theory and (psychological) learning theory: are options with probabilistic outcomes (food after variable numbers of bar presses or waiting times) evaluated in terms of short- or long-term rates and how is past experience weighted in terms of current information (Bateson and Kacelnik 1996; Kacelnik and Bateson 1996)? Perhaps it is time for Foraging Theory and its links with behavioral economics and economic psychology to become fashionable again. With toxic effects and nutritional gains following different time courses and cues varying in reliability, aposematic animals (and their shadows, Batesian mimics) would seem to offer an excellent empirical test-bed for extending the theories developed for, typically, simple foraging choices in rather sparse laboratory paradigms.

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What do predators do? A response to comments on Skelhorn et al.

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It has long been recognized that predators include aposematic prey in their diet when it is beneficial to do so (Marshall 1908; Sherratt 2003; Skelhorn and Rowe 2007; Barnett et al. 2012; Halpin et al. 2014). Indeed the commentaries on our recent review (Skelhorn et al. 2016) show that this is now widely accepted and noncontroversial (Cuthill 2016; Merilaita 2016; Sherratt 2016; Stevens 2016). Yet whilst many authors pay lip service to this idea, it has been slow to influence the mainstream literature on aposematism and mimicry. For example, a quick review of papers published so far this year on Google Scholar with "aposematism" as a search term reveals only one study (Veselý et al. 2016) that has specifically been designed to explore this. This failure to fully consider predator decision-making is hardly surprising given our limited understanding of the subject. Consequently, the purpose of our review was to highlight this major gap in our knowledge, explain why it is important that we fill it, and encourage others to consider predator decision-making when designing experiments and interpreting results. Our review should therefore be read as a "call to arms" rather than a traditional review article.

In a series of thoughtful commentaries on our review, several authors have highlighted a number of mathematical/theoretical approaches that could potentially be adapted to enhance our understanding of predators' decisions to attack aposematic prey (Cuthill 2016; Merilaita 2016; Sherratt 2016). We absolutely agree that these approaches have vast potential, and could enable us to identify the optimal decisions of predators when faced with aposematic prey. But it is worth noting that these approaches do not necessarily tell us how predators arrive at these decisions (Sherratt 2016; Skelhorn et al. 2016). This may not seem important from an evolutionary perspective. After all, if we can identify the decisions being made, we can identify the selection pressures acting on defended prey. However, we would argue that if we do not understand how predators arrive at these decisions it is impossible to determine whether they are capable of making them. If there are constraints on what predators can learn, how they integrate conflicting information or how they weight information when making-decisions, then the decisions that predators actually make may be very different from those that models predict (Halpin et al. 2008; Halpin et al. 2012). This brings us nicely back to the main message of our review: we currently have nowhere near enough information about predator cognition to even begin to determine whether mathematical/theoretical models accurately reflect predator behavior let alone assess the role of predator cognition in driving the evolution of aposematism. There is an urgent need for studies investigating how predators gather and use information about defended prey, and it is crucial that studies investigating the evolution of aposematism attempt to determine why predators are behaving as they do. In short, whenever we consider the evolution of aposematism we should ask ourselves what do predators do?

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