A synthesis of deimatic behaviour

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ABSTRACT

Deimatic behaviours, also referred to as startle behaviours, are used against predators and rivals. Although many are spectacular, their proximate and ultimate causes remain unclear. In this review we aim to synthesise what is known about deimatic behaviour and identify knowledge gaps. We propose a working hypothesis for deimatic behaviour, and discuss the available evidence for the evolution, ontogeny, causation, and survival value of deimatic behaviour using Tinbergen’s Four Questions as a framework. Our overarching aim is to direct future research by suggesting ways to address the most pressing questions in this field.

Key words: antipredator, defence, predator, prey, competition, cognition, behaviour, aposematism, deimatism, startle.

CONTENTS

I. INTRODUCTION

Avoiding predation is essential for prey fitness. Defending against predators can be costly in terms of time, energy, injury, and death. Therefore, traits that reduce these costs are widespread and diverse. The variety of defensive traits includes: camouflage – concealing colours and patterns (Endler, 1978; Stevens & Merilaita, 2011); aposematism – warning colour patterns and sounds (Mappes, Marples & Endler, 2005); retaliation – expulsion of blood, toxins, and hot fluids (Eisner, 1970; Sherbrooke, Middendorf & Guyer, 2001); armour – defensive structures like spines and hard integuments (Speed & Ruxton, 2005); and mimicry in many forms (Skelhorn *et al.*, 2010; Dell'Aglio *et al.*, 2018). How defensive traits such as visual warning signals work against predators is well understood (Mappes *et al.*, 2005), while others like deimatic behaviours (Fig. 1), remain poorly understood. Cott (1940, p. 213) commented on deimatic behaviour stating "*Indeed, we have here an almost untrodden field for future research*". More than 80 years later this statement remains true save for a surge of research in the 1970s, and a more recent second wave. The recent resurgence has precipitated this collaborative review in which we: (1) suggest a hypothesis for deimatism as distinct from other defences; (2) critically evaluate examples of deimatism and their classification; and (3) apply Tinbergen's 'Four Questions' framework (Tinbergen, 1963) on evolution, ontogeny, causation, and survival value, to synthesise the literature and identify the critical knowledge gaps we need to fill to understand the evolution of deimatism.

II. WHAT IS DEIMATIC BEHAVIOUR?

Deimatic behaviour [*sensu* Maldonado (1970) and Edmunds (1974)] is a celebrated 'textbook example' of a spectacular antipredator defence (Fig. 1), but what exactly is it? Despite long-standing scientific interest (see online Supporting Information, Table S1) no strong consensus has so far emerged, nor has a name even been settled on although more than a dozen have been proposed, with 'deimatic behaviour' and 'startle display' persisting into the modern literature (Table S1).

The first occurrence of the phrase 'startle display' in the animal behaviour literature seems to be in Crane's (1952) work on Trinidadian mantises, described as the "*type of behavior in which tegmina and wings are elevated and special associated motions made in the face of a potential threat. The more usual terms 'frightening' or 'intimidating display' seem too strong to apply in most of the current instances*" (p. 261). Since Crane (1952), the term 'startle' has been used to describe the prey's behaviour without knowledge of whether in fact the behaviour releases the startle reflex in the attacker (Skelhorn, Holmes & Rowe, 2016). Maldonado (1970) coined the phrase 'deimatic behaviour'. 'Deimatic' is from the

Greek for ‘frighten’ (Liddell *et al.*, 1996) which we note is the same root as Deimos the Greek God of Terror (Grant & Hazel, 2004). Maldonado (1970) defined deimatic behaviour in prey as “*a conspicuous display when they are faced with a ‘threat’*” (p. 61). Edmunds (1974) expanded Maldonado’s definition and described ‘deimatic behaviour’ in a range of species and stipulated that it “*stimulates an attacking predator to withdraw and move away. This results in a period of indecision on the part of the predator… and this gives the displaying animal an increased chance of escaping*” (p. 150). To avoid assumptions about mechanisms and form, we suggest the use of ‘deimatic behaviour’ instead of ‘startle display’. We suggest avoiding the term ‘startle’ because it is not yet clear by how many or which mechanisms deimatic behaviour can be protective (see Section II.7) and we suggest avoiding the word ‘display’ because it can imply visual signals and exclude other sensory modalities (Edmunds, 1974; Ruxton, Sherratt & Speed, 2004).

Descriptions of deimatic behaviours are inconsistent across the literature. They have been described as behaviours performed by prey as a predator approaches, that cause predators to hesitate long enough for prey to escape. However, many species – including most of those described in the literature – perform their deimatic behaviour during subjugation, long after approach (Table S1). Deimatic behaviours are often described as a ‘bluff’ (Ruxton *et al.*, 2004) which assumes that besides the display, prey pose no further threat. That is, it assumes that prey lack a chemical or physical defence, and disregards any protective value of the performance itself. Also, species have been described as deimatic in ways that imply that their whole antipredator strategy is ‘deimatic’ (Umbers & Mappes, 2015). All of the above approaches have proved problematic when then trying to place deimatism in context with other defences (Skelhorn *et al.*, 2016). We therefore suggest that antipredator strategies can include many ‘defences’ such as crypsis, masquerade, and aposematism; any one of which may be a deimatic behaviour (Umbers *et al.*, 2017) (Fig. 2).

Given the overall lack of clarity, but considering the main conceptual points from previous contributions to the field, we suggest the following hypothesis for what constitutes deimatic behaviour: *a behaviour performed by a target different from fleeing and retaliation that is triggered by it perceiving threat from an attacker during approach or subjugation, and which can trigger an unlearned avoidance response in the attacker causing it to slow or stop its attack.*

There are four key components of our hypothesis and we provide rationales for each below plus a summary of our deliberate exclusions.

(1) Component 1: "A behaviour performed by a target different from fleeing and retaliation…"

"Behaviour" here is to be interpreted very broadly as something an organism can do including body part movements, the emission of sounds or chemicals, or dynamic changes in colour patterns. The inclusion of the word "performed" is intended to emphasise that it is a discrete state that the prey adopts for a time and to distinguish it from more continuous states, such as constantly exposed aposematic colouration. The behaviour may have been selected to induce the attacker's response or the attacker's response may be an accidental by-product of a prey behaviour.

A "target" is the organism or group of organisms that is being attacked, including colonies and other diffuse phenotypes. The target may not always be prey and could be a competitor (Edmunds, 1974). Deimatic behaviours do not involve the target fleeing from an attack. They *can* be performed while fleeing, but their protective value is not in avoiding capture by increasing physical distance. Deimatic behaviours do not include retaliation (*sensu* Edmunds, 1974), in which predators can be physically harmed such as by toxic sprays (Eisner, 1970).

(2) Component 2: "…triggered by it perceiving threat from an attacker during approach or subjugation…"

The implication here is that deimatic behaviour evolves in response to attack, and the form has been influenced by the effect that it has on an attacker, so it is a signal not a cue (Maynard Smith & Harper, 2003). It is triggered by the target perceiving, rightly or wrongly, that it is threatened; it requires the target to detect the attack. With "perceiving" we intend to include the most neurologically simple stimulus–response processes. We predict the behaviour will only be performed outside of a threatening context by mistake, for example when targets misidentify an event as a threat (akin to false alarm). We also predict the behaviour will typically be performed for brief time intervals, or at least not very long beyond the period of interaction with an attacker. While "attacker" often refers to a predator or competitor, it also extends to the range of natural enemies such as parasitoids, parasites, and micropredators (*sensu* Lafferty & Kuris, 2002). Display initiation should coincide with the physical proximity of an attacker within some relevant distance – we suggest the phrase 'display initiation distance' (*sensu* Aguilar-Argüello, Díaz-Fleischer & Rao, 2016) – and it will cease upon the perceived threat passing, such as when the attacker leaves the scene or obviously changes its motivation (e.g. from a focused attack to ignoring, or if the prey escapes the predator). The onset of deimatic behaviour may be sudden if it is the result of a threat threshold being breached, but we suggest leaving the time taken to begin performing the display open because slow transitions may be as effective as fast ones (Holmes *et al.*, 2018). Deimatic behaviours are performed during predator approach or subjugation – they may function to prevent consumption.

(3) Component 3: "…which can trigger an unlearned avoidance response in the attacker …"

We predict that deimatic behaviour can impact the attacker through a change in their perception of their target in any sensory mode. The change does not have to result from learning or prior experience. The attacker's response could involve cognition and/or could be affected by reflexive responses. We also predict that the attacker's response may change in response to sensory adaptation, habituation, confusion, motor fatigue, state of arousal, and, of course, associative learning, perhaps related to withdrawing from a threat. The implication of "can" is that the target's behaviour will occur often enough for the behaviour to be favoured by selection.

(4) Component 4: "…causing it to slow or stop its attack."

Our hypothesis requires that deimatic behaviour causes the attacker to slow or stop its attack. Guilford's (1994) 'go-slow' hypothesis suggests that predators may be more cautious when faced with an aposematic signal, we predict the same may be true for deimatic behaviours. The attacker may continue to attack after responding to deimatic behaviour; this still counts as deimatic. Although displays may not always be effective, the likelihood of survival should be higher for individuals that choose to perform the behaviour compared to those that do not; at least in some circumstances. Any slowing or termination of attack will be adaptive to the prey.

(5) Deliberate exclusions from the hypothesis

Our hypothesis deliberately excludes certain words and phrases to remain inclusive of several concepts. We have avoided the terms predator and prey because although deimatic displays are commonly thought of in predator–prey interactions, they also occur in other contexts such as intraspecific interactions (Edmunds, 1974). We expressly avoid specifying the mechanism underlying the attacker’s response, as several could be exploited. Our hypothesis allows the target to be ‘defended’ or ‘undefended’ because the presence and strength of defences beyond the behaviour are not needed for it to be deimatic and, equally, their presence does not preclude deimatism (Fig. 2). The definition also deliberately does not specify the target’s behavioural state at the end of the display which could include the target returning to its previous state, or fleeing (de-escalation) or retaliation (escalation) (Edmunds, 1972).

(6) Deimatism as a distinct defence

The biggest challenge in articulating the concept of deimatic behaviour is in determining the conceptual boundaries between it and other antipredator defences. Here we discuss the conceptual similarities and differences among deimatism and other defences. For clarity, we use the phrase ‘antipredator strategy’ to mean the combination of defences an animal uses such as crypsis, masquerade, aposematism, deimatism, and/or types of mimicry, each of which may be encountered by predators or deployed by prey at different stages of the predation sequence (Fig. 2) and may be multimodal and/or multicomponent (Rowe & Guilford, 1999). We expand the primary/secondary defences dichotomy to recognise that an antipredator strategy can be a sequence of any length – primary, secondary, tertiary, quaternary, quinery, etc. (Endler, 1986, 1991) (Fig. 2).

Where does deimatism fit among other antipredator defences? The concepts of most antipredator defences are not crystal clear, with many different definitions presented and the distinctions between defences muddy. In addition, relative to other defences like aposematism and camouflage, the mechanisms and functions of deimatism are not well understood. This makes the necessary task of explaining clear conceptual distinctions difficult, particularly compared to flash behaviour, retaliation, and aposematism.

Deimatic behaviour can resemble, although is functionally distinct from, fleeing responses like ‘flash behaviours’ (*sensu* Edmunds, 1974) which often take the form of repeatedly revealed colour patches and/or sounds by escaping prey (Table S2). These signals are thought to impair the ability of attackers to track a fleeing signaller (Loeffler-Henry *et al*., 2018) whereas deimatic behaviours are not protective *via* disrupting prey tracking or increasing the distance between predator and prey (Edmunds, 1974; Loeffler-Henry *et al.*, 2018). Aspects of deimatic behaviour also overlap with retaliatory defences (*sensu* Edmunds, 1974) such as the defensive sprays of bombardier beetles. Such behaviours are also performed when under threat, but differ in that predators are attacked rather than just displayed to.

Debate and confusion has surrounded whether deimatism is distinct from aposematism (Skelhorn *et al.*, 2016; Umbers & Mappes, 2016). In their most general sense, aposematic signals can be loosely defined as ‘go away’ signals to predators. Such a broad definition can include many concepts currently considered distinct: warning colouration, flash colouration, types of mimicry and deimatism. This could mean that deimatism is a type of aposematism, in the same way that crypsis and masquerade are both types of camouflage (Skelhorn *et al.*, 2010). But if the term aposematism is used as an umbrella term for all those concepts, classic warning signals need to be given a new name, which could cause unnecessary confusion.

A more useful and biologically precise definition states that aposematism is “…*the association between the signal and unprofitability*…”, that “*Aposematic signals work best when they are easily detectable and memorable, which facilitates avoidance learning*…”, and that the benefits of aposematism “*…increase as a function of the density of the similarly signalling individuals*…” (Mappes *et al.*, 2005, p. 598). Deimatism does not fit this definition well. There is preliminary evidence that deimatic behaviours are more effective against naïve predators than experienced ones, which is opposite to the expectations of signals that facilitate avoidance learning (Umbers *et al.*, 2019). Deimatic behaviours are not easily detectable; they are temporary and undetectable until they are performed. Learning is not necessary for deimatism to afford protection, which is a major difference from aposematism *via* learned aversion, although learning might be associated with deimatism after the first encounter (Kang *et al.*, 2016). It is currently unclear whether deimatic behaviours facilitate or impede memorability, and both are possible (Kang *et al.*, 2016). Finally, the benefits of deimatic behaviour can in theory decrease as a function of density, rather than increase, as attackers learn to expect the performance (Sargent, 1990; Ingalls, 1993).

