared during the trials at Konnevesi

141   research station and was thus missing for 17 participants, most likely because of

142   a predation attempt by a natural predator. Therefore, our data sets consist of

143   6443 detection/non-detection events with 129 participants in three locations.

144

145

146   *Figure 1. Colour morphs of snake replicas used to test the effect of*

147   *colouration, posture and the zigzag pattern on the detectability of snakes.*

148

149   To analyse the effect of the snake replicas' coloration on their

150   detectability, we used a generalized linear mixed model with binomial

151   distribution and logit link function. The binary response variable (detected or

152   not) was explained by the colour (brown or grey) and the posture (coiled or s-

153   shape) of the snake replica, the presence of a zigzag pattern, and their two and

154   three-way interactions. To control for the fact that participants walked at

155   different speeds, the time that it took for them to finish the trail was included as

156   a covariate. Because of our sampling structure, we included participant ID nested

157   within location as a random effect in our model. The analysis was conducted

158   using the lme4 package in R (Bates et al. 2014).

159

160   *Fleeing speed*

161   To evaluate the possibility of a flicker-fusion effect we measured the fleeing

162   speed of adders (*Vipera berus*). We captured 18 individuals, five females and 13

163   males, from four populations in the Jyväskylä area of Central Finland. Individuals

164   were housed in individual terraria (30 cm x 20 cm x 15 cm, L x W x H) within a

165   climate chamber. Snakes were kept in captivity only a few days and returned to

166   the place of capture after the experiment. They were not fed during captivity, but

167   water was offered ad libitum. They were kept on a 12 h day:12 h night cycle

168   where temperatures were kept between 23.5 - 35°C and at 10°C, respectively.

169   These temperatures were chosen because they are within the range of natural

170   conditions that *V. berus* experiences. The preferred body temperature of the

171   adder is between 31.7°C and 33.8°C (Herczeg et al. 2007). Thus, to avoid over-

172   heating them, they were exposed to the highest temperature for a maximum of

173   two hours.

174   The fleeing performance of adders was measured by placing them at the

175   end of a 190 cm long and 56 cm wide arena with pine bark as substrate. Snake

176   body temperature was measured with a laser thermometer (Prego P-8380B) at

177   the beginning of each fleeing trial. During the trials the snakes were provoked to

178   flee by gently tapping them on the tail, and their fleeing speed was recorded with

179   a video camera (Canon Legria HF R37) placed on top of the arena. The fleeing

180   performance of each snake was measured 7 to 8 times. Snakes were allowed to

181   recover between trials in their housing terraria (minimum 0.5 h), and they were

182   tested a maximum of four times per day.

183   After completing the fleeing trials, we weighed and measured the full

184   body length of each snake, and then photographed them. We used photographs

185   to determine the spatial frequency of adjacent colour patches (i.e. number of

186   zigzags within body length) by counting the number of transitions in the pattern

187   within a 10 cm length at the middle of the body and extrapolating that to total

188   body length (fig 2.). The maximum sprinting speed of snakes was determined

189   from video recordings by measuring the longest distance that snakes reached

190   within a 0.4 s time window in each trial. To obtain the maximum flicker

191   frequency that snakes can achieve, we converted the maximum fleeing speed to

192   body lengths per second, and multiplied the speed by the number of zigzags

193   within body length. This yields our response variable, the number of adjacent

194   colour patches of the zigzag pattern passing by a fixed point within a second

195   during the flee (flicker rate in Hz).

Adjacent colour paches in the zigzag pattern
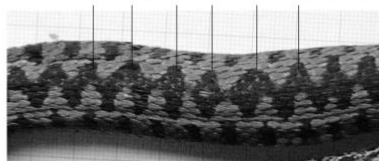
196

197   *Figure 2. To determine the spatial frequency of the zigzag pattern we*

198   *counted the number of adjacent patches in the pattern within ten cm and*

199   *extrapolated that to whole body length.*

200   To test the effects of sex, size and body temperature on maximum flicker

201   rate we used a general linear mixed model with a Gaussian distribution. The

202   response variable, flicker rate, was explained by including weight, sex and body

203   temperature as explanatory variables, and individual ID as a random factor to

204   account for repeated measures within individuals.

205

206   **Results**

207   *Detectability*

208   The probability of detecting snake replicas was best described by the three-way

209   interaction of coloration, presence of zigzag pattern and posture (Table 1; Table

210   2; Fig3). The detectability of black and grey snake replicas without the zigzag

211   pattern appeared to be lower in s-shaped or movement posture compared to the

212   coiled basking posture, whereas the detectability of brown snake replicas

213   without the pattern was similar regardless of their posture. The detection

214   probability of grey and brown zigzag patterned snake replicas was lower

215   compared to the uniform ones in both postures (Fig3), suggesting a cryptic

216   function of the zigzag pattern. The brown zigzag patterned (female adder morph)

217   snake replicas were less likely to be detected compared to the grey zigzag

218   patterned (male adder morph) ones, which indicates asymmetric benefits of

219   zigzag pattern between the sexes of this species. Interestingly, the posture did

220   not affect the detectability of neither brown or grey zigzag patterned snake

221   replicas (Fig3). Thus, it seems that the crypsis provided by the zigzag pattern is

222   not affected by the snake posture.

