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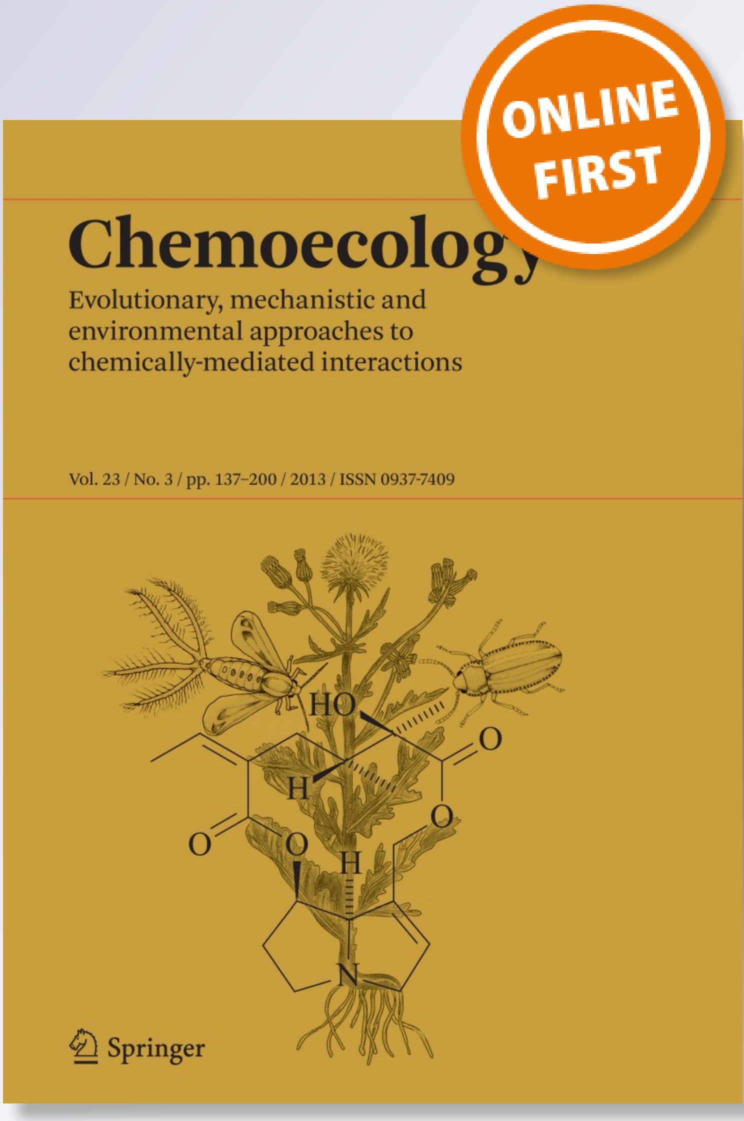

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COMMENTARY

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Abstract Discussions of aposematism traditionally have focused on the visual displays of prey that denote unpalatability or toxicity to predators. However, the construct of aposematism accommodates a spectrum of unprofitable traits signaled through various sensory modalities, including contact and distance chemoreception. Aposematism, involving learned aversions by signal receivers or selection for their unlearned avoidances, arises in predator–prey or other interspecific interactions where a mutually beneficial avoidance of signal emitters by signal receivers exists. Aposematism evolves by selection against signal receivers, e.g., predators, imposed by signal emitters, e.g., unprofitable prey, and vice versa, where both nondiscriminating signal receivers and unrecognized signal emitters are imperiled. Chemical aposematism entails concurrent reciprocal selection where signal emitters select for chemosensory avoidance responses in signal receivers, and where signal receivers select for the emission of identifiable (distinctive) chemicals in signal emitters.

