The complex business of survival by aposematism

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The theory of warning signals dates back to Wallace but is still confusing, controversial and complex. Because predator avoidance of warningly coloured prey (aposematism) is based upon learning and reinforcement, it is difficult to understand how initially rare conspicuous forms subsequently become common. Here, we discuss several possible resolutions to this apparent paradox. Many of these ideas have been largely ignored as a result of implicit assumptions about predator behaviour and assumed lack of variation in the predators, prey and the predation process. Considering the spatial and temporal variation in and mechanisms of behaviour of both predators and prey will make it easier to understand the process and evolution of aposematism.

Introduction

Warning signals manipulate predator foraging behaviour by sending a signal, which can be a distinctive colour, odour or behaviour, to the predator that the prey is unprofitable [1–4] (Figure 1; Box 1). This, in turn, enables and encourages the predator to switch to more profitable prey [5–7]. The association between the signal and unprofitability is called 'aposematism' [1]. Aposematic signals work best when they are easily detectable and memorable, which facilitates avoidance learning [4]. However, by sending conspicuous signals, prey also increase their own risk of damage or death if the predator is immune to their defences [8], has forgotten the association between signal and unprofitability, or is naïve [4]. The benefits of aposematism increase as a function of the density of the similarly signalling individuals [8], making maintenance understandable but origin apparently paradoxical [9]. The concepts and evidence for aposematism have been reviewed recently [4], therefore we discuss the largely neglected mechanisms that might aid or prevent the initial spread and maintenance of aposematism.

Predator behaviour

It is commonly assumed that the initial stages of the evolution of aposematism proceed slowly or inefficiently because learning and reinforcement mechanisms work better at high prey densities [4,10]. This assumption
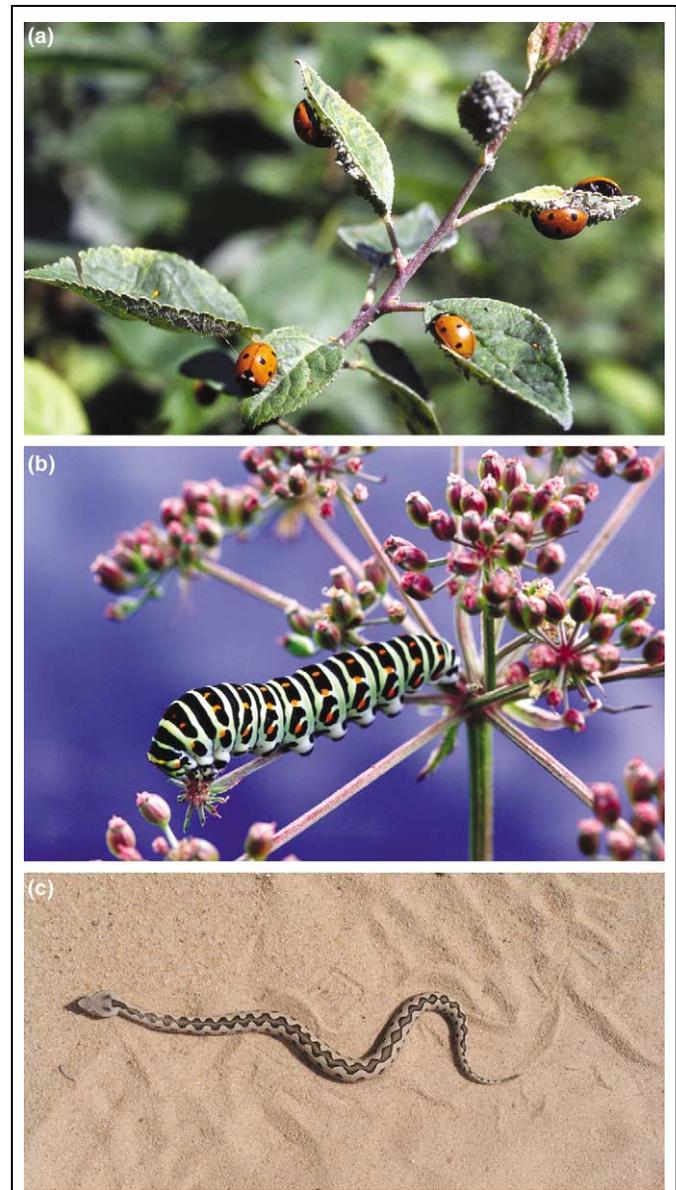

