

Do aposematism and Batesian mimicry require bright colours? A test, using European viper markings

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Predator avoidance of noxious prey, aposematism and defensive mimicry are normally associated with bright, contrasting patterns and colours. However, noxious prey may be unable to evolve conspicuous coloration because of other selective constraints, such as the need to be inconspicuous to their own prey or to specialist predators. Many venomous snakes, particularly most vipers, display patterns that are apparently cryptic, but nevertheless highly characteristic, and appear to be mimicked by other, non-venomous snakes. However, predator avoidance of viper patterns has never been demonstrated experimentally. Here, the analysis of 813 avian attacks on 12 636 Plasticine snake models in the field shows that models bearing the characteristic zigzag band of the adder (*Vipera berus*) are attacked significantly less frequently than plain models. This suggests that predator avoidance of inconspicuously but characteristically patterned noxious prey is possible. Our findings emphasize the importance of mimicry in the ecological and morphological diversification of advanced snakes.

Keywords: aposematism; crypsis; mimicry; vipers; predation; predator avoidance

1. INTRODUCTION

Aposematism, the use of bright colours and patterns by noxious animals to deter predators, is a well-documented phenomenon in nature, as is the mimicry of such patterns by other organisms lacking any noxious qualities (Batesian mimicry). Until now, experimental studies of aposematism and mimicry have focused primarily on systems involving brightly patterned, conspicuous models. Predators learn to avoid brightly patterned or otherwise conspicuous noxious prey items more rapidly than cryptic prey items (Gittleman & Harvey 1980; Sillén-Tullberg 1985; Guilford 1986; Rowe & Guilford 2000), and consequently, aposematism and/or Batesian mimicry have usually been inferred in cases where the presumed mimic matches a brightly patterned model.

Most of aposematism theory is based on two-species interactions, with one noxious prey (the signaller) and one predator (the receiver). However, in nature, animals interact with a multitude of other species, which may include generalist predators that are deterred by aposematic coloration, specialist predators that can overcome the noxious features of the signaller, and, where the signaller is itself a predator, its prey (Endler & Mappes 2004). In this context, conspicuous colours and patterns may have selective disadvantages: although it is in the signaller's interest to advertise its noxious qualities to a generalist predator, it will also be in its interest to avoid detection by specialist predators and by its own prey.

Where specialist predators, generalist predators and prey use different sensory modalities (e.g. sensitivity to

light of different wavelengths), these differences could theoretically be exploited through warning coloration that is visible only to generalist predators. However, where generalist predators operate under similar sensory modalities as either prey or specialized predators, a potential alternative strategy would consist of the use of patterns and colours that do not interfere with crypsis, but are characteristically distinct and easily recognizable when crypsis has failed and the animal is spotted by a generalist predator. Although bright colours and patterns may enhance predator learning, experiments using captive birds have demonstrated that cryptic, noxious prey also gains protection against attack, albeit more slowly than conspicuous prey (Sillén-Tullberg 1985). Fisher (1930) emphasized the primary importance of recognizability for any noxious organism, and Mallet & Joron (1999) argued that any pattern could potentially generate predator avoidance provided it is recognizable and memorable, even if no conspicuous coloration is involved. Likely examples include some transparent ithomiine butterflies in South America, which are part of mimicry rings (Mallet & Joron 1999; Joron 2003), and appear to be avoided by at least some avian predators (Pinheiro 1996). The possibility of predator avoidance of inconspicuous but distinctive noxious prey is also supported by computer modelling (Endler & Mappes 2004) and computer experiments involving human 'predators' (Sherratt & Beatty 2003). If all that is required to generate predator avoidance is recognizability, then one would expect inconspicuous but characteristic patterns denoting unprofitable or well-defended prey to be avoided by predators. However, the avoidance of such patterns by free-ranging predators in nature has never, to our knowledge, been demonstrated experimentally.

