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Author(s): Drinkwater, Eleanor; Allen, William L.; Endler, John A.; Hanlon, Roger T.; Holmes, Grace; Homziak, Nicholas T.; Kang, Changku; Leavell, Brian C.; Lehtonen, Jussi; Loeffler-Henry, Karl; Ratcliffe, John M.; Rowe, Candy; Ruxton, Graeme D.; Sherratt, Tom N.; Skelhorn, John; Skojec, Chelsea; Smart, Hannah R.; White, Thomas E.; Yack, Jayne E.; Young, Catherine M.; Umbers, Kate D. L.

Title: A synthesis of deimatic behaviour

Year: 2022

Version: Accepted version (Final draft)

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Please cite the original version:

Drinkwater, E., Allen, W. L., Endler, J. A., Hanlon, R. T., Holmes, G., Homziak, N. T., Kang, C., Leavell, B. C., Lehtonen, J., Loeffler-Henry, K., Ratcliffe, J. M., Rowe, C., Ruxton, G. D., Sherratt, T. N., Skelhorn, J., Skojec, C., Smart, H. R., White, T. E., Yack, J. E., . . . Umbers, K. D. L. (2022). A synthesis of deimatic behaviour. *Biological reviews*, 97(6), 2237-2267.
<https://doi.org/10.1111/brv.12891>



A synthesis of deimatic behaviour

Journal:	<i>Biological Reviews</i>
Manuscript ID	BRV-10-2021-0388.R4
Manuscript Type:	Original Article
Date Submitted by the Author:	17-Jul-2022
Complete List of Authors:	<p>Drinkwater, Eleanor; University of York, Department of Biology Allen, William; Swansea University, Biosciences Endler, John ; Deakin University, School of Life & Environmental Sciences Holmes, Grace; Newcastle University, Biosciences Institute Homziak, Nicholas; Florida Museum of Natural History, McGuire Center for Lepidoptera and Biodiversity; University of Florida, Entomology and Nematology Department Kang, Changku; Seoul National University, Department of Agricultural Biotechnology; Seoul National University College of Agriculture and Life Sciences, Department of Agriculture and Life Sciences; Mokpo National University, Department of Biosciences Leavell, Brian; Purdue University, Department of Biosciences Lehtonen, Jussi; The University of Sydney, School of Life and Environmental Sciences; University of Jyvaskyla, Department of Biological and Environmental Science Loeffler-Henry, Karl; Carleton University, Department of Biology Ratcliffe, John; University of Toronto, Department of Biology Rowe, Candy; Newcastle University, Biosciences Institute Ruxton, Graeme Sherratt, Tom; Carleton University, Department of Biology Skelhorn, John; Newcastle University, Biosciences Institute Skojec, Chelsea; Florida Museum of Natural History, McGuire Center for Lepidoptera and Biodiversity; University of Florida, Entomology and Nematology Department Smart, Hannah; Western Sydney University, Hawkesbury Institute for the Environment White, Thomas; The University of Sydney, School of Life and Environmental Sciences Yack, Jayne; Carleton University, Department of Biology Young, Catherine; Western Sydney University, School of Science Umbers, Kate; Western Sydney University, School of Science; Western Sydney University, Hawkesbury Institute for the Environment</p>
Keywords:	Antipredator, defense, predator, prey, competition, cognition, behaviour, aposematism, deimatism, startle

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1 A synthesis of deimatic behaviour

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38
39 42 1603).

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42
43 44 **ABSTRACT**

44
45 45 Deimatic behaviours, also referred to as startle behaviours, are used against predators and

46
47 46 rivals. Although many are spectacular, their proximate and ultimate causes remain unclear. In

48
49 47 this review we aim to synthesise what is known about deimatic behaviour and identify

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51 48 knowledge gaps. We propose a working hypothesis for deimatic behaviour, and discuss the

1
2
3 49 available evidence for the evolution, ontogeny, causation, and survival value of deimatic
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5 50 behaviour using Tinbergen's Four Questions as a framework. Our overarching aim is to
6
7 51 direct future research by suggesting ways to address the most pressing questions in this field.
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11
12 53 *Key words:* antipredator, defence, predator, prey, competition, cognition, behaviour,
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14 54 aposematism, deimatism, startle.
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26
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30
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38 138 **I. INTRODUCTION**

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40 139 Avoiding predation is essential for prey fitness. Defending against predators can be costly in
41
42 140 terms of time, energy, injury, and death. Therefore, traits that reduce these costs are
43
44 141 widespread and diverse. The variety of defensive traits includes: camouflage – concealing
45
46 142 colours and patterns (Endler, 1978; Stevens & Merilaita, 2011); aposematism – warning
47
48 143 colour patterns and sounds (Mappes, Marples & Endler, 2005); retaliation – expulsion of
49
50 144 blood, toxins, and hot fluids (Eisner, 1970; Sherbrooke, Middendorf & Guyer, 2001); armour
51
52 145 – defensive structures like spines and hard integuments (Speed & Ruxton, 2005); and
53
54 146 mimicry in many forms (Skelhorn *et al.*, 2010; Dell'Aglio *et al.*, 2018). How defensive traits
55
56 147 such as visual warning signals work against predators is well understood (Mappes *et al.*,
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1
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3 148 2005), while others like deimatic behaviours (Fig. 1), remain poorly understood. Cott (1940,
4
5 149 p. 213) commented on deimatic behaviour stating “*Indeed, we have here an almost untrodden*
6
7 150 *field for future research*”. More than 80 years later this statement remains true save for a
8
9 151 surge of research in the 1970s, and a more recent second wave. The recent resurgence has
10
11 152 precipitated this collaborative review in which we: (1) suggest a hypothesis for deimatism as
12
13 153 distinct from other defences; (2) critically evaluate examples of deimatism and their
14
15 154 classification; and (3) apply Tinbergen’s ‘Four Questions’ framework (Tinbergen, 1963) on
16
17 155 evolution, ontogeny, causation, and survival value, to synthesise the literature and identify
18
19 156 the critical knowledge gaps we need to fill to understand the evolution of deimatism.
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26 158 **II. WHAT IS DEIMATIC BEHAVIOUR?**

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28 159 Deimatic behaviour [*sensu* Maldonado (1970) and Edmunds (1974)] is a celebrated ‘textbook
29
30 160 example’ of a spectacular antipredator defence (Fig. 1), but what exactly is it? Despite long-
31
32 161 standing scientific interest (see online Supporting Information, Table S1) no strong consensus
33
34 162 has so far emerged, nor has a name even been settled on although more than a dozen have
35
36 163 been proposed, with ‘deimatic behaviour’ and ‘startle display’ persisting into the modern
37
38 164 literature (Table S1).
39
40
41

42 165 The first occurrence of the phrase ‘startle display’ in the animal behaviour literature
43
44 166 seems to be in Crane’s (1952) work on Trinidadian mantises, described as the “*type of*
45
46 167 *behavior in which tegmina and wings are elevated and special associated motions made in*
47
48 168 *the face of a potential threat. The more usual terms ‘frightening’ or ‘intimidating display’*
49
50 169 *seem too strong to apply in most of the current instances*” (p. 261). Since Crane (1952), the
51
52 170 term ‘startle’ has been used to describe the prey’s behaviour without knowledge of whether
53
54 171 in fact the behaviour releases the startle reflex in the attacker (Skelhorn, Holmes & Rowe,
55
56 172 2016). Maldonado (1970) coined the phrase ‘deimatic behaviour’. ‘Deimatic’ is from the
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3 173 Greek for ‘frighten’ (Liddell *et al.*, 1996) which we note is the same root as Deimos the
4
5 174 Greek God of Terror (Grant & Hazel, 2004). Maldonado (1970) defined deimatic behaviour
6
7
8 175 in prey as “*a conspicuous display when they are faced with a ‘threat’*” (p. 61). Edmunds
9
10 176 (1974) expanded Maldonado’s definition and described ‘deimatic behaviour’ in a range of
11
12 177 species and stipulated that it “*stimulates an attacking predator to withdraw and move away.*
13
14
15 178 *This results in a period of indecision on the part of the predator... and this gives the*
16
17 179 *displaying animal an increased chance of escaping*” (p. 150). To avoid assumptions about
18
19 180 mechanisms and form, we suggest the use of ‘deimatic behaviour’ instead of ‘startle display’.
20
21 181 We suggest avoiding the term ‘startle’ because it is not yet clear by how many or which
22
23 182 mechanisms deimatic behaviour can be protective (see Section II.7) and we suggest avoiding
24
25 183 the word ‘display’ because it can imply visual signals and exclude other sensory modalities
26
27 184 (Edmunds, 1974; Ruxton, Sherratt & Speed, 2004).

30
31 185 Descriptions of deimatic behaviours are inconsistent across the literature. They have
32
33 186 been described as behaviours performed by prey as a predator approaches, that cause
34
35 187 predators to hesitate long enough for prey to escape. However, many species – including
36
37 188 most of those described in the literature – perform their deimatic behaviour during
38
39 189 subjugation, long after approach (Table S1). Deimatic behaviours are often described as a
40
41 190 ‘bluff’ (Ruxton *et al.*, 2004) which assumes that besides the display, prey pose no further
42
43 191 threat. That is, it assumes that prey lack a chemical or physical defence, and disregards any
44
45 192 protective value of the performance itself. Also, species have been described as deimatic in
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47 193 ways that imply that their whole antipredator strategy is ‘deimatic’ (Umbers & Mappes,
48
49 194 2015). All of the above approaches have proved problematic when then trying to place
50
51 195 deimatism in context with other defences (Skelhorn *et al.*, 2016). We therefore suggest that
52
53 196 antipredator strategies can include many ‘defences’ such as crypsis, masquerade, and
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55 197 aposematism; any one of which may be a deimatic behaviour (Umbers *et al.*, 2017) (Fig. 2).
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3 198 Given the overall lack of clarity, but considering the main conceptual points from previous
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5 199 contributions to the field, we suggest the following hypothesis for what constitutes deimatic
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7 200 behaviour: *a behaviour performed by a target different from fleeing and retaliation that is*
8
9 201 *triggered by it perceiving threat from an attacker during approach or subjugation, and which*
10
11 202 *can trigger an unlearned avoidance response in the attacker causing it to slow or stop its*
12
13 203 *attack.*
14
15

16
17 204 There are four key components of our hypothesis and we provide rationales for each below
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19 205 plus a summary of our deliberate exclusions.
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21

22 206

23
24 207 **(1) Component 1: “A behaviour performed by a target different from fleeing and**
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26 208 **retaliation...”**

27
28 209 “Behaviour” here is to be interpreted very broadly as something an organism can do
29
30 210 including body part movements, the emission of sounds or chemicals, or dynamic changes in
31
32 211 colour patterns. The inclusion of the word “performed” is intended to emphasise that it is a
33
34 212 discrete state that the prey adopts for a time and to distinguish it from more continuous states,
35
36 213 such as constantly exposed aposematic colouration. The behaviour may have been selected to
37
38 214 induce the attacker’s response or the attacker’s response may be an accidental by-product of a
39
40 215 prey behaviour.
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43
44 216 A “target” is the organism or group of organisms that is being attacked, including
45
46 217 colonies and other diffuse phenotypes. The target may not always be prey and could be a
47
48 218 competitor (Edmunds, 1974). Deimatic behaviours do not involve the target fleeing from an
49
50 219 attack. They *can* be performed while fleeing, but their protective value is not in avoiding
51
52 220 capture by increasing physical distance. Deimatic behaviours do not include retaliation (*sensu*
53
54 221 Edmunds, 1974), in which predators can be physically harmed such as by toxic sprays
55
56 222 (Eisner, 1970).
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224 **(2) Component 2: “...triggered by it perceiving threat from an attacker during**
225 **approach or subjugation...”**