Figure 1. Examples of warning colouration. **(a)** Seven-spot ladybirds *Coccinella septempunctata* are a classic example of aposematic species. Conspicuous coloration warns predators that the prey is toxic. **(b)** Aposematism and crypsis combined: the noxious swallowtail butterfly, *Papilio machaon* is cryptic from a distance but conspicuous close up [70]. **(c)** The zig-zag pattern of many venomous snakes is suggested to be an example of a disruptive colour pattern. Recent studies show that the zig-zag pattern of *Vipera* species can also function as a warning to predators [71]. Reproduced with permission from Jarkko Mäkineva/Nature Photo Agency, Aarni Nurmila/Nature Photo Agency and Martti Niskanen.

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Box 1. What determines profitability?

Aposematism depends upon the relationship between a distinctive signal and the low profitability of potential prey [4], but why should a predator make the decision not to attack? Foraging theory and numerous experiments suggest that predators tend to choose prey if the benefits of attacking that prey are higher than the attack costs [5]; we refer to this as the intrinsic profitability of the prey. In addition, a prey should be chosen when its intrinsic profitability is greater than or equal to that of other prey [5]; we refer to this as its relative profitability. Aposematism depends upon the relative profitability and the signal advertising unprofitability, and not necessarily the intrinsic profitability.

Profitability is a function of the benefits and costs to the predator and the physical and physiological state of the predator and prey. Benefits include nutrition and water, and attack costs include time taken away from foraging or mating, pursuit and handling time and energy, damage or poisoning by the prey, and digestion costs. The profitability of the prey depends upon which defences it uses (Table I), and on the properties and relative abundances of prey and predator communities [8,11,38].

Costs of overcoming defences vary with the kind of defences encountered (Table I) and this affects the conditions for establishment of aposematism [38]. For example, the potential fitness loss to predators if prey are unpalatable, distasteful, or require moderate handling time, is likely to be less than if the prey are toxic, have effective or damaging physical defences or high pursuit costs. Consequently, predators should respond differently to weakly defended prey compared to those that damage the predator, which

have relatively much lower profitability. However, if damaging effects are minor, then a higher relative abundance might offset a small difference in defence strength, making better-defended prey more profitable; the predator might thus switch to eating a prey that has what might seem to be a superior defence.

Defences that have a time delay before their effects are felt will generally be more costly to predators than those that take effect immediately [69], not only because of the risk of physical or chemical damage, but also because the costs might be cumulative. Prey species that invoke toxicity and distastefulness after ingestion [70], as well as highly toxic prey, are therefore more likely to evolve aposematism than are weakly defended prey [38]. It might not be a coincidence that the most common forms of aposematism involve these later-acting forms of defence [4]. The costs of such defences are also greater for the prey because they involve greater risk [69]. A predator might decide to abandon the predation attempt at any time in the sequence (Table I) when the cumulative costs are greater than the benefits [5]. From the viewpoints of both predator and prey, this should happen as soon in the sequence as possible [69]. As a result, predators can appear to let their prey escape intentionally during attack stages when the cumulative costs equal the cumulative benefits of completing the sequence. The terms 'unpalatable', 'distasteful', 'aversive', 'toxic', 'defended' and 'unprofitable' have all been used, often interchangeably, in the literature on aposematism, but 'profitability' in the context of optimal foraging captures the consequences of these defences more efficiently than these other terms.

