



Learning to avoid aposematic prey

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The evolution of prey warning coloration is, literally, a textbook example of Darwinian adaptive evolution by natural selection. The cornerstone of this evolutionary process is a predation event, the dynamics of which are poorly understood. Aposematic (warningly coloured) prey are relatively unpalatable and their conspicuous appearance should enable predators to avoid them, but such is not always the case. Based on models of conditioned learning, it has been assumed that the number of aposematic prey that a predator will attack as it learns to avoid such prey should be constant or declining as the prey's abundance increases. However, empirical studies have shown that predators make more attacks on aposematic prey when those prey are more common. I suggest that this failure of theory to predict behaviour probably arises from limitations of the learning models in question. Rather than using mechanistic models of conditioned learning, I used signal detection theory to provide a functional characterization of the uncertainty that inexperienced predators encounter when learning to distinguish prey types. This characterization explains other otherwise puzzling data on predation on aposematic prey and can offer insight on the selective pressures driving the evolution of aposematism and mimicry.

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The combination of conspicuous appearance and unpalatability is an antipredator defence known as aposematism. Their unpalatability makes aposematic prey (aposemes) costly to attack and predators should avoid them. However, predators often fail to discriminate aposematic prey from more cryptic and palatable prey, and discrimination varies with aposeme abundance, gregariousness, palatability and conspicuousness (reviews in [Joron & Mallet 1998](#); [Speed 1999](#)).

This interplay of morphological, physiological and ecological factors with predation has made the evolution of aposematism important in our understanding of the behavioural mechanisms of natural selection in general ([Turner 1987](#); [Joron & Mallet 1998](#); [Speed 2001](#)). As a case study of Darwinian adaptation, topics in aposematism are under active investigation at many levels of biological organization, including ecology, population genetics, genetic control of morphology, toxin metabolism and behaviour. Aposematism also provides an experimentally useful system for the relatively new

perspective in evolutionary biology that examines the effects of cognition as both a selective agent and a character under selection.

The event at the centre of all the excitement is the predatory act. Expectations of the patterns of predation on aposematic prey have assumed either tacitly ([Müller 1879](#); [Endler 1988](#); [Lindström et al. 2001](#)) or explicitly ([Speed 1993](#); [Speed & Turner 1999](#); [Servadio 2000](#)) that a form of conditioned learning underlies predator behaviour. Predators, it is assumed, learn an association between an aposeme's conspicuous appearance and the relative cost accrued upon attacking the unpalatable prey item. The learning theory commonly used is associative learning theory ([Bush & Mosteller 1955](#); [Rescorla & Wagner 1972](#); see also [Domjan 1998](#)). The Rescorla–Wagner model of associative learning ([Rescorla & Wagner 1972](#)) is the most widely known implementation of associative learning theory. However, much has changed since the formulation of the early models. Limitations of the models have been discovered and addressed (e.g. [Miller & Matzel 1988](#); [Van Hamme & Wasserman 1994](#); [Dickenson 2001](#)), and entirely nonassociative learning mechanisms have been put forward (e.g. [Gallistel & Gibbon 2000](#)). For an introduction to the current debate over learning mechanisms, see [Leslie \(2001\)](#) and accompanying articles.

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Within behavioural ecology, learning-oriented research is concerned largely with the effects of learning on ecology and evolution and does not produce studies adequate to differentiate between learning mechanisms. Commitment to a hypothesized mechanism ill suited to the type of learning under study could therefore lead to unwarranted conclusions. A failure to take advantage of modern developments in learning theory may hold back our understanding of how learned behaviours, such as discrimination and choice, affect ecological and evolutionary processes. In the present study, rather than commit to a specific hypothesis of learning mechanism, I used signal detection theory (Green & Swets 1966) as a functional characterization of the uncertainty experienced by predators as they learn to distinguish prey types. By allowing that predators may experience uncertainty about how to respond to prey (i.e. whether a given prey item should be attacked or avoided), signal detection theory offers an alternative account of these predation events and may enhance current theories to produce a more complete understanding of predator response to aposematic or other prey.