Keywords Aposematism · Chemical defense

Charles Darwin and Alfred Russel Wallace, the celebrated co-proponents of natural selection as a mechanism of evolution, proffered different explanations for colorful ostentation among animals. Darwin (1874) posited that bright plumage and other conspicuous traits arise through sexual selection, and are displayed chiefly by males "to charm the female". However, he was puzzled by the gaudy markings of some caterpillars, which, given their life stage, could not plausibly be adorned for mate recognition (Wallace 1867). Wallace (1867) suggested that these patterns in caterpillars evolved as signals to potential predators denoting unpalatability: "… distaste alone would be insufficient to protect a larva unless there were some outward sign to indicate to its would-be destroyer that his contemplated prey would prove a disgusting morsel, and so deter him from attack". Poulton (1890) coined the term aposematism (Gr *άπό*, away; *σῆμά*, sign) for the phenomenon postulated by Wallace, defining it as "an appearance which warns off enemies because it denotes something unpleasant or dangerous".

As Poulton's definition of aposematism licenses, the range of known or suspected features supporting the aposematic status of signalers has been expanded beyond prey unpalatability to embrace a spectrum of unprofitable traits, including toxicity, pugnacity, and mechanical inaccessibility. In addition, some authors have justly amended Poulton's definition to accommodate aposematism that is manifest by means other than through appearance, i.e., where signals are perceived through non-visual sensory channels.

Eisner and Grant (1980) proposed the idea of "olfactory aposematism", whereby consumers associate odors with, and hence refrain from attacking, toxic or otherwise noxious animals and plants. Inspired by studies of conditioned taste aversion, they hypothesized that predators and herbivores, using olfaction, learn to identify noxious organisms, often responding to volatiles from them that are unrelated to the toxins they harbor.

Since its inception, aposematic features have been portrayed as a prey's "warning" to (chiefly vertebrate)

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predators. "Warning" here must be understood in a metaphorical sense; neither a signaler's intent nor a responding organism's anticipation of danger necessarily is entailed. In a parallel vein, many authors contend that learned avoidance of predators, established in sub-lethal interactions with conspicuous prey, is integral to the evolution of aposematism; this notion was embraced by Eisner and Grant (1980). However, the many demonstrated examples of naive predators that avoid dangerous prey, or particular aspects of prey organisms presented in stimulus control experiments, affirm that aposematism is not invariably predicated on learned aversions (see Lindström et al. 1999). An operational construct of aposematism entails merely a mutually beneficial avoidance of signal emitters by signal receivers in interspecific interactions. In the lexicon of chemical ecology, aposematic chemicals are synomones.

A considered outlook on aposematism, then, acknowledges signals denoting diverse kinds of unprofitability; a panoply of sensory channels mediating them, including various types of contact and distance chemoreception; and different mechanisms by which phenotypic features acquire iconic value. For chemical ecologists, aposematism clearly has relevance beyond the visually conspicuous, unpalatable caterpillars that captivated Darwin and Wallace. For evolutionary biologists, in general, these chemically mediated responses present opportunities to examine participating taxa and trophic interactions not conventionally entertained by those who study aposematism, and from which new insights may be drawn.

Consider, for example, arthropod-vertebrate interactions where the familiar roles of arthropods as aposematic signalers (prey) and vertebrates as aposematic signal respondents (predators) are reversed. This occurs in some cases involving nonhost odors (NHO) where mosquitoes, ticks, and other nuisance arthropods use chemoreception to avoid dangerous or otherwise unprofitable vertebrate hosts (Weldon 2010). These semiochemicals, which typically emanate from a nonhost's integument, repel arthropods or inhibit their attraction. Phytophagous insects similarly respond to NHO from unpreferred plants (Andersson 2007).

Responses to NHO, on one hand, constitute a foraging adaptation by host-seeking arthropods; arthropods that fail to avoid unprofitable hosts are selected against. On the other hand, the emission of NHO may constitute a defense by unprofitable hosts whereby they avoid lethal attacks, wounding, and tissue damage that could admit vectored and opportunistic pathogens; hosts that fail to elaborate identifiable chemicals are selected against. In this paradigm of concurrent reciprocal selection—where signal receivers select against signal emitters, and vice versa—both nondiscriminating signal receivers and unrecognized signal emitters are imperiled. Chemical aposematism entails selection by signal emitters for chemosensory avoidance responses in signal receivers, and selection by signal receivers for the emission of identifiable (distinctive) chemicals in signal emitters. This proposition accords with the premise that aposematic features arise by selection on defended prey to avoid being confused with undefended prey (e.g., Sherratt and Beatty 2003).

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