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Among terrestrial vertebrates, venomous snakes are particularly likely participants in aposematism and mimicry systems, owing to the extreme potency of their venoms. The severe consequences for any non-specialist predator that attacks them will either accelerate avoidance learning (Czaplicki *et al.* 1976; Goodale & Sneddon 1977) or result in innate avoidance (Smith 1975, 1977; Pough 1988). Predator avoidance of the characteristic, brightly coloured banding of neotropical coral snakes (*Micrurus*, *Micruroides*) has been demonstrated in field experiments (Brodie 1993; Brodie & Janzen 1995), and appears to be innate in some generalist predatory birds (Smith 1975, 1977). These snakes form the focus of extensive mimicry rings (Greene & McDiarmid 1981; Brodie & Brodie 2004).

However, many venomous snakes, particularly the vipers (Viperidae), are cryptic sit-and-wait predators (Greene 1997). However, despite their remarkable crypsis (at least to the human eye), many viperid patterns are highly distinctive and characteristic once the snake has been seen, and their potential as models for defensive mimicry was realized from the very beginning of mimicry theory by Bates (1862), who described the 'most extraordinary instance of imitation' of a viperid head by a caterpillar. Some non-venomous snakes display very similar patterns to those of sympatric vipers (e.g. Gans 1961; Sweet 1985; Sazima 1992; Greene 1997). These resemblances are often interpreted as Batesian mimicry, but predator avoidance of viper patterns has never been demonstrated experimentally (Brodie & Brodie 2004).

Experimental testing of the function of viperid patterns is hampered by their potentially dual function of crypsis and aposematism (Sweet 1985; Brodie & Brodie 2004), and the likelihood of generalized avoidance of such patterns by predators (Pough 1988). Predator avoidance of viper patterns would be most easily testable in a simple system, in which a viper with a cryptic, and yet distinctive pattern occurs in the absence of other similar snakes. In northern Europe, the European adder (*Vipera berus*) is the only venomous snake, and, except in the case of melanistic individuals, almost invariably displays a characteristic dark dorsal zigzag band on a greyish, yellowish, brownish or reddish background. No other northern European snake bears any pronounced resemblance to it (Arnold 2002). The exact function of the zigzag band has been debated, but always with the underlying assumption of crypsis (e.g. Andrén & Nilson 1981; Luiselli 1992; Shine & Madsen 1994).

In recent years, the use of Plasticine models has become the standard method for studies of aposematism and mimicry in snakes (e.g. Madsen 1987; Brodie 1993; Brodie & Janzen 1995; Pfennig *et al.* 2001). Predatory attacks leave marks in the models, which can be recorded, and allow identification of the predator (Brodie 1993). Placing a proportion of the models on a plain background (Brodie 1993) controls for the confounding effects of crypsis. We use the same approach to test the hypothesis that free-ranging avian predators avoid the zigzag pattern of European vipers. Whereas a solely cryptic function would predict lower rates of attack on zigzag-patterned models than on plain models on a natural background but not on a plain background, predator avoidance would predict significantly lower rates of attack on both a plain background and a natural background.

2. MATERIAL AND METHODS

Our methods largely follow Brodie (1993). We constructed models of snakes using Plasticine (Hobbicraft, Leeds, UK) of two colours, grey and terracotta, loosely chosen to represent male and female adders, as well as controlling for potential artefacts relating to Plasticine colour. The models measured *ca.* 20 cm in length and 1 cm in diameter, corresponding roughly to the size of a yearling adder, and had a tapering tail end and a slightly enlarged head distinct from a thinner neck (electronic Appendix A, available on The Royal Society's Publications Web site). Using black acrylic paint, we painted a mid-dorsal zigzag band similar to that of *V. berus* onto approximately half the models. The remainder were left plain and acted as controls. Painted controls featuring non-viper patterns were considered but not used: owing to the potential confounding effects of predator generalization (Brodie & Janzen 1995), neophobia (Marples *et al.* 1998; Lindström *et al.* 2001) or unexpected avoidance of characteristics of other seemingly harmless animals (Madsen 1987), painted controls cannot unambiguously reject the hypothesis that viper patterns deter avian predators.