Table I. Anti-predator defences operating at various stages of predation[a]

Stage	Defence[b]	
Encounter (get within detection distance)	Rarity	Apparent rarity
Detection Stage	Immobility	Disruptive colouration[c]
	Crypsis[d]	Other sensory or cognitive tricks[d]
	Confusion[c]	
Identification as profitable and attack decision	Rarity relative to more-profitable species[c]	Aposematism[c]
	Masquerade (resemble inedible objects)	Müllerian mimicry[c]
	Confusion[c]	Batesian mimicry
Approach and attack	Difficult to pursue or capture[c]	Redirection of attack to body parts of low damage cost[d]
	Unpredictable behaviour	Encouraging premature attack[c]
	Rush for cover	Aggregation and predator saturation[c]
	Startle, bluff, threat behaviour[c]	
Subjugation (prevent escape)	Strength of escape[c]	Lethality[c]
	Mechanical defence[c]	Group defence[c]
	Noxiousness[c] (hairy, distasteful)	Resistance to venom[d]
	Toxic to handle[c]	
Consumption (eat)	Safe passage through the gut	Toxic[c]
	High digestion cost[c]	Lethality[c]
	Emetic[c]	

[a]Modified from [25,69].
[b]Defences are any mechanism that reduces the probability of damage or death. These defences reduce profitability to varying degrees. Different defences are not mutually exclusive.
[c]Commonly used by aposematic species.
[d]Defences that aposematic species might also use.

results from conflating the mechanisms of the maintenance and origination of aposematism. Several aspects of the behaviour of predators towards rare prey can favour new forms long enough for them to increase in frequency, enabling the positive frequency dependence of aposematism to take over the maintenance of aposematism [11,12].

Predators often prefer familiar foods and avoid those that are novel (neophobia) [13]; some individuals are also

reluctant to add new items to their diet (dietary conservatism) [14–16]. For brevity, we call these two phenomena 'wariness'. Wariness has been demonstrated in a variety of species, including slugs [17], fish [18], amphibians [19], reptiles [20], birds [21], cattle [22] and humans [23]. If many predators are conservative in their food preferences, then even very conspicuous novel prey morphs are not necessarily at a selective disadvantage [15,16,24]. Wariness

should work best when new aposematic forms are rare because it depends on other prey being more familiar to the predator (but see [10]). Wariness might favour new forms long enough for them to increase in frequency, an idea that has only just begun to be explored empirically [15,24]. We do not yet know whether predator wariness proceeds, follows, or evolves simultaneously with aposematism. Phylogenetic considerations suggest that wariness evolves with aposematism [14], but no studies have approached this question in detail to our knowledge.

Predators can also induce negative frequency-dependent selection (i.e. features are advantageous when rare) on equally familiar prey types, through optimal foraging in patches and by using search images, selective attention and other psychological mechanisms [26–30]. The resulting predation thus benefits rare prey forms and might aid the initial spread of new aposematic forms, especially if they are not very conspicuous. But, depending upon whether predators are immune to the defences of these new aposematic forms, negative frequency-dependent selection might also prevent their fixation [8]. More work is needed on the frequency- and density-dependent effects of predation on aposematic species.

When presented with a new food, the choice that the predator makes is unlikely to be related to the profitability of that food given that its costs and benefits would be unknown to the predator (Box 1). The predator would have to make a judgement about relative profitability, and decide accordingly whether to eat the food. This judgement might be based upon the similarity in appearance and/or taste between the new prey and the most similar prey with which the individual is familiar [31,32]. For example, if the most similar known prey is relatively unprofitable, then the predator should refuse the new prey, and vice versa. In addition, any new form that uses colours or colour combinations that the prey already knows to avoid will have an initial advantage over those forms with unfamiliar colours [7,33,34]. Many experiments show that typical aposematic colours (i.e. black with yellow, black with red) are innately aversive whereas typically cryptic colours (i.e. green, brown) are preferred by a variety of species [4,33,35] although avoidance can be context dependent [36].

Any or all of these factors might enable a sufficient increase in the frequency of a rare form for the positive frequency dependence of predator learning to take over the system and maintain or elaborate new forms [11,12].

Effects of variation in prey profitability
Aposematism is often treated as a distinct alternative to crypsis (i.e. being inconspicuous and palatable); that is, all aposematic prey are equally conspicuous and unprofitable, and a cryptic alternative (if it is present) is always fully palatable. An exception is müllerian mimicry (having the same colouration but different degrees of defence), although this is likely to evolve after aposematism has established [26,37]. However, constant profitability is unlikely to occur even in non-mimetic aposematic systems, because prey will vary genetically and at random in the efficacy of their defences. Defence efficacy might also vary with prey age or experience in defence. Thus, profitability

varies with the state of the prey [5,38]. This variance in (un)profitability might decrease the learning rate of predators [58], thus affecting negatively the success of aposematism. However, this success also depends on the fraction and degree of the unprofitability of the prey population; thus, any outcome (successful or unsuccessful spread of aposematism) is theoretically possible.