Deimatic behaviours can, however, be part of an antipredator strategy that includes an aposematic signal (Umbers *et al.*, 2017) (Fig. 2). If an antipredator strategy includes deimatism and aposematism, deimatic behaviour may cause a predator to break off its attack before directly experiencing any of the prey's other defences. The deimatic function may then hamper development of avoidance learning and reduce the efficacy of, or requirement for, aposematism. Antipredatory strategies that include deimatism can also include Batesian mimicry (for example through revealing markings that mimic a dangerous predator), the use of eyespot signals, or retaliation, and equally, deimatic behaviour can be followed by no further defence (Fig. 2).

(7) Mechanisms by which predators respond to initial encounters with deimatic behaviour

The sensory and cognitive mechanisms deimatic behaviours exploit in predators are currently unclear. Several non-mutually exclusive hypotheses have been suggested: release of the startle reflex, the looming reflex, the release of fear in the predator, sensory overload, confusion, and neophobia. Experimentally distinguishing among these mechanisms is an important challenge to meet.

(*a*) *Startle reflex*

Deimatic behaviours are often colloquially referred to as 'startle displays', in that when predators encounter them they appear to be startled (Crane, 1952; Schlenoff, 1985). But this description is largely anthropomorphic and requires biological specificity. Vaughan (1983) tested the responses of blue jays (*Cyanocitta cristata*) to artificial prey in which 'startle response' was defined as "*a measurable hesitation in the normal feeding sequence of a predator*" (Vaughan, 1983, p. 385). Further measures of 'startle' have included response variables of mixed specificity: increased heart rate, latency to reinvestigate, hesitating, jumping back, diving away, fleeing, contraction of facial and skeletal muscles, jumping, rearing, running, grinding teeth, and quivering (Burnham, 1939; Bura *et al.*, 2011; Ramirez-Moreno & Sejnowski, 2012; Fischer, Franco & Romero, 2016; Holmes *et al.*, 2018). These behaviours and physiological responses could occur for several reasons and not necessarily as a result of eliciting a startle reflex as defined in its strictest sense.

The 'startle reflex' is a response that interrupts what an animal is currently doing and produces physiological and behavioural changes that help it evade an immediate threat (Eaton, Bombardieri & Meyer, 1977; Gotz & Janik, 2011; Yilmaz & Meister, 2013; Skelhorn *et al.*, 2016). The startle reflex appears to be triggered by stimuli, whether auditory or visual, that have a high intensity and a rapid onset (Koch & Schnitzler, 1997; Koch, 1999; Deuter *et al.*, 2012). For example, in laboratory experiments where sounds are produced in close proximity to subjects (usually primates and rodents), sounds typically need to be above 80–90 dB with rapid rise times (the time taken for the stimulus to reach its maximum amplitude) of less than 12 ms (Davis, 1984), but sounds of 60 dB can also be effective if they have close to instantaneous rise times (Åsli & Flaten, 2012). Caterpillars that make sounds in response to attack can produce them close to instantaneously at 70–90 dB when the predator is at close range, but the limited data available suggest that deimatic behaviours rarely have such intense and rapid onset, at least for auditory signals. Therefore, although the startle reflex is taxonomically widespread, and exploiting it could protect against many enemies, it is unlikely to be the mechanism by which all deimatic behaviours protect.

(*b*) *Looming reflex*

Deimatic displays may trigger the 'looming reflex', an adaptive response to avoid rapidly approaching objects, including predators (Yamawaki, 2011). The looming reflex has been studied across a wide range of species including insects (Rind, Santer & Wright, 2008; Yamawaki, 2011), crustaceans (Shragai *et al.*, 2017), cephalopods (King & Adamo, 2006; Hanlon & Messenger, 2018) and chordates (Temizer *et al.*, 2015), and is characterised by receivers taking rapid evasive action to avoid contact with the approaching object. Like startle reflexes, the stimuli that induce this response are specific – looming-sensitive neurons respond to stimuli that increase rapidly in surface area on the retina (Yilmaz & Meister, 2013). For example, mice respond to rapidly looming discs, but only when they come from above at speeds that resemble an incoming aerial predator (Yilmaz & Meister, 2013). Some deimatic behaviours involve a rapid increase in size (Table S3) and although it is not known if such changes are sufficient in size or speed, it is possible they evoke the looming response. To take advantage of predator looming reflexes we predict that deimatic behaviour may have the greatest survival value when it appears to make the apparent size of the prey increase rapidly, and perhaps at close range so that they can stimulate a larger area of the predator's retina.

(*c*) *Fear responses*

Responses to deimatic behaviour seem to occur very quickly (i.e. reflex-like), and may use specific neural systems that do not involve time-consuming identification of the approaching stimulus in order to enable rapid life-saving responses (Lin, Murray & Boynton, 2009). However, another hypothesis for how deimatic behaviours work is that they elicit fear responses because a stimulus is recognised and misclassified as a potential threat (Skelhorn *et al.*, 2016). Phasic fear is a state of apprehension elicited by a specific and imminent perceived threat, that dissipates once the danger is removed (Davis *et al.*, 2010; Miles, Davis & Walker, 2011; Sato & Yamawaki, 2014; Tovote *et al.*, 2016). It produces responses that can be rapid, occurring within 100 ms of stimulus onset, and could mediate observers' responses to deimatic behaviour (Pomeroy & Heppner, 1977; Åsli & Flaten, 2012). The kinds of stimuli perceived as threatening can be influenced by an animal's evolutionary history (Blumstein, 2006) or ontogeny, or by what it has learned from its own experiences or observations (Griffin, 2004). This means that features of dangerous stimuli in a predator's environment that are likely to elicit phasic fear responses could be exploited by deimatic behaviour. For example, deimatic behaviour could include the revealing of eyespots that resemble sympatric predatory eyes (Janzen, Hallwachs & Burns, 2010; De Bona *et al.*, 2015), or auditory signals that sound like sympatric (or at least historically so) predatory alarm calls (Dookie *et al.*, 2017).

(*d*) *Sensory overload*

Deimatic behaviours could somehow overwhelm a predator's ability to process sensory information by presenting them with more information or noise than they can process at once (Hebets & Papaj, 2004; Low, 2012). This popular idea has been referred to as 'sensory overload' (Hebets & Papaj, 2004; Bro-Jørgensen, 2010). However, this term is often used loosely, and clear conceptual definitions are rare (Scheydt *et al.*, 2017), particularly in the animal signalling literature. From a mechanistic point of view, the behavioural phenomena that appear to be associated with sensory overload (e.g. behavioural immobilization and confusion) may be caused when excessive stimulation from at least two sensory modes blocks the reticular formation; a complex network of brainstem nuclei involved in (amongst other things) perception, attention and maintaining behavioural arousal (Lindsley, 2013). Related concepts probably include visual or auditory distraction, sensory filtering, cognitive overload (Dukas & Kamil, 2000) and breakdown of multimodal/sensory integration.

Understanding the mechanisms by which deimatic behaviours protect prey from predators requires directly measuring what the predator is experiencing, which may demand more technically difficult and invasive data collection (Fullard, Dawson & Jacobs, 2003) than measuring predator behaviour and carries important ethical considerations. The difficulty of determining the mechanisms involved increases substantially when attempted in field conditions (Skelhorn *et al.*, 2016; Umbers & Mappes, 2016). Both are worthy goals if we are to understand how deimatic behaviours provide survival value.

(*e*) *Confusion effect*

As stated above, deimatic behaviour often involves the exposure of a previously hidden signal that functions to startle a would-be attacker. However, the deployment of hidden signals may also prevent attacks through other mechanisms. Specifically, a cryptic organism revealing a conspicuous signal as it flees may confuse the attacker as to the organism's appearance when at rest, hindering subsequent search. This defensive strategy is known as 'flash behaviour' and appears to be widespread in nature with putative examples having been described in cephalopods, insects, fish, amphibians, reptiles, birds, and mammals (Edmunds 1974; Hanlon & Messenger, 2018). It has been postulated that the confusion effect of flash behaviour may function in tandem with a startle effect to dissuade attackers (Edmunds, 1974; Cott, 1940). However, a ‘proof of concept’ experiment demonstrated that the confusion effect of flash behaviour alone is sufficient to prevent attacks (Loeffler-Henry *et al*., 2018). Moreover, flash displays may be more effective in reducing predation when the signaller flees from a distance, so that the signaller’s cryptic resting state is not observed (Loeffler-Henry, Kang & Sherratt, 2021). Since hidden signals are less likely to frighten the observer when exposed from a distance, then deimatic and flash displays are functionally distinct and may often be incompatible.

III. DEIMATIC BEHAVIOUR ACROSS TAXA

We collated all studies on deimatic behaviour and its analogues from the primary literature. We include studies on deimatic and related phenomena based on descriptions in the literature by the authors and as such may have included behaviours eventually deemed not to fit deimatism and may have excluded deimatic behaviours that will be included in the future. With those limitations, here we synthesise the literature on deimatic behaviour and discuss the marginal cases.

(1) Literature search methods

We searched titles, abstracts, and key words in the *Web of Science* database, with relevant terms gathered from Edmunds (1974), proposed definitions and iteratively, based on preliminary descriptions we found in the literature (Table S1). Our search terms in the Title [TI] field were: deimatic display OR deimatic response OR frightening attitude OR startl* display OR defensive display OR startle behaviour OR deimatic behaviour OR startl* sound OR startl* colour* OR startl* response OR startl* reaction OR dymantic display. This search returned 1535 hits in February 2021. In addition, we searched for papers using the taxon-specific terms: ‘unken reflex’ (amphibians), ‘hooding’ (cobras) and ‘disturbance stridulation’ (insects).

(2) Results from literature search

75 publications met at least one of two inclusion criteria: describing the form of putative deimatic behaviour or describing a manipulative experiment on an aspect of deimatic behaviour (Table S3). In total our data set included 224 species from 246 separate studies within 75 publications (with ‘studies’ defined as descriptions or experiments within a publication) with 16 species represented multiple times (Table S3) . Because so few species have been studied multiple times, the number of studies is roughly representative of the number of species, for a summary of the number of species see Fig. 3. Most studies were descriptive accounts of putative deimatic behaviour (N = 198/246, 80%) rather than manipulative experiments (N = 48/246, 20%), providing an important natural history base from which to work but little evidence on the mechanistic and functional drivers of deimatic behaviour. In the following sections we report trends from descriptive accounts. The results from manipulative experiments are discussed in later sections.

(*a*) *History of describing deimatic behaviour*

Deimatic behaviour is no doubt known by indigenous people the world over, but to the detriment of this review we found no modern indigenous accounts. However, we found some evidence of ancient knowledge on snakes with putative deimatic behaviours in images and written accounts. A rattlesnake’s rattle is prominently depicted in a pictograph dated to approximately 1000 CE at the Pony Hills archaeological site, New Mexico (Schollmeyer, 2020). The Brooklyn Medical Papyrus dated 450 BCE, describes the hooding behaviour of the Egyptian cobra (*Naja haja*), scale stridulation of saw-scaled vipers (*Echis* sp.), and sounds of puff adders (*Bitis arietanis*) (Golding, 2020). The earliest written description of deimatic behaviour in the scientific literature we could find is that of Goureau (1841) about *Mantis religiosa* which roughly translates from French to: "*she raised her long corselet vertically, carried her forelegs forward, as if to catch her prey, half spread her wings and elytra, and moved her abdomen up and down with a rapid movement; during this movement, the sides of the belly rubbed against the inner edges of the wings and elytra, and produced a noise analogous to that obtained by crumpling parchment*" (Goureau, 1841, p. 354). Löhner (1919) described the unken reflex (arched-back posture) in *Bombinator igneus* toads as potentially hypnotising. Varley (1939) published a comprehensive summation of the literature on mantis 'frightening attitudes' citing 29 publications including Roonwal's (1938) account of the 'frightening display' of the mantis *Eremiaphila braueri*. After a three-year residence in the jungles of Trinidad, Crane (1952) published her comparative account of the 'defensive behaviour' of 15 Trinidad mantis species. Blest (1957*a*) published a detailed account of 'protective displays' in some Saturnioidea and Sphingidae Lepidoptera. Throughout the 1970s there was a flourish of work on deimatic behaviour. Maldonado described details of the form, habituation and ontogeny of deimatic behaviour in the double eye-spot mantis (*Stagmatoptera biocellata*) (Maldonado, 1970; Balderrama & Maldonado, 1971, 1973).

In the early and mid 1970s, Edmunds published two extensive descriptions of the 'defensive behaviour' of dozens of African mantises (Edmunds, 1972, 1976) and his influential book *Defence in Animals: A Survey of Anti-predator Defences* (Edmunds, 1974), in which he describes 'deimatic behaviour' across species and contexts. Also in the 1970s, Brodie Jr led a series of publications that described the 'defensive posturing' of the newt *Taricha granulosa* and dozens of salamander species (Johnson & Brodie Jr, 1975; Nowak & Brodie, 1978). Since then, the field has progressed steadily including seminal works on the underwing moths (*Catocala* spp.) in the 1980s and 1990s (Schlenoff, 1985; Sargent, 1990; Ingalls, 1993) and peacock butterflies (*Aglais io*) in the 2000s (Vallin *et al*., 2005, Olofsson, Jakobsson & Wiklund, 2012*b*).

(*b*) *Taxonomic coverage, descriptions, predators and life stages*

The majority of studies describe the deimatic behaviour of salamanders (Urodela), moths and butterflies (Lepidoptera), mantises (Mantodea), and frogs (Anura) (Table S3, Fig. 3) but this is likely to be a poor summary because the concept and the kinds of behaviours included has not been clear or applied consistently. Deimatic behaviour of 16 species has been described multiple times, for example the European cuttlefish (*Sepia officinalis*), peacock butterfly, and promethea silkmoth (*Callosamia promethia*) (Table S3). Words most often used in the descriptions are shown in Fig. 3E. Most studies focused on displays of adults (around 80%), with just a handful of studies on juveniles (Table S3). A few studies covered both adult and juvenile life stages and around 10% provided no information about life stage (Table S3). The vast majority of studies used humans as predators with birds and non-human mammals a distant second and third (Table S3, Fig. 3D).