226 The implication here is that deimatic behaviour evolves in response to attack, and the form
227 has been influenced by the effect that it has on an attacker, so it is a signal not a cue
228 (Maynard Smith & Harper, 2003). It is triggered by the target perceiving, rightly or wrongly,
229 that it is threatened; it requires the target to detect the attack. With “perceiving” we intend to
230 include the most neurologically simple stimulus–response processes. We predict the
231 behaviour will only be performed outside of a threatening context by mistake, for example
232 when targets misidentify an event as a threat (akin to false alarm). We also predict the
233 behaviour will typically be performed for brief time intervals, or at least not very long
234 beyond the period of interaction with an attacker. While “attacker” often refers to a predator
235 or competitor, it also extends to the range of natural enemies such as parasitoids, parasites,
236 and micropredators (*sensu* Lafferty & Kuris, 2002). Display initiation should coincide with
237 the physical proximity of an attacker within some relevant distance – we suggest the phrase
238 ‘display initiation distance’ (*sensu* Aguilar-Argüello, Díaz-Fleischer & Rao, 2016) – and it
239 will cease upon the perceived threat passing, such as when the attacker leaves the scene or
240 obviously changes its motivation (e.g. from a focused attack to ignoring, or if the prey
241 escapes the predator). The onset of deimatic behaviour may be sudden if it is the result of a
242 threat threshold being breached, but we suggest leaving the time taken to begin performing
243 the display open because slow transitions may be as effective as fast ones (Holmes *et al.*,
244 2018). Deimatic behaviours are performed during predator approach or subjugation – they
245 may function to prevent consumption.

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3 247 **(3) Component 3: “...which can trigger an unlearned avoidance response in the**
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5 248 **attacker ...”**

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7 249 We predict that deimatic behaviour can impact the attacker through a change in their
8
9 250 perception of their target in any sensory mode. The change does not have to result from
10
11 251 learning or prior experience. The attacker’s response could involve cognition and/or could be
12
13 252 affected by reflexive responses. We also predict that the attacker’s response may change in
14
15 253 response to sensory adaptation, habituation, confusion, motor fatigue, state of arousal, and, of
16
17 254 course, associative learning, perhaps related to withdrawing from a threat. The implication of
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19 255 “can” is that the target’s behaviour will occur often enough for the behaviour to be favoured
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23
24 256 by selection.

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26 257
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28 258 **(4) Component 4: “...causing it to slow or stop its attack.”**

29
30 259 Our hypothesis requires that deimatic behaviour causes the attacker to slow or stop its attack.
31
32
33 260 Guilford’s (1994) ‘go-slow’ hypothesis suggests that predators may be more cautious when
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35 261 faced with an aposematic signal, we predict the same may be true for deimatic behaviours.
36
37 262 The attacker may continue to attack after responding to deimatic behaviour; this still counts
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39 263 as deimatic. Although displays may not always be effective, the likelihood of survival should
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41 264 be higher for individuals that choose to perform the behaviour compared to those that do not;
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43
44 265 at least in some circumstances. Any slowing or termination of attack will be adaptive to the
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46 266 prey.

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51 268 **(5) Deliberate exclusions from the hypothesis**

52
53 269 Our hypothesis deliberately excludes certain words and phrases to remain inclusive of several
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55 270 concepts. We have avoided the terms predator and prey because although deimatic displays
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57 271 are commonly thought of in predator–prey interactions, they also occur in other contexts such
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3 272 as intraspecific interactions (Edmunds, 1974). We expressly avoid specifying the mechanism
4
5 273 underlying the attacker's response, as several could be exploited. Our hypothesis allows the
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8 274 target to be 'defended' or 'undefended' because the presence and strength of defences beyond
9
10 275 the behaviour are not needed for it to be deimatic and, equally, their presence does not
11
12 276 preclude deimatism (Fig. 2). The definition also deliberately does not specify the target's
13
14
15 277 behavioural state at the end of the display which could include the target returning to its
16
17 278 previous state, or fleeing (de-escalation) or retaliation (escalation) (Edmunds, 1972).
18
19 279

20 21 22 280 **(6) Deimatism as a distinct defence**

23
24 281 The biggest challenge in articulating the concept of deimatic behaviour is in determining the
25
26 282 conceptual boundaries between it and other antipredator defences. Here we discuss the
27
28 283 conceptual similarities and differences among deimatism and other defences. For clarity, we
29
30 284 use the phrase 'antipredator strategy' to mean the combination of defences an animal uses
31
32 285 such as crypsis, masquerade, aposematism, deimatism, and/or types of mimicry, each of
33
34 286 which may be encountered by predators or deployed by prey at different stages of the
35
36 287 predation sequence (Fig. 2) and may be multimodal and/or multicomponent (Rowe &
37
38 288 Guilford, 1999). We expand the primary/secondary defences dichotomy to recognise that an
39
40 289 antipredator strategy can be a sequence of any length – primary, secondary, tertiary,
41
42 290 quaternary, quinary, etc. (Endler, 1986, 1991) (Fig. 2).

43
44
45 291 Where does deimatism fit among other antipredator defences? The concepts of most
46
47 292 antipredator defences are not crystal clear, with many different definitions presented and the
48
49 293 distinctions between defences muddy. In addition, relative to other defences like
50
51 294 aposematism and camouflage, the mechanisms and functions of deimatism are not well
52
53 295 understood. This makes the necessary task of explaining clear conceptual distinctions
54
55 296 difficult, particularly compared to flash behaviour, retaliation, and aposematism.
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3 297 Deimatic behaviour can resemble, although is functionally distinct from, fleeing
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5 298 responses like ‘flash behaviours’ (*sensu* Edmunds, 1974) which often take the form of
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7
8 299 repeatedly revealed colour patches and/or sounds by escaping prey (Table S2). These signals
9
10 300 are thought to impair the ability of attackers to track a fleeing signaller (Loeffler-Henry *et al.*,
11
12 301 2018) whereas deimatic behaviours are not protective *via* disrupting prey tracking or
13
14 302 increasing the distance between predator and prey (Edmunds, 1974; Loeffler-Henry *et al.*,
15
16 303 2018). Aspects of deimatic behaviour also overlap with retaliatory defences (*sensu* Edmunds,
17
18 304 1974) such as the defensive sprays of bombardier beetles. Such behaviours are also
19
20 305 performed when under threat, but differ in that predators are attacked rather than just
21
22 306 displayed to.
23
24

25
26 307 Debate and confusion has surrounded whether deimatism is distinct from
27
28 308 aposematism (Skelhorn *et al.*, 2016; Umbers & Mappes, 2016). In their most general sense,
29
30 309 aposematic signals can be loosely defined as ‘go away’ signals to predators. Such a broad
31
32 310 definition can include many concepts currently considered distinct: warning colouration,
33
34 311 flash colouration, types of mimicry and deimatism. This could mean that deimatism is a type
35
36 312 of aposematism, in the same way that crypsis and masquerade are both types of camouflage
37
38 313 (Skelhorn *et al.*, 2010). But if the term aposematism is used as an umbrella term for all those
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40 314 concepts, classic warning signals need to be given a new name, which could cause
41
42 315 unnecessary confusion.
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46 316 A more useful and biologically precise definition states that aposematism is “...*the*
47
48 317 *association between the signal and unprofitability...*”, that “*Aposematic signals work best*
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50 318 *when they are easily detectable and memorable, which facilitates avoidance learning...*”, and
51
52 319 that the benefits of aposematism “...*increase as a function of the density of the similarly*
53
54 320 *signalling individuals...*” (Mappes *et al.*, 2005, p. 598). Deimatism does not fit this definition
55
56 321 well. There is preliminary evidence that deimatic behaviours are more effective against naïve
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3 322 predators than experienced ones, which is opposite to the expectations of signals that
4
5 323 facilitate avoidance learning (Umbers *et al.*, 2019). Deimatic behaviours are not easily
6
7 324 detectable; they are temporary and undetectable until they are performed. Learning is not
8
9 325 necessary for deimatism to afford protection, which is a major difference from aposematism
10
11 326 *via* learned aversion, although learning might be associated with deimatism after the first
12
13 327 encounter (Kang *et al.*, 2016). It is currently unclear whether deimatic behaviours facilitate or
14
15 328 impede memorability, and both are possible (Kang *et al.*, 2016). Finally, the benefits of
16
17 329 deimatic behaviour can in theory decrease as a function of density, rather than increase, as
18
19 330 attackers learn to expect the performance (Sargent, 1990; Ingalls, 1993).

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21
22 331 Deimatic behaviours can, however, be part of an antipredator strategy that includes an
23
24 332 aposematic signal (Umbers *et al.*, 2017) (Fig. 2). If an antipredator strategy includes
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26 333 deimatism and aposematism, deimatic behaviour may cause a predator to break off its attack
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28 334 before directly experiencing any of the prey's other defences. The deimatic function may
29
30 335 then hamper development of avoidance learning and reduce the efficacy of, or requirement
31
32 336 for, aposematism. Antipredatory strategies that include deimatism can also include Batesian
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34 337 mimicry (for example through revealing markings that mimic a dangerous predator), the use
35
36 338 of eyespot signals, or retaliation, and equally, deimatic behaviour can be followed by no
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38 339 further defence (Fig. 2).

