Animal Behaviour xxx (2016) e1–e3

Contents lists available at ScienceDirect

Animal Behaviour

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

Forum

Towards a tractable working hypothesis for deimatic displays

Kate D. L. Umbers [a, *], Johanna Mappes [b]

[a] School of Science and Health, Western Sydney University, Hawkesbury, Richmond, NSW, Australia
[b] Centre of Excellence in Biological Interactions, Department of Biological and Environmental Science, University of Jyväskylä, Jyväskylä, Finland

ARTICLE INFO

Article history:
Received 2 September 2015
Initial acceptance 29 September 2015
Final acceptance 14 December 2015
Available online xxx
MS. number: 15-00758R

Keywords:
aposematic
colour
deimatic
startle
Tettigoniidae
warning colours

Upon being agitated, the mountain katydid, *Acripeza reticulata*, performs a remarkable defensive display that includes a defensive posture, a display of conspicuous coloration and the release of distasteful, possibly toxic, exudate. From our initial investigations this display appears to be best described as a deimatic display. Deimatic displays are conspicuous behaviours that a prey animal performs when it perceives the threat of an imminent attack by a predator. It can cause a predator to stop, slow or pause its attack, allowing the potential prey to escape (Edmunds, 1974). In Umbers and Mappes (2015) and Umbers, Lehtonen, and Mappes (2015) we recommended that the definition be extended to include both displays performed early, for example before predators make physical contact, and displays that take place late in the predation sequence, for example after physical attacks by the predator (Endler 1991; Umbers & Mappes, 2015). This forum article provides a valuable opportunity to reflect on the classic definition of deimatic displays, how the definition has been used and how it can be refined.

THE SURVIVAL VALUE OF DEIMATIC DISPLAYS

Skelhorn, Holmes, and Rowe (2016) questioned our definition of deimatic displays as applied to the mountain katydid and argued that only observations with katydids' natural predators can be used to demonstrate whether their behaviour is deimatic or not. We agree that to understand the survival value of a deimatic display, we must understand how natural predators respond. However, in light of recently acquired evidence, we stand by our definition of the mountain katydid's behaviour as a deimatic display, and contend that deimatic displays can be performed after physical attack (simulated or natural). Although our previous experiment did not measure the survival value of display, our recent experiments on the responses of Australian magpies, *Cracticus tibicen*, and domestic chickens, *Gallus gallus domesticus*, to mountain katydids have yielded data supporting our observations of the simulated attacks. In these new experiments katydids only performed their display after the initial attack and in some instances this successfully stopped the predator continuing the attack (Umbers, Haff, DeBona, & Mappes, 2015).

ARE DEIMATIC SIGNALS ALSO APOSEMATIC?

Skelhorn et al. (2016) point out that deimatic displays have historically been associated with undefended animals, but acknowledge that a definition that includes defended animals is sensible. Examples of deimatic displays in nontoxic (undefended) insects come from praying mantises (Crane, 1952; Edmunds, 1972, 1974, 1976; Maldonado, 1970), and examples of defended animals (e.g. with toxins) from the Colombian four-eyed frog, *Pleurodema*

* Correspondence: K. Umbers, School of Science and Health, Western Sydney University, Hawkesbury, Richmond, NSW 2753, Australia.
E-mail address: k.umbers@westernsydney.edu.au (K. D. L. Umbers).

http://dx.doi.org/10.1016/j.anbehav.2016.01.002

brachyops (Martins, 1989). Skelhorn et al. suggest that it is important to make a distinction between aposematic and deimatic strategies. We wish to point out that aposematic and deimatic displays are not necessarily mutually exclusive strategies: deimatic displays can function as warning signals to predators as, of course, can aposematic signals. We consider the difference between deimatic and aposematic displays to be that deimatic displays can include bluffs whereas aposematic signals must include a punishment via an unprofitable experience. Additionally, deimatic displays could also signal unprofitability with prey advertising that they are too difficult to catch or chase (Edmunds, 1974), but this idea is unexplored. We agree that using movement alone, unexpected or otherwise, to distinguish between deimatic and aposematic displays is not useful; we did not, and do not advocate it.

SKELHORN ET AL.'S DEFINITION

Skelhorn et al. present their definition of deimatic displays as 'any defensive display that causes a predator to misclassify a prey as a potential threat to its immediate safety' and go on to suggest that there are three scenarios that can lead to a display being considered deimatic. We address each of these in turn.

Displays that mimic the appearance of one of the predator's own predators, or part of one (e.g. the eyes)

Although many prey animals with deimatic displays utilize, for example, sudden flash of eye patterns in their display (De Bona, Valkonen, López-Sepulcre, & Mappes, 2015), this description would exclude many prey animals that are classically described as deimatic such as salamanders performing the unken reflex (Toledo & Haddad, 2009; Toledo, Sazima, & Haddad, 2011). In addition, the requirement to show mimicry raises a challenge common to the study of mimicry: from which of the prey's predators' perspectives should it be defined? For example, while we may see a crocodile face on the peanut-head bug, *Fulgora laternaria*, it is unlikely that their natural predators (or at least all of them) would misclassify a peanut bug as an actual crocodile. Of course this problem of predator identity is not exclusive to deimatic display but common to most studies on antipredator adaptations. So while mimicry can and does appear in deimatic displays we do not agree that mimicry is required for a display to fall under the classification.

