

Evolving détente: the origin of warning signals via concurrent reciprocal selection

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Casualties and impediments inflicted on consumers by defended prey, and *vice versa*, may be averted by vocalizations, postures, coloration, scents, and other warning or, so-called aposematic, displays. The existence of aposematic signals has challenged biologists who have sought plausible mechanisms for their evolution. Here, we elaborate on the rationale for the hypothesis that aposematic signals arise via concurrent reciprocal selection (CRS) enacted between inimical signal receivers and signal emitters, where signal emitters, e.g., defended prey, select against non-discriminating signal receivers, e.g., predators, and signal receivers select against unrecognized signal emitters. It is postulated that this mutual selective interaction culminates in the survival of discriminating signal receivers that avoid signal emitters, and recognized (distinctive) signal emitters that are avoided by signal receivers. A CRS hypothesis for the evolution of aposematism, therefore, maintains that distinctive features of prey arise in response to selection imposed by consumers, and that avoidances of those features by consumers arise in response to selection imposed by defended prey. We discuss the plausible inception of aposematism via CRS in light of related hypotheses, and describe points of concordance with previous observations and suggestions on the origin of aposematism. Aposematism arising via CRS is not contingent upon the relatedness of signalers, aversions acquired by learning, or other conditions postulated for some other evolutionary hypotheses. CRS is a credible alternative hypothesis for the evolution of warning signals in diverse consumer-prey interactions. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, **00**: 000–000.

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INTRODUCTION

Not all encounters between predators and formidably defended prey result in injury. Nature is replete with vocalizations, postures, coloration, scents, and other displays that suppress attacks by consumers. The tendencies of organisms to avoid injurious confrontations by responding to or displaying warnings or, so-called aposematic, signals have beguiled naturalists and challenged biologists who have sought plausible mechanisms for their evolution (Harlin & Harlin, 2003; Mappes, Marples & Endler, 2005). Consensus on even the level of selection thought to operate for such displays to evolve has been difficult to achieve

as investigators choose between or attempt to balance individual and/or kin selection paradigms (Harvey & Paxton, 1981; Järvi, Sillén-Tullberg & Wiklund, 1981; Wiklund & Järvi, 1982; Turner, 1984; Mallet & Singer, 1987; Guilford, 1988, 1990). Recently, Weldon (2013) suggested that chemical aposematic signals arise via concurrent reciprocal selection (CRS) operating at the individual level between inimical signal receivers and signal emitters. Here, we elaborate on the rationale for this hypothesis, discuss it in light of related evolutionary hypotheses, and describe points of concordance with previous observations and suggestions pertaining to the evolution of aposematism. However, we do not attempt to review the substantial evidence for aposematism.

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Alfred Russel Wallace (1867) first posited the existence of warning signals in predator-prey interactions, suggesting that the gaudy colour patterns of some caterpillars denote unpalatability, and hence discourage attack by would-be predators. Caterpillars benefit when predators avoid them, and predators benefit when they avoid noxious prey. Poulton (1890: 337–340) referred to the phenomenon postulated by Wallace as ‘aposematic colours’, characterizing it as a type of defence entailing ‘an appearance which warns off enemies because it denotes something unpleasant or dangerous’. During the nearly 150 years since Wallace’s conjecture on brightly colored caterpillars, numerous examples have been proposed of animal and plant ornamentation signifying distastefulness or toxicity, including venomousness (Ruxton, Sherratt & Speed, 2004; Lev-Yadun, 2009; Stevens & Ruxton, 2012).

Although aposematism entailing visual cues is most frequently alleged, chemical (Lev-Yadun, 2009; Weldon, 2013), auditory (e.g., Connor, 2014), and other non-visual cues occasionally are hypothesized to serve as aposematic signals; different attendant cues may, in some cases, contribute to multimodal aposematism (e.g., Hauglund, Hagen & Lampe, 2006; Wheeler, Millar & Cardé, 2015). In addition to features that denote distastefulness or toxicity, a variety of protective qualities can support an organism’s status of unprofitability vis-à-vis predators. Wallace (1889: 266–267), for example, wrote, ‘The brilliant colours of the scallops (*Pecten*) and some other bivalve shells are perhaps an indication of their hardness and consequent inedibility, as in the case of hard beetles...’ Other types of mechanical protection, such as spines and thorns (Inbar & Lev-Yadun, 2005; Speed & Ruxton, 2005; Lev-Yadun, 2009), and behavioral defences, including pugnacity (Eisner *et al.*, 1977), evasiveness (pursuit deterrence) (Mallet & Singer, 1987; Ruxton *et al.*, 2004; Caro, 2005), and the ability to launch mobbing attacks (Tan *et al.*, 2013), may be denoted by aposematic signals.