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46 47 341 **(7) Mechanisms by which predators respond to initial encounters with deimatic** 48 49 342 **behaviour**

50
51 343 The sensory and cognitive mechanisms deimatic behaviours exploit in predators are currently
52
53 344 unclear. Several non-mutually exclusive hypotheses have been suggested: release of the
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55 345 startle reflex, the looming reflex, the release of fear in the predator, sensory overload,
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1
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3 346 confusion, and neophobia. Experimentally distinguishing among these mechanisms is an
4
5 347 important challenge to meet.
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9
10 349 *(a) Startle reflex*

11
12 350 Deimatic behaviours are often colloquially referred to as ‘startle displays’, in that when
13
14 351 predators encounter them they appear to be startled (Crane, 1952; Schlenoff, 1985). But this
15
16 352 description is largely anthropomorphic and requires biological specificity. Vaughan (1983)
17
18 353 tested the responses of blue jays (*Cyanocitta cristata*) to artificial prey in which ‘startle
19
20 354 response’ was defined as “*a measurable hesitation in the normal feeding sequence of a*
21
22 355 *predator*” (Vaughan, 1983, p. 385). Further measures of ‘startle’ have included response
23
24 356 variables of mixed specificity: increased heart rate, latency to reinvestigate, hesitating,
25
26 357 jumping back, diving away, fleeing, contraction of facial and skeletal muscles, jumping,
27
28 358 rearing, running, grinding teeth, and quivering (Burnham, 1939; Bura *et al.*, 2011; Ramirez-
29
30 359 Moreno & Sejnowski, 2012; Fischer, Franco & Romero, 2016; Holmes *et al.*, 2018). These
31
32 360 behaviours and physiological responses could occur for several reasons and not necessarily as
33
34 361 a result of eliciting a startle reflex as defined in its strictest sense.
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39

40 362 The ‘startle reflex’ is a response that interrupts what an animal is currently doing and
41
42 363 produces physiological and behavioural changes that help it evade an immediate threat
43
44 364 (Eaton, Bombardieri & Meyer, 1977; Gotz & Janik, 2011; Yilmaz & Meister, 2013; Skelhorn
45
46 365 *et al.*, 2016). The startle reflex appears to be triggered by stimuli, whether auditory or visual,
47
48 366 that have a high intensity and a rapid onset (Koch & Schnitzler, 1997; Koch, 1999; Deuter *et*
49
50 367 *al.*, 2012). For example, in laboratory experiments where sounds are produced in close
51
52 368 proximity to subjects (usually primates and rodents), sounds typically need to be above 80–
53
54 369 90 dB with rapid rise times (the time taken for the stimulus to reach its maximum amplitude)
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56 370 of less than 12 ms (Davis, 1984), but sounds of 60 dB can also be effective if they have close
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3 371 to instantaneous rise times (Åsli & Flaten, 2012). Caterpillars that make sounds in response
4
5 372 to attack can produce them close to instantaneously at 70–90 dB when the predator is at close
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7
8 373 range, but the limited data available suggest that deimatic behaviours rarely have such intense
9
10 374 and rapid onset, at least for auditory signals. Therefore, although the startle reflex is
11
12 375 taxonomically widespread, and exploiting it could protect against many enemies, it is
13
14 376 unlikely to be the mechanism by which all deimatic behaviours protect.
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19 378 *(b) Looming reflex*

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21 379 Deimatic displays may trigger the ‘looming reflex’, an adaptive response to avoid rapidly
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23 380 approaching objects, including predators (Yamawaki, 2011). The looming reflex has been
24
25 381 studied across a wide range of species including insects (Rind, Santer & Wright, 2008;
26
27 382 Yamawaki, 2011), crustaceans (Shragai *et al.*, 2017), cephalopods (King & Adamo, 2006;
28
29 383 Hanlon & Messenger, 2018) and chordates (Temizer *et al.*, 2015), and is characterised by
30
31 384 receivers taking rapid evasive action to avoid contact with the approaching object. Like
32
33 385 startle reflexes, the stimuli that induce this response are specific – looming-sensitive neurons
34
35 386 respond to stimuli that increase rapidly in surface area on the retina (Yilmaz & Meister,
36
37 387 2013). For example, mice respond to rapidly looming discs, but only when they come from
38
39 388 above at speeds that resemble an incoming aerial predator (Yilmaz & Meister, 2013). Some
40
41 389 deimatic behaviours involve a rapid increase in size (Table S3) and although it is not known
42
43 390 if such changes are sufficient in size or speed, it is possible they evoke the looming response.
44
45 391 To take advantage of predator looming reflexes we predict that deimatic behaviour may have
46
47 392 the greatest survival value when it appears to make the apparent size of the prey increase
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49 393 rapidly, and perhaps at close range so that they can stimulate a larger area of the predator’s
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51 394 retina.
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3 396 (c) *Fear responses*
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5 397 Responses to deimatic behaviour seem to occur very quickly (i.e. reflex-like), and may use
6
7 398 specific neural systems that do not involve time-consuming identification of the approaching
8
9 399 stimulus in order to enable rapid life-saving responses (Lin, Murray & Boynton, 2009).
10
11 400 However, another hypothesis for how deimatic behaviours work is that they elicit fear
12
13 401 responses because a stimulus is recognised and misclassified as a potential threat (Skelhorn *et*
14
15 402 *al.*, 2016). Phasic fear is a state of apprehension elicited by a specific and imminent perceived
16
17 403 threat, that dissipates once the danger is removed (Davis *et al.*, 2010; Miles, Davis & Walker,
18
19 404 2011; Sato & Yamawaki, 2014; Tovote *et al.*, 2016). It produces responses that can be rapid,
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21 405 occurring within 100 ms of stimulus onset, and could mediate observers' responses to
22
23 406 deimatic behaviour (Pomeroy & Heppner, 1977; Åsli & Flaten, 2012). The kinds of stimuli
24
25 407 perceived as threatening can be influenced by an animal's evolutionary history (Blumstein,
26
27 408 2006) or ontogeny, or by what it has learned from its own experiences or observations
28
29 409 (Griffin, 2004). This means that features of dangerous stimuli in a predator's environment
30
31 410 that are likely to elicit phasic fear responses could be exploited by deimatic behaviour. For
32
33 411 example, deimatic behaviour could include the revealing of eyespots that resemble sympatric
34
35 412 predatory eyes (Janzen, Hallwachs & Burns, 2010; De Bona *et al.*, 2015), or auditory signals
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37 413 that sound like sympatric (or at least historically so) predatory alarm calls (Dookie *et al.*,
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39 414 2017).
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49 416 (d) *Sensory overload*

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51 417 Deimatic behaviours could somehow overwhelm a predator's ability to process sensory
52
53 418 information by presenting them with more information or noise than they can process at once
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55 419 (Hebets & Papaj, 2004; Low, 2012). This popular idea has been referred to as 'sensory
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57 420 overload' (Hebets & Papaj, 2004; Bro-Jørgensen, 2010). However, this term is often used
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3 421 loosely, and clear conceptual definitions are rare (Scheydt *et al.*, 2017), particularly in the
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5 422 animal signalling literature. From a mechanistic point of view, the behavioural phenomena
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7 423 that appear to be associated with sensory overload (e.g. behavioural immobilization and
8
9 424 confusion) may be caused when excessive stimulation from at least two sensory modes
10
11 425 blocks the reticular formation; a complex network of brainstem nuclei involved in (amongst
12
13 426 other things) perception, attention and maintaining behavioural arousal (Lindsley, 2013).
14
15 427 Related concepts probably include visual or auditory distraction, sensory filtering, cognitive
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17 428 overload (Dukas & Kamil, 2000) and breakdown of multimodal/sensory integration.
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22 429 Understanding the mechanisms by which deimatic behaviours protect prey from
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24 430 predators requires directly measuring what the predator is experiencing, which may demand
25
26 431 more technically difficult and invasive data collection (Fullard, Dawson & Jacobs, 2003) than
27
28 432 measuring predator behaviour and carries important ethical considerations. The difficulty of
29
30 433 determining the mechanisms involved increases substantially when attempted in field
31
32 434 conditions (Skelhorn *et al.*, 2016; Umbers & Mappes, 2016). Both are worthy goals if we are
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34 435 to understand how deimatic behaviours provide survival value.
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40 437 *(e) Confusion effect*

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42 438 As stated above, deimatic behaviour often involves the exposure of a previously hidden
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44 439 signal that functions to startle a would-be attacker. However, the deployment of hidden
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46 440 signals may also prevent attacks through other mechanisms. Specifically, a cryptic organism
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48 441 revealing a conspicuous signal as it flees may confuse the attacker as to the organism's
49
50 442 appearance when at rest, hindering subsequent search. This defensive strategy is known as
51
52 443 'flash behaviour' and appears to be widespread in nature with putative examples having been
53
54 444 described in cephalopods, insects, fish, amphibians, reptiles, birds, and mammals (Edmunds
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56 445 1974; Hanlon & Messenger, 2018). It has been postulated that the confusion effect of flash
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3 446 behaviour may function in tandem with a startle effect to dissuade attackers (Edmunds, 1974;
4
5 447 Cott, 1940). However, a ‘proof of concept’ experiment demonstrated that the confusion effect
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7 448 of flash behaviour alone is sufficient to prevent attacks (Loeffler-Henry *et al.*, 2018).
8
9
10 449 Moreover, flash displays may be more effective in reducing predation when the signaller
11
12 450 flees from a distance, so that the signaller’s cryptic resting state is not observed (Loeffler-
13
14 451 Henry, Kang & Sherratt, 2021). Since hidden signals are less likely to frighten the observer
15
16 452 when exposed from a distance, then deimatic and flash displays are functionally distinct and
17
18 453 may often be incompatible.
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24 455 **III. DEIMATIC BEHAVIOUR ACROSS TAXA**

25
26 456 We collated all studies on deimatic behaviour and its analogues from the primary literature.
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28 457 We include studies on deimatic and related phenomena based on descriptions in the literature
29
30 458 by the authors and as such may have included behaviours eventually deemed not to fit
31
32 459 deimatism and may have excluded deimatic behaviours that will be included in the future.
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34 460 With those limitations, here we synthesise the literature on deimatic behaviour and discuss
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36 461 the marginal cases.
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42 463 **(1) Literature search methods**

43
44 464 We searched titles, abstracts, and key words in the *Web of Science* database, with relevant
45
46 465 terms gathered from Edmunds (1974), proposed definitions and iteratively, based on
47
48 466 preliminary descriptions we found in the literature (Table S1). Our search terms in the Title
49
50 467 [TI] field were: deimatic display OR deimatic response OR frightening attitude OR startl*
51
52 468 display OR defensive display OR startle behaviour OR deimatic behaviour OR startl* sound
53
54 469 OR startl* colour* OR startl* response OR startl* reaction OR dymantic display. This search
55
56 470 returned 1535 hits in February 2021. In addition, we searched for papers using the taxon-
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3 471 specific terms: ‘unken reflex’ (amphibians), ‘hooding’ (cobras) and ‘disturbance stridulation’
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5 472 (insects).
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10 474 **(2) Results from literature search**
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12 475 75 publications met at least one of two inclusion criteria: describing the form of putative
13
14 476 deimatic behaviour or describing a manipulative experiment on an aspect of deimatic
15
16 477 behaviour (Table S3). In total our data set included 224 species from 246 separate studies
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18 478 within 75 publications (with ‘studies’ defined as descriptions or experiments within a
19
20 479 publication) with 16 species represented multiple times (Table S3) . Because so few species
21
22 480 have been studied multiple times, the number of studies is roughly representative of the
23
24 481 number of species, for a summary of the number of species see Fig. 3. Most studies were
25
26 482 descriptive accounts of putative deimatic behaviour ($N = 198/246$, 80%) rather than
27
28 483 manipulative experiments ($N = 48/246$, 20%), providing an important natural history base
29
30 484 from which to work but little evidence on the mechanistic and functional drivers of deimatic
31
32 485 behaviour. In the following sections we report trends from descriptive accounts. The results
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34 486 from manipulative experiments are discussed in later sections.
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42 488 *(a) History of describing deimatic behaviour*
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44 489 Deimatic behaviour is no doubt known by indigenous people the world over, but to the
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46 490 detriment of this review we found no modern indigenous accounts. However, we found some
47
48 491 evidence of ancient knowledge on snakes with putative deimatic behaviours in images and
49
50 492 written accounts. A rattlesnake’s rattle is prominently depicted in a pictograph dated to
51
52 493 approximately 1000 CE at the Pony Hills archaeological site, New Mexico (Schollmeyer,
53
54 494 2020). The Brooklyn Medical Papyrus dated 450 BCE, describes the hooding behaviour of
55
56 495 the Egyptian cobra (*Naja haja*), scale stridulation of saw-scaled vipers (*Echis* sp.), and
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3 496 sounds of puff adders (*Bitis arietanis*) (Golding, 2020). The earliest written description of
4
5 497 deimatic behaviour in the scientific literature we could find is that of Goureau (1841) about
6
7 498 *Mantis religiosa* which roughly translates from French to: “*she raised her long corselet*
8
9 499 *vertically, carried her forelegs forward, as if to catch her prey, half spread her wings and*
10
11 500 *elytra, and moved her abdomen up and down with a rapid movement; during this movement,*
12
13 501 *the sides of the belly rubbed against the inner edges of the wings and elytra, and produced a*
14
15 502 *noise analogous to that obtained by crumpling parchment*” (Goureau, 1841, p. 354). Löhner
16
17 503 (1919) described the unken reflex (arched-back posture) in *Bombinator igneus* toads as
18
19 504 potentially hypnotising. Varley (1939) published a comprehensive summation of the
20
21 505 literature on mantis ‘frightening attitudes’ citing 29 publications including Roonwal’s (1938)
22
23 506 account of the ‘frightening display’ of the mantis *Eremiaphila braueri*. After a three-year
24
25 507 residence in the jungles of Trinidad, Crane (1952) published her comparative account of the
26
27 508 ‘defensive behaviour’ of 15 Trinidad mantis species. Blest (1957a) published a detailed
28
29 509 account of ‘protective displays’ in some Saturnioidea and Sphingidae Lepidoptera.
30
31 510 Throughout the 1970s there was a flourish of work on deimatic behaviour. Maldonado
32
33 511 described details of the form, habituation and ontogeny of deimatic behaviour in the double
34
35 512 eye-spot mantis (*Stagmatoptera biocellata*) (Maldonado, 1970; Balderrama & Maldonado,
36
37 513 1971, 1973).