(*c*) *Primary defence associated with deimatic behaviour and stage of predation sequence deployed*

For most species, deimatic behaviour was associated with a form of camouflage (Fig. 3C) as its primary defence. Exceptions were the salamanders which were considered aposematic except for two *Pseudotriton* Batesian mimics, and the Io moths (*Automeris* spp.) which were deemed putatively aposematic in the literature. Work on the co-evolution of primary defences, deimatic behaviour, and further defences is key to understanding how different defences interact to protect prey.

(*d*) *Multimodality of deimatic behaviour*

About half the studies suggested that deimatic behaviours target more than one sensory mode (Higham & Hebets, 2013) (Table S3). However, most studies focused on behaviours involving movement of large body parts (the wings, body, tail, or head; Table S3, Fig. 3E). Several visual components were reported: movement and body size increase, colour pattern reveal including eyespots, light production (e.g. bioluminescence), and the revealing or highlighting of a weapon. Most studies (~ 65%) involved visual components in addition to movement. We found a few cases of putative Batesian mimicry where posturing alone was thought to be protective. For example, the stick insect (*Oncotophasma martini*) curves its abdomen over giving it the appearance of a scorpion (Robinson, 1968*b*), while the lobster moth (*Stauropus fagi*) caterpillar adopts a spider-like posture (Poulton, 1890). The most common incorporation of Batesian mimicry was in the reveal of eyespots (18 Lepidoptera (especially Saturniidae: *Automeris*), two manitses, one cuttlefish and one frog]. Only about one quarter of the studies included a focus on auditory, vibrational or olfactory components and around 40% reported a gustatory or olfactory component (Table S3). It is unclear whether visual components are more commonly associated with deimatic behaviour or just more often studied (Rowe & Halpin, 2013).

(*e*) *Speed and duration of deimatic behaviour*

The movement involved in deimatic behaviour may be important for its protective value (Holmes *et al.*, 2018) but speed and duration were rarely measured. We found no clear information on the speed of state change (rise time) between resting and deimatic behaviours. One exception was for the common octopus (*Octopus vulgaris*), which initiated changes to its visual appearance in 270 ms and completed a dramatic colour pattern and skin texture change in 2 s using its capacity for rapid neural polyphenism (Hanlon, 2007; Hanlon & Messenger, 2018). The European cuttlefish initiates dramatic changes in appearance over a similar time frame, and varied these responses across three different species of teleost fish predators (Staudinger, Hanlon & Juanes, 2011). In other taxa, display duration varied enormously among species from milliseconds to more than 30 min (Table S3). In the most extreme case a mantis held its pose for 6 h while sharing a cage with a predatory bird (Maldonado, 1970). Deimatic behaviours were described as sustained and/or rhythmical (repeated) (*sensu* Blest, 1957*b*), around half the studies report on sustained behaviours, around 30% on rhythmical and 15% on behaviours that have both sustained and rhythmical elements. We found no reports describing movements that were performed only once and thus were neither sustained nor rhythmical.

(*f*) *Stage of predation sequence in which deimatic behaviour is performed*

Although deimatic behaviours are thought to be performed during approach by a predator in order for prey to be able to escape, only about 20% of studies reported deimatic behaviour solely during the approach phase, while roughly half reported behaviours during subjugation, and about 10% reported behaviours during both phases. These suggest that prior assumptions about deimatic behaviours being deployed only during the approach phase may be unfounded, and are consistent with our definition of deimatism as performed “during approach or subjugation”. However, our ability to draw conclusions is limited because around half of all studies (134/246, 54%) used humans as ‘predators’ to poke, drop or otherwise disturb prey to evoke deimatic behaviour. Thus, it is possible that against natural predators deimatic behaviour may be performed at an earlier stage. A key hypothesis to test is that ‘defended’ species are more likely to display during subjugation whereas ‘undefended’ species display during approach. To understand the evolution of deimatic behaviour, it is critical that an ecologically appropriate stimulus is used (see Section VIII.2).

(3) Potential deimatic behaviours

Confusion as to which behaviours are deimatic became obvious from our survey of the literature. Common sources of ambiguity included defensive spray liquids, body inflation, bioluminescent signals, alarm calls, vibrations, and electrical emissions. Given this uncertainty, we briefly discuss these cases below and attempt to clarify the information required to include or exclude them as deimatic, which will mostly depend on the receiver's response.

(*a*) *Defensive sprays*

Edmunds (1974) described defensive sprays as retaliatory defences but the posturing before the spray, such as that of a skunk, as deimatic. Skunks (Mephitidae) squirt strong-smelling liquid at their attackers from glands (Medill, Renard & Larivière, 2011; Fisher & Stankowich, 2018) and reflexive bleeders like horned lizards (*Phrynosoma* spp.) squirt blood at their attackers (Sherbrooke *et al.*, 2001). More harmful sprays include the hot, caustic, liquid sprays of bombardier beetles, stinging peppermint stick insect (*Megacrania batesii*) sprays, and the entangling toxic 'glue' shot by termites (Eisner, 1970; Eisner & Adams, 1975; Eisner, Yack & Aneshansley, 2001*b*; Eisner *et al.*, 2001*a*; Dossey, 2011). Interestingly, bombardier beetles and skunks have warning colours as their primary defence, whereas peppermint stick insects and horned lizards use crypsis. We hypothesise that posturing and/or non-harmful sprays are deimatic in that they have an aversive effect when initially encountered and then, on subsequent encounters, have an aposematic effect. The distinction lies in whether the posturing before sprays are employed has a deimatic effect and whether spraying the predator qualifies as retaliation (*sensu* Edmunds, 1974) rather than deimatism, but no clear line has yet been drawn. Future work could focus on the effect of posturing and the degree of physical harm done to the attacker during the spraying behaviour to disentangle these defences.

(*b*) *Body inflation*

Body inflation, using gases or liquids, occurs in many species, including frogs in which it is considered part of their deimatic behaviour (Martins, 1989). Body inflation is also used by many reptiles and fish in which it has not been described as deimatic *per se*, but is considered defensive (Badiane *et al.*, 2018). Pufferfish (Tetraodontidae) inflate their bodies with the added effect of raising spines, which is assumed to make them more difficult to bite and/or swallow, but the inflation also may elicit an aversive response qualifying this behaviour as deimatic (Wainwright & Turingan, 1997). Similarly, during their deimatic behaviour cephalopods use 'sustained hyperinflation'; this may interfere with their circulation hinting at a measurable cost to performing this behaviour (King & Adamo, 2006). It has been suggested that their inflation in response to a perceived threat could have a deimatic effect, be an aposematic signal, highlight weapons, and/or mechanically impede predation. Whether the inflation process deters an attacker owing to induced fear of the inflated animal suddenly looming, or whether the resulting large body size exceeds the gape limit of the attacker is untested.

(*c*) *Electrical discharge*

Electrical signals are surprisingly ubiquitous in nature (England & Robert, 2021). The electrical discharges generated by numbfishes (Narcinidae), electric rays (Torpedinidae), and electric eels (*Electrophorus electricus*) could be deimatic behaviours. They are not typically described as deimatic in the literature perhaps because it is mechanism focused (Sheridan, 1965; Mellinger *et al.*, 1978; Macesic & Kajiura, 2009). Electrical signals are, however, known to function in antipredator contexts in some species. Macesic & Kaijura (2009) showed that the lesser electric ray (*Narcine brasiliensis*) generates electric organ discharges against simulated predatory attacks. As there is still limited research into the use of electrical discharges as a defence, it is currently unclear whether this should be considered retaliation to make the prey less profitable, or whether it is a deimatic display. It may be speculated that this could be context dependent, as the same charge could, for example, simply startle a larger predator, whereas it could stun a smaller predator. The mechanism of defence could therefore be related to both the type of predator and the type of prey (for example juvenile lesser electric rays are capable of weaker discharges than adults), however further work is needed to determine whether retaliation and deimatic behaviour can be separated in this example. Behavioural studies on predator responses to electrical discharges are needed to understand how they fit among antipredator defences especially in terms of retaliation and aposematism.

(*d*) *Bioluminescence*

Bioluminescence, the chemical production of light by living organisms (Kahlke & Umbers, 2016), is used in anti-predatory contexts and can resemble deimatic behaviour (Stanger-Hall & Oakley, 2019). Bioluminescence can be aposematic, as chemically defended adult and larval fireflies elicit avoidance learning in anurans (De Cock & Matthysen, 2003), bats (Leavell *et al.*, 2018), mice (Underwood, Tallamy & Pesek, 1997), and spiders (Long *et al.*, 2012), or it may ‘frighten’ potential predators (Lloyd, 1973). Esaias & Curl (1972) hypothesised that dinoflagellate (*Gonyaulax* spp.) bioluminescent flashes function as a protean display “*which startles or confuses the copepod*” (p. 901) suggesting both fleeing and deimatism (Humphries & Driver, 1970; Edmunds, 1974; Driver & Humphries, 1989). Similarly, lantern fish (Myctophidae) emit bioluminescent flashes in response to their predators, southern elephant seals (*Mirounga leonina*), which result in longer prey capture attempts (Goulet *et al.*, 2020). Where feasible, direct tests of predator responses could identify examples of deimatism in bioluminescent systems.

(*e*) *Alarm calls and burglar alarms*

It is currently unclear whether ‘alarm calls’ (alerting conspecific receivers to a potential danger), or ‘burglar alarms’ (attracting the attention of an enemy’s enemy) should be considered as deimatic behaviour (Burkenroad, 1943; Haddock, Moline & Case, 2010; Hanley & Widder, 2017). Vervet monkey (*Chlorocebus pygerythrus*) predator-specific alarm calls signal the presence of a predator to conspecifics (Cheney & Seyfarth, 1981). However, it could be speculated that the surprise (or ‘startle’) caused by an unexpected alarm call may also directly deter predators if the prey’s call releases a threat-avoidance response. In response to copepod (*Acartia tonsa*) attack some dinoflagellates (*Pyrodinium bahamense* and *Lingulodinium polyedrum*) use bioluminescent flashes as ‘burglar alarms’ to draw in copepod predators, but such flashes may also act to release a rapid threat response in the copepods directly (Hanley & Widder, 2017).

(*f*) *Vibrations*

Substrate and airborne signals may constitute vibratory deimatism if they cause a threat-avoidance response in an attacker. In many species disturbance-induced vibration increases handling time and decreases predation risk (Bauer, 1976; Smith & Langley, 1978; Masters, 1979; Buchler, Wright & Brown, 1981; Lewis & Cane, 1990; Guedes *et al.*, 2012; Low, 2012), although some studies have found no evidence for protection against predation

(Gotch, 1997; Corey & Hebets, 2020). The studies that showed little protective value tested vertebrate predators, which may not be the target receivers. For example, vibrations that can successfully reduce parasitoid attacks (Low, 2012), and vibrations by spiders (Corey & Hebets, 2020) could be deimatic to predatory piratid spiders but useless against birds or predacious damselflies. However, further work is needed to determine definitively whether these actions cause a threat-avoidance response in an attacker (and therefore are deimatic), or whether the vibrations function to reduce attack by other mechanisms, such as making the prey more challenging to handle.

(*g*) *Moth clicks*

Moth clicks, produced by tymbalation and stridulation (Corcoran & Hristov, 2014), have been attributed many functions including startling predators and sonar jamming, and are performed by both chemically defended and undefended species. Fullard & Fenton (1977) suggested that while most sound-producing tiger moths in southern Ontario respond to simulated bat echolocation calls with sound, others do not, and must be physically handled to elicit defensive sound production. Playback experiments suggested that substrate-gleaning bats are deterred by contact-elicited tiger moth clicks (Stoneman & Fenton, 1988; Bates & Fenton, 1990). However, flight room interactions between wild bats and live tiger moths suggest that while they click in response to being handled by a gleaning bat, in the wild sound-producing tiger moths suffer similarly high mortality as silent species (Ratcliffe & Fullard, 2005). Hristrov & Conner (2005) showed that naïve big brown bats (*Eptesicus fuscus*) are repelled by tiger moth clicks (four species of Arctiidae), but that they rapidly learn to ignore the clicks unless the prey is also unpalatable. An intriguing, but untested, possibility is that these sounds are more readily associated with chemical defence precisely because they are deimatic, under the assumption that a negative signal can be more easily associated with a negative consequence than can a neutral or positive acoustic signal (Guilford & Dawkins, 1991; Ratcliffe & Fullard, 2005; Ter Hofstede & Ratcliffe, 2016).

(*h*) *Rattles*

The antipredator strategy of rattlesnakes, porcupines, and other animals that ‘rattle’ may include deimatism (Edmunds, 1974). In rattlesnakes, the sound is produced by the impact of keratin scales against each other (Gans & Maderson, 1973), while in porcupines the sound is from knocking quills together and is made when a threat is perceived (Edmunds, 1974). Data on how naïve and experienced predators respond to rattles are required to determine their function. Presumably many predators can learn to associate the sound with a threat and thus rattles likely have an aposematic function, while in naïve individuals the sound may have a deimatic effect.

(*i*) *Facultative flatulence*

Herring (*Clupea harengus*) facultatively force air through the anus in an antipredator context (Wahlberg & Westerberg, 2003). Air is apparently actively gulped at the water surface and then later expelled from the herring’s anus when they are under duress. The resultant sounds and bubbles may function as an acoustic and optic screen to confuse a pursuing predator (Wahlberg & Westerberg, 2003)

The use of facultative flatulence in fish is still poorly understood, and it may be the case that it is used more often in the context of inter-individual communication than defence (Wilson, Batty & Dill, 2004). However, it may be speculated that rapid bursts of bubbles could trigger reflexive responses in a predator, such as avoiding a crashing wave. Therefore, facultative flatulence could have the potential to be a deimatic defence, but further work is needed to determine definitively whether this is the case.