Aposematism can arise in interactions other than those with conventional predators. Plants and vertebrates that are inhospitable to ectoparasitic or hematophagous arthropods emit aposematic semiochemicals called non-host odours (NHO) that repel or inhibit attraction by these nuisance consumers (Andersson, 2007; Weldon, 2010). The emission of NHO benefits would-be hosts by deterring harmful arthropods; on the other hand, responses to NHO benefit foraging arthropods by directing them away from unprofitable hosts. NHO from inhospitable plants appear to deter infestation by parasitic plants, as well (Lev-Yadun, 2013). Warning signals also may be involved in competitive interactions, as recently

described for the warning buzz of bumblebees (*Bombus* spp.) that prompts birds to abandon their nests, which the bees subsequently occupy (Jablonski *et al.*, 2013). We know of no explicit suggestions for aposematism in microbial interactions, but chemical signals fostering mutually beneficial avoidances among microorganisms likely are widespread.

MECHANISMS FOR A PERVASIVE PHENOMENON

Batesian mimicry often involves counterfeit aposematic signals and, as such, it has frequently drawn the attention of biologists to (chiefly visual) warning displays. As Mallet & Singer (1987: 339) state, ‘The detailed analogous resemblances between species we call mimicry are the best evidence for the existence of warning signals’. Aposematism, however, is neither dependent upon nor necessarily coupled with mimicry, hence aposematic signals may be more diverse and more prevalent than mimetic resemblances alone suggest. Even a lone focus on classical aposematism – visual ornamentation denoting distastefulness or toxicity – discloses numerous purported examples evolved independently among a taxonomically and ecologically diverse array of signal emitters and signal receivers (Ruxton *et al.*, 2004; Stevens & Ruxton, 2012). Expanded appreciation for the panoply of sensory channels by which aposematism is communicated, the various defensive qualities of signal emitters that support aposematism, and the spectrum of trophic relationships of signal emitters and signal receivers engaged in aposematic communications suggests that aposematism is rife in nature.

To account for the biodiverse representation of aposematism, specifically conspicuous (warning) coloration, some authors have invoked kin selection: predatory attack on conspicuous individuals enhances their inclusive fitness when predators, having learned to associate prey features with distastefulness, avoid their conspicuous relatives (Harvey & Greenwood, 1978; Gittleman & Harvey, 1980; Harvey *et al.*, 1982). Guilford (1988, 1990) suggested that warning coloration under certain conditions works primarily because of an altruistic effect associated not with kin selection but with ‘green-beard’ selection. According to this hypothesis, conspicuous altruists engage predators so as to benefit individuals whose phenotype denotes shared gene(s) for altruism.

A fundamental assumption for kin-based aposematism is that conspicuous prospective prey reside within the foraging ranges of the same predators that had attacked their conspicuous relatives, thus

permitting kin to benefit when these experienced consumers avoid them. For this reason, the purported association of conspicuous coloration with gregariousness in insects has been thought to support kin-based aposematism (e.g., Fisher, 1930; Harvey & Greenwood, 1978; Malcolm, 1986) (see Ruxton & Sherratt (2006) for review and analyses). Some authors, however, point out that cohorts of unpalatable, conspicuous butterflies, a focal group in discussions of aposematism, often disperse beyond the ranges of potentially shared predators (Mallet & Singer, 1987), and that, more generally, many visually aposematic organisms live solitarily and not in family groups (Järvi *et al.*, 1981; Sillén-Tullberg, 1988).

Documentations of the survival of distasteful insects following attacks by predators (Wiklund & Järvi, 1982 and references therein) have prompted some investigators to consider that aposematism evolves via individual selection rather than by kin selection. These hypotheses generally posit that conspicuous, distasteful organisms rejected in initial encounters with predators subsequently are recognized and avoided by them (Sillén-Tullberg & Bryant, 1983; Engen, Järvi & Wiklund, 1986; Halpin, Skelhorn & Rowe, 2008). Gohli & Högstedt (2009) developed a stochastic model in which reliable chemical signalling involving secreted prey toxins detected via olfaction by predators selects for visually conspicuous prey. Their model assumes no initial aversion toward aposematic traits or conspicuousness, i.e., it operates without neophobia and dietary conservatism.