The diet choice of individual predators depends on the availability as well as the characteristics (states) of alternative prey [38–40]. If the profitability of a conspicuous prey species is less than that of other prey species (regardless of conspicuousness), then the conspicuous prey species will be protected because the predators might prefer other species with relatively higher profitability [5,38]. Curiously, densities (or characteristics) of alternative prey have rarely [40,42] been considered in either models or experiments in aposematism research, although their effects on population dynamics [6,41] and mimicry [4] are well known. The few experiments that vary density of alternative prey show that, when alternative prey are scarce, predators attack more-defended prey, but when alternative prey are common, the profitability of the defended prey is relatively low and they are either eaten infrequently or ignored [43,44]. This suggests that the spread and maintenance of aposematism requires an intermediate abundance of alternative prey, at least initially [40]. Predators routinely make decisions based upon relative profitability even if all prey are undefended [5,6]. Consequently, adding a weak defence and a conspicuous signal to an already rare form might reduce its profitability further and make the initial spread of aposematic forms possible [4]. In the early stages of spread, even if rare, a relatively low profitability might protect the new form long enough for it to increase in frequency, and also enable it to evolve stronger defences, which will decrease its profitability further. Alternatively, locally abundant profitable prey can attract increased numbers of predators [45], which might lead to lower survival of aposematic prey. The composition of the prey community will therefore have a significant effect on the evolution of aposematism. However, this is an area of research that requires further study.

Effect of variation among predators
Aposematism is usually treated as though all predators have the same properties and experience. However, there is among-species variation in dietary conservatism, predatory behaviour, general wariness, susceptibility to anti-predator defences, how they can handle prey and other ways that affect the efficiency of prey defence (reviewed in [8]). Predator differences can arise as a result of divergence in evolutionary history, differences in experience and in the potency of aposematic and alternative prey (which affect optimal foraging decisions), interspecific competition, genetic differences, arms races and other factors. Similar variation is found among individuals of a species [8]. For example, individuals can differ in their previous experience and learning of defended forms, or in their hunger level. Hunger makes animals, including humans, take more risks [46] and be less choosy about food [5,23,41], inducing individual variation.

Preferences can also vary according to predator experience. Often juveniles are more wary than are adults when they attack aposematic prey [47,48], and even adults vary greatly in attack latency and tendency [8,49]. Experiments show that some individuals are more exploratory than others and readily search out and utilize new prey types [14,50,51]. Although individual variation in foraging and feeding behaviour can result from local differences in age and experience, it can also have a genetic basis [50]. However, aversions are not necessarily fixed; negative experiences can reinforce them [51] and positive experience can relax them [52]. In less wary species, some individuals might learn how to remove the noxious parts of prey insects, whereas others might not [53]. Although many predators have innate avoidances against warningly coloured prey [54] or novel odours [55, 56], most vertebrate predators have to learn to distinguish edible prey from inedible prey. Consequently, even if all individuals had equal defence-breaking learning ability, young ones might be more deterred than older individuals because they have not yet learned to deal with the prey. This also illustrates how, if learning ability is well developed, predators can either learn to avoid aposematic prey or learn how to handle and eat them.

Because food is often limited, natural selection should favour both learned and heritable predatory mechanisms that bypass prey defences [57,58]. Toxins are often not evenly spread throughout the body of an organism, and many predators remove the more toxic parts before eating, reducing the advantage of aposematism [8]. Mechanisms that bypass prey defences can lead to arms races between predators and their prey. For instance, newts of the aposematic salamander genus *Taricha* sequester TTX neurotoxin in their skin, which can kill their main predator, garter snakes. However, a few populations of snakes have evolved a high level of TTX resistance, which is phenotypically and genetically variable within populations [59]. Such arms races between predator and prey can result in incomplete defences and inefficient predation [60]. The results of such effects on both the maintenance and the end point of the aposematic strategy need further study.