223

224
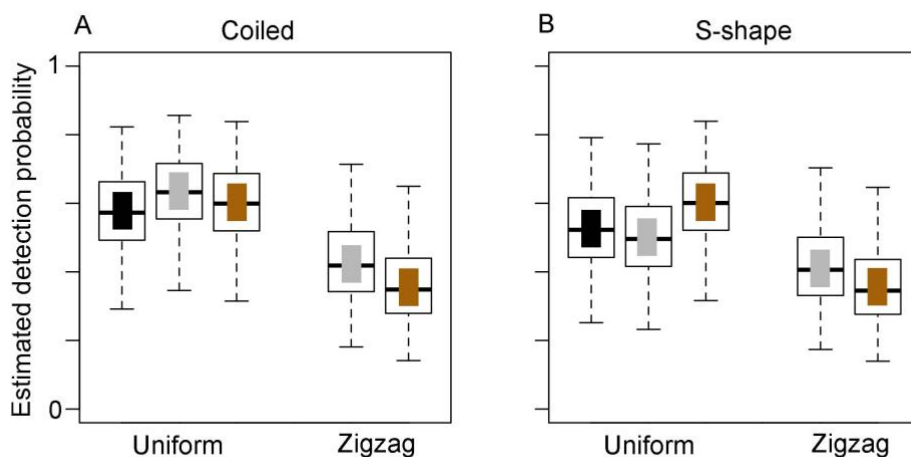
Figure 3. Estimated detection probabilities of zigzag patterned and uniformly

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

231

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

234

235

236 *Fleeing speed*

237   Fourteen out of 18 adders achieved a fleeing speed fast enough to cause

238 the flicker rate of their zigzag pattern to exceed 80 Hz. This speed is very likely to

239 exceed the flicker threshold of most of their mammalian predators (Fig4.; Loop

240 and Berkley 1975; Coile et al. 1995). The maximum detected fleeing speed was

241 89.7 cms^{-1} (min. 53.9 and mean 74.2), and the corresponding flicker rate of the

242 zigzag pattern was 138.8 Hz (min. 52.5 and mean 94.4). This however indicates

243 that the fleeing speed of adders is probably not fast enough to allow their zigzag

244 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).
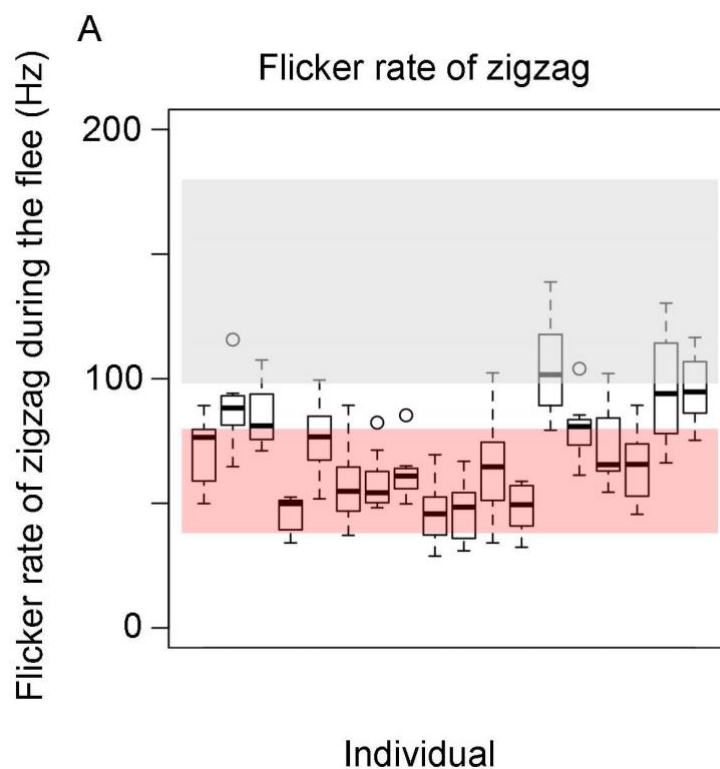
Figure 4. Flicker frequencies of adder zigzag pattern during the flee. The grey shaded rectangle represents the critical flicker threshold range of avian vision (Olsen 2005; Boström et al. 2016; Krautwald-Junghanns et al. 2008) and the red one the flicker threshold range of mammalian predators (Loop 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

284   1980; Roper and Redston 1987; Lindström et al. 1999; Nokelainen et al. 2012).