IV. EVOLUTION OF DEIMATIC BEHAVIOUR

Understanding the evolution of complex traits like deimatism is challenging, especially because behaviours are difficult and costly to measure. Evolutionary models are required to provide explicit hypotheses for experimental testing. Where data are available, comparative approaches also provide important opportunities to generate and test hypotheses on the evolution of deimatic behaviours. This can be done by establishing when and in what lineages deimatism has evolved or been lost, and what ecological factors may be associated with its evolution.

(1) Evolutionary pathways to deimatism

Umbers *et al.* (2017) formally proposed two potential pathways for the evolutionary origins of deimatic behaviour; the 'defence-first' and 'startle-first' hypotheses. The defence-first hypothesis suggests that the acquisition of some form of chemical defence or weapon precedes the acquisition of a deimatic behaviour (itself also a defence). Under this hypothesis, the acquired defence facilitates the evolution of, for example, a conspicuous aposematic colour signal, the costs of which can be offset by concealment, revealing it only when the prey perceives a threat. The defence-first hypothesis can also include revealing or highlighting weapons, possibly from the ritualisation of counter-attack behaviour (Lieshout, Elgar & Wilgenburg, 2005). For example, during their deimatic behaviour, many mantises highlight their large raptorial forelimbs which are used in prey capture and retaliation (O'Hanlon *et al.*, 2018; Vidal-García *et al.*, 2020). However, unless further defences are lost upon the evolution of deimatic behaviour, the numerous examples of deimatism not obviously associated with a chemical or weaponry defence require other evolutionary routes.

The startle-first hypothesis suggests that the act of performing the behaviour itself has protective value and can allow the evolution of further defences. Given our objections above concerning the use of the word ‘startle’, perhaps ‘behaviour-first hypothesis’ is a better name. Vidal-García *et al*. (2020) found indirect evidence to support this behaviour-first hypothesis, as they reported that wings were used by 29 of 31 displaying mantis species including 11 species in relatively basal phylogenetic positions that lacked hidden colours. In a behavioural study, Holmes *et al*. (2018) showed that movement alone can be protective but that a combination of colour and movement increased survival. Similarly, using a robotic moth and wild black-capped chickadees (*Poecile atricapillus*), Kang, Zahiri & Sherratt (2017) showed that prey movement alone, without other defensive components like colours, can elicit responses consistent with responses to deimatic behaviour in birds.

Flash behaviour – repeated signalling while fleeing that inhibits predator pursuit – could represent an intermediate step in either the startle-first or defence-first trajectories; after signals are obtained but before they are used in deimatic behaviour (Umbers *et al.*, 2017) (Table S2). In their study of the *Pleurodema* frogs, Faivovich *et al*. (2012) mapped flash behaviour and deimatic behaviour on a phylogeny and suggested that deimatic behaviour occurs in more derived species and flash behaviour in more basal species. However, it is unclear how flash behaviour and deimatic behaviour were defined and quantified (Faivovich *et al.*, 2012). Further comparative analyses that map the evolution of flash behaviour and deimatic behaviour are needed to test this hypothesis.

(2) Modelling the evolution of deimatic behaviour

Theoretical models of deimatic behaviour have so far been mostly descriptive, qualitative arguments, although mathematical models of related phenomena have been developed. Theory in this area is necessary to formalise arguments and make testable predictions. Below we highlight key considerations when developing mathematical models of deimatic behaviour.

The evolution of antipredator defences is best considered as a co-evolutionary process, in which any adaptation in prey that reduces their vulnerability to predation also affects the nature of selection on predators and *vice versa* (Dawkins & Krebs, 1979; Abrams, 2000). A self-consistent co-evolutionary model (Houston & McNamara, 2006) of the evolution of deimatic behaviour therefore requires an understanding of the nature of selection on *both* predators and prey, with the aim of characterising their plausible co-evolutionary states (such as a mutual equilibrium and/or stable limit cycle; Otto & Day, 2011). Importantly, deimatism may not necessarily involve co-evolution. It might simply be a result of the 'wiring' of the attacker's brain and cognitive processes that developed in other contexts, thereby requiring no co-evolution and no learning. However, the fitness consequences of these processes should be considered for both the attacker and the displaying individual. Several co-evolutionary models of predator–prey interactions have been developed (Abrams, 2000; Mougi & Iwasa, 2010; Tien & Ellner, 2012; Bateman, Vos & Anholt, 2014), but we are not aware of any developed specifically for understanding the evolution of deimatic behaviour.

Deimatic behaviours are typically not primary defences but rather back-up defences deployed at the prey's discretion (Umbers, Lehtonen & Mappes, 2015). This can be formalised in modelling terms by viewing deimatic behaviours as one defence in a sequence of antipredator defences (Fig. 2). If the primary defensive strategy is highly effective in preventing predation, this may impede selection on further defences that are invoked only when the primary defence fails (Britton, Planqué & Franks, 2007; Wang *et al.*, 2019). Such 'strategy blocking' may lead to cross-species associations between primary and subsequent defences (such as deimatism) mediated by factors that affect the upper limit on the primary defence, such as body size (Kang *et al.*, 2017) (for further discussion of body size, see Section IV.4*a*). From an evolutionary perspective, perhaps the most fundamental question is: *what is the selective advantage for a predator responding to deimatic behaviour*? It is a behavioural response that comes at the cost of energy expenditure and opportunities missed, so what are its benefits? If it is a rapid response to a potential threat (Simons, 1996), it may save the life of the receiver, or prevent injury. Signal detection theory quantifies the optimal trade-off between type I error (such as twigs treated as snakes, 'false alarms') and type II errors (snakes treated as twigs, 'misses') (Leavell & Bernal, 2019). If the costs of mistaking a snake for a twig far outweigh the costs of mistaking a twig for a snake, then a conservative threshold with a high false alarm rate would be optimal, even when the likelihood of the stimulus coming from a true threat is small (Castellano & Cermelli, 2015). While signal detection models identify the optimal response under uncertainty, speed–accuracy trade-offs need to be included (Chittka, Skorupski & Raine, 2009). If the stimulus is sudden, such as that caused by dangerous events like the rush of a potential predator or a tree falling, then quick action will be favoured over careful deliberation. As Janzen *et al.* (2010, p. 11659), puts it "*pause a millisecond to ask whether that eye belongs to acceptable prey or to a predator, you are likely to be—and it takes only once—someone's breakfast*".

Models that combine signal detection and speed–accuracy trade-offs have been developed and take the form of sequential sampling models in which additional inspections to gain more information come at a cost (e.g. Getty, 1996; Abbott & Sherratt, 2011). Complementary models have separated the two processes almost entirely. For example, motivated by empirical evidence, Trimmer *et al.* (2008) represented mammalian brains as having two decision-making systems, both Bayesian in nature but acting at different speeds. The first quick-but-inaccurate thalamic decision is assumed to be based on a one-off application of signal-detection theory involving a simple (and conservative) threshold for treating stimuli as threats, whereas the slow-but-accurate cortical decision is based on the sequential probability ratio test (SPRT) as more evidence governing how to act is gathered over time (Wald, 1945; Castellano, 2015). Natural selection appears to have favoured an ‘act now, think later’ response to certain stimuli because only quick action can save the observer’s life and, like many behaviours, this response can be exploited by potential prey. Modelling can help clarify why the responses are rapid, and how they continue to be maintained despite a high propensity for false alarms.

Finally, there are other features of the response to deimatic behaviour that can be understood using mathematical models. For example, the prior presentation of a stimulus associated with an undesirable event tends to generate a more vigorous response to an unrelated stimulus (Brown, Kalish & Farber, 1951); a result readily understood through Bayesian conditioning models (Bach, 2015). Likewise, habituation to a stimulus can be modelled through Bayesian learning in which the conditional probability of the signaller being a threat is updated over time as more information is gained. A related set of questions revolve around why some species’ deimatic behaviours inhibit would-be predators long after the initial reflex-like response. Of course, even if rapid habituation occurs under experimental conditions, then it may not be realised under more natural conditions. In particular, it is possible that some observers and/or signallers would flee following a deimatic display if it they were able to do so. Even if only a small proportion of attackers or signallers respond in this way, it can still be selected for as a last-resort defence even if there is no long-lasting inhibitory effect from the display.

(3) Comparative analyses and the evolution of deimatic behaviour

Crane (1952), Edmunds (1972, 1976), Blest (1957*b*), and Brodie (1983) on mantises, moths and salamanders were the first to compare the diversity and systematic patterns of deimatic behaviour among species. The detailed descriptions and observations of deimatic behaviour now available allow phylogenetic analyses (Vidal-García *et al.*, 2020) to investigate when and why deimatism evolves and is lost. Kang *et al*. (2017) assessed the evolution of hidden hindwing colours in erebid moths (Noctuoidea: Lepidoptera) assuming that their hidden colours are used in deimatic behaviour. Their results suggested that basal erebid moths lack hidden colours, that hidden colours are a derived trait, and that it has evolved multiple times across the family. In phylogenetically controlled analysis of hidden colours in a further five insect taxa, Orthoptera, Mantodea, Phasmatodea, Saturniidae and Sphingidae, Loeffler-Henry, Kang & Sherratt (2019) found evidence for the repeated evolution of hidden contrasting colours dozens of times among these five groups. A comparative analysis by Bura, Kawahara & Yack (2016) found that what they termed acoustic startle defences (Dookie *et al.*, 2017) have evolved multiple times in caterpillars from multiple lepidopteran subfamilies in Sphingidae and Saturniidae. They found that short clicking sounds were typically followed by regurgitation while longer, louder sounds were not and thus the short clicking sound form seems to be associated with the expulsion of chemical defence. The ancestral state reconstruction of deimatic displays in 58 mantis genera by Vidal-García *et al*. (2020) included behavioural data as well as descriptions of colour patterns and body size on the presence and absence of deimatic behaviour. Their findings suggest that some form of camouflage without deimatic behaviour is the ancestral state in mantises, and that it has evolved at least four times across the Mantodea (Vidal-García *et al.*, 2020). They also show that deimatic behaviour has evolved in species without any associated colour patterns and that inclusion of behavioural data is important. By contrast, placing data from 25 of Brodie's salamander descriptions into a phylogenetic context shows gains, losses, and variability of deimatic behaviour, but deimatic behaviour is found in the most basal lineages included in the tree (Fig. 4). These studies all confirm the conclusions of the earlier comparative studies, that deimatic behaviours are frequently gained and lost as a lineage diversifies.

The processes driving gains and losses of deimatic behaviour are unclear. In praying mantises there is a hint that deimatic behaviour evolved in response to the evolution of birds, appearing roughly 60 million years ago (Vidal-García *et al.*, 2020). So far, no phylogenetic comparative studies have included the required data to test hypotheses on ecological drivers such as predator diversity, population density, habitat type and activity time, but such analyses would make a valuable contribution to elucidating the evolutionary timing and ecological correlates of deimatic behaviour.

(4) Traits associated with the evolution of deimatic behaviour

Several hypotheses have been proposed suggesting that the evolution of deimatic behaviour is related to body size, degree of unprofitability, and phenology.

(*a*) *Deimatic behaviour and body size*

The literature provides mixed support for the hypothesis that larger species are more likely to perform deimatic behaviours. Kang *et al*. (2017) suggested that hidden colours are more common in large species than in small species of Erebidae moths. In a taxonomically broader study, Loeffler-Henry *et al*. (2019) also found evidence of a positive correlation between body size and hidden colouration for four insect taxa (Orthoptera, Phasmatidae, Mantidae, Saturniidae) but not for Sphingidae. More nuanced still, particular colours may be correlated with body size. Emberts *et al.* (2020) studied 26 species of leaf-footed bugs (Coriidae) and found an association between large size and deimatic behaviour only in species with white hidden patches, but not in those with red/orange patches. These studies suggest that certain colours of signals revealed by deimatic behaviour are more common in larger species but do not address whether deimatic behaviour itself is more common in larger species. However, a phylogenetically controlled analysis on 58 praying mantis species that included behaviour, sound production, and hidden colours found no support for the hypothesis that larger species were more likely to exhibit deimatic behaviour (Vidal-García *et al.*, 2020). Discrepancies between this study and that of Loeffler-Henry *et al*. (2019) are likely due to differences in the sizes of species sampled. Some deimatic species lacked hidden colouration suggesting that a relationship between the presence of hidden colours and size does not extend to deimatic behaviour *per se*.

If larger prey have deimatic behaviour because they are more likely to be attacked due to their profitability as a larger meal, then why do so many deimatic behaviours include an apparent body size increase? One hypothesis is that it is not their profitability, but their conspicuousness that puts larger species under greater predation pressure (Pembury Smith & Ruxton, 2021). If this is true, then appearing to become larger only when performing a deimatic behaviour would lower predation risk only if the behaviour was performed once the prey had already been detected. One species which may be using this defence is the European cuttlefish. Underwater trials with young laboratory-reared cuttlefish released into natural habitats demonstrated that predatory groupers (*Serranus cabrilla*) ceased their attack sequence when the cuttlefish rapidly deployed their deimatic body pattern (Fig. 1I) while flattening their body to create the illusion of a larger body size. When this deimatic behaviour was not deployed, attacks continued and some cuttlefish were eaten (Hanlon & Messenger, 1988).

Additionally, larger prey may be more effective at confusing predators or eliciting the looming reflex in receivers during deimatic behaviour (see Section II.7*b*). Alternatively, an increase in size could be related to making the prey more challenging to consume, particularly if the increased size exceeds the maximum gape size of the predator. New theory and further research are needed to determine how body size and deimatic behaviour interact considering trophic level, predator diversity, and other ecological factors.