The involvement of learning in establishing predators' avoidances of aposematic cues has been averred by many authors over the years. Poulton (1890: 160), for example, wrote, 'The object of warning colours is to assist the education of enemies, enabling them to easily learn and remember the animals which are to be avoided'. Cott (1940), in his seminal volume, dismissed the existence of 'instinctive' aversions by predators of aposematic prey, and suggested that each predator learns to associate a conspicuous signal with its unprofitability. Learned avoidances have been embraced broadly in recent kin-based and individual selection models of aposematism (e.g., Mappes *et al.*, 2005).

Some studies, however, show that the avoidance of unprofitable prey by predators does not depend upon learning (Edmunds, 1974; Lindström, Alatalo & Mappes, 1999 and references therein). Smith (1975, 1977), for example, reared turquoise-browed motmots (*Emomota superciliosa*) and great kiskadees (*Pitangus sulphuratus*) in controlled settings and demonstrated that naive subjects avoid the red-yellow-black banding patterns of venomous coral snakes (Micrurinae, Elapidae), which occur

throughout the ranges of these birds in the Neotropics. We reconcile both unlearned and learned aversions in aposematic interactions, acknowledging the latter as arising ultimately from selection-ordained sensory biases and associative-learning propensities. Influences on the expression of avoidance responses by natural predators likely will differ, with learned and unlearned elements of behavioral aversions variously contributing to the evolution of aposematic traits.

RECIPROCAL SELECTION: TANDEM VS. CONCURRENT

Aposematism evolves where would-be signal receivers and signal emitters detract from one another's fitness; selection is mutually enacted between them. Weldon (2013) suggested that chemical aposematism arises via CRS enacted between signal emitters and signal receivers, where signal emitters, e.g., defended prey, select against non-discriminating signal receivers, e.g., predators (Fig. 1A), and where signal receivers select against unrecognized signal emitters (Fig. 1B). Non-discriminating consumers may suffer when, for example, they attempt to dispatch noxious or toxic prey; in nonlethal interactions, selection may act against consumers that pursue organisms that are nutritionally deficient or require protracted handling (Gohli & Högstedt, 2010). Likewise, unrecognized prey that are attacked indiscriminately may be killed or wounded, and hence become debilitated and vulnerable to opportunistic pathogens. From the mutual selective interactions between these signal receivers and signal emitters emerge discriminating signal receivers that avoid signal emitters, and recognized (distinctive) signal emitters that are avoided by signal receivers (Fig. 1C).

The evolution of aposematism by CRS is predicated upon the existence of variation in: (1) the responses by would-be signal receivers to signal emitters, among which is the avoidance of phenotypic features of signal emitters (possibly entailing learned aversions arising from prior encounters with signalers or observations of them); and (2) the observable phenotypes of would-be signal emitters, among which are distinctive features that arise coincidentally in defended organisms. Although the original proposal for aposematism arising via CRS pertains to the evolution of aposematic semiochemicals, the rationale for this process is germane to aposematism involving any observable aspect of the phenotype of signal emitters, including vocalizations, coloration, and behaviour.

Reciprocal selection often is discussed in connection with coevolutionary 'arms races', where tandem sequential ploys and counter-ploys typically are envi-

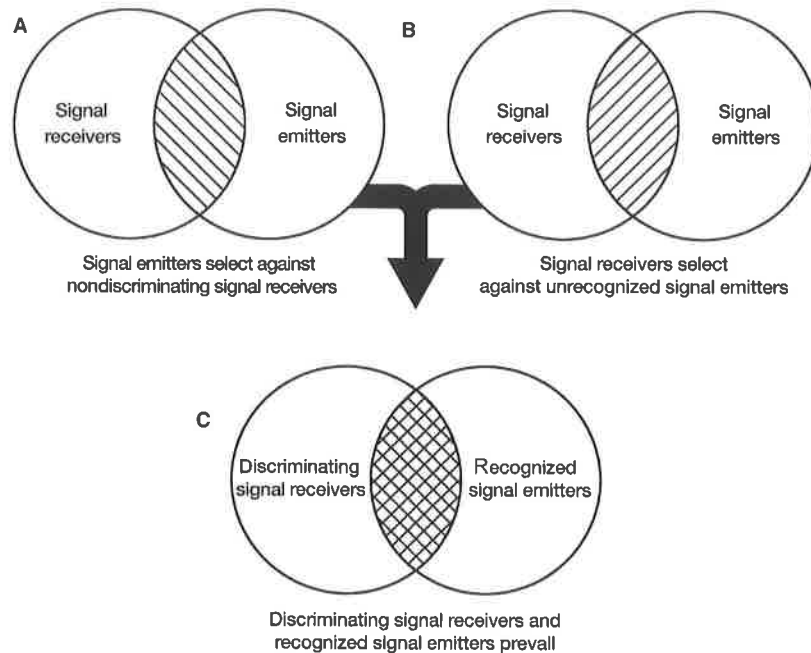


Figure 1. Elements of concurrent reciprocal selection (CRS) participating in the inception of aposematism. (A) Signal emitters select against non-discriminating signal receivers. Upward left-slanted lines denote selection by defended prey against predators. (B) Signal receivers select against unrecognized signal emitters. Upward right-slanted lines denote selection by predators against undistinguished prey. Arrow denotes convergence of trends represented in (A) and (B) Culmination of CRS. (C) Discriminating signal receivers and recognized signal emitters prevail. Open area of circle on left denotes predators that avoid aposematic prey, and open area of circle on right denotes aposematic prey that are avoided by predators.