Selection for aposematism is variable in space and time
The components of aposematic strategies are usually treated as though they are invariant, although this is unlikely. We have already discussed how variation in predators and prey leads to variation in profitability among species and individuals. This variation might have a spatial and/or temporal pattern depending on predator and prey individual states and community structure. For example, prey might vary over time and space in their nutritional value and defence efficacy, affecting each individual's intrinsic profitability. Relative profitability is affected by the characteristics and abundances of other prey species. The state of health, hunger level and experience of the predator with that prey species will vary over time and in different localities. This results in the gains of eating a given prey item being higher for a hungry than for a satiated predator, and the losses being lower for a healthy than for an unhealthy or injured

predator. The net result is that profitability will vary over the lifetime of an individual predator, even if the prey individuals are all identical, which is unlikely.

The abundance of alternative prey will vary among seasons, years and geographical locations, as does the predator community. Thus, conditions for the spread of aposematism might only occur in a few locations and/or during a few years. On a smaller geographical scale, predator territory quality can vary significantly. For example, birds with low-quality territories might use aposematic species more often than those in average territories, unless there are significant harmful effects [61]. Variation among predator individuals, territories and family groups can also occur because animals can learn from their parents and relatives; such cultural transmissions can lead to localized 'feeding cultures' that can vary among locations or among families [62]. This results in microgeographical variation in selection for or against aposematism. This variation can also occur as a joint result of learning and genetic predisposition [63,64] or a general effect of variation in wariness [65]. Shifts in diet can occur at geographical range boundaries and other marginal habitats where alternative food might be scarce enough to encourage the consumption of aposematic prey. Range extensions can change the local intensity of selection for aposematism; predators can colonize new areas, resulting in completely new selection on the prey, and defended prey species can colonize new areas, challenging the local predator fauna [66]. If either kind of range extension affects the relative abundance of alternative more-palatable prey, or the relative abundance of defence-immune predators, then selection for aposematism might be either weakened or strengthened accordingly. Geographical and microgeographical variation in the conditions for aposematism need to be investigated, both theoretically and empirically.

Clumped prey distributions help the spread and maintenance of aposematism (reviewed in [4]). Optimal foraging can interact with prey clumping behaviour in positive or negative ways depending upon variation in predator territory quality. In a bad year or territory, the advantage to prey of aggregation [67] might be greatly reduced (or become negative) because hungry predators will find a good patch and stay in it until all prey are eaten, selecting against aposematism. If the prey are moderately well defended, and there are few alternative prey, then less-clumped distributions will be better, even in good years. This might lead to aggregation being more common in species-rich prey communities and seasons, at least for prey that do not negatively affect the predator. Clumped or patchy predator distributions could also aid the initial spread if, by chance, a new form appeared in a location in which there were few predators [68].

Variation in selection in space and time can make the conditions for the origin of aposematism more relaxed and the conditions for maintenance more variable than is usually assumed. For example, in good territories or years, predators might be more selective and avoid even weakly protected and weakly aposematic prey, enabling their initial spread in those territories. In intermediate territories and years, the profitability of weakly protected

and/or weakly aposematic prey will be reduced and selection will maintain and enhance the evolution of aposematism. In poor territories or years, if there are no emetic or weakening effects of defences, aposematism might not work, and the initial spread of aposematism might be stalled or reversed. However, if aposematism has advanced enough to include emetic or other predator-weakening effects, then aposematism will be maintained or enhanced even in poor territories or years. Variation among individuals in dietary conservatism will also enable aposematism to spread in predator territories with more conservative occupants [14–16,24]. If conditions for spread are stable enough within territories, then new forms can increase enough for gene flow to raise the frequency of aposematic forms throughout the species range.

