Animal Behaviour 79 (2010) 63–74

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Can dietary conservatism explain the primary evolution of aposematism?

Thomas J. Lee [a,*], Nicola M. Marples [b,1], Michael P. Speed [a]

[a] School of Biological Sciences, University of Liverpool
[b] Department of Zoology, School of Natural Sciences, Trinity College, University of Dublin

ARTICLE INFO

Article history:
Received 22 December 2008
Initial acceptance 4 February 2009
Final acceptance 1 October 2009
Available online 8 November 2009
MS. number: 08-00821R

Keywords:
aposematism
avoidance learning
crypsis
dietary conservatism
frequency-dependent selection
individual-based modelling
neophobia

Predators are often unwilling to eat prey with novel appearances (so called dietary conservatism). It has repeatedly, although controversially, been argued that such wariness can contribute to the evolution of bright coloration in prey animals with effective secondary defences such as toxins. In this paper we report the results of novel evolutionary simulations in which bright prey emerge in otherwise cryptic, defended populations, and predators vary in their level of dietary wariness. A novel prediction from our simulations is that rare aposematic prey can evolve to a dynamic equilibrium with their cryptic conspecifics, and persist for long evolutionary timescales without ever reaching fixation in prey populations. Furthermore, we show that when conditions are more beneficial for new aposematic forms, for example because there are many palatable prey in a habitat, then dietary conservatism can indeed explain the evolution of aposematism, but the generality of this result was considerably restricted by variation in levels of dietary conservatism seen within predator populations and by increased predator longevity. We use the results to consider the case that 'receiver biases' could explain aposematism, rather than recently suggested models of signal reliability.

Aposematism is a well known antipredator mechanism in which a prey advertises a secondary defence, such as a toxin, with a distinctive and usually bright warning signal (Poulton 1890; Cott 1940; Edmunds 1974). Conspicuous warning signals have a number of effects on predators that favour prey survival; for example causing wariness and cautious handling of brightly coloured prey (Sillén-Tullberg 1985; Gamberale & Tullberg 1998; Kelly & Marples 2004), accelerating predator avoidance learning (Gittleman et al. 1980; Roper & Wistow 1986; Lindström et al. 2001) and reducing predator forgetting (Roper & Redston 1987; Yachi & Higashi 1998; Speed 2000; Siddall & Marples 2008). Furthermore, as Wallace (1867, 1889) originally proposed when devising the idea of aposematism, warning signals may be used by educated predators to help them reliably discriminate defended prey from edible, cryptic prey.

It is widely hypothesized that aposematic warning displays must have initially evolved from defended cryptic prey populations (Harvey et al. 1982; Leimar et al. 1986; Yachi & Higashi 1998). In the literature it is assumed that rare novel mutants emerging from within these populations are especially vulnerable to extinction because, having attracted the attention of ignorant predators (because of their enhanced conspicuousness), they are very likely to be attacked and killed (Mallet & Singer 1987). Their low initial numbers would heighten the risk of extinction, since with low absolute numbers all individuals may be consumed before predators learn to associate their appearance with the defences they experience. Given that aposematism is observed across many species and in many diverse habitats, it appears there is some paradox to resolve: the existence of a trait whose persistence is easy to explain when it is common, but difficult to explain when it is new and rare (Mallet & Singer 1987; Servedio 2000; Speed & Ruxton 2005, 2007).

We can consider the problem in two ways: first is the 'primary' evolution of aposematism, in which aposematism as a class of antipredator defence is absolutely novel, and did not previously exist. The challenge here is to explain how aposematism evolved from rarity even though predators had no initial reason to treat conspicuous prey with caution. In addition, we could consider 'secondary' evolution in which aposematism is relatively novel, turning up for the first time in a particular species, but already existing in other species. The evolution of aposematism is easier to explain in this 'secondary' context, because it is often reasonable to expect that evolution has already prepared predators to be wary of aposematic colour patterns (see empirical studies such as Coppinger 1970; Schuler & Hesse 1985; Sillén-Tullberg 1985; Roper & Cook 1989; Gamberale & Tullberg 1998). Hence, when new aposematic prey emerge, predators are already biased to 'go slow',

---

[*] Correspondence: T. J. Lee, School of Biological Sciences, Biosciences Building, Crown Street, University of Liverpool, Liverpool L69 7ZB, U.K.
E-mail address: thomas.lee@liv.ac.uk (T.J. Lee).

[1] N. M. Marples is at the Department of Zoology, School of Natural Sciences, Trinity College, University of Dublin, Dublin 2, Ireland.

0003-3472/$38.00 © 2009 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
doi:10.1016/j.anbehav.2009.10.004

to handle them cautiously and to learn about them quickly (Guilford 1994).

The recent literature provides two competing hypotheses to explain the more challenging case of the primary evolution of aposematism. First, it has been argued by Sherratt (2002) that predator biases and bright aposematic coloration originally emerged from a coevolutionary process. Cautious handling of bright prey by predators emerges in Sherratt's theoretical model because bright, edible prey are increasingly eaten and removed from the prey population while bright defended prey tend to escape and reproduce. If appearance and defence are heritable traits, then brightness consequently becomes a reliable signifier of unprofitability, and at evolutionary stability it pays predators to be wary, and to avoid eating conspicuous prey.