285   This, together with our findings here, suggests asymmetric benefits of the zigzag

286   pattern between the sexes: more conspicuous males may be more protected

287   against predation than less conspicuous females via aposematism, whereas

288   females can be better protected than males via crypsis. This asymmetric benefit

289   of the protective coloration may explain the existence of sexual dimorphism in

290   the adder. However, based on evidence from previous studies (Wüster et al.

291   2004; Niskanen and Mappes 2005; Valkonen et al. 2011a; Santos et al. 2014) and

292   our present study, it is evident that both zigzag patterned colour morphs, grey

293   and brown, gain some degree of protection via the simultaneous effects of the

294   aposematic and cryptic functions of the zigzag pattern.

295   Adders (*Vipera berus*) have been suggested to enhance their probability of

296   escaping predator attacks through a flicker-fusion illusion made possible by their

297   colour patterns (Shaine and Madsen 1994; Lindell and Forsman 1996). The

298   flicker-fusion illusion requires movement of an object across the visual field of a

299   perceiver at a speed fast enough to cause the object's adjacent colour patterns to

300   blur together and form perception of a uniform average colour (Pough 1976). So

301   far, suggestions about the flicker-fusion effect of the zigzag pattern have been

302   based on observations of antipredator behaviour and survival of differently

303   coloured snakes (Shaine and Madsen 1994; Lindell and Forsman 1996). Our

304   measurements of fleeing speed show that most adders are capable of reaching a

305   speed high enough to induce a flicker-fusion effect in mammalian predators (up

306   to 80 Hz; Loop and Berkley 1975; Coile et al. 1995). However, it is very unlikely

307   this would be efficient against avian predators because their critical flicker

308   threshold can be as high as 180 Hz (Olsen 2005; Boström et al. 2016; Krautwald-

309   Junghanns et al. 2008). The critical flicker threshold of vision systems is expected

310   to decrease in low light conditions and thus flicker fusion should happen in

311   lower speed (reviewed in Titcomb et al. 2014; Umeton et al. 2017). Adders (*V.*

312   *berus*), however, are diurnal and most active in good weather conditions. Thus

313   they are most likely exposed to predation when viewing conditions are optimal

314   for visual predators.

315   Interestingly, when the dorsal zigzag pattern of a fleeing adder blurs

316   together it appears as a uniform dorsal stripe (fig5). Striped patterns can hinder

317   the estimation of speed and trajectory of movement and, thus, enhance the

318   probability that a fleeing snake escapes from a predator's attack (Jackson et al

319   1976; Pough 1976; Scott-Samuel et al. 2011; Hämäläinen et al. 2015; Murali &

320   Kodandaramaiah 2016). The zigzag pattern has been found to cause a similar

321   effect, but it is unclear if one of the patterns is more effective than the other

322   (Stevens et al. 2008; Scott-Samuel et al. 2011). The flicker-fusion effect was

323   defined by Pough (1976) as an antipredator strategy where adjacent colours of

324   prey blur together to form an "average" coloration that changes the prey's

325   background matching. This is also how the flicker-fusion effect is often

326   considered in current literature, which has led to both the formulation of

327   confusing hypotheses and equally confusing interpretation of results (reviewed

328   in Umeton et al. 2017). Although the existence of the flicker-fusion effect is a

329   well-known phenomenon in vision science, its role in predator avoidance by

330   prey is rarely demonstrated (Umeton et al. 2019). Our results highlight again the

331   importance of considering the adaptive value of each antipredator strategy from

332   the point of view of the receiver(s). As our results show, flicker-fusion may not

333   work toward raptors but can be effective against other predator types.

334   Furthermore, the flicker-fusion effect does not seem to change prey colouration

335   to make it more 'background-matching', as originally suggested by Pough (1976)

336   (see Fig 5). Instead, the flicker-fusion effect seems to change the snake's

337   patterning appearance such that it may more effectively induce motion dazzle

338   camouflage. In line with Umeton et al. 2017, we suggest that the flicker-fusion

339   effect should be viewed as a mechanism (not as an antipredator strategy) that

340   can change the appearance of a moving prey if it moves fast enough. How prey

341   appearance changes mainly depends on its colour patterning and the visual

342   capabilities of the receiver (i.e., the predator).

343

344

345   *Figure 5. Illustration of flicker-fusion effect induced change in appearance of a*

346   *male adder (Vipera berus). In panel A the snake is moving slow enough for the*

347   *perceiver to separate adjacent colour patches of the zigzag pattern that blend*

348   *together at a higher speed (B), forming a more uniform striped colour pattern.*

349   Understanding the conceptual differences between the mechanisms

350   shaping animal protective colouration is undeniably important for recognising

351   the evolutionary forces behind antipredator strategies. We would like to

352   highlight that it is equally important to understand that these conceptually

353   opposing strategies and mechanisms (e.g. aposematism, crypsis, motion dazzle

354   camouflage and flicker-fusion effect) are not mutually exclusive, but they can all

355   work sequentially during a single predation event.

356

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