Signal detection theory provides a model of how animals choose between stimuli under conditions of uncertainty. Typically, that uncertainty is considered to arise from perceived similarity in the appearance of stimuli (e.g. Straddon & Gendron 1983; Getty 1985, 1987, 1996; Greenwood 1986; Sherratt 2001). In cases of mimicry, for example, any given prey item has some probability of being either a model or a mimic (e.g. Getty & Krebs 1985; Davies et al. 1996; Rodríguez-Gironés & Lotem 1999). Perceived variability in prey appearance might mirror phenotypic variability in the prey or arise from sensory noise (Boneau & Cole 1967). Signal detection theory might seem to be a poor candidate for describing predator response to aposematism, then, because aposemes are by definition conspicuous and should be distinguishable from cryptic prey without perceptual uncertainty. More generally, however, the uncertainty modelled by signal detection theory arises from stimulus generalization (Blough 1967, 1969), a process dependent on reinforcement history in addition to perception. I suggest that inexperienced animals may be able to perceptually distinguish stimuli very well, yet be uncertain as to the appropriate response to give to a particular stimulus. The application of signal detection theory that I have developed differs from applications within behavioural ecology, in that the uncertainty of interest arises from inexperience rather than from perceptual confusion.

Under signal detection theory, the likelihood of appropriate response (attacking S+, the prey type to which response is relatively beneficial, or ignoring S-, the prey type to which response is relatively costly) is a function of variation in prey appearance (Fig. 1). Predators place a response threshold on a continuum of prey appearance. Attacks on S+ are considered 'correct detections', whereas S- prey suffer 'false alarm' attacks. Placement of the threshold is guided by a utility function (equation 1), the maximum of which is sensitive to three signal parameters: abundance of the two prey types relative to each other, the distributions of appropriate response to each

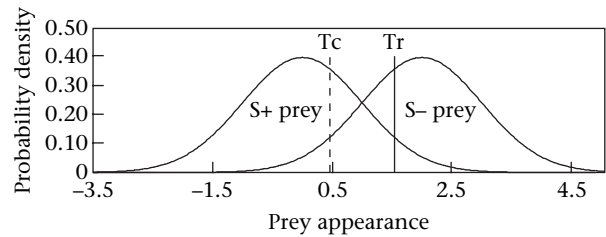


Figure 1. Avoidance learning as a signal detection task involves discrimination of two prey types: S+, the prey type to which response is relatively beneficial (e.g. cryptic palatable prey or moderately defended aposemes), and S-, the type to which response is relatively costly (e.g. strongly defended aposemes). The likelihood of appropriate response to the two types (i.e. bell-shaped signal distributions) varies over a continuum of prey perceptual similarity. Signal distributions correspond to stimulus generalization gradients, not to perceived visual similarity. That gradients tend to be bell-shaped and decrease in variance with training is well established (e.g. Rilling 1977). Overlapping distributions represent uncertainty about which response is appropriate to give to any given prey item. Overlap does not necessarily indicate that the predator perceives S+ to look similar to S-. Such uncertainty exists, for example, when predators are inexperienced or when aposematic and cryptic palatable prey types may be confused for one another because of similar morphology (e.g. both are crickets; Sword 1999). The predator behaves as though it places a threshold on the appearance continuum, attacking all prey with an appearance left of threshold, incurring both correct detections of S+ prey and false alarm attacks on S- prey. Prey abundance affects false alarm probabilities via its influence on utility (equation 1): Tc, the conservative 'S- common' threshold, denotes the optimal decision criterion (utility maximum) for a relative abundance of S- prey = 0.75. Tr, the more permissive 'S- rare' threshold, denotes the optimal decision criterion for a relative abundance of S- prey = 0.25. Other utility function parameter values producing Tc and Tr in this example: difference between distribution means = 2.0; variance of both prey distributions = 1; benefit of correct detection, $h = 1.0$; cost of false alarm $a = -1.0$; cost of missed detection, m , and benefit of correct rejection, $j = 0.0$.

prey type over the perceptual domain, and costs and benefits accrued for responding to or ignoring the prey types. Following Sperling (1984), utility is estimated as:

$$U(x) = \alpha h P(\text{CD}) + \alpha m P(\text{MD}) + (1 - \alpha) a P(\text{FA}) + (1 - \alpha) j P(\text{CR}) \quad (1)$$

where P(CD) is the probability of correct detection (measured as the integral of the S+ distribution from threshold to $-\infty$), P(MD) is the probability of missed detection ($= 1 - P(\text{CD})$), P(FA) is the probability of false alarm (integral of the S- distribution from threshold to $-\infty$), P(CR) is the probability of correct rejection ($= 1 - P(\text{FA})$), α is the relative probability of encountering an S+ prey item ($1 - \alpha =$ the relative probability of encountering an S- prey item), h is the benefit of correct detection, m is the cost of missed detection, a is the cost of false alarm and j is the benefit of correct rejection ($h > m, j > a$).