The models were distributed in the field at 12 sites in the UK, and one site in Finland, in June–August 2001 and June–August 2003 (electronic Appendix B). Field sites were situated in regions where *V. berus* is known to occur, and contained plausible snake habitat, even if no snakes were known from the actual site. *Vipera berus* is the only venomous snake found near any of the sites, and the only snake in northwestern Europe with a dorsal zigzag band. The non-venomous colubrid *Natrix natrix* and the lizard *Anguis fragilis* are the only other legless reptiles occurring in or near the sites, but do not bear any pronounced resemblance to the adder (Arnold 2002). Potential avian snake predators at the sites included various corvids, and buzzards (*Buteo buteo*). All are residents in the UK, where most of the work was done, and thus unlikely to have had past interactions with other snake species than those found in the study sites, although Finnish *B. buteo* migrate to Africa (Cramp & Simmons 1980; Cramp & Perrins 1994).

Models were placed singly, following transect lines or natural vegetational or physiographic features. To control for the effect of crypsis, approximately half the models were placed on A4 sheets of white card, the corners of which were weighted down with stones to avoid wind damage or curling due to humidity. A distance of at least 10 m was left between any two models. To avoid any subconscious bias in how models were placed, we first identified the exact placement for each individual model. Three flips of a coin determined the colour (terracotta or grey), pattern (zigzag or plain) and background (natural or card) of the model. Models were arranged in an S-shaped curve.

Models were gathered and inspected at approximately weekly intervals, reshaped and randomly relocated in the habitat. Each such iteration was counted as a separate event. The models were inspected carefully for beak marks (Brodie 1993). Models with multiple beak marks were conservatively scored as one single attack. Only marks unambiguously caused by birds were recorded. Non-avian attacks were excluded, as they are unlikely to be biologically relevant attempts at visual predation on a snake. Similarly, lost models were ignored, because many factors other than avian predation may be responsible for model loss.

We used two statistical approaches to determine the significance of differences in attack rates between different model-background combinations. In the first instance, we used binary logistic regression of all individual events, run on SPSS v. 12. To identify the appropriate regression model, we used forward binary

logistic regression, which uses likelihood ratio tests to identify those factors that are significant predictors of attack rates. The factors initially entered into the analysis were background, pattern, colour and field site, as well as pairwise interactions between background, colour and pattern.

Because this almost certainly involves an element of pseudo-replication (single individual birds may have been responsible for multiple attacks at any one field site), we used a second, much more conservative approach, in which each individual field site was treated as a single data point: we repeated the binary logistic regressions for each individual locality and scored the odds ratio for pattern in each case. Using Minitab v. 13.1, we then tested the distribution of the resulting odds ratios for normality by means of the Ryan–Joiner test, and then applied a one-sample *t*-test to determine whether the mean odds ratio differs significantly from the value of 1.0 expected under the null hypothesis that a similar number of sites should show higher attack rates on zigzag models as on plain models

Finally, because birds attack predominantly the head end of snakes (Smith 1973, 1976), and especially of venomous snakes (Brodie 1993), the position of attacks on the models may indicate how the predators perceived them, and whether model types were perceived differently. In eight of the experiments performed in 2003, representing a range of geographical locations and habitats (electronic Appendix B), we divided the length of each attacked model into quarters, and noted the most intensively attacked quarter. Attacks on natural and card backgrounds were pooled for this. Differences in the part of the body attacked were compared among model types by χ^2 -tests.

3. RESULTS

We recorded a total of 12 636 events. Out of these, 813 (6.57%) were attacks, the rest non-attacks. The distribution of attacks between different model and background types is shown in figure 1. The forward binary logistic regression analysis identified field site, pattern and background as significant predictors of attack rates (table 1), confirming that models with adder patterns were attacked significantly less frequently than plain models, models on a card background were attacked less frequently than models on a natural background, and that there were significant differences between field sites. Overall, adder-patterned models suffered less than half the rate of attacks of plain models (odds ratio = 0.457). The difference between attack rates on plain and adder models was slightly greater on the card background (3.46% for adder models, 7.48% for plain models, odds ratio = 0.41) than on a natural background (5.04% and 9.49%, odds ratio = 0.48).

Among the 14 locality–year combinations, 13 had odds ratios of less than one (i.e. models with zigzag patterns were subject to fewer attacks). The distribution of odds ratio values did not differ significantly from normality (Ryan–Joiner test, $R = 0.9778$, $p > 0.1$), but its mean differed significantly from the value of 1.0 expected under the null hypothesis that the zigzag pattern does not reduce predation rates (mean = 0.4821, $t = -6.71$, $p < 0.001$).

