Quick guide

Deimatic displays

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What are deimatic displays? 'Deimatic' comes from the Greek δειματσω, 'to frighten', and is generally used to describe behaviour in which, when under attack, prey suddenly unleash unexpected defences to frighten their predators and stop the attack. Deimatic displays have also been referred to as deimatic reaction, startle display, responsive defence, dymantic display, dymantic coloration, frightening display and frightening attitude. Some of the most dazzling examples of deimatic displays include those of katydids, lepidopterans, praying mantises, frogs, salamanders and cephalopods (Figure 1). We use deimatic displays (*sensu* Maldonado) as an umbrella term that includes those that are observed through vision. The broader term, deimatic behaviour, may include other sensory modalities.

Isn't this just a variant of aposematism? And how does it relate to camouflage? In some ways, deimatic displays are a combination of aposematism and camouflage, but importantly, they also include an element of surprise, which the other two do not have. Classically, aposematic animals are conspicuously coloured to warn a potential predator that they are unprofitable as prey. Unlike aposematic displays, which are mostly static and perpetually 'switched-on', in deimatic displays revealing the visual cue (or signal) is a choice or a reflex (*e.g*. uken reflex in amphibians; Figure 1E).

At rest, animals with deimatic displays are often camouflaged and sometimes resemble other animals (mimics) or environmental objects (masquerade), e.g. the 'dead leaf' *Deroplatys* mantises (Figure 1). While animals that rely mostly on camouflage — with no deimatic display — often have reduced activity to minimize detection risk, those with hidden deimatic displays may be somewhat released from this pressure. If their camouflage fails, deimatic displayers have a formidable secondary defence to deploy. Deimatic displays, therefore, may enable a 'best of both worlds' adaptation, allowing animals with this ability to remain undetected longer than aposematic animals, but be better defended than camouflaged ones. Furthermore, they may avoid paying the costs aposematic animals pay when encountering a naive predator. As with all effective defence strategies, and adaptations in general, this raises the following question: if deimatic displays offer a 'best of both worlds' strategy, are they common in nature and if

Figure 1. Deimatic displays.
(A) Mountain katydid (*Acripeza reticulata*, Australia), image: Kate D.L. Umbers. (B) European swallowtail (*Papilio machaon*, Europe), image: Christer Wiklund. (C) Dead leaf mantis (*Deroplatys* sp., Asia), image: James C. O'Hanlon. (D) Four-eyed frog (*Pleurodema branchyops*, South America), image: Daniel Hoops. (E) Rough-skinned newt (*Taricha granulosa*, North America), image: Edmund D. Brodie III. (F) Common cuttlefish (*Sepia officinalis*, Europe), image reproduced with permission from Langridge *et al.,* 2007.

not, why not? Data on the survival value and costs of deimatic displays are required to begin answering questions like these.

Are deimatic displays usually associated with honest or dishonest signaling? Deimatic displays are used by profitable and unprofitable prey animals. While some animals' deimatic displays honestly indicate their unprofitability as prey, many seem to be bluffing, being, in reality, a tasty prey item. Deimatic displays are, therefore, either an honest or dishonest signal of prey profitability; however, whether honest or dishonest, showing the signal always involves a surprise element that may in itself delay the attack. Praying mantises, for example, are camouflaged at rest and are palatable, but when approached and/or touched by a predator, some mantises adopt their deimatic defensive posture revealing bright colours, 'eye' spots and producing a rasping sound (Figure 1). The remarkable and elaborate displays mantises perform do not reflect any real threat to a predator, because no known mantis is toxic. However, frightening the predator by all-of-a-sudden presenting it with a much larger, brightly coloured object, the mantis' deimatic display is thought to stop the predator's attack or make it pause long enough for the mantis to escape.

On the other hand, some species with deimatic display, such as mountain katydids (*Acripeza reticulata*), are toxic. At rest, mountain katydids are well camouflaged but when approached they clumsily attempt to flee and when touched reveal a brightly coloured abdomen below the tegmina (tough wings) (Figure 1). As with mantis displays, their deimatic display makes the katydid appear larger than before and the sudden appearance of bright colours presumably startles the predator preventing further attack. Unlike the mantis, the katydid's display is an honest signal of unpalatability because if the predator eats it, it will encounter a nasty toxin.

Under what circumstances do prey perform deimatic displays? Deimatic displays can be classified as pre-emptive defences or counter defences depending on when throughout the attempted predation event they are performed. Traditionally, deimatic displays are expected to pre-emptively confuse or shock the predator, making it pause in its attack long enough for prey to escape. For example, European swallowtail butterflies (*Papilio machaon*) deter bird attacks by flashing conspicuous wing colours when approached (Figure 1). However, while applicable to a subset of predator-prey interactions, this definition fails to account for circumstances where prey wait for tactile stimulation before performing their display as a counter defence.

Mountain katydids (*Acripeza reticulata*) and four-eyed frogs (*Pleurodema branchyops*) only perform their deimatic display after physical contact from an attacker. The tough cuticle or toxic skin may protect them from a predator's initial investigations and allow the deimatic display to occur late in the predation attempt. More robust animals may avoid performing their display until they are aware a predator has detected them. Alternatively, deimatic displays may be performed during subjugation if prey secrete a toxin and are likely to be spat out, thus providing a reinforcing visual display with a bad/toxic taste. Interestingly, when deimatic displays are performed only after attempted subjugation, the opportunity for predators to transfer the lesson from one encounter to the next is limited unless the predator learns to associate the resting camouflaged state with the bad/toxic taste and display. If predators do not learn that association, individuals in the prey population are not protected by predators' previous experience with conspecifics. However, this strategy may work well for prey species that regularly encounter naïve predators. In this way, deimatic displays are fundamentally different to the classic aposematic strategy.

How do deimatic displays evolve? Very little empirical data on either the costs or benefits of deimatic displays exist. As such, our understanding of the selective forces driving the evolution and maintenance of these traits is poor. On the theoretical side, this question is relatively little studied, although it is related to the evolution of the timing of antipredator defences, which has received recent attention (see below for reference).

Little modelling effort has been directed toward the evolution of deimatic displays, despite some fascinating open questions. For example, the above-mentioned strategy of deimatic display during subjugation poses an interesting evolutionary question, given that there is little opportunity for learning if the visual signal comes only after the attack, as opposed to normal aposematism in which predator experience is an important part of the strategy's protective value.

In general we expect that deimatic displays involve co-evolutionary processes, as they are exposed to selection only when prey primary defences (*e.g*. camouflage) fail. There is then selection on two levels in both prey and predator: the primary defence, the secondary deimatic defence, and coevolution in the predator to circumvent each of these defences. There is significant scope for more theoretical and empirical work to be done in this field.

Where do I find out more?

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