In this paper, I contrast associative learning theory approaches to aposeme predation with this 'signals' approach. I describe how the perspectives make different predictions about the number of prey that a predator will attack but make similar predictions about frequency-dependent selection, although for different reasons.

ABSOLUTE NUMBER OF PREY ATTACKED

The two common approaches to aposeme predation have assumed that the total number of aposemes attacked, n , during the period in which a predator learns to avoid aposemes should be constant at any level of aposeme abundance. Müller's influential 'number-dependent' theory specifies this constant directly (Müller 1879; Joron & Mallet 1998; Mallet & Joron 1999; Speed 1999). Models based more formally on associative learning theory (Speed 1993; Turner & Speed 1996; MacDougall & Dawkins 1998; Servidio 2000) do not specify n explicitly, but use a combination of associative learning parameters that are constant over all prey abundance. In situations where predators have any ability to distinguish prey, the effect is constant n . Theories based on conditioning posit that a predator will require some fixed amount of experience to show a particular level of avoidance of an aposematic prey type relative to alternative prey. That amount of conditioning may be produced by, for example, $n = 10$ encounters with aposematic prey of a given appearance and unpalatability. Some accounts posit that conditioning decays (i.e. animals forget; Speed 1993; Turner & Speed 1996; Servidio 2000). When aposematic prey are at low abundance, predators that forget may need a greater absolute number of encounters to learn to avoid those rare, infrequently encountered prey. Models with forgetting thus predict a declining n as aposeme abundance increases. At moderate to high aposeme abundance, both Müller's and the associative models predict that predators should require a fixed (i.e. at 10) number of encounters to learn to avoid aposemes (Joron & Mallet 1998). Attacks on aposematic prey are thus attributed to poor learning and/or forgetting.

Three experiments have reported the number of aposematic prey attacked at different levels of aposeme abundance. Each used avian predators with artificial prey. Greenwood et al. (1989) used a polymorphic aposematic system. Two prey types were each conspicuous against the background, easy to discriminate from one another and equally unpalatable. Speed et al. (2000; see also Speed 1999, page 761) used five prey types, including a quasi-Batesian mimic. All prey were conspicuous against the background. Prey types included a palatable type, and strongly defended model and distinct types, and moderately defended mimic and distinct types. Lindström et al. (2001) used a classically aposematic system. Aposemes were easily distinguished from background and palatable prey. Palatable prey were cryptic.

In none of these experiments did predators support either the declining or constant n predictions. Rather, predators made higher absolute numbers of attacks on aposematic prey during treatments in which aposemes were at high abundance levels than in those in which aposemes were in low abundance levels relative to alternative prey types. In low abundance conditions, predators showed that they were capable of making relatively few mistakes. According to the conventional models, that minimum number of mistakes is all that should be required by predators to show a given level of avoidance, no matter what the abundance. In high abundance

conditions, however, predators made more mistakes under otherwise identical conditions. Such results remain unexplained (Speed 1999; Lindström et al. 2001). Paradoxically, the conclusion drawn has been that, to learn to avoid aposemes, predators must eat more of these conspicuous, unpalatable prey when such prey are common than when they are rare (Mallet 2001).

Signal detection theory suggests a different perspective. If predators are uncertain about whether to attack or avoid a particular prey item, then the absolute number of S- (e.g. aposematic) prey attacked, n , will vary as a function of the probability of false alarm (Fig. 2). When S- prey are rare, the predator's permissive threshold (Fig. 1) will lead that prey type to suffer a high probability of false alarm attacks (Fig. 2a). At low abundance, false alarm attacks will be small in absolute number (Fig. 2b) because there are few S- prey to attack (although these attacks may encompass a large fraction of the S- population). As S- prey become more common, the utility function (equation 1) dictates that the threshold will become more restrictive, lowering the probability of false alarm (Fig. 1). During this process, the number of attacks on S- prey will initially increase, then decrease (Fig. 2b). Predators are predicted to make the most false alarm