In contrast, Marples et al. (2005) proposed an alternative argument, focusing on the repeated demonstration that predators often avoid contact with new foods (neophobia) and subsequently they may be reluctant to include them in their diet (so called dietary conservatism). There is considerable evidence that both neophobia and dietary conservatism can be invoked in predators by novel prey forms whether these are conspicuous or not (Mastrota & Mench 1994; Marples & Brakefield 1995; Marples & Kelly 1999; Kelly & Marples 2004; Marples et al. 2007, 1998). Marples et al. (2005) argued that such wariness of novelty is likely to be a general consequence of optimal-foraging decision making and thus easily preceded the primary evolution of aposematism. For foraging animals, novelty implies some degree of uncertainty and risk of injury; if valuable familiar foods are already present in a habitat, then the optimal strategy in relation to new food items will often be avoidance for some period. In field and laboratory experiments, dietary conservatism has been shown to facilitate the evolution of novel prey forms (Thomas et al. 2003, 2004), and consequently Marples et al. (2005) argued that the primary evolution of aposematism could easily be explained if avoidance of novel prey forms caused by dietary conservatism in predators is sufficiently high.

Although this argument is plausible, some important issues require quantitative evaluation before a well-founded judgement can, in our view, be made. For example, field data indicate that (within a population) predators can be very variable in their levels of dietary conservatism; without numerical investigation, it is not clear how likely it is for a novel morph to survive and prosper when, for example a majority of mobile predators are willing to eat novel prey without hesitation (see data in Marples et al. 1998). Furthermore, if predators typically outlive their prey (e.g. with invertebrate prey and vertebrate predators) it is possible that the benefits to rare prey of predatory dietary conservatism apply only to the first prey generation, so that even if novel morphs are initially favoured, they subsequently face a rapid extinction because of long-lived predators that are no longer wary (a similar point is made rather forcefully in Mallet & Singer 1987).

In fact, there are only two published theoretical models that evaluate the importance of predator wariness of novelty on the initial evolution of aposematic warning displays (Speed 2001; Puurtinen & Kaitala 2006; note that different authors use different terms to describe the reluctance of predators to ingest novel prey; for simplicity we term this dietary conservatism throughout). Of these papers Puurtinen & Kaitala (2006) is by far the most rigorous and extensive. While both of these papers demonstrate that dietary conservatism could benefit aposematic mutants, neither includes the kind of ecological details, such as variability in predator life span and wariness, that are key to evaluating the plausibility of the arguments of Marples et al. (2005). In addition, neither used evolutionary modelling as a tool and, as we describe in this paper, a stochastic-evolutionary approach yields some important, and so far unreported, findings about the dynamics of aposematic evolution.

If Marples et al. (2005) were correct to assert that wariness of novel prey explains aposematism, then an important evolutionary paradox is easily resolved by a simple and easily generalized argument. If, on the other hand, Mallet & Singer's (1987) view is correct, that the ephemeral nature of dietary conservatism makes it unimportant, the primary evolution of aposematism is more problematic and may require a coevolutionary solution like that proposed by Sherratt (2002). In this paper we therefore present a stochastic-evolutionary model in which rare, bright prey forms emerge in populations of cryptic defended prey. We examine whether dietary conservatism on its own can explain the initial evolution of aposematism, and whether additional psychological biases such as accelerated learning of conspicuous signals are necessary. Unlike previous theoretical models we consider the interaction of dietary conservatism with ecologically relevant conditions such as varied duration of predator life span, migration of predators into a focal habitat and the number of predators attacking at any one time.

MODEL DESCRIPTION

Using stochastic, evolutionary simulations we consider the evolution of aposematism in a prey population that possesses some kind of effective secondary defence such as a toxin. At the start of the simulations the prey are overwhelmingly cryptic in appearance, and we introduce a single mutant individual that has a more conspicuous appearance than the rest of the population. We simulate interactions between members of the prey population and one or more predators for a specified period (a season) after which the prey species reproduces by asexual reproduction. We iterate this sequence over many prey generations and follow evolutionary change in the abundances of cryptic and aposematic forms of the prey. We make some simplifying assumptions: specifically (1) that there is only one predator and one prey population (which is closed to immigration and emigration), (2) that the life span of the prey and the predator are equal and (3) that the habitat contains only the focal defended prey species. As we develop the model some of these assumptions are relaxed. We first present a general framework within which the predator–prey environment is described, and then consider how dietary conservatism is represented computationally, before describing and developing scenarios for simulation.

Simple Single-habitat Models (One Predator, Life Span Equal to that of the Prey)

A MATLAB script was produced (The Mathworks Inc., Natick, MS, U.S.A.; a sample is available in the Supplementary Material) to model a finitely sized habitat in which one predator and a number of prey (N) reside. Within the prey population two distinct prey types exist, cryptic (c_c, of number N_c) and aposematic (c_a, of number N_a). We assume that both prey types are equally distasteful to the predator. At the start of the simulation we assume that a single aposematic mutant exists (although the number of aposematic prey within the prey population could be varied). The model is run for a finite number of generations each of finite time limit (T). Each prey type is assigned an arbitrary conspicuousness value, (c_a) for the aposematic prey type and (c_c) for the cryptic type which represents the probability of detection by the predator, given that a predator and prey are within some minimum level of proximity. The two prey types are also each assigned an avoidance learning rate, (α_a) for the aposematic prey type and (α_c) for the cryptic prey, used to determine the rate at which the predator learns to avoid each prey type as a result of its distastefulness. A full summary of model parameters is given in Table 1.