Displays that exploit predators' innate startle reflexes (such as those performed in response to loud sounds or sudden movements)

We agree that the definition of deimatic displays should include that the predator's startle reflex is released. We would like to make the point that startle responses are challenging to experimentally manipulate and to measure in the field and difficult to measure directly (see below our discussion about 'fear'). Such measures may be beyond the logistical scope of some studies but data from such studies should still be valued.

Displays that cause predators to mistake them for prey that have the potential to inflict harm (e.g. by making individual prey look bigger or more aggressive)

We agree that dangerous prey could be scary for predators if they pose a real threat (e.g. if they are defended); however, we disagree that the scare alone can make a display deimatic. Consider the situation where a predator aborts the predation sequence when approaching a yellow-black caterpillar because it is frightened when it misclassifies it as a wasp. According to Skelhorn et al.'s definition this is classifiable as deimatic but it is in fact a static signal and a classic example of aposematism.

ARGUMENTS AGAINST THE REQUIREMENT OF MEASURING THE PREDATOR'S FEAR

We agree with Skelhorn et al.'s statement: 'deimatic displays, like other prey defences, should be defined by the mechanisms through which they prevent predation rather than by the form taken by the display'. However, we disagree that 'what defines deimatic displays is their ability to exploit classic fear responses in predators that have evolved, not to avoid prey, but to avoid imminent danger' and that 'direct evidence that deimatic displays elicit fear responses… is absolutely critical if we want to determine whether a display is actually deimatic' (Skelhorn et al. 2016). We see two problems with the hypothesis that predators must be shown to feel fear in interactions with potential prey to classify the prey's defence as a deimatic display. First, fear is an underlying emotional state (Murphy, 1978) and manifests physiologically with the production of adrenaline and heightened arousal (Funkenstein, 1958), whereas responses to deimatic displays are not fear per se because they occur before there is time for a fear reaction to take place (e.g. for adrenaline to be released). In observational studies, responses to deimatic displays are described as reflexes, more akin to 'getting a fright', 'being spooked', 'being shocked' (in the colloquial sense, not the medical or electrocuted sense), 'being surprised', performing a 'jumpy' reflex response, reacting to sensory overload Stevens (2015), being confused (Humphries & Driver, 1970) or experiencing something unexpected or unusual (Edmunds, 1972, 1974, 1976; Ingalls, 1993; Johnson & Brodie Jr, 1975; Maldonado, 1970; Martins, 1989; Olofsson, Eriksson, Jakobsson, & Wiklund, 2012). We advocate that it is not necessary for prey to be misclassified as something frightening, or classified at all. Thus, despite the fact that deimatic is supposed to be Greek for 'to frighten' (Maldonado, 1970; although this is not confirmed by any Greek–English dictionary so far consulted), it is not fear that we expect the predator to feel. Thus the requirement of showing a predator to be frightened or fearful is inaccurate when trying to determine whether a display is deimatic.

Second, while the difficultly of data collection per se should not negate the use of a behaviour in a definition, biologists must have testable hypotheses with which to make progress and increase knowledge. Measuring fear, especially in a wild predator, is challenging, with most studies using proxies for fear (Murphy, 1978; Stankowich & Blumstein, 2005). Furthermore, observations of predation events in the wild are among the rarest that field biologists can hope to make. In most cases, the natural predators of candidate aposematic species are unknown; for example the identity of natural predators of most species of poison frogs, iconic examples of aposematism, and how those predators respond to live adult frogs in the wild is unknown (for tadpoles see: Gray & Christy, 2000). Therefore, while Skelhorn et al. argue that it is critical to make observations in the wild as to whether a putative deimatic display elicits the fear response of a predator, we assert that studies on predators' reactions to defended prey conducted in the laboratory that use model predators and/or hold prey animals in artificial settings can still be useful (Gamberale-Stille & Tullberg, 1999; Lindstedt, Lindström, & Mappes, 2008; Skelhorn, Rowland, Delf, Speed, & Ruxton, 2011; Skelhorn, Rowland, Speed, & Ruxton, 2010; Skelhorn & Ruxton, 2010; Svádová et al., 2009; Tullberg, Merilaita, & Wiklund, 2005).

OUR PROPOSED DEFINITION

We agree with Skelhorn et al. that it is important to define any phenomenon in science as clearly as possible. We contend that it is

Please cite this article in press as: Umbers, K. D. L., & Mappes, J., Towards a tractable working hypothesis for deimatic displays, Animal Behaviour (2016), http://dx.doi.org/10.1016/j.anbehav.2016.01.002

also important to define animal behaviour in the way that it is beneficial for developing workable, testable hypotheses. We therefore suggest the following working definition of deimatic displays: a momentary, transient, conspicuous signal that induces a startle response or overloads the senses of an attacking predator, such that the predator pauses, slows or stops the attack. Under this definition it is possible to measure aspects of the displayer's behaviour (momentary, transient, conspicuous) and the predator's behaviour (performs startle response, pauses or stops attack) without having to know the internal state of either animal. In this definition we intend to account for the 'startle' or 'spook' element of the predator's sensory system that prey are exploiting. To understand the proximate mechanisms of deimatic displays it may be necessary to measure the internal state of one or both parties, but we argue that this is not necessary for the definition.

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Please cite this article in press as: Umbers, K. D. L., & Mappes, J. Towards a tractable working hypothesis for deimatic displays. Animal Behaviour (2016), http://dx.doi.org/10.1016/j.anbehav.2016.01.002