Conclusions

The function of aposematism is currently well understood, but many questions still exist about its origin and maintenance (Box 2). Not all predator species are susceptible to anti-predator defences and, even within species, susceptibility varies [6]. Aposematism should not be seen as an anti-predator strategy that is an alternative to crypsis but rather as part of a continuum of strategies from very protected highly conspicuous to weakly protected less conspicuous forms. Different strategies, such as crypsis and aposematism, are not mutually exclusive [70,71] (Figure 1). We also need to account for spatial and temporal variation in selection. Small- and large-scale variation in ecological, behavioural and genetic factors in predator–prey interactions can cause variable selection pressures that influence both the origin

and maintenance of aposematism in ways that are not fully covered by current theory and experiments.

References

1 Poulton, E.B. (1890) *The Colours of Animals: Their Meaning and Use Especially Considered in the Case of Insects*, Kegan Paul, Trench, Trubner and Co

2 Cott, H.B. (1940) *Adaptive Coloration of Animals*, Methuen

3 Edmunds, M. (1974) *Defence in Animals: A Survey of Antipredator Defences*, Longman

4 Ruxton, G.D. *et al*. (2004) *Avoiding Attack. The Evolutionary Ecology of Crypsis, Warning Signals & Mimicry*, Oxford University Press

5 Stephens, D.W. and Krebs, J.R. (1987) *Foraging Theory*, Princeton University Press

6 Murdoch, W.W. (1969) Switching in general predators: experiments on predators and stability of prey populations. *Ecol. Monogr.* 39, 354–355

7 Lindström, L. *et al*. (1999) Can aposematic signals evolve by gradual change? *Nature* 397, 249–251

8 Endler, J.A. and Mappes, J. (2004) Predator mixes and the conspicuousness of aposematic signals. *Am. Nat.* 163(4), 532–547

9 Guilford, T. (1990) Evolutionary pathways to aposematism. *Acta Oecologia* 11, 835–841

10 Lindström, L. *et al*. (2001) Strong antiapostatic selection against novel rare aposematic prey. *Proc. Natl. Acad. Sci. U. S. A.* 98, 9181–9184

11 Sherratt, T.N. (2002) The coevolution of warning signals. *Proc. R. Soc. London B Biol. Sci.* 269, 741–746

12 Speed, M.P. (2001) Can receiver psychology explain the evolution of aposematism? *Anim. Behav.* 61, 205–216

13 Bravemen, N.S. and Jarvis, P.S. (1978) Independence of neophobia and taste aversion learning. *Anim. Learn. Behav.* 6, 406–412

14 Marples, N.M. *et al*. (1998) Response of wild birds to novel prey: evidence of dietary conservatism. *Oikos* 83, 161–165

15 Thomas, R.J. *et al*. (2003) Dietary conservatism may facilitate the initial evolution of aposematism. *Oikos* 101, 458–466

16 Marples, N.M. *et al*. (2005) The evolution of warning coloration is not paradoxical. *Evolution* 59, 933–940

17 Delaney, K. and Gelperin, A. (1986) Post-ingestive food-aversion learning to amino-acid deficient diets by the terrestrial slug *Limax maximus*. *Behaviour* 159, 281–295

18 Bryant, J.E. (1972) Feeding history, parental stock, and food selection in rainbow trout. *Behaviour* 45, 123–153

19 deCock, R. and Matthysen, E. (2003) Glow-worm larvae bioluminescence (Coleoptera: Lampyridae) operates as an aposematic signal upon toads (*Bufo bufo*). *Behav. Ecol.* 14, 103–108

20 Sword, G.A. *et al*. (2000) Density-dependent aposematism in the desert locust. *Proc. R. Soc. London B Biol. Sci.* 267, 63–68

21 Alcock, J. (1973) The feeding response of hand-reared red-winged blackbirds (*Agelaius phoeniceus*) to a stinkbug (*Euschistus consperus*). *Am. Midl. Nat.* 89, 307–313

22 Herskin, M.S. *et al*. (2003) Behavioural and adrenocortical responses of dairy cows toward novel food: effects of food deprivation, milking frequency and energy density in the daily ration. *Appl. Anim. Behav. Sci.* 82, 251–261

23 Pliner, P. *et al*. (1995) The effects of fear on food neophobia in humans. *Appetite* 25, 77–87

24 Thomas, R.J. *et al*. (2004) Prey selection by wild birds can allow novel and conspicuous colour morphs to spread in prey populations. *Oikos* 106, 285–294