sioned in interactions between populations, as, for example, between some predator–prey (e.g., Brodie & Ridenhour, 2003) or host–parasite lineages (e.g., Clayton *et al.*, 1999). The type of reciprocal selection that we contend pertains to the inception of warning signals entails concurrent processes, with an outcome that can be likened to ‘détente’: selection imposed by signal emitters against non-discriminating signal receivers coincides with selection imposed by signal receivers against unrecognized signal emitters, culminating in the survival of non-interactive signal receivers and signal emitters. CRS as a mechanism for the installation of aposematic signals does not necessitate counter-adaptation, hence it does not accord with Janzen (1980: 611) popular definition of coevolution: ‘an evolutionary change in a trait of the individuals in one population in response to a trait of the individuals of a second population, followed by an evolutionary response by the second population to the change in the first’ [italics added].

Sherratt (2002) developed coevolutionary models of warning signals in which he stipulated that more than one individual predator, of the same or different species, interacts with many prey species, and

that both the conspicuousness of prey and the foraging behavior of predators are subject to selection. He envisioned novel conspicuous prey, including defended individuals, migrating into a new area and selecting for predator wariness. The greater the conspicuousness of a prey item, the more likely it presumably has survived previous encounters with other predators. Sherratt (2002: 745) wrote, “In broad anthropocentric terms, the models proposed suggest that predators should be wary of overtly conspicuous prey because they are ‘too good to be true’.” Sherratt hypothesized that once aposematic species become established and disperse, their presence would select in predators for an even greater sensitivity and phobia towards conspicuousness under which further aposematic phenotypes would evolve in a ‘runaway process’. Mallet & Singer (1987) also posited a runaway process of coevolution between predators and conspicuous prey.

Sherratt (2002) model for the evolution of aposematism involves multiple species. In contrast, aposematism arising via CRS operates with as few as two interacting populations, one consisting of discriminating and non-discriminating consumers,

and another consisting of distinguished and undistinguished defended prey. Neither does a CRS hypothesis necessarily entail migration as the mechanism for populations of signal receivers and signal emitters to interface.

CRS is inherent in another phenomenon postulated by Wallace (1889), the so-called Wallace effect, also known as reinforcement. This is a type of subpopulation-isolating mechanism that occurs when the progeny of incipient species are less fit than are the offspring of matings from within the general population. Here, males of one subpopulation select against females of another subpopulation, and vice versa, by contributing to the formation of unfit hybrids. The elimination of these hybrids accentuates the incompatibility of the two subpopulations. Wallace (1889: 176) hypothesized that ‘...with each modification of form and habits, and especially with modifications of colour, there arises a disinclination of the two forms to pair together...’.

CONCORDANCE AND PARSIMONY

A central, longstanding premise for the construct of aposematism, and a key assumption for a CRS hypothesis, is that signals are ‘honest’, i.e., they reliably denote unprofitability (although, of course, not for mimics) (e.g., Sherratt & Beatty, 2003). Studies demonstrating a strong coupling of conspicuous visual displays with the possession of toxic (e.g., Cortesi & Cheney, 2010; Vidal-Cordero *et al.*, 2012) or noxious chemicals (e.g., Wheeler *et al.*, 2015) support this contention in the classic context of ‘aposematic colours’ and chemically defended organisms. Maan & Cummings (2012) reported a positive correlation between coloration brightness (conspicuousness) and toxicity in the strawberry poison frog [*Oophaga (= Dendrobates) pumilio*] from Panama, a signalling system that they suggest evolved largely in response to bird predation. However, their bioassay, which entailed injecting sleeping laboratory mice with methanolic frog skin extracts and treating the latency of mice to fall back to sleep as index of toxicity, is not clearly relevant to natural predators; hence, we regard their results as suggestive, at best.