(*b*) *Deimatic behaviour and prey profitability*

Many textbooks suggest that deimatic behaviour is performed by 'undefended' species and is therefore a 'bluff'. We disagree with this description for two reasons. One, we argue that deimatic behaviour itself has protective value and therefore cannot be a bluff, and two this stands regardless of the presence of any further defences such as repellent tastes (Rowland, Ruxton & Skelhorn, 2013), toxins (Barnett *et al.*, 2012), weapons (Speed & Ruxton, 2005), protean escape (Edmunds 1974), and impenetrable armour (Wang *et al.*, 2018). In the venomous cottonmouth snake (*Agkistrodon piscivorus*) the use of deimatic behaviour has been found to be a reliable indicator of an individual's willingness to strike (Glaudas & Whine, 2007). Beyond this we are not aware of any formal studies testing what drives or correlates with deimatic behaviours and the presence of further defences. The main challenge is defining ecologically relevant unprofitability and a model taxon.

(*c*) *Deimatic behaviour and phenology*

Kim *et al.* (2020) compiled data on colour, phenology, and abundance for 1,568 macro-lepidopteran species on three continents (Asia, Europe, and North America) and found that species with hidden contrasting colours that are putatively used in deimatic behaviour appear later in the season than the species with other colour defences. This finding is interesting as it may be expected that deimatic behaviour would be most effective against naïve predators, and therefore would be most protective earlier in the season. However, it could be that a protective effect against naïve predators may be quickly diluted by predator learning. Thus, the fitness benefit of appearing early in the season may not be significant because this protective effect does not contribute significantly to the survival of adult insects (until they reproduce). On the other hand, a protective effect through mimicry may remain stable because predators' avoidance learning remains for longer and more consistently (and perhaps reinforced continuously through their experience with various aposematic prey).

Some species with deimatic behaviours may gain protection because they reveal a signal that is a Batesian mimic of defended species. This could be an effective defence if predators generalise signals or if those signals are highly effective against naïve predators. If species with deimatic behaviours derive a selective advantage by delaying their activities until local predators have learned to avoid aposematic signals, it would be interesting to test how this fits into mimic–model systems in Batesian mimicry theory (Waldbauer, Sternburg & Maier, 1977).

V. ONTOGENY OF DEIMATIC BEHAVIOUR

Juveniles and adults differ in important ecological and morphological ways and thus may employ different defences. However, ontogenic changes in the presence and absence of deimatic behaviour, and more subtle differences in their performance during development, are only known for multiple life stages in a few species (Table S4).

In animals that undergo 'complete' metamorphosis, the differences between juveniles and adults may require different defensive strategies due to differences in mobility, habitat, and diet. Holometabolous insects provide many examples of deimatic behaviour at only one life stage, and we found no descriptions of deimatism for both larval and adult life stages (Table S4). Lepidopteran larvae (caterpillars) provide excellent examples of deimatic behaviour as juveniles but the presence of deimatic behaviours in their adult forms is often unknown. However, in peacock butterflies the reverse is true: adults use deimatic behaviour, whereas we found no evidence of deimatic behaviour in their caterpillars. Ambystomid salamanders also undergo a dramatic metamorphosis, only after which do they exhibit deimatic behaviour. In Anderson’s crocodile newt (*Echinotriton andersoni*), aquatic larvae do not posture, but just one day after they reabsorb their gills terrestrial juveniles can perform an extreme version of the deimatic behaviours seen in mature adults, in which they can bring their ribs forward at an angle of 90° to their spine to pierce the skin (Brodie, Nussbaum & Digiovanni, 1984). The posturing behaviour could be deimatic, with the protrusion of ribs perhaps preparation for retaliation, or a deterrent by exceeding a predator’s gape. Such differences between adult and juvenile defences may reflect adaptations to their different aquatic and terrestrial habitats.

For animals that undergo relatively gradual changes in morphology over their life stages, data on changes in deimatic behaviour with ontogeny were available for some mantises, orthopterans, and squid (Table S4). The double eye-spot mantis (*Stagmatoptera biocellata*) uses crypsis as its sole method of predator defence in the first and second instar, whereas intermediate instars (3–7) use both crypsis and deimatic behaviours, and adults primarily use deimatic behaviours (Balderrama & Maldonado, 1973). The authors suggested that relying on deimatic displays may be too risky when individuals are small and relatively easy prey, and that their stick-like morphology may allow camouflage. Adults with their more prominent head may prevent them from mimicking sticks as effectively, reducing their camouflage and increasing pressure for the evolution of deimatism as a secondary defence. In the mantis *Angela guianensis*, adults use deimatic wing displays, while juveniles rely on running and dropping. In the Texas unicorn mantis (*Phyllovates chlorophaea*) and Peruvian shield mantis (*Choeradodis rhombicollis*) juveniles also run and drop in defence. The deimatic behaviour of adult *P. chlorophaea*, on the other hand, reveals yellow and black bands on their dorsal abdomen, while that of adult *C. rhombicollis* includes rearing up and posturing towards the attacker. Juveniles also rely on fleeing in several orthopterans. In the katydid *Scorpiorinus fragilis* (Pseudophyllinae), nymphs rely on escape while adults reveal their yellow dorsal abdomen in response to touch by lifting their wings which produces a stridulatory sound (Robinson, 1969). Adults of the stick insect, *Metriotes diocles* raise their wings in a deimatic display while nymphs tend to drop and use thanatosis to avoid consumption (Robinson, 1969). Differences during ontogeny have also been reported in the defensive behaviour of two species of squid, Atlantic brief squid (*Lolliguncula brevis*) and longfin inshore squid (*Doryteuthis pealeii*) (York & Bartol, 2016). Paralarvae (hatchlings) of *D. pealeii* were more likely to use transparency in response to predators whereas juveniles and adults of *L. brevis* were more likely to perform deimatic behaviours. It is possible that relying on crypsis alone for adults is too costly or risky, or that deimatic behaviour in juveniles is less effective, or perhaps both. By contrast, juvenile cottonmouth snakes (*Agkistrodon piscivorus*) are more likely than adults to use deimatic behaviour (Glaudas, Winne & Fedewa, 2006). A possible explanation is that adult cottonmouths may face a sufficiently low predation risk that the energetic costs of deimatic behaviour are not justified. Together, these findings suggest a species-specific use of deimatic displays at different life stages.

Changes in deimatic behaviour across development can be more subtle than simple presence or absence. For example, in European cuttlefish, hatchlings, juveniles and adults use different body patterns and postures as deimatic displays (Hanlon & Messenger, 1988). Similar examples of subtle changes in deimatic behaviour during development have been observed in the mountain katydid (*Acripeza reticulata*). Subadults have orange and black intersegmental abdominal membranes which are visible when they move (Table S4). Adults, by contrast, have large mottled brown wings which completely hide their red, blue, and black striped abdominal surface. Umbers & Mappes (2015) found that when performing deimatic behaviour, subadult mountain katydids held their position for longer than adults, perhaps because they lack the tough wings of adults. Lacking tough wings may mean juveniles rely more on their deimatic behaviour and the aposematic signal it reveals which could select for longer display times (Baker, 2019). Because subadults lack wings and therefore cannot fly, their extended display may compensate for their reduced opportunity to escape. By contrast, the Western Australian katydid (*Mygalopsis marki*) develops auditory deimatic behaviour very early in life. Both adults and nymphs stridulate, producing a sound within their head capsule, and this behaviour is maintained throughout ontogeny despite major morphological changes (Bailey & Sandow, 1983), however nymphs are more likely to attempt to escape during the early stages of the predation sequence and stridulate when caught, whereas adults posture while stridulating when faced with a predator. This example may suggest that the constraints on deimatic behaviours involving visual signals and auditory signals may vary, and may arise at different stages across ontogeny.

The level of cognition involved in prey display performances is mostly undocumented but there is some evidence that individuals improve their displays as they develop. Sunbitterns (*Eurypyga helias*) are large birds that reveal eyespots on their wings when threatened. Thomas & Strahl (1990) described young sunbitterns practicing their wing displays from seven days old and performing full wing displays from 12 days old until they left the nest two to three weeks later. They observed nestlings displaying to falling leaves and butterflies, perhaps mistakenly or instinctively. These results may suggest that the risk of drawing attention to themselves on the nest before they can fly is outweighed by the benefit of mastering the behaviour before fledging, a hypothesis for future testing.

Taken together, the available evidence seems to support the view that deimatic behaviours are more likely to be found in adult animals, but whether this is a research bias or is biologically important is unclear. Body size could be a factor driving the presence and absence of displays at different life stages (see Section IV.4*a*), but this and alternative explanations such as differing niches or activity levels remain to be tested.

VI. CAUSATION OF DEIMATIC BEHAVIOUR

Tinbergen (1963) described causation as the physiology of behaviour, encompassing both the underlying molecular, physiological and cognitive processes, now more commonly called mechanisms. We summarise what is known about triggers that release deimatic behaviour, and special mechanisms by which the behaviours are performed. Predator cognition and behaviour drive the evolution of deimatic behaviour and we discuss the putative psychological mechanisms involved (Fawcett, Marshall & Higginson, 2015).

(1) Releasers of deimatic behaviour

Deimatic behaviours may be released by being touched, hearing a sound, detecting a smell, or seeing a visual signal (Table S3). Experimental evidence from studies using ecologically relevant predators is rare, with most data coming from experiments where predation is simulated by humans. Triggers in some sensory modes may be more likely to release deimatic behaviour than others, more likely to release different components of deimatic behaviour, and/or release different levels of intensity. In some katydids and mantises most individuals perform their deimatic behaviour in response to tactile rather than visual stimuli, and more invasive stimuli evoke more intense displays (Umbers & Mappes, 2015; O'Hanlon *et al.*, 2018). Maldonado (1970) experimentally investigated the effects of visual and tactile triggers on mantises. When visual cues were obliterated by covering the eyes, tactile cues still released the full display, however, a visual releaser resulted in a longer display. More work needs to be done to determine which cues, signals, and their components are most effective in releasing deimatic behaviour. Mechanistic and sensory constraints, including noise, probably determine the type of stimuli prey respond to and the fitness consequences of their responses (Cooper & Blumstein, 2015).

(2) Mechanisms of components of deimatic behaviour

Deimatic behaviour can target any sensory mode although most work has focused on visual components. We assume many of the physiological and psychological mechanisms associated with deimatic behaviour have not evolved *de novo*, but were co-opted from other functions. For example, the muscles used in butterfly flight are presumably the same as those used to move their wings during deimatic behaviour. We note that well-understood pathways present opportunities to measure costs and their evolutionary history.

(*a*) *Visual components: colour, movement, and size*

Many deimatic behaviours reveal colour patterns hidden under wings, legs, fins, bellies, inside mouths, and/or on flaps of neck skin. To date there is no evidence that colours associated with deimatic behaviour are produced *via* mechanisms different from those used in other signals, although some observations suggest that hiding colour patches could reduce maintenance costs. For example, in mountain katydids that have one tegmen missing, abdominal colours are bleached where they are exposed but retained where they are covered (K.D.L. Umbers, personal observation).

Most insect deimatic behaviour includes the movement of legs and/or wings. The mechanisms of movement involved in deimatic behaviour have been directly manipulated in the nervous system of praying mantises. Maldonado (1970) determined that the components of deimatic behaviour performed varied depending on which nerves were severed. A cut between the suboesophageal and prothoracic ganglia resulted in only the head and mouth responding to visual stimuli, and the rest of the body required tactile stimulation to respond (Maldonado, 1970).

The ‘unken reflex’, named after the fire-bellied toads ‘Feuerunke’ (Löhner, 1919), is a proximate cause of deimatic behaviour but little is known about its mechanistic underpinnings. Typically only applied to amphibians, it manifests as a rigid arching or lifting of the body, legs, and/or tail in which ventral surfaces become visible and sometimes body parts are ‘hypnotically’ swayed (Brodie, 1977). For example, Colombian four-eyed frogs (*Pleurodema brachyops*) lift their hind quarters to reveal eyespots and colour patches, and highlight poison glands (Martins, 1989). In some salamanders, deimatic behaviour includes their ribs penetrating the skin in special areas of the integument with poison glands. Whether this is caused by the same process as the posturing is unclear (Brodie, 1977, 1983; Nowak & Brodie, 1978).

Few morphological structures seem to have evolved for use in deimatic behaviour. A promising candidate, however, is ‘hooding’ in snakes (Table S3). During hooding, cobras (*Naja* spp.) use eight muscles and putatively novel nervous rewiring to elevate and protract the ribs, while flattening and expanding the neck (Young & Kardong, 2010; Jara & Pincheira-Donoso, 2015). Other specialised structures may exist and future work beyond traditional model systems will probably highlight other traits.

Cephalopods provide a clear exception to movement of large body parts in deimatic behaviour, with their colour patterns displayed and changed by chromatophores (Langridge, 2009). Chromatophore colour change is controlled by the dispersal and concentration of pigments *via* intracellular innervated radial muscles (Messenger, 2001; Hanlon & Messenger, 2018). The most well-studied cephalopod deimatic behaviour is that of the European cuttlefish, which produce dark rings around the eyes and dark eyespots on the dorsum (Holmes, 1940; Langridge, Broom & Osorio, 2007) (Fig. 1I). Their deimatic pattern is complex, comprising six signalling elements that can be expressed in different combinations: (1) flattened body posture; (2) paling of the skin; (3) paired mantle spots that look like eyes; (4) a dark fin line; (5) a dark eye ring; and (6) a dilated pupil. They can also produce directional displays presenting deimatic patterning only towards the predator and cryptic patterning away from the predator (Langridge, 2006), indicating that their neural mechanisms allow targeted responses.