25 Lindström, L. *et al*. (2001) Predator experience on cryptic prey affects the survival of conspicuous aposematic prey. *Proc. R. Soc. London B Biol. Sci.* 268, 357–361

26 Endler, J.A. (1991) Interactions between predators and prey. In *Behavioural Ecology* (3rd edn) (Krebs, J.R. and Davies, N.B., eds), pp. 169–196, Blackwell Scientific Publications

27 Blough, P. and Lacourse, D.M. (1994) Sequential priming in visual search – contributions of stimulus-driven facilitation and learned expectancies. *Anim. Learn. Behav.* 11, 275–281

28 Bond, A.B. and Kamil, A.C. (1998) Apostatic selection by blue jays produces balanced polymorphism in virtual prey. *Nature* 395, 594–596

29 Allen, J.A. and Weale, M.E. (2005) Anti-apostatic selection by wild birds on quasi-natural morphs of the land snail *Cepaea hortensis*: a generalised linear mixed models approach. *Oikos* 108, 335–343

30 Dukas, R. and Kamil, A.C. (2001) Limited attention: the constraint underlying search image. *Behav. Ecol.* 12, 192–199

31 Mappes, J. and Alatalo, R.V. (1997) Batesian mimicry and signal accuracy. *Evolution* 51, 2050–2053

32 Loewen, R. and Pliner, P. (1999) Effects of prior exposure to palatable and unpalatable novel foods on children's willingness to taste other novel foods. *Appetite* 32, 351–366

33 Smith, S.M. (1977) Coral-snake pattern recognition and stimulus generalisation by naive great kiskadees (Aves: Tyrannidae). *Nature* 265, 535–536

34 Alatalo, R.V. and Mappes, J. (1996) Tracking the evolution of warning signals. *Nature* 382, 708–710

35 Schuler, W. and Hesse, E. (1985) On the function of warning coloration – a black and yellow pattern inhibits prey-attack by naïve domestic chicks. *Behav. Ecol. Sociobiol.* 16, 249–255

36 Gamberale-Stille, G. and Tullberg, B. (2001) Fruit or aposematic insect? Context-dependent colour preferences in domestic chicks. *Proc. R. Soc. London B Biol. Sci.* 268, 2525–2529

37 Flanagan, N.S. *et al.* (2004) Historical demography of Müllerian mimicry in the neotropical *Heliconius* butterflies. *Proc. Natl. Acad. Sci. U. S. A.* 101, 9704–9709

38 Sherratt, T.N. (2003) State-dependent risk-taking by predators in systems with defended prey. *Oikos* 103, 93–100

39 Leimar, O. *et al.* (1986) Evolutionary stability of aposematic coloration and prey unprofitability: a theoretical analysis. *Am. Nat.* 128, 469–490

40 Merilaita, S. and Kaitala, V. (2002) Community structure and the evolution of aposematic coloration. *Ecol. Lett.* 5, 495–501

41 Elkinton, J.S. *et al.* (2004) Effects of alternative prey on predation by small mammals on gypsy moth pupae. *Popul. Ecol.* 46, 171–178

42 Kokko, H. *et al.* (2003) Alternative prey can change model–mimic dynamics between parasitism and mutualism. *Ecol. Lett.* 6, 1068–1076

43 Hetz, M. and Slobodcikoff, C.N. (1988) Predation pressure on an imperfect Batesian mimicry complex in the presence of alternative prey. *Oecologia* 76, 570–573

44 Lindström, L. *et al.* (2004) The effect of alternative prey on the dynamics of imperfect batesian and müllerian mimicries. *Evolution* 58, 1294–1302

45 Holt, R.D. (1997) Community modules. In *Multitrophic Interactions in Terrestrial Systems* (Gange, A.C. and Brown, V.K., eds), pp. 333–349, Blackwell Scientific Publications

46 Krebs, J.R. and Davies, N.B. (1993) *An Introduction to Behavioural Ecology*, Blackwell Scientific Publications

47 Reznick, D.N. *et al.* (1981) Initial prey preferences in the lizard *Sceloporus malachiticus*. *Copedia* 1981, 681–686