38
39 514 In the early and mid 1970s, Edmunds published two extensive descriptions of the
40
41 515 ‘defensive behaviour’ of dozens of African mantises (Edmunds, 1972, 1976) and his
42
43 516 influential book *Defence in Animals: A Survey of Anti-predator Defences* (Edmunds, 1974),
44
45 517 in which he describes ‘deimatic behaviour’ across species and contexts. Also in the 1970s,
46
47 518 Brodie Jr led a series of publications that described the ‘defensive posturing’ of the newt
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49 519 *Taricha granulosa* and dozens of salamander species (Johnson & Brodie Jr, 1975; Nowak &
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51 520 Brodie, 1978). Since then, the field has progressed steadily including seminal works on the
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3 521 underwing moths (*Catocala* spp.) in the 1980s and 1990s (Schlenoff, 1985; Sargent, 1990;
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5 522 Ingalls, 1993) and peacock butterflies (*Aglais io*) in the 2000s (Vallin *et al.*, 2005; Olofsson,
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7 523 Jakobsson & Wiklund, 2012b).

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10 524

11
12 525 *(b) Taxonomic coverage, descriptions, predators and life stages*

13
14 526 The majority of studies describe the deimatic behaviour of salamanders (Urodela), moths and
15
16 527 butterflies (Lepidoptera), mantises (Mantodea), and frogs (Anura) (Table S3, Fig. 3) but this
17
18 528 is likely to be a poor summary because the concept and the kinds of behaviours included has
19
20 529 not been clear or applied consistently. Deimatic behaviour of 16 species has been described
21
22 530 multiple times, for example the European cuttlefish (*Sepia officinalis*), peacock butterfly, and
23
24 531 promethea silkmoth (*Callosamia promethia*) (Table S3). Words most often used in the
25
26 532 descriptions are shown in Fig. 3E. Most studies focused on displays of adults (around 80%),
27
28 533 with just a handful of studies on juveniles (Table S3). A few studies covered both adult and
29
30 534 juvenile life stages and around 10% provided no information about life stage (Table S3). The
31
32 535 vast majority of studies used humans as predators with birds and non-human mammals a
33
34 536 distant second and third (Table S3, Fig. 3D).

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42 538 *(c) Primary defence associated with deimatic behaviour and stage of predation sequence*

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44 539 *deployed*

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46 540 For most species, deimatic behaviour was associated with a form of camouflage (Fig. 3C) as
47
48 541 its primary defence. Exceptions were the salamanders which were considered aposematic
49
50 542 except for two *Pseudotriton* Batesian mimics, and the Io moths (*Automeris* spp.) which were
51
52 543 deemed putatively aposematic in the literature. Work on the co-evolution of primary
53
54 544 defences, deimatic behaviour, and further defences is key to understanding how different
55
56 545 defences interact to protect prey.

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3 546
45 547 *(d) Multimodality of deimatic behaviour*

6
7 548 About half the studies suggested that deimatic behaviours target more than one sensory mode
8
9 549 (Higham & Hebets, 2013) (Table S3). However, most studies focused on behaviours
10
11 550 involving movement of large body parts (the wings, body, tail, or head; Table S3, Fig. 3E).
12
13 551 Several visual components were reported: movement and body size increase, colour pattern
14
15 552 reveal including eyespots, light production (e.g. bioluminescence), and the revealing or
16
17 553 highlighting of a weapon. Most studies (~ 65%) involved visual components in addition to
18
19 554 movement. We found a few cases of putative Batesian mimicry where posturing alone was
20
21 555 thought to be protective. For example, the stick insect (*Oncotophasma martini*) curves its
22
23 556 abdomen over giving it the appearance of a scorpion (Robinson, 1968*b*), while the lobster
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25 557 moth (*Stauropus fagi*) caterpillar adopts a spider-like posture (Poulton, 1890). The most
26
27 558 common incorporation of Batesian mimicry was in the reveal of eyespots [18 Lepidoptera
28
29 559 (especially Saturniidae: *Automeris*), two manitises, one cuttlefish and one frog]. Only about
30
31 560 one quarter of the studies included a focus on auditory, vibrational or olfactory components
32
33 561 and around 40% reported a gustatory or olfactory component (Table S3). It is unclear
34
35 562 whether visual components are more commonly associated with deimatic behaviour or just
36
37 563 more often studied (Rowe & Halpin, 2013).
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47 565 *(e) Speed and duration of deimatic behaviour*

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49 566 The movement involved in deimatic behaviour may be important for its protective value
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51 567 (Holmes *et al.*, 2018) but speed and duration were rarely measured. We found no clear
52
53 568 information on the speed of state change (rise time) between resting and deimatic behaviours.
54
55 569 One exception was for the common octopus (*Octopus vulgaris*), which initiated changes to its
56
57 570 visual appearance in 270 ms and completed a dramatic colour pattern and skin texture change
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3 571 in 2 s using its capacity for rapid neural polyphenism (Hanlon, 2007; Hanlon & Messenger,
4
5 572 2018). The European cuttlefish initiates dramatic changes in appearance over a similar time
6
7 573 frame, and varied these responses across three different species of teleost fish predators
8
9 574 (Staudinger, Hanlon & Juanes, 2011). In other taxa, display duration varied enormously
10
11 575 among species from milliseconds to more than 30 min (Table S3). In the most extreme case a
12
13 576 mantis held its pose for 6 h while sharing a cage with a predatory bird (Maldonado, 1970).
14
15 577 Deimatic behaviours were described as sustained and/or rhythmical (repeated) (*sensu* Blest,
16
17 578 1957*b*), around half the studies report on sustained behaviours, around 30% on rhythmical
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19 579 and 15% on behaviours that have both sustained and rhythmical elements. We found no
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21 580 reports describing movements that were performed only once and thus were neither sustained
22
23 581 nor rhythmical.
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31 583 *(f) Stage of predation sequence in which deimatic behaviour is performed*

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33 584 Although deimatic behaviours are thought to be performed during approach by a predator in
34
35 585 order for prey to be able to escape, only about 20% of studies reported deimatic behaviour
36
37 586 solely during the approach phase, while roughly half reported behaviours during subjugation,
38
39 587 and about 10% reported behaviours during both phases. These suggest that prior assumptions
40
41 588 about deimatic behaviours being deployed only during the approach phase may be
42
43 589 unfounded, and are consistent with our definition of deimatism as performed “during
44
45 590 approach or subjugation”. However, our ability to draw conclusions is limited because
46
47 591 around half of all studies (134/246, 54%) used humans as ‘predators’ to poke, drop or
48
49 592 otherwise disturb prey to evoke deimatic behaviour. Thus, it is possible that against natural
50
51 593 predators deimatic behaviour may be performed at an earlier stage. A key hypothesis to test is
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53 594 that ‘defended’ species are more likely to display during subjugation whereas ‘undefended’
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3 595 species display during approach. To understand the evolution of deimatic behaviour, it is
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5 596 critical that an ecologically appropriate stimulus is used (see Section VIII.2).
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9
10 598 **(3) Potential deimatic behaviours**

11
12 599 Confusion as to which behaviours are deimatic became obvious from our survey of the
13
14 600 literature. Common sources of ambiguity included defensive spray liquids, body inflation,
15
16 601 bioluminescent signals, alarm calls, vibrations, and electrical emissions. Given this
17
18 602 uncertainty, we briefly discuss these cases below and attempt to clarify the information
19
20 603 required to include or exclude them as deimatic, which will mostly depend on the receiver's
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22 604 response.
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28 606 *(a) Defensive sprays*

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30 607 Edmunds (1974) described defensive sprays as retaliatory defences but the posturing before
31
32 608 the spray, such as that of a skunk, as deimatic. Skunks (Mephitidae) squirt strong-smelling
33
34 609 liquid at their attackers from glands (Medill, Renard & Larivière, 2011; Fisher &
35
36 610 Stankowich, 2018) and reflexive bleeders like horned lizards (*Phrynosoma* spp.) squirt blood
37
38 611 at their attackers (Sherbrooke *et al.*, 2001). More harmful sprays include the hot, caustic,
39
40 612 liquid sprays of bombardier beetles, stinging peppermint stick insect (*Megacrania batesii*)
41
42 613 sprays, and the entangling toxic 'glue' shot by termites (Eisner, 1970; Eisner & Adams, 1975;
43
44 614 Eisner, Yack & Aneshansley, 2001*b*; Eisner *et al.*, 2001*a*; Dossey, 2011). Interestingly,
45
46 615 bombardier beetles and skunks have warning colours as their primary defence, whereas
47
48 616 peppermint stick insects and horned lizards use crypsis. We hypothesise that posturing and/or
49
50 617 non-harmful sprays are deimatic in that they have an aversive effect when initially
51
52 618 encountered and then, on subsequent encounters, have an aposematic effect. The distinction
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54 619 lies in whether the posturing before sprays are employed has a deimatic effect and whether
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3 620 spraying the predator qualifies as retaliation (*sensu* Edmunds, 1974) rather than deimatism,
4
5 621 but no clear line has yet been drawn. Future work could focus on the effect of posturing and
6
7 622 the degree of physical harm done to the attacker during the spraying behaviour to disentangle
8
9 623 these defences.
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12 624