Movements included in deimatic behaviour are not restricted simply to the performer changing state from resting to displaying, they may continue throughout the performance as re-orienting or rhythmical repetition. For example, during deimatic behaviour mountain katydids reorient their distasteful brightly coloured abdomen towards their attacker (Umbers & Mappes, 2015; Umbers *et al.*, 2019). The peacock butterfly's rhythmic deimatic behaviour involves their wings being opened and closed in succession at a constant rate (Blest, 1957*b*). The devil's flower mantis (*Indolomantis diabolica*) moves its outstretched forelimbs back and forth in a pendulum-like fashion. Many salamanders sway or undulate their tails 'hypnotically' throughout their display. The efficacy of displays with and without repeated movement has not been compared but in many cases rhythmical movements are associated with sound production which adds further complexity (Blest, 1957*b*; Vallin *et al.*, 2005) (Table S3). Rhythmic signals may be much more effective in stimulating the receiver than sustained displays if they avoid sensory adaptation in the predator. Signalling at random time intervals may be more effective still if doing so eliminates synchronous sensory adaptation.

(*b*) *Acoustic components: sounds and vibration*

Sounds (i.e. air and water-borne vibrations) and vibrations (i.e. solid-borne vibrations) are widely used in defence across several taxa (Low, Naranjo & Yack, 2021). We discussed vibrations in the context of deimatic behaviour in Section III.3*f*, and alarm calls in Section

III.3*e*. Here we focus on sounds produced during an encounter with a predator which have been proposed to function in aposematism, jamming echolocation calls, and as deimatic behaviour (see Low *et al*., 2021). Continuous sound production is presumably too costly in terms of conspicuousness or energy (Low *et al*., 2021). One notable exception occurs in cicadas which as a group produce incessant mate-attraction calls *via* tymbalation [the flexing of corrugated regions of exoskeleton (tymbals)] that may have a dual function in aposematism (Simmons, Wever & Pylka, 1971). Cicadas can drive bird predators out of forests both due to the dangerously loud and painful sound, and its disruption to their communication (Simmons *et al*., 1971). Their sound can certainly drive human visitors away (K.D.L. Umbers & J.A. Endler, personal observations).

Sounds used in defence are produced by a huge diversity of body parts or specialised organs (Bura *et al*., 2016; Low *et al*., 2021) – knocking or rubbing body parts together as in stridulation (Bura *et al*., 2016; Rosi-Denadai *et al*., 2018), forced air (Bura *et al*., 2011; Rosi-Denadai *et al*., 2018), percussion, or tymbalation (Ewing, 1989; Dookie *et al*., 2017).

Sound created by 'forced air' is used across animals. Walnut sphinx (*Amorpha juglandis*) caterpillars whistle by expelling air *via* muscular contractions through special sound-producing spiracles on the A8 abdominal segment (Bura *et al*., 2011) and can successfully deter red-winged blackbirds (*Agelaius phoeniceus*) despite having no further defences (Dookie *et al*., 2017). In the walnut sphinx deimatic sounds are loud, sudden, and of longer duration than those produced in other defensive contexts (Low *et al*., 2021). Other caterpillars 'vocalise' when attacked, by forcing air out of their gut (Rosi-Denadai *et al*., 2018; Bura *et al*., 2016). Many reptiles including lizards such as the blue-tongued skink (*Tiliqua scincoides*) (Badiane *et al*., 2018) and the frill-necked lizard (*Chlamydosaurus kingii*) (Perez-Martinez, Riley & Whiting, 2020) also use 'hissing' during their deimatic behaviour by forcing air from their lungs across the glottis, but its effect on predator behaviour has not been assessed in this context.

Deimatic behaviour can include stridulation and rasping sounds, for example when mantises move their wings and abdomens rhythmically (Hill, 2007; Olofsson *et al*., 2012*b*). Hill (2007) showed that *Mantis religiosa* have tooth-studded venation on their hindwings and denticles on their abdomen and the sound is produced as the former are moved over the latter. The peacock butterfly also produces ‘swooshing’ sounds by opening and closing its wings, and ultrasonic clicks audible to rodents and bats by a ‘costal clicker’ on the base of the dorsal side of the forewing (Møhl & Miller, 1976). Orthoptera also have a wide repertoire of defensive stridulatory mechanisms which are performed upon the approach of a predator and function to slow or stop its attack (Bedford & Chinnick, 1966; Robinson, 1969; Maldonado, 1970; Edmunds, 1972). In the katydid *Mygalopsis marki* both adults and nymphs use stridulation produced within the head capsule (Bailey & Sandow, 1983). The nymph usually attempts to escape by jumping or running but if held in the hand, head stridulation is produced.

(*c*) *Olfactory/gustatory components: oozing and regurgitating*

Chemical defences are typically associated with aposematism, which predators encounter if they dare to attempt consumption. They may, however, also appear as components of deimatic behaviour which are released when prey perceive a threat from an attacker during approach or subjugation, and which can cause predators to slow or stop their attack (Fig. 2). Deimatic chemical defences are those released during the behaviour, not those simply present in the organism regardless of an attacker’s proximity. That is, deimatic chemical defences are produced upon attack.

Chemical defences may be oozed, frothed, or foamed from joints and glands during deimatic behaviour, and may have olfactory and/or visual effects on predator behaviour. Amphibians exude chemical defences from glands during deimatic behaviour (Ferraro, Topa & Hermida, 2013) and defensive posturing can enhance the effect (Williams *et al.*, 2000). Fire-bellied toads (*Bombina* spp.) can increase the amount of toxin released through physical pressure on the glands when the back is arched (Bajger, 1980; Choi, Lee & Ricklefs, 1999). During their deimatic behaviour four-eyed frogs (*Physalaemus nattereri*) reveal large black discs on their rumps where bradykinin peptides and correspondingly strong signals of related gene expression are concentrated (Barbosa *et al.,* 2015). Similarly, many salamanders have noxious skin secretions and combine their presentation with various postures to orient the glands and associated secretions towards the predator (Brodie, 1977). Mountain katydids exude droplets of a bitter secretion from the surface of the abdomen when attacked, presumably from glands as yet undescribed, with compounds that originate from their preferred diet of *Senecio* daisies (Baker, 2019), such as senecionines and sceneciophyllines. Some lepidopterans exude noxious chemicals *via* froth which seems to be deimatic behaviour rather than retaliation because they are not shot at the attacker. The saturniid moth *Citheronia brisottii* is a yellow and orange moth with black intersegmental membranes from which newly emerged adult males can expel a tar-like substance (Blest, 1957*a*). Other lepidopteran ‘frothers’ include the arctiine moth *Amerila bubo* which emits a ‘sizzling’ sound from the thorax as it produces an odorous froth from two large vesicles, as well as its congener *A. leucoptera* which displays a bright pink body by spreading its wings and expelling a yellow froth from the thorax when disturbed (Carpenter, 1938).

Regurgitation is almost ubiquitous among insects when they are attacked, and in lepidopteran larvae is also a common accompaniment to acoustic components of deimatic behaviour (Bura *et al*., 2016). Brown, Boettner & Yack (2007) found that defensive regurgitation often preceded or accompanied the clicking sounds produced by the polyphemus moth (*Antheraea polyphemus*) and was an effective deterrent against predators. Similarly, caterpillars of the giant peacock moth (*Saturnia pyri*) produce a chemical secretion from integumental bristles when attacked repeatedly while ‘chirping’ (Bura, Fleming & Yack, 2009). These examples provide some insight into the chemical components of deimatic behaviour but leave many questions unanswered about their proximate mechanisms. In particular, it is currently unclear whether both the regurgitation and noise function as a deimatic defence, or whether the noises produced are deimatic, and the regurgitation consists of toxic secondary plant compounds.

(3) Changes in deimatic behaviour in response to repeated attack

Deimatic behaviours can be highly repeatable – performed the same way by the same individual every time – or can vary among performances. The limited available evidence suggests variability both within and among individuals. For example, over ‘long’ 24-h intervals between repeated attacks, consistency in display intensity varied substantially among individual mountain katydids and were only somewhat repeatable in the magnitude of their displays (De Bona, White & Umbers, 2020). One explanation may be that performing deimatic behaviour is condition dependent, but the proximate cause for this variation requires future research.

Many species increase the intensity of their deimatic behaviour with repeated exposure to stimuli. In simulated sequential, repeated attacks over short intervals (10 s), mountain katydids increased the intensity of their display (used more components) (F. Mourmourakis, S. De Bona & K. D. L. Umbers, unpublished data). Similarly, Brown *et al.* (2007) investigated the response of clicking polyphemus moth caterpillars to different numbers of simulated repeated attacks and showed that the number of clicks per individual increased with attack number. In a different measure, Vallin *et al*. (2005) showed that the second time peacock butterflies were approached by a predator, they displayed when the predator was at a greater distance away than in the first encounter. Increased intensity of deimatic behaviour might increase prey survival if displaying maximally upon first stimulus carries costs (e.g. conspicuousness) or if the prey are protected from sub-lethal investigative predator behaviour by a tough exterior, and may also depend on their perceived certainty or intensity of danger. The degree to which prey are defended may influence their propensity to exhibit deimatic behaviour when repeatedly accosted by potential predators. The chemically defended cottonmouth snake reduces its expression of deimatic behaviours with repeated exposure to human model predators (Glaudas, 2004). However, comparatively less-defended juveniles do so to a lesser degree (Glaudas *et al.*, 2006). Predictions around the mechanisms underlying prey responses to repeated attacks is fertile ground for future theory and experiments.

VII. SURVIVAL VALUE OF DEIMATIC BEHAVIOUR

A limited number of studies have quantified the survival value of deimatic behaviour in the field and the laboratory with respect to prey survival probability (Table S5) and effects on predators (Table S6).

(1) Does deimatic behaviour increase the probability of prey survival?

Ten publications have measured the survival value of deimatic behaviour and/or further signals revealed by them using live prey animals, of which eight were laboratory-based and two field-based (Table S5). Some prey were putatively profitable, others putatively unprofitable (i.e. ‘chemically defended’), and most were insects. The efficacy of visual components, acoustic components, and their combination have all been investigated. Most studies did not address whether the experimental predators were natural predators thus leaving questions about the ecological and evolutionary significance of the results.

(*a*) *Survival value of deimatic behaviour that reveals colour patterns without chemical defence*

Vallin *et al*. (2006) examined the effect of the wing-flicking display with eyespots of the peacock butterfly against wild-caught blue tits (*Parus caeruleus*). Peacock butterflies, which are seemingly palatable to all their known predators, initiated their deimatic behaviour during the predator's approach (average 12 cm distance) and all survived (*N* = 10) (Vallin *et al.*, 2006). Vallin, Jakobsson & Wiklund (2007) found that peacock butterfly visual displays were protective against both blue tits and great tits (*Parus major*), in contrast to those of the larger hawkmoth *Smerinthus ocellatus*. Both insects had eyespots which were revealed on the approach of a predator, however the type of display was different as the hawkmoth *S. ocellatus* protracted its upper wings to show the eyespots then rocked with its legs, while the peacock butterfly continually flicked its wings to hide and reveal its eyespots. Peacock butterflies survived 12/12 blue tit attacks and 9/12 great tit attacks whereas only 5/13 hawkmoths survived blue tit attacks and 1/14 survived great tit attacks. These findings suggest that the type of visual display is more important than the presence of eyespots alone.

Mollusc deimatic behaviour can include a combination of posturing and colour pattern expression *via* chromatophores without a chemical defence. In a field study, young European cuttlefish altered their defensive responses and deimatic behaviour according to predator type and avoided attacks (Hanlon & Messenger, 1988). In a laboratory-based study, Staudinger *et al*. (2011) showed that longfin squid (*Loligo pealeii*) also alter their defence response depending on predator type. Against bluefish (*Pomatomus saltatrix*), a 'pursuit' predator, longfin squid primarily used deimatic behaviours, whereas protean behaviours (erratic escape behaviours, *sensu* Edmunds, 1974) were used against summer flounder (*Paralichthys dentatus*) an ambush predator. Overall, while deimatic behaviours saved the prey's life in 40–64% of interactions, prey were more likely to survive when confronted with predators if they fled rather than performed deimatic behaviours (87–92% survival rate). The authors suggest that deimatic behaviours are not always the most effective strategy but may be employed when prey are unlikely to 'outrun' their predators (Staudinger *et al.*, 2011).

(*b*) *Survival value of deimatic behaviour that reveals colour patterns with chemical defence*

Mountain katydids perform deimatic behaviour: they lift their wings to reveal a brightly coloured abdomen that exudes a *Senecio*-derived secretion (Umbers & Mappes, 2015; Baker, 2019; De Bona *et al.*, 2020). Umbers *et al*. (2019) used a field-based experiment to test whether the survival value of the katydid's display relates to the prior experience of one of their native predators, the Australian magpie (*Gymnorhina tibicen*). In interactions with naïve allopatric Australian magpies, katydids survived 70% of encounters, while only 24% of katydids survived interactions with sympatric predators. During the experiments katydids revealed their display in the subjugation phase of the predation sequence, suggesting that camouflage may be their primary defence and that their tough tegmina might help them withstand initial predator investigations (Umbers *et al.*, 2019). Katydids were more vulnerable to experienced (sympatric) magpies than naïve (allopatric) ones despite the katydid's abdominal exudate (Baker, 2019); perhaps they are profitable due to their large size (up to 3 g) or perhaps magpies are unaffected by their chemical defence, or both.

Brodie *et al.* (1984) investigated the survival value of deimatic behaviour in three Asian salamander species, *Paramesotriton chinensis* (*N* = 15), *Paramesotriton caudopunctatus* (*N* = 17) and *Pachytriton brevipes* (*N* = 10), against short-tailed shrews (*Blarina brevicauda*). All three species displayed and survived 100% of encounters despite biting and mouthing by shrews (Brodie *et al.*, 1984). Whether shrews were deterred by the visual component of the behaviour or by the taste or toxic effect of the exudate is unclear, and more work is required to determine the selective advantage of each component.