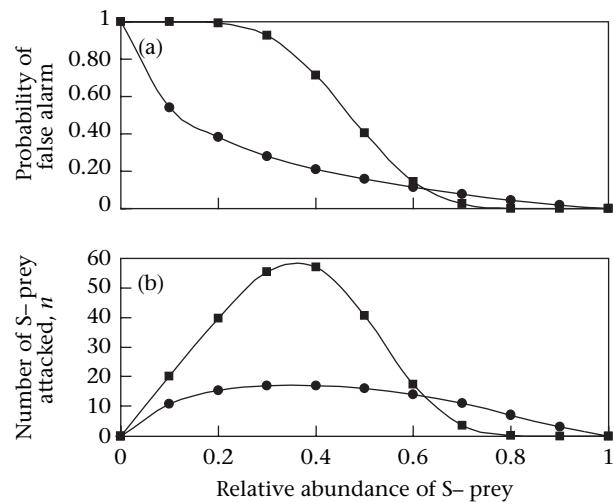


Figure 2. Under signal detection theory, an S- prey type will suffer a similar pattern of false alarm attacks whether generalization gradients overlap strongly (e.g. discrimination between mimics; difference between distribution means = 0.5, ■) or weakly (e.g. discrimination between distinct prey types; difference between distribution means = 2.0, ●). (a) As a result of the influence of abundance on the threshold location, false alarm attacks on S- occur with high probability when S- are rare relative to other prey and with low probability when S- are more common. (b) The absolute number of S- prey attacked, n , varies as a function of false alarm probability. For S- prey, n is low when they are either rare or common and highest at intermediate abundance. Data are from a model in which the total number of S- and S+ individuals = 200, the number used in Lindström et al.'s (2001) experiments. Number of S- prey attacked = $200 \times (1 - \alpha) \times P(\text{FA})$. Other utility function parameter values producing (a) and (b): variance of both prey distributions = 1; benefit of correct detection, $h = 1.0$; cost of false alarm, $a = -1.0$; cost of missed detection, m , and benefit of correct rejection, $j = 0.0$.

attacks at intermediate S– abundance. When S– prey are very abundant relative to alternative prey, the threshold will be restrictive, and once again very few false alarm attacks will be made.

Within the associative framework, one way to conceptualize this issue may be that when aposemes are more common, predators must exert greater control over their own behaviour. This additional control would require additional associative strength, and so require additional S– encounters to achieve. This frequency-dependent behavioural restraint is not captured by the traditional associative equations. Those equations model the accumulation of association strength of a single stimulus in isolation, not the optimization of choice between stimuli. Under signal detection theory, predators attack aposematic prey because optimizing their behaviour under uncertainty requires some probability of false alarm. Signal detection theory predicts that when aposematic prey are relatively rare, the number of attacks on aposematic prey will increase as abundance rises to intermediate levels. This prediction is contrary to traditional expectations, but offers an explanation for the otherwise paradoxical findings of the empirical data.

FREQUENCY-DEPENDENT SELECTION

Although signal detection theory differs from the other theories regarding predictions of the number of prey attacked, it preserves a critical prediction regarding frequency-dependent selection against aposemes. For aposematic prey, predation is predicted to be antiapostatic (i.e. to show a pattern of strong selection against aposemes when they are rare and weaker selection against them when they are common; Endler 1988; Lindström et al. 2001). This pattern of selection is considered to be central to understanding the evolution of aposematism and Müllerian mimicry (i.e. mimicry between aposematic species; Alatalo & Mappes 1996; Mallet & Joron 1999; Speed 1999). Conspicuousness draws attention, putting rare aposemes in danger of extinction, and creating strong pressure for the evolution of a shared appearance between aposematic species (Sherratt & Beatty 2003). The shared appearance increases a prey type's apparent abundance, and individuals share the costs of conspicuousness among a larger pool of potential prey. However, the diversity of aposematic appearance and the existence of mimetic polymorphism argue for a relaxation of selective pressure at some point, and an antiapostatic selection pattern fits these expectations nicely (Joron & Mallet 1998; Mallet & Joron 1999). Empirical results support the predicted frequency-dependent selection (Greenwood et al. 1989; Mallet & Barton 1989; Speed et al. 2000; Lindström et al. 2001).