48 Lindström, L. *et al.* (1999) Reactions of hand-reared and wild-caught predators toward warningly colored, gregarious, and conspicuous prey. *Behav. Ecol.* 10, 317–322

49 Marples, N.M. and Kelly, D.J. (2001) Neophobia and dietary conservatism: two distinct processes? *Evol Ecol.* 13, 641–653

50 Marples, N.M. and Brakefield, P.M. (1995) Genetic variation for the rate of recruitment of novel insect prey into the diet of a bird. *Biol. J. Linn. Soc.* 55, 17–27

51 Domjan, M. (1975) Poison-induced neophobia in rats – role of stimulus generalization of conditioned taste aversions. *Anim. Learn. Behav.* 3, 205–211

52 Roper, J.T. (1990) Responses of domestic chicks to artificially colored insect prey – effects of previous experience and background color. *Anim. Behav.* 39, 466–473

53 Fink, L.S. and Brower, L.P. (1981) Birds can overcome the cardenolida defence of monarch butterflies in Mexico. *Nature* 291, 67–70

54 Smith, S.M. (1975) Innate recognition of coral snake pattern by a possible avian predator. *Science* 187, 759–760

55 Marples, N.M. and Roper, T.J. (1996) Effects of novel colour and smell on the response of naive chicks towards food and water. *Anim. Behav.* 51, 1417–1424

56 Rowe, C. and Guilford, T. (1999) Novelty effects in a multimodal warning signal. *Anim. Behav.* 57, 341–346

57 Turner, J.G.R. *et al.* (1984) Mimicry and the Monte Carlo predator: the palatability spectrum and the origins of mimicry. *Biol. J. Linn. Soc.* 23, 247–268

58 Speed, M.P. (1999) Batesian, quasi-Batesian or Müllerian mimicry? Theory and data in mimicry research. *Evol. Ecol.* 13, 755–776

59 Geffeney, S. *et al.* (2002) Mechanisms of adaptation in a predator–prey arms race: TTX-resistant sodium channels. *Science* 297(5585), 1336–1339

60 Dawkins, R. and Krebs, J.R. (1979) Arms race between and within species. *Proc. R. Soc. London B Biol. Sci.* 205, 489–511

61 Eeva, T. *et al.* Pollution–related changes in diets of two insectivorous passerines. *Oecologia* (in press)

62 Altbaecker, V. *et al.* (1995) Rabbit-mothers' diet influences pups' later food choice. *Ethology* 99, 107–116

63 Turro-Vincent, I.F. *et al.* (1995) Experiential and genetic influences on learnt food aversions in Japanese quail selected for high or low levels of fearfulness. *Behav. Proc.* 34, 23–42

64 Van Oers, K. *et al.* (2004) Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities. *Proc. R. Soc. London B Biol. Sci.* 271, 65–73

65 Pliner, P. and Loewen, R.E. (1997) and food neophobia in children and their mothers. *Appetite* 28, 239–254

66 Phillips, B.L. and Shine, R. (2004) Adapting to an invasive species: toxic cane toads induce morphological change in Australian snakes. *Proc. Acad. Natl. Sci. U. S. A.* 101, 17150–17155

67 Riipi, M. *et al.* (2001) Multiple benefits of gregariousness cover detectability costs in aposematic aggregations. *Nature* 413, 512–514

68 Sherratt, T.N. and Beatty, D.C. (2003) The evolution of warning signals as reliable indicators of prey defense. *Am. Nat.* 162, 377–389

69 Endler, J.A. (1986) Defence against predation. In *Predator–Prey Relationships, Perspectives and Approaches from the Study of Lower Vertebrates* (Feder, M.E. and Lauder, G.E., eds), pp. 109–134, University of Chicago Press

70 Tullberg, B.S. *et al.* (2005) Aposematism and crypsis combined as a result of distance dependence: functional versatility of the colour pattern in the swallowtail butterfly larva. *Proc. R. Soc. London B Biol. Sci.* (in press)

71 Niskanen, M. and Mappes, J. (2005) Significance of the dorsal zig-zag pattern of *Vipera latastei graditana* against avian predators *J. Anim. Ecol.* (in press)