(*c*) *Survival value of deimatic behaviour that reveals sounds*

Two studies have examined the survival value of the auditory component of deimatic behaviour in the peacock butterfly by studying a population in the wild during its vulnerable over-wintering period (Olofsson *et al.*, 2011, 2012*b*). Hibernating butterflies were placed in eight different sites accessible by wild predators and filmed to observe predator–prey interactions (Olofson *et al*., 2011). Cameras revealed yellow-necked mice (*Apodemus flavicollis*) and wood mice (*A. sylvaticus*) as the main predators and that the sound of wing-flicking displays made predators retreat in 41 out of 52 encounters. Olofsson *et al.* (2012*b*) experimentally tested this auditory component against wild-caught mouse predators in a laboratory setting. To isolate the auditory component of the display, experiments were conducted in dark arenas. In 30 min trials in dark arenas mice were presented with either ‘mute’ butterflies which had both ultrasound and stridulatory sound disabled, and ‘sound’ individuals which were sham-manipulated. 96% of butterflies (23/24) survived the first encounter, with no difference in survival between ‘mute’ and ‘sound’ butterflies. However, 18/24 mice fled when butterflies flicked their wings and fled further from ‘sound’ butterflies than from ‘mute’ butterflies. The likelihood of predator-associated wing-flicking behaviour varied among individuals. Eight butterflies only required one interaction with mice before initiating wing-flicking, while some required up to six interactions or to be physically touched. It is not clear whether the sound itself was the deterrent. Olofsson *et al.* (2012*b*) suggested that tactile stimulation arising from the sudden movement of air caused by wing-flicking or being physically touched by the wings themselves could have deterred the mice.

Further, whether the sound is mimetic of a rodent predator, or simply surprising, is unknown but would be an interesting avenue for further research.

Vallin *et al.* (2005) tested the effects of the visual and auditory components in the peacock butterfly by presenting various combinations of eyespots and sound to blue tits. No difference in survival was found between the sound and no-sound treatments, whereas 33/34 butterflies with intact eyespots survived the trials, and only 7 of 20 butterflies with covered eyespots survived. Taking all the peacock butterfly studies together, eyespots seem to be effective against blue tits (Vallin *et al.*, 2005) whereas sound seems to be effective against rodents (Olofsson *et al.*, 2011, 2012*b*). A role of airborne chemical signals was not tested.

Deimatic behaviour has been studied in detail in a few lepidopteran larvae (Low *et al.*, 2021). Brown *et al.* (2007) experimentally examined the survival value of mandible clicks in the polyphemus moth which are accompanied by regurgitation when the moth is grasped by forceps or a beak. In experimental trials, domestic chicks (*Gallus gallus domesticus*) induced sound production in 100% and regurgitation in 87.5% of larvae (*N* = 16) during subjugation and 100% of the caterpillars survived the encounter. Data on long-term survival after attack and any sub-lethal effects are needed. The survival value and function of walnut sphinx whistles and clicks was tested against yellow warblers (*Setophaga petechia*) (*N* = 3) and showed that when caterpillars produced whistles upon attack, the birds hesitated and even flew away (Bura *et al.*, 2011). All three caterpillars survived with no visible harm to their bodies suggesting potential long-term survival, but to confirm this, a larger sample is needed. In simulated attack trials regurgitation in *A. juglandis* was rare (3% of trials) suggesting that in nature they may rely on the sound alone.

Sandow & Bailey (1978) experimentally tested the visual and acoustic components of the deimatic behaviour of the sluggish snout-nosed katydid (*Mygalopsis ferruginea* (Redtenbacher) syn., *M. pauperculus*) against the salmon-bellied skink, *Ergenia napoleonis*.

Both ‘muted’ katydids ($N = 20$) and intact katydids ($N = 20$) raised their legs, flared their mandibles, vibrated their antennae, and attempted stridulation when the predator approached (Sandow & Bailey, 1978). Despite both treatments performing stridulation behaviour, only intact insects were able to produce a discernible sound. A total of 35 out of 40 katydids (87.5%) survived predator encounters and, while there was no difference in survival of sound-producing insects compared with muted individuals, the duration of encounters was longer for muted katydids (average 4 min) than intact katydids (average 1 min) perhaps suggesting that sound production saves the katydid energy by reducing interaction time (Sandow & Bailey, 1978).

(2) Does deimatic behaviour actually deter predators?

Prey defences should be categorised by the effect they have on predators and, while the underlying mechanisms may be unclear, direct measures of predator behaviour can indicate survival value (Fenton & Licht, 1990; Skelhorn *et al.*, 2016). We found 17 studies on predator behavioural responses to deimatic behaviour on 15 species: five species of mammal including three bats and two rodents, and 10 species of bird, all passerines except for domestic chicks (Galliformes) (Table S6). Experiments tested predator responses to deimatic behaviour that revealed colour patterns (including eyespots) both accompanied and unaccompanied by chemical defences, and deimatic behaviours with auditory components and no further defences. Fifteen of the 17 studies were laboratory-based studies with small sample sizes, two field-based investigations had larger sample sizes. In all studies, predator behaviours were either expressly or implicitly considered proxies for a ‘startle response’. Qualitative measures of behaviour typically included descriptions of discrete states such as ‘wing flap’, ‘hesitation’ (latency to attack), or ‘fleeing’ (increasing the distance between themselves and the prey; Table S6). Most studies did not decouple the visual signals revealed by the deimatic behaviour from the deimatic behaviour itself. Overall, the ways in which predator responses have been measured have made direct conclusions about survival value difficult to draw and fitness implications difficult to assess.

(*a*) *Measures of predator 'startle responses'*

The 'startle responses' of predators have typically been measured in response to artificial prey. Schlenoff (1985) showed that blue jays ($N = 6$) 'startled' in around 50% of their initial interactions with models featuring *Catocala*-coloured hindwings (red, orange, and yellow), which were revealed when cardboard forewings were removed, but never startled in response to models with grey hindwings. The startle response was mostly 'low intensity' ("*dropped prey model, raised crest, moved in a jerky rapid fashion*"; p. 1059), as opposed to 'high intensity', which included the low-intensity behaviours plus flying against the side of the cage, emitting an alarm call, and wiping beak. Whether these responses correspond to a 'startle response', whether they constitute 'slowing' their attack, whether they would protect real moths, and what the moths might do in response, is mostly unknown. However, Sargent (1973) found that blue jays often released *Catocala* moths when their hindwings became exposed during prey handling. They left a beak imprint but did not tear the moth's wings, thereby suggesting that exposure of *Catocala* hindwings triggered blue jays to release the moths, perhaps involuntarily.

Dookie *et al*. (2017) showed that the whistling sounds of walnut sphinx moth caterpillars 'startled' red-winged blackbirds. Predators experienced a playback of the caterpillar's sound in response to contacting a sensor on a feeding dish. The behaviours recorded included 'shoulder flinch', 'wing flap', 'ruffle feathers', 'body flinch', 'startle hop', and 'fly away'. The number of behaviours recorded was greater for birds that received a sound compared to birds that did not (Dookie *et al.*, 2017). An interesting future direction would be to compare the responses of birds to control sounds to test if aspects of the caterpillar’s sounds are especially effective as a deterrent or whether any sound has a similar effect.

(*b*) *Measures of predator hesitation*

A long-standing hypothesis about deimatic displays is that they cause predators to pause their attack for long enough for prey to escape (Ruxton *et al.*, 2004) and latency to attack seems to be the response variable most often measured to test this idea. Experiments have usually presented artificial stimuli such as sound recordings, computer imagery, and abstract models (concentric circles) (Table S6). Of the studies that included experiments on live insects (6/17), prey escape behaviour was not described. Vaughan (1983) tested the effect of model *Catocala* moth deimatic behaviour on blue jays ($N = 8$) under the hypothesis that the anomaly (unexpected), novelty (never previously encountered), and/or rarity (previously encountered but uncommon) of moth hindwing colours may cause predators to hesitate. Vaughan (1983) showed that novelty can cause blue jays to hesitate in an experiment where they interacted with an experimental apparatus consisting of a series of flaps behind each of which was hidden colourful discs resembling *Catocala* hindwing colours and mealworms (*Tenebrio molitor* larvae). When the jays encountered discs of a colour they had not encountered during training, they took longer to eat the reward mealworm than when they encountered colours they had experienced before (Vaughan, 1983), and that hesitancy increased with colour rarity.

Using the same apparatus as Vaughan (1983), Ingalls (1993) tested the latency of naïve hand-raised blue jays ($N = 8$) to respond to the combined effects of novel colours and patterns. She showed that birds took longer to touch discs with novel colours presented in a striped pattern with black bands than solid novel colours. Despite potentially confounding order effects, these data suggest that the presence of black bands resulted in the greatest latencies compared to discs without black bands as did colour combinations similar to those found naturally in *Catocala* spp. (Ingalls, 1993). Further, Ingalls (1993) reported interesting variation in predator responses, with some birds never habituating to the stimuli and others habituating relatively quickly, perhaps suggesting that variability within predator species may select for variation in prey defences.

Holmes *et al*. (2018) tested the protective value of deimatic behaviour using computer-generated ‘moths’ with and without colourful hindwings that were revealed rhythmically at three different speeds to domestic chicks (*Gallus gallus domesticus*). In a laboratory setting they showed that rapid movement alone in the absence of conspicuous colours delayed a chick’s attack, and that the combination of movement and coloured hindwings led to longer latencies. These results suggest that movement alone can increase latency in predator responses, that this effect can be enhanced by colourful hindwings and, by extension, that movement could precede colour in the evolution of deimatic behaviour.

(*c*) *Measures of predators fleeing*

Predators might flee when they experience deimatic behaviour (De Bona *et al.*, 2015). Olofsson *et al*. (2012*b*) showed that when field-caught yellow-necked mice and wood mice hear the sound of the peacock butterfly’s display, the majority flee quickly (N = 18/24). Whether they simply flee or if fleeing is initiated after their startle reflex is released would be interesting ground for further testing. Olofsson *et al*. (2012*b*) also suggested that mice respond as they would to a real predator and hypothesised that the peacock butterfly’s sound may involve Batesian mimicry of snake hisses (Vane-Wright, 1986; Skelhorn *et al.*, 2016).

(3) Do predator responses change across repeat encounters?

Changes in predator behaviour across repeated encounters with prey are central to understanding the evolution of deimatism. In some environments deimatic prey may be rare enough for encounter and re-encounter rates to be very low. However, when repeat encounters do occur, predator responses may change depending on encounter rate, predator age [younger predators may be more neophobic (Lindstrom, Alatalo & Mappes, 1999; Marples & Kelly, 1999) or conservative (Thomas *et al.*, 2003)], variability in deimatic behaviours, and whether or how quickly deimatic behaviours are learned and remembered by predators.

(*a*) *Responses to deimatism that reveals colour patterns with no chemical defences*

In 12 studies that exposed predators to repeated trials (Table S6), four used prey stimuli with colour patterns and no chemical defence. Of those four, two found evidence that predators learn to ignore the signals and attack the prey (Vaughan, 1983; Schlenoff, 1985), one showed that predators learn to avoid the prey (Ingalls, 1993), and one found no clear pattern (Kang *et al.*, 2017).

Using the *Catocala*-inspired apparatus described above, Vaughan (1983) showed that blue jays became habituated to the rarity of colours after the first of four experimental days. Initially the latency to attack a rare colour was >200% of that for a common colour, but after one day this dropped to ~110% despite the rarity of the rare colour remaining consistent. Schlenoff (1985), also using the *Catocala*-inspired apparatus, tested blue jay (N = 6) responses to different colour patterns. Habituation took 6–25 days for models resembling red-banded, yellow-banded and black *Catocala* hindwings and the deterring effect lasted longest when trained on two sequential banded patterns rather than a black followed by a banded pattern. The flight periods of *Catocala* species last for several weeks, which is enough time for predator habituation to hamper the effectiveness of startle displays. Sargent & Hessel

(1970) observed flight periods exceeding two months for many *Catocala* species in the north-eastern USA, and adults can survive for at least 60 days in some species (Gall, 1991).

With a further seven wild-caught blue jays, Schlenoff (1985) trained them to two different forewing types with corresponding hindwings, and found that a startle response could be elicited by swapping hindwing colours. She suggested that the anomalous nature of the prey's form combined with the striking colour pattern caused the birds to perform startle behaviours, not simply that the hindwings colours were unexpected, and that it is unnecessary for the patterns to be unknown to the bird. Schlenoff (1985) also showed that encountering an unexpected difference in hindwing colour is not enough to elicit a startle response because birds trained on *Catocala* patterns do not startle to unexpected grey hindwings.

Ingalls (1993) surmised that *Catocala* hindwings may deter blue jays for several reasons: (*a*) they mimic sympatric aposematic species; (*b*) they are novel; and/or (*c*) their patterns include strong contrasts. She suggested that an optimal number of types of forewings must exist. Although an unexpected hindwing colour pattern can deter a predator, if they are presented with a new type in every encounter, in theory they could habituate to the rule that the hindwing will always be new (Ingalls, 1993). Ingalls' (1993) data suggest that blue jays take longer to habituate to startle signals as a function of the diversity of the signals; birds presented with a single stimulus colour habituated far more quickly than those presented with five colours. However, there was also evidence of consistent individual variation in feeding strategy. For example, within a group of birds presented with food associated with five different startle colours, two birds habituated after less than 50 trials, while a third was not habituated after 149 presentations. This variation in individual predator performance could suggest that differences in dietary conservativism (Marples & Kelly, 1999) coupled with differences in levels of neophobia could have a significant impact on predator perception of defences involving multiple stimuli. Overall, this detailed work on *Catocala* and replica stimuli suggests that colour pattern novelty could be protective but does not provide information for responses with real prey. The spatial distribution of hindwing colours in *Catocala* would merit further study.