As a corollary to the proposition of honest warning signalling, a CRS hypothesis accords with a fundamental assumption on the chronology of the appearance of defences and aposematic signals: distinctive features arise in signal emitters after or in conjunction with the evolution of defences (e.g., Harvey & Paxton, 1981), hence prey potentially detract from the fitness of predators at the commencement of aposematic signalling. Guilford (1988) outlined different possible sequences for the appearance of conspicuousness

and unpalatability, and considered conspicuousness most likely related to aposematism when it follows or evolves jointly with unpalatability. Similarly, Ruxton & Sherratt (2006), commenting on investigations of the association of aposematism, unpalatability, and gregariousness among the Lepidoptera, stated that conspicuous signals are unlikely to evolve in the absence of defence, and that the establishment of defence most likely preceded aposematic signalling.

A CRS hypothesis also maintains that the avoidance of aposematic features by consumers arises in response to selection imposed by defended prey. This contention may be examined by assessing the fitness of predators that vary in their tendency to avoid aposematic signalers, as was done in a study documenting the differential responses of predatory fishes from the Atlantic and Pacific Oceans to the yellowbelly sea snake [*Hydrophis (= Pelamis) platurus*], a highly venomous, brightly colored species widely ranging in the Pacific Ocean (Rubinoff & Kropach, 1970). Captive Pacific fishes in more than 300 trials attacked live *H. platurus* only once, while Atlantic fishes did so 36 times. Of the 21 Atlantic fish predators tested, three that had attacked snakes died. One fish died while eating its first snake; another fish consumed 22 snakes in 31 days before succumbing to a snake bite. Rubinoff & Kropach (1970) concluded that Pacific predators have been selected to avoid visual and possibly chemical cues from *H. platurus*. Additional studies of the survivorship of predators following encounters with aposematic prey are needed.

A key component of a CRS hypothesis, noted by both Wallace (1889) and Fisher (1930), is that selection acts on defended prey to avoid being confused with undefended prey. Support for this contention, as it relates to visual aposematism, derives from model simulations and computer-assisted studies of predator-prey interactions (see Franks, Ruxton & Sherratt (2008) for literature). Merilaita & Ruxton (2007), for example, developed a neural network model of prey detection and attack decision-making by predators that operated in combination with evolving virtual prey. Their results suggest that, while prey need not always advertise their level of defensiveness with conspicuous coloration, a key driver of conspicuousness, when it occurs, is the differentiation of defended prey from undefended reference prey. Sherratt & Beatty (2003) presented human volunteers with computer-generated ‘prey’ in which both the reliability of a given trait as a sign of defence and its conspicuousness were controlled. The defended prey in their study invariably evolved traits that distinguished them from undefended prey. Even inconspicuous prey were avoided if they were distinct and reliably defended. Subtle, distinctive aposematic

patterns are as plausibly evolved by CRS as are conspicuous, colorful ones; to wit, the displays merely must be recognizable to consumers.

The prospect of aposematic displays that are inconspicuous opens new possible interpretations of distinctive colour patterns. For example, European vipers (*Vipera* spp.) possess a black zigzag band on their dorsum that was presumed by many investigators to disrupt the visual image of these venomous snakes, rendering them less detectable to predators. Field experiments, however, demonstrate that avian predators sympatric with *Vipera* spp. avoid the zigzag pattern painted on plasticine models of snakes, suggesting that this inconspicuous but characteristic band is a warning signal (Wüster *et al.*, 2004; Valkonen *et al.*, 2011); no evidence was obtained that this pattern is visually disruptive. Neotropical ithomiine butterflies (Nymphalidae), which are highly distasteful due to sequestered alkaloids (Beccaloni, 1997), possess wing patterns – mottled ‘tiger’ brown or transparent with brown or black edges – that also are believed to be inconspicuously aposematic (Mallet & Singer, 1987). Distinctive traits other than visual features may act as aposematic cues. For example, novel compounds on the skin of some reptiles are hypothesized to warn predators and ectoparasites (Weldon, Flachsbarth & Schulz, 2008).

A CRS hypothesis for aposematism additionally is compelling because it operates without the special conditions postulated for some other evolutionary hypotheses; it represents a parsimonious alternative hypothesis that may apply broadly. Aposematism arising by CRS is not limited with respect to the number of interacting consumer or prey species; it could entail interaction between one or many predator populations and one or many prey populations (cf. Sherratt, 2002). Neither is a CRS hypothesis contingent upon either the gregariousness or the relatedness of signallers. Indeed, CRS may beget Müllerian mimicry, where different, sometimes distantly related, defended taxa exhibit similar aposematic phenotypes (reviewed by Sherratt, 2008). Importantly, CRS as a mechanism for the inception of aposematism is not contingent upon learning and may account for consumers that shun aposematic prey when first encountered.

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