The explanation for the antiapostatic pattern traditionally has been based on the constant n assumption. From Müller's perspective, for any constant n , the fraction of the aposeme population killed will be high when the population is small and decline as the population size increases (Mallet & Joron 1999). From the conditioned learning perspective, low encounter rates with rare

aposematic prey produce a weak association between the prey's appearance and the unpalatable reinforcement received for attacking the prey item (i.e. poor learning of the association). For a given level of unpalatability and similarity of appearance to other prey types, it is therefore more difficult for a predator to learn to avoid aposematic prey when such prey are rare, putting rare aposemes at higher risk of attack than common aposemes (Lindström et al. 2001).

In contrast, antiapostatic predation is also readily explained by signal detection theory, although for different reasons. The probability of false alarm shows an antiapostatic pattern (Fig. 2a), which arises from the effect of the relative abundance of the two prey types on threshold placement (Fig. 1). For given prey appearance and pay-offs, when S– prey are rare, threshold placement is permissive because of the low probability of encountering S– prey. Both the probability of correct detection and the probability of false alarm are high. When S– prey are common, however, the predator will be more cautious. The corresponding threshold is more restrictive, admitting few false alarms but also fewer correct detections.

EVOLUTION OF APOSEMATISM AND MIMICRY

As an operational account of stimulus discrimination, the signals approach can be considered to rephrase the fairly abstract and hypothetical parameters of associative learning theory, such as stimulus salience and the amount of associative strength that a stimulus can support, into functional ecological and behavioural terms representing the distribution, abundance and quality of resources. For example, Endler (1988) suggested that antiapostatic selective pressure might be generated by factors other than constant n , such as effects of abundance on detectability (e.g. via search image efficiency) or on profitability (e.g. from increased practise). Signal detection theory parameters seem to accommodate these additional mechanisms very well: detectability corresponds to the separation between signal distributions, and profitability is embodied in the payoff terms of the utility function (Getty 1985; Wiley 1994).

The critical event in the predation-driven evolution of aposematism and mimicry is the predation. If current models are making inaccurate predictions of the number of predation events at different prey abundances, then conclusions based on those numbers may also be inaccurate. Empirical research indicates that encounters with cryptic palatable prey influence predation rates on conspicuous unpalatable prey (Lindström et al. 2001). The classic approaches to associative learning developed in the 1950s through 1970s, and in common use by behavioural ecologists today, do not permit such interactions. Attempts to model predator psychology based on, for example, the Rescorla–Wagner equation (Rescorla & Wagner 1972) or its antecedents (e.g. Speed 1993; Turner & Speed 1996; MacDougall & Dawkins 1998; Speed & Turner 1999; Servadio 2000) cannot predict the empirical pattern of variation in aposeme attacks, because they have no mechanism of allowing encounters with one stimulus to

influence the association strength of another. More modern approaches to associative learning theory (e.g. Miller & Matzel 1988; Van Hamme & Wasserman 1994; Dickenson 2001) are designed to permit such interactions between stimuli and should prove to be more successful models of aposeme predation, and of discrimination in general.

Use of a more appropriate model may change theoretical conclusions. For example, Servedio (2000), using a classic associative model, concluded that a combination of extreme parameters (one-trial learning, strong unpalatability and no forgetting) is needed for aposematism to reach a stable equilibrium unless the aposematic population is already at very high abundance. However, interactions between stimuli, such as permitted by modern associative learning theory or signal detection theory, could allow for less extreme parameter values to more easily support the evolution of aposematism.

Signal detection theory has several natural strengths that suggest that it could be a powerful tool for investigating the role of receiver learning in the evolution of both aposematism and mimicry. In addition to permitting encounters with one stimulus to influence reactions to another, and the straightforward ecological interpretation afforded by the three signal parameters relative to that of the more abstract associative learning parameters, signal detection theory can permit relaxation of an assumption widespread in models of mimicry (Getty 1985). Current models of the evolution of Müllerian mimicry are based on classic associative learning theory and also assume perfect morphological similarity between model and mimic (e.g. Turner et al. 1984; Speed 1993; Turner & Speed 1996; MacDougall & Dawkins 1998; Speed & Turner 1999). This assumption of identical stimuli mitigates the lack of interaction between associative strengths of the stimuli, because distinguishing between the stimuli is impossible. However, if real predators have any ability to distinguish between real mimics and models, then the classic associative models are no longer appropriate. Unlike even modern associative theories, signal detection theory was developed specifically for situations in which animals experience uncertainty about whether to respond to one stimulus (e.g. an aposematic model) or another (e.g. a mimic, whatever its palatability).