(*b*) *Responses to deimatic behaviour that reveals colour patterns with chemical defences*

Two studies used prey with colour patterns and chemical defences (Kang *et al.*, 2016; Umbers *et al.*, 2019). Both showed that predators can learn to avoid the prey, while Umbers *et al.* (2019) also found that experienced predators can learn to ignore the deimatic behaviour and consume the prey. The latter study measured repeated interactions between wild live predators and live prey with a deimatic behaviour that reveals a colour pattern and an associated chemical defence. Umbers *et al*. (2019) found that Australian magpies naïve (allopatric) to mountain katydids learn to avoid them after just one trial, but that experienced (sympatric) birds consume katydids at a rate of 50%. This suggests that the initial deterrent effect of the display can be lost, perhaps due to the absence of an emetic effect, but the conditions that promote repeated sampling of initially repellent prey remain unclear. Using chemically defended artificial paper prey, Kang *et al*. (2016) tested whether deimatic behaviours facilitate predator avoidance, and in particular whether predators learn to associate a cryptic resting appearance with distastefulness. They showed that the speed of predator learning was similar between classically aposematic prey and deimatic–aposematic prey (Kang *et al.*, 2016).

(*c*) *Responses to deimatic behaviour that reveals sounds*

Three studies investigated predator responses to repeated sound stimuli (Table S6). In two of these predators learned to ignore the sound and in the third the result was unclear. Dookie *et al*. (2017) tested for effects of repeated exposure of red-winged blackbirds to the whistle emitted by the walnut sphinx caterpillar. They found short-term habituation to the sound within each of their two experimental phases but found no difference in habituation between phases, indicating that during this two-day period the birds dishabituated despite no changes to the experimental set-up (Dookie *et al.*, 2017).

VIII. FUTURE DIRECTIONS

To understand the evolution of deimatic behaviour, further research is required in four broad areas: (1) deimatism as part of an antipredator sequence and the need to define antipredator 'space'; (2) quantifying the underlying mechanisms of predator responses to deimatic behaviours and how these change with experience; (3) gathering richer data for comparative analyses; and (4) ecological patterns of deimatic behaviour. Collaboration across the breadth of behavioural sciences while conducting laboratory and field-based experiments and including indigenous knowledge will enable advances in this field.

(1) Deimatism in the antipredator sequence

Deimatic behaviour is one part of an antipredator strategy. To understand both the benefits of this behaviour and how/when individuals should perform it, we need to establish how it is distinct from and interacts with other defensive strategies. The defences that precede and follow deimatic behaviour in an antipredator strategy vary among species, among individuals, and within individuals. Predators may encounter different sequences of defences when encountering different prey (Fig. 2), but equally, prey can, with different degrees of control, choose which defences to deploy and when. We predict that the protective value of defences can change depending on the combination and order in which they are experienced by predators and that recognising, quantifying, and analysing this variation is key to understanding the proximate and ultimate aspects of antipredator strategies in general.

Recognising that antipredator strategies include multiple defences experienced by predators in a sequence has profound implications (Endler, 1991). It requires us to reframe our view of predator–prey interactions as multi-level escalating interactions rather than a simplistic single-level signal and response. Therefore, understanding deimatism is complicated by how well other defences are defined and the clarity of the conceptual boundaries between them. We therefore encourage mapping the full breadth of antipredator defences (i.e. antipredator 'space') to define these conceptual boundaries (Fig. 2).

(2) Predator responses to deimatic behaviour and prey survival advantage

To arrive at a universally accepted definition of deimatism and establish how it differs from other defensive strategies, it is crucial to experimentally demonstrate the proximate causes(s) by which deimatism deters predators and to test how these differ from other defences within and among attacks and predator individuals. This is needed for predator responses to initial and repeat encounters as well as for predators over the course of a single deimatic performance. Understanding the mechanisms requires working with ecologically relevant predators in natural field settings complemented by controlled laboratory experiments or well-designed field experiments to disentangle interacting effects. We need to make careful choices about how to measure appropriate behaviours for predator species and assumptions as to what these measures represent must be made explicit. Measures that allow us to distinguish among proposed mechanisms by which deimatism deters predators are needed. They include behaviour, physiology, and the stimuli themselves. A coordinated effort to use comparable measurements across studies where possible will allow meta-analyses and systematic reviews in the future.

Limited evidence suggests that deimatic behaviours are more effective against naïve predators. If this is true, we predict that they should be more common in areas where their predators learn slowly, forget quickly, have non-synchronous phenology, or short lifespans resulting in a lower frequency of experienced predators. In these cases, predators are unlikely to learn or habituate so protection could be maintained even if prey possess no additional defences. Interestingly, deimatism might also be favoured where predators learn quickly and retain memory efficiently if those traits are associated with reluctance to attack, for example when attempting to subjugate dangerous prey. Deimatism unaccompanied by subsequent defences should be common, even among populations of predators that are good learners, if the phenologies of the prey and predator only overlap for a short time, minimising time for learning. Similarly, if deimatism is most effective against naïve predators, it may be more common in prey species that are only active when young and naïve predators are more common than experienced predators. Deimatism may be rare if predators are long-lived and overlap extensively in time with prey.

If it is true that the protective value of deimatism is directly related to predator naïvety, it may allow prey to invade new habitats [e.g. lantern bugs (*Lycorma delicatula*) in North America]. Prey species with more effective deimatic displays may expand their geographic ranges faster than species without or with inefficient deimatic displays and might even displace them. This pattern may be stronger when most predators in the new area are naïve. If predators are good learners, then the expanding geographic range may stabilise quickly.

(3) Richer data on prey form and predator response for comparative analyses

To understand the evolutionary pathway(s) *via* which deimatism evolves we need to perform comparative analyses. However, comprehensive quantitative descriptions of deimatic behaviour are currently too rare, most are missing critical measures such as rise time, speed, duration, number of components and sensory modes, the qualities of the components (colours, frequencies), whether the behaviour is sustained or includes rhythmical elements (*sensu* Blest, 1958), and if and when during the predation sequence the behaviour is performed. Data on how deimatism differs among life stages, between sexes, and among species and higher taxonomic groups are also required.

IX. CONCLUSIONS

(1) Deimatic behaviour has evolved and been lost multiple times and is widespread across a diverse range of taxonomic groups.

(2) Deimatic behaviours vary greatly in modality, and may be used singly or in combination with other defences triggering one or more of the predator's sensory systems.

(3) Multiple non-exclusive hypotheses have been put forward to suggest the mechanism(s) by which deimatic behaviour is protective including the looming reflex, the startle reflex, fear, sensory overload, and confusion. Determining whether deimatic behaviours exploit one or more of these mechanisms is an area of high priority.

(4) Deimatic behaviour can be one defence in an antipredator strategy and therefore the impact of the display can vary depending on both the predator's physiology and experience, and the sequence of defences the prey deploys.

(5) Limited evidence suggests that deimatic behaviours are more effective against naïve predators, which could have implications for range expansion and inter-individual conflict.

(6) To develop our understanding of deimatic behaviour, further research is required into: (*a*) deimatism as part of an antipredator sequence; (*b*) quantifying the underlying mechanisms of predator responses; (*c*) comparative analyses; and (*d*) ecological patterns of deimatic behaviour.

X. ACKNOWLEDGEMENTS

We thank Melanie Low for comments and discussion, Audrey Manuel, Science Illustrator, for the salamander images, and Michael Kelly for contributing to data extraction. We are grateful to the two anonymous reviewers who provided very helpful and insightful comments. K.D.L.U. and E.D. were funded by a Hermon Slade Grant (HSF 14/3), K.D.L.U. was funded by an Australian Research Council Discovery Early Career Research Award (project DE180100026) from the Australian Government, and Western Sydney University's Women's Fellowship, Carer's Grant and Early Career Grant. G.H. was funded by a BBSRC Studentship (BB/L017709/1) awarded to J.S. and C.R. C.K. was supported by National Research Foundation of Korea (NRF-2019R1C1C1002466). B.C.L. was supported by a National Science Foundation Graduate Research Fellowship (DGE-1842166). J.L. was funded by an Australian Research Council Discovery Early Career Research Award (project DE180100526) and by an Academy of Finland grant (340130). J.E.Y. was supported by Natural Science and Engineering Council of Canada (2020-07056).

XI. AUTHOR CONTRIBUTIONS

Overall concept and structure – K.D.L.U, E.D. and C.M.Y.; hypothesis and rationales – all authors; data extraction – E.D., K.D.L.U., C.M.Y. and C.S.; results from literature search – E.D., K.D.L.U. and T.E.W.; potential deimatic behaviours – K.D.L.U., B.C.L., J.A.E., R.T.H. and J.E.Y.; evolution – C.K., W.L.A., C.S., K.D.L.U., T.N.S and J.L.; ontogeny – C.M.Y., K.D.L.U. and R.T.H.; causation – J.S., C.R., G.H. and K.D.L.U.; survival value – E.D., K.D.L.U., H.R.S. and N.T.H.; future directions – J.A.E, C.K., J.S. and K.D.L.U.; figures – K.D.L.U., B.C.L., T.E.W. and J.R.; comprehensive editing – E.D., J.A.E., J.E.Y, C.R., J.S. and K.D.L.U.; intellectual property, ideas, and feedback in meetings – all authors.

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XIII. SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of the article.

Table S1. Past descriptions of deimatic displays and terms used to describe the concept.

Table S2. Deimatic behaviours in the context of other similar antipredator defences adapted from Umbers *et al*. (2017).

Table S3. Descriptions of deimatic behaviour from the literature. NA: unclear from text or not included in study, varied: too many different approaches to mention. For the five display mode columns, 0 = absent, 1 = present.

Table S4. Comparison of the defensive strategies of juvenile and adult life stages of species for which both have been studied and at least one stage uses a deimatic display.

Table S5. Summary of studies that have assessed the survival value of deimatic displays in prey.

Table S6. Summary of studies that have assessed predator responses to deimatic displays.

FIGURE LEGENDS

Fig. 1. Examples of deimatic behaviour across three phyla. Icons in the upper right of images indicate additional non-visual signals: sounds (three curved lines) and chemical defence (flask shape). (A) Peacock butterfly (*Aglais io*), image: Charles J. Sharp; (B) Io moth (*Automeris io*), image: Patrick Coin; (C) rosy underwing (*Catocala electa*), image: Yale Peabody Museum, Entomology Division, Catalog #: YPM ENT 563513; (D) spotted lanternfly (*Lycorma delicatula*), image: Changku Kang; (E) walnut sphinx (*Amorpha juglandis*) caterpillar, image: Andy Reago & Chrissy McClarren; (F) mountain katydid (*Acripeza reticulata*), image: Kate Umbers; (G) dead leaf mantis (*Derplatys dessicata*), image James O'Hanlon; (H) sunbittern (*Eurypyga heilas*), image: Minor Torres Salazar; (I) European cuttlefish (*Sepia officinalis*), image: Gavan Cooke; (J) Appenine yellow-bellied toad (*Bombina pachypus*), image: Stefano Canessa; (K) blue-spotted salamander (*Ambystoma laterale*), image: Brock Struecker; (L) rough-skinned newt (*Taricha granulosa*), image: Gary Nafis.

Fig. 2. Five species of insect with their suite of antipredator defences presented together to highlight the differences and similarities in their sequences. The phrases below the prey represent the signal sent by different defences: 'I'm dangerous!' is aposematic; 'I'm not here!' is camouflage (crypsis or masquerade); 'Wait!' is deimatism; 'I told you so!' indicates that the predator has encountered a bad taste or toxin. The dotted rectangle highlights the deimatic component, the defensive phase refers to the order in which the defences are deployed or encountered. The predation sequence phase indicates when during the interaction the predator typically encounters the given defence (Endler, 1991). The seven-spot ladybird represents what is considered classic aposematism, a conspicuous ever-present signal coupled with a defence, in this case a chemical defence. Most of the species are camouflaged at rest as

their primary defence. The walnut sphinx caterpillar represents a deimatic sound, a sound that occurs only when a predator approaches or attempts subjugation; the sound acts as a deterrent but in this case is not coupled with a chemical defence (the sound would still be deimatic even if a chemical defence was present; and then would be both deimatic and aposematic). The peacock butterfly represents deimatic behaviour that includes a sound and a Batesian defence (eyespots). As far as is currently known mantises also fall into this category, as do cephalopods. The hash symbol on the peacock butterfly's caption 'I'm dangerous?!#' is intended to indicate that it is in fact not dangerous; the arrows indicate that the wings open and close and that this movement is repeated. The mountain katydid reveals its colourful abdomen as a predator attempts subjugation and then holds this posture and exudes defensive chemicals from the abdomen in a putative aposematic defence. Finally, the spotted lanternfly's primary defence is aposematism but it too has a deimatic element with the opening of its wings to reveal conspicuous colour patterns, followed by a second aposematic display as the colours are held exposed. If the lanternfly is consumed, the predator will encounter a bad taste and if the predator continues despite the bad taste and swallows the bug, the predator may regurgitate. Illustrations: Kate Umbers

Fig. 3. Summary of the literature to date on deimatic behaviour showing (A) order of species studied, (B) components of deimatic behaviour, (C) type of primary defence for species in study, (D) order of predator species in study, (E) word cloud from the text of all descriptions of deimatic behaviour highlighting the most common phrases used. Illustration: James O'Hanlon.

Fig. 4. Cladogram adapted from Shen *et al.* (2016), with species lacking data removed from the original tree, showing the presence and absence of various traits of deimatic displays in

25 species of plethodontid salamanders. 1, Brodie & Howard (1972); 2, Brodie (1977); 3, Hubbard (1903).