14 625 *(b) Body inflation*

16
17 626 Body inflation, using gases or liquids, occurs in many species, including frogs in which it is
18
19 627 considered part of their deimatic behaviour (Martins, 1989). Body inflation is also used by
20
21 628 many reptiles and fish in which it has not been described as deimatic *per se*, but is considered
22
23 629 defensive (Badiane *et al.*, 2018). Pufferfish (Tetraodontidae) inflate their bodies with the
24
25 630 added effect of raising spines, which is assumed to make them more difficult to bite and/or
26
27 631 swallow, but the inflation also may elicit an aversive response qualifying this behaviour as
28
29 632 deimatic (Wainwright & Turingan, 1997). Similarly, during their deimatic behaviour
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31 633 cephalopods use ‘sustained hyperinflation’; this may interfere with their circulation hinting at
32
33 634 a measurable cost to performing this behaviour (King & Adamo, 2006). It has been suggested
34
35 635 that their inflation in response to a perceived threat could have a deimatic effect, be an
36
37 636 aposematic signal, highlight weapons, and/or mechanically impede predation. Whether the
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39 637 inflation process deters an attacker owing to induced fear of the inflated animal suddenly
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41 638 looming, or whether the resulting large body size exceeds the gape limit of the attacker is
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43 639 untested.
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51 641 *(c) Electrical discharge*

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54 642 Electrical signals are surprisingly ubiquitous in nature (England & Robert, 2021). The
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56 643 electrical discharges generated by numbfishes (Narcinidae), electric rays (Torpedinidae), and
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58 644 electric eels (*Electrophorus electricus*) could be deimatic behaviours. They are not typically
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3 645 described as deimatic in the literature perhaps because it is mechanism focused (Sheridan,
4
5 646 1965; Mellinger *et al.*, 1978; Macesic & Kajiuura, 2009). Electrical signals are, however,
6
7 647 known to function in antipredator contexts in some species. Macesic & Kaijura (2009)
8
9 648 showed that the lesser electric ray (*Narcine brasiliensis*) generates electric organ discharges
10
11 649 against simulated predatory attacks. As there is still limited research into the use of electrical
12
13 650 discharges as a defence, it is currently unclear whether this should be considered retaliation to
14
15 651 make the prey less profitable, or whether it is a deimatic display. It may be speculated that
16
17 652 this could be context dependent, as the same charge could, for example, simply startle a
18
19 653 larger predator, whereas it could stun a smaller predator. The mechanism of defence could
20
21 654 therefore be related to both the type of predator and the type of prey (for example juvenile
22
23 655 lesser electric rays are capable of weaker discharges than adults), however further work is
24
25 656 needed to determine whether retaliation and deimatic behaviour can be separated in this
26
27 657 example. Behavioural studies on predator responses to electrical discharges are needed to
28
29 658 understand how they fit among antipredator defences especially in terms of retaliation and
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31 659 aposematism.
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40 661 (d) *Bioluminescence*

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42 662 Bioluminescence, the chemical production of light by living organisms (Kahlke & Umbers,
43
44 663 2016), is used in anti-predatory contexts and can resemble deimatic behaviour (Stanger-Hall
45
46 664 & Oakley, 2019). Bioluminescence can be aposematic, as chemically defended adult and
47
48 665 larval fireflies elicit avoidance learning in anurans (De Cock & Matthysen, 2003), bats
49
50 666 (Leavell *et al.*, 2018), mice (Underwood, Tallamy & Pesek, 1997), and spiders (Long *et al.*,
51
52 667 2012), or it may ‘frighten’ potential predators (Lloyd, 1973). Esaias & Curl (1972)
53
54 668 hypothesised that dinoflagellate (*Gonyaulax* spp.) bioluminescent flashes function as a
55
56 669 protean display “*which startles or confuses the copepod*” (p. 901) suggesting both fleeing and
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2
3 670 deimatism (Humphries & Driver, 1970; Edmunds, 1974; Driver & Humphries, 1989).
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5 671 Similarly, lantern fish (Myctophidae) emit bioluminescent flashes in response to their
6
7 672 predators, southern elephant seals (*Mirounga leonina*), which result in longer prey capture
8
9 673 attempts (Goulet *et al.*, 2020). Where feasible, direct tests of predator responses could
10
11 674 identify examples of deimatism in bioluminescent systems.
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17 676 *(e) Alarm calls and burglar alarms*

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19 677 It is currently unclear whether ‘alarm calls’ (alerting conspecific receivers to a potential
20
21 678 danger), or ‘burglar alarms’ (attracting the attention of an enemy’s enemy) should be
22
23 679 considered as deimatic behaviour (Burkenroad, 1943; Haddock, Moline & Case, 2010;
24
25 680 Hanley & Widder, 2017). Vervet monkey (*Chlorocebus pygerythrus*) predator-specific alarm
26
27 681 calls signal the presence of a predator to conspecifics (Cheney & Seyfarth, 1981). However,
28
29 682 it could be speculated that the surprise (or ‘startle’) caused by an unexpected alarm call may
30
31 683 also directly deter predators if the prey’s call releases a threat-avoidance response. In
32
33 684 response to copepod (*Acartia tonsa*) attack some dinoflagellates (*Pyrodinium bahamense* and
34
35 685 *Lingulodinium polyedrum*) use bioluminescent flashes as ‘burglar alarms’ to draw in copepod
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37 686 predators, but such flashes may also act to release a rapid threat response in the copepods
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39 687 directly (Hanley & Widder, 2017).
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47 689 *(f) Vibrations*

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49 690 Substrate and airborne signals may constitute vibratory deimatism if they cause a threat-
50
51 691 avoidance response in an attacker. In many species disturbance-induced vibration increases
52
53 692 handling time and decreases predation risk (Bauer, 1976; Smith & Langley, 1978; Masters,
54
55 693 1979; Buchler, Wright & Brown, 1981; Lewis & Cane, 1990; Guedes *et al.*, 2012; Low,
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57 694 2012), although some studies have found no evidence for protection against predation
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3 695 (Gotch, 1997; Corey & Hebets, 2020). The studies that showed little protective value tested
4
5 696 vertebrate predators, which may not be the target receivers. For example, vibrations that can
6
7 697 successfully reduce parasitoid attacks (Low, 2012), and vibrations by spiders (Corey &
8
9 698 Hebets, 2020) could be deimatic to predatory piratid spiders but useless against birds or
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11 699 predacious damselflies. However, further work is needed to determine definitively whether
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13 700 these actions cause a threat-avoidance response in an attacker (and therefore are deimatic), or
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15 701 whether the vibrations function to reduce attack by other mechanisms, such as making the
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17 702 prey more challenging to handle.
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704 (g) *Moth clicks*

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26 705 Moth clicks, produced by tymbalation and stridulation (Corcoran & Hristov, 2014), have
27
28 706 been attributed many functions including startling predators and sonar jamming, and are
29
30 707 performed by both chemically defended and undefended species. Fullard & Fenton (1977)
31
32 708 suggested that while most sound-producing tiger moths in southern Ontario respond to
33
34 709 simulated bat echolocation calls with sound, others do not, and must be physically handled to
35
36 710 elicit defensive sound production. Playback experiments suggested that substrate-gleaning
37
38 711 bats are deterred by contact-elicited tiger moth clicks (Stoneman & Fenton, 1988; Bates &
39
40 712 Fenton, 1990). However, flight room interactions between wild bats and live tiger moths
41
42 713 suggest that while they click in response to being handled by a gleaning bat, in the wild
43
44 714 sound-producing tiger moths suffer similarly high mortality as silent species (Ratcliffe &
45
46 715 Fullard, 2005). Hristov & Conner (2005) showed that naïve big brown bats (*Eptesicus*
47
48 716 *fuscus*) are repelled by tiger moth clicks (four species of Arctiidae), but that they rapidly
49
50 717 learn to ignore the clicks unless the prey is also unpalatable. An intriguing, but untested,
51
52 718 possibility is that these sounds are more readily associated with chemical defence precisely
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54 719 because they are deimatic, under the assumption that a negative signal can be more easily
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3 720 associated with a negative consequence than can a neutral or positive acoustic signal
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5 721 (Guilford & Dawkins, 1991; Ratcliffe & Fullard, 2005; Ter Hofstede & Ratcliffe, 2016).

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10 723 *(h) Rattles*

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12 724 The antipredator strategy of rattlesnakes, porcupines, and other animals that ‘rattle’ may
13
14 725 include deimatism (Edmunds, 1974). In rattlesnakes, the sound is produced by the impact of
15
16 726 keratin scales against each other (Gans & Maderson, 1973), while in porcupines the sound is
17
18 727 from knocking quills together and is made when a threat is perceived (Edmunds, 1974). Data
19
20 728 on how naïve and experienced predators respond to rattles are required to determine their
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22 729 function. Presumably many predators can learn to associate the sound with a threat and thus
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24 730 rattles likely have an aposematic function, while in naïve individuals the sound may have a
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26 731 deimatic effect.

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33 733 *(i) Facultative flatulence*

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35 734 Herring (*Clupea harengus*) facultatively force air through the anus in an antipredator context
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37 735 (Wahlberg & Westerberg, 2003). Air is apparently actively gulped at the water surface and
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39 736 then later expelled from the herring’s anus when they are under duress. The resultant sounds
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41 737 and bubbles may function as an acoustic and optic screen to confuse a pursuing predator
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43 738 (Wahlberg & Westerberg, 2003)

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46 739 The use of facultative flatulence in fish is still poorly understood, and it may be the
47
48 740 case that it is used more often in the context of inter-individual communication than defence
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50 741 (Wilson, Batty & Dill, 2004). However, it may be speculated that rapid bursts of bubbles
51
52 742 could trigger reflexive responses in a predator, such as avoiding a crashing wave. Therefore,
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54 743 facultative flatulence could have the potential to be a deimatic defence, but further work is
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56 744 needed to determine definitively whether this is the case.

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3 745
45 746 **IV. EVOLUTION OF DEIMATIC BEHAVIOUR**

7 747 Understanding the evolution of complex traits like deimatism is challenging, especially
8 748 because behaviours are difficult and costly to measure. Evolutionary models are required to
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10 749 provide explicit hypotheses for experimental testing. Where data are available, comparative
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12 750 approaches also provide important opportunities to generate and test hypotheses on the
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14 751 evolution of deimatic behaviours. This can be done by establishing when and in what
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16 752 lineages deimatism has evolved or been lost, and what ecological factors may be associated
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18 753 with its evolution.
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26 755 **(1) Evolutionary pathways to deimatism**

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28 756 *Umbers et al.* (2017) formally proposed two potential pathways for the evolutionary
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30 757 origins of deimatic behaviour; the ‘defence-first’ and ‘startle-first’ hypotheses. The defence-
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32 758 first hypothesis suggests that the acquisition of some form of chemical defence or weapon
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34 759 precedes the acquisition of a deimatic behaviour (itself also a defence). Under this
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36 760 hypothesis, the acquired defence facilitates the evolution of, for example, a conspicuous
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38 761 aposematic colour signal, the costs of which can be offset by concealment, revealing it only
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40 762 when the prey perceives a threat. The defence-first hypothesis can also include revealing or
41
42 763 highlighting weapons, possibly from the ritualisation of counter-attack behaviour (Lieshout,
43
44 764 Elgar & Wilgenburg, 2005). For example, during their deimatic behaviour, many mantises
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46 765 highlight their large raptorial forelimbs which are used in prey capture and retaliation
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48 766 (*O’Hanlon et al.*, 2018; *Vidal-García et al.*, 2020). However, unless further defences are lost
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50 767 upon the evolution of deimatic behaviour, the numerous examples of deimatism not
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52 768 obviously associated with a chemical or weaponry defence require other evolutionary routes.
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3 769 The startle-first hypothesis suggests that the act of performing the behaviour itself has
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5 770 protective value and can allow the evolution of further defences. Given our objections above
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7
8 771 concerning the use of the word ‘startle’, perhaps ‘behaviour-first hypothesis’ is a better name.
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10 772 Vidal-García *et al.* (2020) found indirect evidence to support this behaviour-first hypothesis,
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12 773 as they reported that wings were used by 29 of 31 displaying mantis species including 11
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14 774 species in relatively basal phylogenetic positions that lacked hidden colours. In a behavioural
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17 775 study, Holmes *et al.* (2018) showed that movement alone can be protective but that a
18
19 776 combination of colour and movement increased survival. Similarly, using a robotic moth and
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21 777 wild black-capped chickadees (*Poecile atricapillus*), Kang, Zahiri & Sherratt (2017) showed
22
23 778 that prey movement alone, without other defensive components like colours, can elicit
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25
26 779 responses consistent with responses to deimatic behaviour in birds.