The most heavily attacked part of the model was recorded in 402 attacks. Models with adder patterns were attacked predominantly on the anterior quarter of the body, whereas in plain models, attacks were scattered along the entire body, with the tail quarter accumulating the

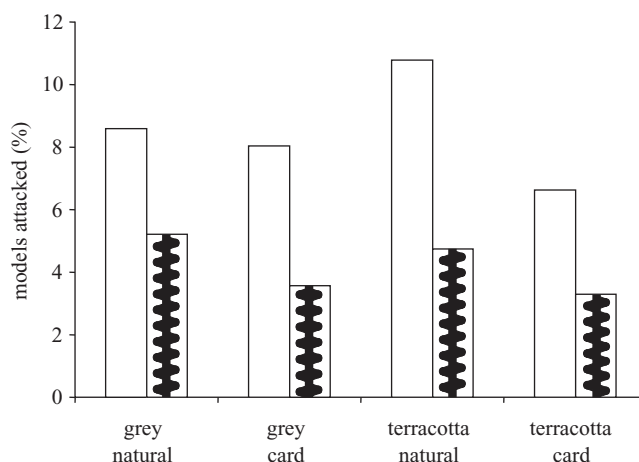


Figure 1. Percentage of different models attacked. Plain columns indicate plain models, bars with zigzag band indicate models painted with viper patterns. Grey/terracotta and natural/card indicate model ground colour and background, respectively.

highest number (figure 2). The difference between plain and patterned models was significant both in grey and terracotta ($\chi^2 = 19.997$ and 26.614 , respectively; d.f. = 3, $p < 0.001$) models, but there was no significant difference between grey and terracotta plain or grey and terracotta patterned models ($\chi^2 = 1.356$ and 2.926 , respectively; d.f. = 3, $p > 0.1$).

4. DISCUSSION

Our results show that, independent of background and model colour, Plasticine models bearing the distinctive zigzag mark of *V. berus* receive fewer avian attacks than plain models. The differences in attack rates are paralleled by differences in the site of attack along the body: adder-patterned models were attacked primarily in the anterior quarter of the body, whereas plain models were not. These differences suggest that the predators perceived the adder-patterned models as posing a greater threat than plain models.

In much of the literature, the function of the dorsal zigzag band of European vipers is assumed to be primarily cryptic (e.g. Andr n & Nilson 1981; Luiselli 1992; Shine & Madsen 1994). However, in our study, the avoidance of ‘adder’ models was in fact more pronounced on a plain card background than on a natural background. This strongly suggests that our avian predators were actively avoiding models with an adder pattern, as opposed to being unable to find them because of crypsis resulting from the zigzag band.

The fact that free-ranging avian predators selectively avoided models patterned like the generally inconspicuous adder suggests that, contrary to classical aposematism theory based on receiver psychology, bright, conspicuous colours are not a prerequisite for predator avoidance under some conditions. As noted by Pough (1988), viperids are able to inflict severe or lethal retaliation on most potential vertebrate predators, resulting in severe loss of fitness from an inappropriate attack. Consequently, although relatively cryptic patterns such as those of the adder may be less effective in engendering predator avoidance than bolder

Table 1. Binary logistic regression analysis. The odds ratios refer to card : natural background and zigzag : plain models.

| predictor | χ^2 | d.f. | <i>p</i> | odds ratio | lower 95% CI | upper 95% CI |
|------------|----------|------|----------|------------|--------------|--------------|
| site | 759.46 | 13 | <0.001 | n.a. | | |
| pattern | 99.82 | 1 | <0.001 | 0.457 | 0.39 | 0.53 |
| background | 11.88 | 1 | 0.001 | 0.766 | 0.66 | 0.89 |