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References

- Alatalo, R. V. & Mappes, J. 1996. Tracking the evolution of warning signals. *Nature*, **382**, 708–710.
- Blough, D. S. 1967. Stimulus generalization as signal detection in pigeons. *Science*, **158**, 940–941.
- Blough, D. S. 1969. Generalization gradient shape and summation in steady-state tests. *Journal of the Experimental Analysis of Behavior*, **12**, 91–104.
- Boneau, C. A. & Cole, J. L. 1967. Decision theory, the pigeon, and the psychophysical function. *Psychological Review*, **74**, 123–135.
- Bush, R. R. & Mosteller, F. 1955. *Stochastic Models for Learning*. New York: J. Wiley.
- Davies, N. B., Brooke, M. de L. & Kacelnik, A. 1996. Recognition errors and probability of parasitism determine whether reed warblers should accept or reject mimetic cuckoo eggs. *Proceedings of the Royal Society of London, Series B*, **263**, 925–931.
- Dickenson, A. 2001. Causal learning: an associative analysis. *Quarterly Journal of Experimental Psychology*, **54B**, 3–25.
- Domjan, M. 1998. *The Principles of Learning and Behavior*. 4th edn. Pacific Grove, California: Brooks/Cole.
- Endler, J. A. 1988. Frequency-dependent predation, crypsis and aposematic coloration. *Philosophical Transactions of the Royal Society of London, Series B*, **319**, 505–523.
- Gallistel, C. R. & Gibbon, J. 2000. Time, rate, and conditioning. *Psychological Review*, **107**, 219–275.
- Getty, T. 1985. Discriminability and the sigmoid functional response: how optimal foragers could stabilize model–mimic complexes. *American Naturalist*, **125**, 239–256.
- Getty, T. 1987. Crypsis, mimicry, and switching: the basic similarity of superficially different analyses. *American Naturalist*, **130**, 793–797.
- Getty, T. 1996. Mate selection by repeated inspection: more on pied flycatchers. *Animal Behaviour*, **51**, 739–745.
- Getty, T. & Krebs, J. R. 1985. Lagging partial preferences for cryptic prey: a signal detection analysis of great tit foraging. *American Naturalist*, **125**, 39–60.
- Green, D. M. & Swets, J. A. 1966. *Signal Detection Theory and Psychophysics*. New York: J. Wiley.
- Greenwood, J. J. D. 1986. Crypsis, mimicry, and switching by optimal foragers. *American Naturalist*, **128**, 294–300.
- Greenwood, J. J. D., Cotton, P. A. & Wilson, D. M. 1989. Frequency-dependent selection on aposematic prey: some experiments. *Biological Journal of the Linnean Society*, **36**, 213–226.
- Joron, M. & Mallet, J. L. B. 1998. Diversity in mimicry: paradox or paradigm? *Trends in Ecology and Evolution*, **13**, 461–466.
- Leslie, A. L. 2001. Learning: association or computation? Introduction to a special section. *Current Directions in Psychological Science*, **10**, 124–127.
- Lindström, L., Alatalo, R. V., Lytinen, A. & Mappes, J. 2001. Strong antiapostatic selection against novel rare aposematic prey. *Proceedings of the National Academy of Sciences, U.S.A.*, **98**, 9181–9184.
- MacDougall, A. & Dawkins, M. S. 1998. Predator discrimination error and the benefits of Müllerian mimicry. *Animal Behaviour*, **55**, 1281–1288.
- Mallet, J. 2001. Mimicry: an interface between psychology and evolution. *Proceedings of the National Academy of Sciences, U.S.A.*, **98**, 8928–8930.
- Mallet, J. & Barton, N. H. 1989. Strong natural selection in a warning-color hybrid zone. *Evolution*, **43**, 421–431.
- Mallet, J. & Joron, M. 1999. Evolution of diversity in warning color and mimicry: polymorphisms, shifting balance, and speciation. *Annual Review of Ecology and Systematics*, **30**, 201–233.