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28 780 Flash behaviour – repeated signalling while fleeing that inhibits predator pursuit –
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30 781 could represent an intermediate step in either the startle-first or defence-first trajectories; after
31
32 782 signals are obtained but before they are used in deimatic behaviour (Umbers *et al.*, 2017)
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34 783 (Table S2). In their study of the *Pleurodema* frogs, Faivovich *et al.* (2012) mapped flash
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36 784 behaviour and deimatic behaviour on a phylogeny and suggested that deimatic behaviour
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38 785 occurs in more derived species and flash behaviour in more basal species. However, it is
39
40 786 unclear how flash behaviour and deimatic behaviour were defined and quantified (Faivovich
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42 787 *et al.*, 2012). Further comparative analyses that map the evolution of flash behaviour and
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44 788 deimatic behaviour are needed to test this hypothesis.

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50 51 790 **(2) Modelling the evolution of deimatic behaviour**

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53 791 Theoretical models of deimatic behaviour have so far been mostly descriptive, qualitative
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55 792 arguments, although mathematical models of related phenomena have been developed.

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57 793 Theory in this area is necessary to formalise arguments and make testable predictions. Below
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3 794 we highlight key considerations when developing mathematical models of deimatic
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5 795 behaviour.

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8 796 The evolution of antipredator defences is best considered as a co-evolutionary
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10 797 process, in which any adaptation in prey that reduces their vulnerability to predation also
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12 798 affects the nature of selection on predators and *vice versa* (Dawkins & Krebs, 1979; Abrams,
13
14 799 2000). A self-consistent co-evolutionary model (Houston & McNamara, 2006) of the
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16 800 evolution of deimatic behaviour therefore requires an understanding of the nature of selection
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18 801 on *both* predators and prey, with the aim of characterising their plausible co-evolutionary
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20 802 states (such as a mutual equilibrium and/or stable limit cycle; Otto & Day, 2011).
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22 803 Importantly, deimatism may not necessarily involve co-evolution. It might simply be a result
23
24 804 of the ‘wiring’ of the attacker’s brain and cognitive processes that developed in other
25
26 805 contexts, thereby requiring no co-evolution and no learning. However, the fitness
27
28 806 consequences of these processes should be considered for both the attacker and the displaying
29
30 807 individual. Several co-evolutionary models of predator–prey interactions have been
31
32 808 developed (Abrams, 2000; Mougi & Iwasa, 2010; Tien & Ellner, 2012; Bateman, Vos &
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34 809 Anholt, 2014), but we are not aware of any developed specifically for understanding the
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36 810 evolution of deimatic behaviour.

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42 811 Deimatic behaviours are typically not primary defences but rather back-up defences
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44 812 deployed at the prey’s discretion (Umbers, Lehtonen & Mappes, 2015). This can be
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46 813 formalised in modelling terms by viewing deimatic behaviours as one defence in a sequence
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48 814 of antipredator defences (Fig. 2). If the primary defensive strategy is highly effective in
49
50 815 preventing predation, this may impede selection on further defences that are invoked only
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52 816 when the primary defence fails (Britton, Planqué & Franks, 2007; Wang *et al.*, 2019). Such
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54 817 ‘strategy blocking’ may lead to cross-species associations between primary and subsequent
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56 818 defences (such as deimatism) mediated by factors that affect the upper limit on the primary
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3 819 defence, such as body size (Kang *et al.*, 2017) (for further discussion of body size, see
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5 820 Section IV.4a). From an evolutionary perspective, perhaps the most fundamental question is:
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7 821 *what is the selective advantage for a predator responding to deimatic behaviour?* It is a
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9 822 behavioural response that comes at the cost of energy expenditure and opportunities missed,
10
11 823 so what are its benefits? If it is a rapid response to a potential threat (Simons, 1996), it may
12
13 824 save the life of the receiver, or prevent injury. Signal detection theory quantifies the optimal
14
15 825 trade-off between type I error (such as twigs treated as snakes, ‘false alarms’) and type II
16
17 826 errors (snakes treated as twigs, ‘misses’) (Leavell & Bernal, 2019). If the costs of mistaking a
18
19 827 snake for a twig far outweigh the costs of mistaking a twig for a snake, then a conservative
20
21 828 threshold with a high false alarm rate would be optimal, even when the likelihood of the
22
23 829 stimulus coming from a true threat is small (Castellano & Cermelli, 2015). While signal
24
25 830 detection models identify the optimal response under uncertainty, speed–accuracy trade-offs
26
27 831 need to be included (Chittka, Skorupski & Raine, 2009). If the stimulus is sudden, such as
28
29 832 that caused by dangerous events like the rush of a potential predator or a tree falling, then
30
31 833 quick action will be favoured over careful deliberation. As Janzen *et al.* (2010, p. 11659),
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33 834 puts it “*pause a millisecond to ask whether that eye belongs to acceptable prey or to a*
34
35 835 *predator, you are likely to be—and it takes only once—someone’s breakfast*”.

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42 836 Models that combine signal detection and speed–accuracy trade-offs have been
43
44 837 developed and take the form of sequential sampling models in which additional inspections to
45
46 838 gain more information come at a cost (e.g. Getty, 1996; Abbott & Sherratt, 2011).
47
48 839 Complementary models have separated the two processes almost entirely. For example,
49
50 840 motivated by empirical evidence, Trimmer *et al.* (2008) represented mammalian brains as
51
52 841 having two decision-making systems, both Bayesian in nature but acting at different speeds.
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54 842 The first quick-but-inaccurate thalamic decision is assumed to be based on a one-off
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56 843 application of signal-detection theory involving a simple (and conservative) threshold for
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3 844 treating stimuli as threats, whereas the slow-but-accurate cortical decision is based on the
4
5 845 sequential probability ratio test (SPRT) as more evidence governing how to act is gathered
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7 846 over time (Wald, 1945; Castellano, 2015). Natural selection appears to have favoured an ‘act
8
9 847 now, think later’ response to certain stimuli because only quick action can save the observer’s
10
11 848 life and, like many behaviours, this response can be exploited by potential prey. Modelling
12
13 849 can help clarify why the responses are rapid, and how they continue to be maintained despite
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15 850 a high propensity for false alarms.

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19 851 Finally, there are other features of the response to deimatic behaviour that can be
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21 852 understood using mathematical models. For example, the prior presentation of a stimulus
22
23 853 associated with an undesirable event tends to generate a more vigorous response to an
24
25 854 unrelated stimulus (Brown, Kalish & Farber, 1951); a result readily understood through
26
27 855 Bayesian conditioning models (Bach, 2015). Likewise, habituation to a stimulus can be
28
29 856 modelled through Bayesian learning in which the conditional probability of the signaller
30
31 857 being a threat is updated over time as more information is gained. A related set of questions
32
33 858 revolve around why some species’ deimatic behaviours inhibit would-be predators long after
34
35 859 the initial reflex-like response. Of course, even if rapid habituation occurs under experimental
36
37 860 conditions, then it may not be realised under more natural conditions. In particular, it is
38
39 861 possible that some observers and/or signallers would flee following a deimatic display if it
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41 862 they were able to do so. Even if only a small proportion of attackers or signallers respond in
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43 863 this way, it can still be selected for as a last-resort defence even if there is no long-lasting
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45 864 inhibitory effect from the display.

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52 53 866 **(3) Comparative analyses and the evolution of deimatic behaviour**

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55 867 Crane (1952), Edmunds (1972, 1976), Blest (1957*b*), and Brodie (1983) on mantises, moths
56
57 868 and salamanders were the first to compare the diversity and systematic patterns of deimatic
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2
3 869 behaviour among species. The detailed descriptions and observations of deimatic behaviour
4
5 870 now available allow phylogenetic analyses (Vidal-García *et al.*, 2020) to investigate when
6
7 871 and why deimatism evolves and is lost. Kang *et al.* (2017) assessed the evolution of hidden
8
9 872 hindwing colours in erebid moths (Noctuoidea: Lepidoptera) assuming that their hidden
10
11 873 colours are used in deimatic behaviour. Their results suggested that basal erebid moths lack
12
13 874 hidden colours, that hidden colours are a derived trait, and that it has evolved multiple times
14
15 875 across the family. In phylogenetically controlled analysis of hidden colours in a further five
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17 876 insect taxa, Orthoptera, Mantodea, Phasmatodea, Saturniidae and Sphingidae, Loeffler-
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19 877 Henry, Kang & Sherratt (2019) found evidence for the repeated evolution of hidden
20
21 878 contrasting colours dozens of times among these five groups. A comparative analysis by
22
23 879 Bura, Kawahara & Yack (2016) found that what they termed acoustic startle defences
24
25 880 (Dookie *et al.*, 2017) have evolved multiple times in caterpillars from multiple lepidopteran
26
27 881 subfamilies in Sphingidae and Saturniidae. They found that short clicking sounds were
28
29 882 typically followed by regurgitation while longer, louder sounds were not and thus the short
30
31 883 clicking sound form seems to be associated with the expulsion of chemical defence. The
32
33 884 ancestral state reconstruction of deimatic displays in 58 mantis genera by Vidal-García *et al.*
34
35 885 (2020) included behavioural data as well as descriptions of colour patterns and body size on
36
37 886 the presence and absence of deimatic behaviour. Their findings suggest that some form of
38
39 887 camouflage without deimatic behaviour is the ancestral state in mantises, and that it has
40
41 888 evolved at least four times across the Mantodea (Vidal-García *et al.*, 2020). They also show
42
43 889 that deimatic behaviour has evolved in species without any associated colour patterns and
44
45 890 that inclusion of behavioural data is important. By contrast, placing data from 25 of Brodie's
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47 891 salamander descriptions into a phylogenetic context shows gains, losses, and variability of
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49 892 deimatic behaviour, but deimatic behaviour is found in the most basal lineages included in
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3 893 the tree (Fig. 4). These studies all confirm the conclusions of the earlier comparative studies,
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5 894 that deimatic behaviours are frequently gained and lost as a lineage diversifies.
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7
8 895 The processes driving gains and losses of deimatic behaviour are unclear. In praying
9
10 896 mantises there is a hint that deimatic behaviour evolved in response to the evolution of birds,
11
12 897 appearing roughly 60 million years ago (Vidal-García *et al.*, 2020). So far, no phylogenetic
13
14 898 comparative studies have included the required data to test hypotheses on ecological drivers
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16 899 such as predator diversity, population density, habitat type and activity time, but such
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18 900 analyses would make a valuable contribution to elucidating the evolutionary timing and
19
20 901 ecological correlates of deimatic behaviour.
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24 902