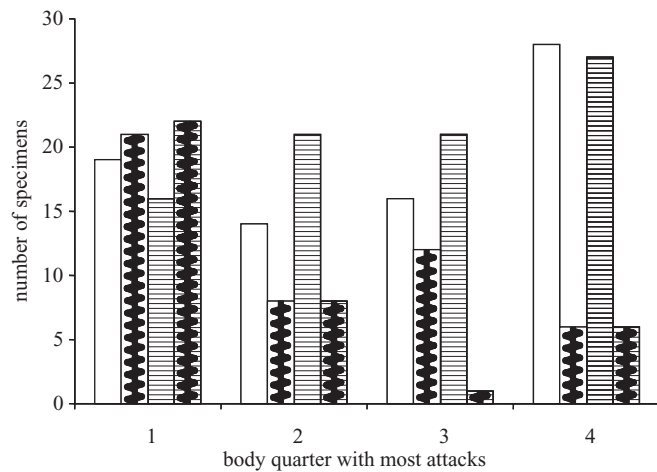


Figure 2. Position of most heavily attacked body quarter. Columns with white background denote grey models, shaded columns indicate terracotta models, plain columns indicate plain models, and columns with zigzag band indicate models painted with viper patterns.

colours, our results provide the first clear experimental evidence that free-ranging avian predators can indeed avoid inconspicuous but characteristically coloured noxious models in nature.

Our results also call for a re-evaluation of hypotheses on the causation of pattern polymorphism, and especially melanism, in *V. berus*. Andrén & Nilson (1981) sought to explain different predation rates between models of patterned and melanistic adders in the context of a trade-off between the benefits of crypsis in zigzag patterned adders and the thermoregulatory benefits of melanism, resulting in faster growth but higher mortality in melanistic adders. However, their models were all positioned on a natural background, confounding the effects of crypsis (model not seen) and aposematism (model seen but avoided). Other workers have invoked crypsis resulting from flicker-fusion to explain the zigzag band of adders and sexual dimorphism in the frequency of melanism (Shine & Madsen 1994; Lindell & Forsman 1996). All these hypotheses rest on the fundamental assumption that the function of the zigzag is primarily cryptic, but do not consider the possibility of an aposematic effect.

We suggest that these observations are also consistent with a hypothesis of aposematism: the particularly contrasting coloration of roaming males in the mating season emphasizes the warning pattern, and the trade-off between melanism and zigzag patterns may be a three-way trade-off between crypsis, aposematism and thermoregulation, rather than just between crypsis and thermoregulation. Aposematism may thus be an important but hitherto neglected factor in the causation and maintenance of pattern polymorphism in *V. berus*. Future experiments

testing the function and consequences of polymorphism in European viperids should seek explicitly to differentiate between crypsis and predator avoidance.

Although our results do not provide evidence of a cryptic function for the zigzag band, it would be premature to dismiss the idea. Aposematism relies on a few specific, easily abstracted cues, whereas crypsis relies on a subtle combination of traits to cause the blending of prey and environment. The limitations of Plasticine models prevent us from fully investigating the role of crypsis, and our models may have been more conspicuous to birds than real snakes would have been. The adder's zigzag pattern may thus fulfil a dual role of crypsis (allowing the snake to remain unseen in many encounters, whether through somatolysis or through flicker-fusion) and warning coloration (repelling potential attacks from predators when crypsis fails). Our results are thus complementary to, rather than contradictory of, the hypotheses based on an assumption of crypsis. Whether predator avoidance of adder patterns is innate (like the avoidance of coral snake and sea snake patterns by some birds; Smith 1975, 1977; Caldwell & Rubinoff 1983) or learned remains to be ascertained.

Finally, our findings also support the pervasive influence of venom on the evolution and diversification in snakes (Greene 1997). A venom apparatus capable of causing severe loss of fitness to any non-specialist predator can provide relative immunity from predation not only to those snakes that possess it, but also to others sufficiently similar to be mistaken for a venomous snake. Up to 18% of all neotropical snake species have been proposed to be coral snake mimics (Pough 1988). Our data confirm the possibility that the many harmless snakes that have been flagged as potential Batesian mimics of vipers (e.g. Gans 1961; Brodie & Brodie 2004) may indeed be exactly that. To the numerous documented mimics of coral snakes, we can now add various potential mimics of highly venomous but inconspicuously patterned vipers. The extent of viper mimicry in colubrid snakes is harder to assess than coral snake mimicry, owing to the difficulty of separating convergent crypsis and mimicry. Nevertheless, the likelihood that several colubrid species may be Batesian mimics of vipers emphasizes the fundamental importance of mimicry as a major factor in the evolution and diversification of snakes, by allowing otherwise vulnerable species the relative immunity from predation required to occupy niches involving exposure to visual predators.

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