- Miller, R. R. & Matzel, L. D.** 1988. The comparator hypothesis: a response rule for the expression of associations. In: *The Psychology of Learning and Motivation*. Vol. 22 (Ed. by G. H. Bower), pp. 51–92. San Diego: Academic Press.
- Müller, F.** 1879. *Ituna* and *Thyridia*: a remarkable case of mimicry in butterflies. *Transactions of the Entomological Society of London*, **1879**, xx–xxix.
- Rescorla, R. A. & Wagner, A. R.** 1972. A theory of Pavlovian conditioning: variations in the effectiveness of reinforcement and non-reinforcement. In: *Classical Conditioning II: Current Theory and Research* (Ed. by A. H. Black & W. F. Prokasy), pp. 64–99. New York: Appleton–Century–Crofts.
- Rilling, M.** 1977. Stimulus control and inhibitory processes. In: *Handbook of Operant Behavior* (Ed. by W. K. Honig & J. E. R. Staddon), pp. 432–480. Englewood Cliffs, New Jersey: Prentice Hall.
- Rodríguez-Gironés, M. A. & Lotem, A.** 1999. How to detect a cuckoo egg: a signal detection theory model for recognition and learning. *American Naturalist*, **153**, 633–648.
- Servedio, M. R.** 2000. The effects of predator learning, forgetting, and recognition errors on the evolution of warning coloration. *Evolution*, **54**, 751–763.
- Sherratt, T. N.** 2001. The evolution of female-limited polymorphisms in damselflies: a signal detection model. *Ecology Letters*, **4**, 22–29.
- Sherratt, T. N. & Beatty, C. D.** 2003. The evolution of warning signals as reliable indicators of prey defense. *American Naturalist*, **162**, 377–389.
- Speed, M. P.** 1993. Müllerian mimicry and the psychology of predation. *Animal Behaviour*, **45**, 571–580.
- Speed, M. P.** 1999. Batesian, quasi-Batesian or Müllerian mimicry? Theory and data in mimicry research. *Evolutionary Ecology*, **13**, 755–776.
- Speed, M. P.** 2001. Can receiver psychology explain the evolution of aposematism? *Animal Behaviour*, **61**, 205–216.
- Speed, M. P. & Turner, J. R. G.** 1999. Learning and memory in mimicry: II. Do we understand the mimicry spectrum? *Biological Journal of the Linnean Society*, **67**, 281–312.
- Speed, M. P., Alderson, N. J., Hardman, C. & Ruxton, G. D.** 2000. Testing Müllerian mimicry: an experiment with wild birds. *Proceedings of the Royal Society of London, Series B*, **267**, 725–731.
- Sperling, G.** 1984. A unified theory of attention and signal detection. In: *Varieties of Attention* (Ed. by R. Parasuraman & R. R. Davies), pp. 103–181. Orlando, Florida: Academic Press.
- Straddon, J. E. R. & Gendron, R. P.** 1983. Optimal detection of cryptic prey may lead to predator switching. *American Naturalist*, **122**, 843–848.
- Sword, G. A.** 1999. Density-dependent warning coloration. *Nature*, **397**, 217.
- Turner, J. R. G.** 1987. The evolutionary dynamics of Batesian and Müllerian mimicry: similarities and differences. *Ecological Entomology*, **12**, 81–95.
- Turner, J. R. G. & Speed, M. P.** 1996. Learning and memory in mimicry. I. Simulations of laboratory experiments. *Philosophical Transactions of the Royal Society of London, Series B*, **351**, 1157–1170.
- Turner, J. R. G., Kearney, E. P. & Exton, L. S.** 1984. Mimicry and the Monte Carlo predator: the palatability spectrum and the origins of mimicry. *Biological Journal of the Linnean Society*, **23**, 247–268.
- Van Hamme, L. J. & Wasserman, E. A.** 1994. Cue competition in causality judgments: the role of nonpresentation of compound stimulus elements. *Learning and Motivation*, **25**, 127–151.
- Wiley, R. H.** 1994. Errors, exaggeration, and deception in animal communication. In: *Behavioral Mechanisms in Evolutionary Ecology* (Ed. by L. A. Real), pp. 157–189. Chicago: University of Chicago Press.