25 26 903 **(4) Traits associated with the evolution of deimatic behaviour**

27
28 904 Several hypotheses have been proposed suggesting that the evolution of deimatic behaviour
29
30 905 is related to body size, degree of unprofitability, and phenology.
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34 35 907 *(a) Deimatic behaviour and body size*

36
37 908 The literature provides mixed support for the hypothesis that larger species are more likely to
38
39 909 perform deimatic behaviours. Kang *et al.* (2017) suggested that hidden colours are more
40
41 910 common in large species than in small species of Erebiidae moths. In a taxonomically broader
42
43 911 study, Loeffler-Henry *et al.* (2019) also found evidence of a positive correlation between
44
45 912 body size and hidden colouration for four insect taxa (Orthoptera, Phasmatidae, Mantidae,
46
47 913 Saturniidae) but not for Sphingidae. More nuanced still, particular colours may be correlated
48
49 914 with body size. Emberts *et al.* (2020) studied 26 species of leaf-footed bugs (Coriidae) and
50
51 915 found an association between large size and deimatic behaviour only in species with white
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53 916 hidden patches, but not in those with red/orange patches. These studies suggest that certain
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55 917 colours of signals revealed by deimatic behaviour are more common in larger species but do
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2
3 918 not address whether deimatic behaviour itself is more common in larger species. However, a
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5 919 phylogenetically controlled analysis on 58 praying mantis species that included behaviour,
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7 920 sound production, and hidden colours found no support for the hypothesis that larger species
8
9 921 were more likely to exhibit deimatic behaviour (Vidal-García *et al.*, 2020). Discrepancies
10
11 922 between this study and that of Loeffler-Henry *et al.* (2019) are likely due to differences in the
12
13 923 sizes of species sampled. Some deimatic species lacked hidden colouration suggesting that a
14
15 924 relationship between the presence of hidden colours and size does not extend to deimatic
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17 925 behaviour *per se*.

21 926 If larger prey have deimatic behaviour because they are more likely to be attacked due
22
23 927 to their profitability as a larger meal, then why do so many deimatic behaviours include an
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25 928 apparent body size increase? One hypothesis is that it is not their profitability, but their
26
27 929 conspicuousness that puts larger species under greater predation pressure (Pembury Smith &
28
29 930 Ruxton, 2021). If this is true, then appearing to become larger only when performing a
30
31 931 deimatic behaviour would lower predation risk only if the behaviour was performed once the
32
33 932 prey had already been detected. One species which may be using this defence is the European
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35 933 cuttlefish. Underwater trials with young laboratory-reared cuttlefish released into natural
36
37 934 habitats demonstrated that predatory groupers (*Serranus cabrilla*) ceased their attack
38
39 935 sequence when the cuttlefish rapidly deployed their deimatic body pattern (Fig. 11) while
40
41 936 flattening their body to create the illusion of a larger body size. When this deimatic behaviour
42
43 937 was not deployed, attacks continued and some cuttlefish were eaten (Hanlon & Messenger,
44
45 938 1988).

51 939 Additionally, larger prey may be more effective at confusing predators or eliciting the
52
53 940 looming reflex in receivers during deimatic behaviour (see Section II.7b). Alternatively, an
54
55 941 increase in size could be related to making the prey more challenging to consume,
56
57 942 particularly if the increased size exceeds the maximum gape size of the predator. New theory
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3 943 and further research are needed to determine how body size and deimatic behaviour interact
4
5 944 considering trophic level, predator diversity, and other ecological factors.
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10 946 *(b) Deimatic behaviour and prey profitability*

11
12 947 Many textbooks suggest that deimatic behaviour is performed by ‘undefended’ species and is
13
14 948 therefore a ‘bluff’. We disagree with this description for two reasons. One, we argue that
15
16 949 deimatic behaviour itself has protective value and therefore cannot be a bluff, and two this
17
18 950 stands regardless of the presence of any further defences such as repellent tastes (Rowland,
19
20 951 Ruxton & Skelhorn, 2013), toxins (Barnett *et al.*, 2012), weapons (Speed & Ruxton, 2005),
21
22 952 protean escape (Edmunds 1974), and impenetrable armour (Wang *et al.*, 2018). In the
23
24 953 venomous cottonmouth snake (*Agkistrodon piscivorus*) the use of deimatic behaviour has
25
26 954 been found to be a reliable indicator of an individual’s willingness to strike (Glaudas &
27
28 955 Whine, 2007). Beyond this we are not aware of any formal studies testing what drives or
29
30 956 correlates with deimatic behaviours and the presence of further defences. The main challenge
31
32 957 is defining ecologically relevant unprofitability and a model taxon.
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40 959 *(c) Deimatic behaviour and phenology*

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42 960 Kim *et al.* (2020) compiled data on colour, phenology, and abundance for 1,568 macro-
43
44 961 lepidopteran species on three continents (Asia, Europe, and North America) and found that
45
46 962 species with hidden contrasting colours that are putatively used in deimatic behaviour appear
47
48 963 later in the season than the species with other colour defences. This finding is interesting as it
49
50 964 may be expected that deimatic behaviour would be most effective against naïve predators,
51
52 965 and therefore would be most protective earlier in the season. However, it could be that a
53
54 966 protective effect against naïve predators may be quickly diluted by predator learning. Thus,
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56 967 the fitness benefit of appearing early in the season may not be significant because this
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3 968 protective effect does not contribute significantly to the survival of adult insects (until they
4
5 969 reproduce). On the other hand, a protective effect through mimicry may remain stable
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7
8 970 because predators' avoidance learning remains for longer and more consistently (and perhaps
9
10 971 reinforced continuously through their experience with various aposematic prey).

12 972 Some species with deimatic behaviours may gain protection because they reveal a
13
14 973 signal that is a Batesian mimic of defended species. This could be an effective defence if
15
16
17 974 predators generalise signals or if those signals are highly effective against naïve predators. If
18
19 975 species with deimatic behaviours derive a selective advantage by delaying their activities
20
21 976 until local predators have learned to avoid aposematic signals, it would be interesting to test
22
23 977 how this fits into mimic–model systems in Batesian mimicry theory (Waldbauer, Sternburg &
24
25 978 Maier, 1977).

28 979

30 980 **V. ONTOGENY OF DEIMATIC BEHAVIOUR**

31
32
33 981 Juveniles and adults differ in important ecological and morphological ways and thus may
34
35 982 employ different defences. However, ontogenic changes in the presence and absence of
36
37 983 deimatic behaviour, and more subtle differences in their performance during development,
38
39 984 are only known for multiple life stages in a few species (Table S4).

40
41
42 985 In animals that undergo 'complete' metamorphosis, the differences between juveniles
43
44 986 and adults may require different defensive strategies due to differences in mobility, habitat,
45
46 987 and diet. Holometabolous insects provide many examples of deimatic behaviour at only one
47
48 988 life stage, and we found no descriptions of deimatism for both larval and adult life stages
49
50 989 (Table S4). Lepidopteran larvae (caterpillars) provide excellent examples of deimatic
51
52 990 behaviour as juveniles but the presence of deimatic behaviours in their adult forms is often
53
54 991 unknown. However, in peacock butterflies the reverse is true: adults use deimatic behaviour,
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56 992 whereas we found no evidence of deimatic behaviour in their caterpillars. Ambystomid
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1
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3 993 salamanders also undergo a dramatic metamorphosis, only after which do they exhibit
4
5 994 deimatic behaviour. In Anderson's crocodile newt (*Echinotriton andersoni*), aquatic larvae
6
7
8 995 do not posture, but just one day after they reabsorb their gills terrestrial juveniles can perform
9
10 996 an extreme version of the deimatic behaviours seen in mature adults, in which they can bring
11
12 997 their ribs forward at an angle of 90° to their spine to pierce the skin (Brodie, Nussbaum &
13
14 998 Digiovanni, 1984). The posturing behaviour could be deimatic, with the protrusion of ribs
15
16
17 999 perhaps preparation for retaliation, or a deterrent by exceeding a predator's gape. Such
18
19 1000 differences between adult and juvenile defences may reflect adaptations to their different
20
21
22 1001 aquatic and terrestrial habitats.

23
24 1002 For animals that undergo relatively gradual changes in morphology over their life
25
26 1003 stages, data on changes in deimatic behaviour with ontogeny were available for some
27
28 1004 mantises, orthopterans, and squid (Table S4). The double eye-spot mantis (*Stagmatoptera*
29
30 1005 *biocellata*) uses crypsis as its sole method of predator defence in the first and second instar,
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32
33 1006 whereas intermediate instars (3–7) use both crypsis and deimatic behaviours, and adults
34
35 1007 primarily use deimatic behaviours (Balderrama & Maldonado, 1973). The authors suggested
36
37 1008 that relying on deimatic displays may be too risky when individuals are small and relatively
38
39 1009 easy prey, and that their stick-like morphology may allow camouflage. Adults with their
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41
42 1010 more prominent head may prevent them from mimicking sticks as effectively, reducing their
43
44 1011 camouflage and increasing pressure for the evolution of deimatism as a secondary defence. In
45
46
47 1012 the mantis *Angela guianensis*, adults use deimatic wing displays, while juveniles rely on
48
49 1013 running and dropping. In the Texas unicorn mantis (*Phyllovates chlorophaea*) and Peruvian
50
51 1014 shield mantis (*Choeradodis rhombicollis*) juveniles also run and drop in defence. The
52
53 1015 deimatic behaviour of adult *P. chlorophaea*, on the other hand, reveals yellow and black
54
55 1016 bands on their dorsal abdomen, while that of adult *C. rhombicollis* includes rearing up and
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57 1017 posturing towards the attacker. Juveniles also rely on fleeing in several orthopterans. In the
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1
2
3 1018 katydid *Scorpiorinus fragilis* (Pseudophyllinae), nymphs rely on escape while adults reveal
4
5 1019 their yellow dorsal abdomen in response to touch by lifting their wings which produces a
6
7 1020 stridulatory sound (Robinson, 1969). Adults of the stick insect, *Metriotes diocles* raise their
8
9 1021 wings in a deimatic display while nymphs tend to drop and use thanatosis to avoid
10
11 1022 consumption (Robinson, 1969). Differences during ontogeny have also been reported in the
12
13 1023 defensive behaviour of two species of squid, Atlantic brief squid (*Lolliguncula brevis*) and
14
15 1024 longfin inshore squid (*Doryteuthis pealeii*) (York & Bartol, 2016). Paralarvae (hatchlings) of
16
17 1025 *D. pealeii* were more likely to use transparency in response to predators whereas juveniles
18
19 1026 and adults of *L. brevis* were more likely to perform deimatic behaviours. It is possible that
20
21 1027 relying on crypsis alone for adults is too costly or risky, or that deimatic behaviour in
22
23 1028 juveniles is less effective, or perhaps both. By contrast, juvenile cottonmouth snakes
24
25 1029 (*Agkistrodon piscivorus*) are more likely than adults to use deimatic behaviour (Glaudas,
26
27 1030 Winne & Fedewa, 2006). A possible explanation is that adult cottonmouths may face a
28
29 1031 sufficiently low predation risk that the energetic costs of deimatic behaviour are not justified.
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31 1032 Together, these findings suggest a species-specific use of deimatic displays at different life
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33 1033 stages.

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39 1034 Changes in deimatic behaviour across development can be more subtle than simple
40
41 1035 presence or absence. For example, in European cuttlefish, hatchlings, juveniles and adults use
42
43 1036 different body patterns and postures as deimatic displays (Hanlon & Messenger, 1988).
44
45 1037 Similar examples of subtle changes in deimatic behaviour during development have been
46
47 1038 observed in the mountain katydid (*Acripeza reticulata*). Subadults have orange and black
48
49 1039 intersegmental abdominal membranes which are visible when they move (Table S4). Adults,
50
51 1040 by contrast, have large mottled brown wings which completely hide their red, blue, and black
52
53 1041 striped abdominal surface. Umbers & Mappes (2015) found that when performing deimatic
54
55 1042 behaviour, subadult mountain katydids held their position for longer than adults, perhaps
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2
3 1043 because they lack the tough wings of adults. Lacking tough wings may mean juveniles rely
4
5 1044 more on their deimatic behaviour and the aposematic signal it reveals which could select for
6
7 1045 longer display times (Baker, 2019). Because subadults lack wings and therefore cannot fly,
8
9 1046 their extended display may compensate for their reduced opportunity to escape. By contrast,
10
11 1047 the Western Australian katydid (*Mygalopsis marki*) develops auditory deimatic behaviour
12
13 1048 very early in life. Both adults and nymphs stridulate, producing a sound within their head
14
15 1049 capsule, and this behaviour is maintained throughout ontogeny despite major morphological
16
17 1050 changes (Bailey & Sandow, 1983), however nymphs are more likely to attempt to escape
18
19 1051 during the early stages of the predation sequence and stridulate when caught, whereas adults
20
21 1052 posture while stridulating when faced with a predator. This example may suggest that the
22
23 1053 constraints on deimatic behaviours involving visual signals and auditory signals may vary,
24
25 1054 and may arise at different stages across ontogeny.

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30
31 1055 The level of cognition involved in prey display performances is mostly undocumented
32
33 1056 but there is some evidence that individuals improve their displays as they develop.
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35 1057 Sunbitterns (*Eurypyga helias*) are large birds that reveal eyespots on their wings when
36
37 1058 threatened. Thomas & Strahl (1990) described young sunbitterns practicing their wing
38
39 1059 displays from seven days old and performing full wing displays from 12 days old until they
40
41 1060 left the nest two to three weeks later. They observed nestlings displaying to falling leaves and
42
43 1061 butterflies, perhaps mistakenly or instinctively. These results may suggest that the risk of
44
45 1062 drawing attention to themselves on the nest before they can fly is outweighed by the benefit
46
47 1063 of mastering the behaviour before fledging, a hypothesis for future testing.

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51 1064 Taken together, the available evidence seems to support the view that deimatic
52
53 1065 behaviours are more likely to be found in adult animals, but whether this is a research bias or
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55 1066 is biologically important is unclear. Body size could be a factor driving the presence and
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3 1067 absence of displays at different life stages (see Section IV.4a), but this and alternative
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5 1068 explanations such as differing niches or activity levels remain to be tested.
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10 1070 **VI. CAUSATION OF DEIMATIC BEHAVIOUR**

11
12 1071 Tinbergen (1963) described causation as the physiology of behaviour, encompassing both the
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14 1072 underlying molecular, physiological and cognitive processes, now more commonly called
15
16 1073 mechanisms. We summarise what is known about triggers that release deimatic behaviour,
17
18 1074 and special mechanisms by which the behaviours are performed. Predator cognition and
19
20 1075 behaviour drive the evolution of deimatic behaviour and we discuss the putative
21
22 1076 psychological mechanisms involved (Fawcett, Marshall & Higginson, 2015).
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26 1077 27 28 1078 **(1) Releasers of deimatic behaviour**

29
30 1079 Deimatic behaviours may be released by being touched, hearing a sound, detecting a smell, or
31
32 1080 seeing a visual signal (Table S3). Experimental evidence from studies using ecologically
33
34 1081 relevant predators is rare, with most data coming from experiments where predation is
35
36 1082 simulated by humans. Triggers in some sensory modes may be more likely to release
37
38 1083 deimatic behaviour than others, more likely to release different components of deimatic
39
40 1084 behaviour, and/or release different levels of intensity. In some katydids and mantises most
41
42 1085 individuals perform their deimatic behaviour in response to tactile rather than visual stimuli,
43
44 1086 and more invasive stimuli evoke more intense displays (Umbers & Mappes, 2015; O'Hanlon
45
46 1087 *et al.*, 2018). Maldonado (1970) experimentally investigated the effects of visual and tactile
47
48 1088 triggers on mantises. When visual cues were obliterated by covering the eyes, tactile cues still
49
50 1089 released the full display, however, a visual releaser resulted in a longer display. More work
51
52 1090 needs to be done to determine which cues, signals, and their components are most effective in
53
54 1091 releasing deimatic behaviour. Mechanistic and sensory constraints, including noise, probably
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2
3 1092 determine the type of stimuli prey respond to and the fitness consequences of their responses
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5 1093 (Cooper & Blumstein, 2015).
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10 1095 **(2) Mechanisms of components of deimatic behaviour**
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12 1096 Deimatic behaviour can target any sensory mode although most work has focused on visual
13
14 1097 components. We assume many of the physiological and psychological mechanisms
15
16 1098 associated with deimatic behaviour have not evolved *de novo*, but were co-opted from other
17
18 1099 functions. For example, the muscles used in butterfly flight are presumably the same as those
19
20 1100 used to move their wings during deimatic behaviour. We note that well-understood pathways
21
22 1101 present opportunities to measure costs and their evolutionary history.
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26 1102
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28 1103 *(a) Visual components: colour, movement, and size*
29

30 1104 Many deimatic behaviours reveal colour patterns hidden under wings, legs, fins, bellies,
31
32 1105 inside mouths, and/or on flaps of neck skin. To date there is no evidence that colours
33
34 1106 associated with deimatic behaviour are produced *via* mechanisms different from those used in
35
36 1107 other signals, although some observations suggest that hiding colour patches could reduce
37
38 1108 maintenance costs. For example, in mountain katydids that have one tegmen missing,
39
40 1109 abdominal colours are bleached where they are exposed but retained where they are covered
41
42 1110 (K.D.L. Umbers, personal observation).
43
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46 1111 Most insect deimatic behaviour includes the movement of legs and/or wings. The
47
48 1112 mechanisms of movement involved in deimatic behaviour have been directly manipulated in
49
50 1113 the nervous system of praying mantises. Maldonado (1970) determined that the components
51
52 1114 of deimatic behaviour performed varied depending on which nerves were severed. A cut
53
54 1115 between the suboesophageal and prothoracic ganglia resulted in only the head and mouth
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1
2
3 1116 responding to visual stimuli, and the rest of the body required tactile stimulation to respond
4
5 1117 (Maldonado, 1970).

7 1118 The 'unken reflex', named after the fire-bellied toads 'Feuerunke' (Löhner, 1919), is a
9
10 1119 proximate cause of deimatic behaviour but little is known about its mechanistic
11
12 1120 underpinnings. Typically only applied to amphibians, it manifests as a rigid arching or lifting
13
14 1121 of the body, legs, and/or tail in which ventral surfaces become visible and sometimes body
15
16 1122 parts are 'hypnotically' swayed (Brodie, 1977). For example, Colombian four-eyed frogs
17
18 1123 (*Pleurodema brachyops*) lift their hind quarters to reveal eyespots and colour patches, and
19
20 1124 highlight poison glands (Martins, 1989). In some salamanders, deimatic behaviour includes
21
22 1125 their ribs penetrating the skin in special areas of the integument with poison glands. Whether
23
24 1126 this is caused by the same process as the posturing is unclear (Brodie, 1977, 1983; Nowak &
25
26 1127 Brodie, 1978).

30 1128 Few morphological structures seem to have evolved for use in deimatic behaviour. A
31
32 1129 promising candidate, however, is 'hooding' in snakes (Table S3). During hooding, cobras
33
34 1130 (*Naja* spp.) use eight muscles and putatively novel nervous rewiring to elevate and protract
35
36 1131 the ribs, while flattening and expanding the neck (Young & Kardong, 2010; Jara &
37
38 1132 Pincheira-Donoso, 2015). Other specialised structures may exist and future work beyond
39
40 1133 traditional model systems will probably highlight other traits.

44 1134 Cephalopods provide a clear exception to movement of large body parts in deimatic
45
46 1135 behaviour, with their colour patterns displayed and changed by chromatophores (Langridge,
47
48 1136 2009). Chromatophore colour change is controlled by the dispersal and concentration of
49
50 1137 pigments *via* intracellular innervated radial muscles (Messenger, 2001; Hanlon & Messenger,
51
52 1138 2018). The most well-studied cephalopod deimatic behaviour is that of the European
53
54 1139 cuttlefish, which produce dark rings around the eyes and dark eyespots on the dorsum
55
56 1140 (Holmes, 1940; Langridge, Broom & Osorio, 2007) (Fig. 1I). Their deimatic pattern is
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1
2
3 1141 complex, comprising six signalling elements that can be expressed in different combinations:
4
5 1142 (1) flattened body posture; (2) paling of the skin; (3) paired mantle spots that look like eyes;
6
7 1143 (4) a dark fin line; (5) a dark eye ring; and (6) a dilated pupil. They can also produce
8
9 1144 directional displays presenting deimatic patterning only towards the predator and cryptic
10 1145 patterning away from the predator (Langridge, 2006), indicating that their neural mechanisms
11
12 1146 allow targeted responses.
13
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16
17 1147 Movements included in deimatic behaviour are not restricted simply to the performer
18
19 1148 changing state from resting to displaying, they may continue throughout the performance as
20
21 1149 re-orienting or rhythmical repetition. For example, during deimatic behaviour mountain
22
23 1150 katydids reorient their distasteful brightly coloured abdomen towards their attacker (Umbers
24
25 1151 & Mappes, 2015; Umbers *et al.*, 2019). The peacock butterfly's rhythmic deimatic behaviour
26
27 1152 involves their wings being opened and closed in succession at a constant rate (Blest, 1957*b*).
28
29 1153 The devil's flower mantis (*Indolomantis diabolica*) moves its outstretched forelimbs back
30
31 1154 and forth in a pendulum-like fashion. Many salamanders sway or undulate their tails
32
33 1155 'hypnotically' throughout their display. The efficacy of displays with and without repeated
34
35 1156 movement has not been compared but in many cases rhythmical movements are associated
36
37 1157 with sound production which adds further complexity (Blest, 1957*b*; Vallin *et al.*, 2005)
38
39 1158 (Table S3). Rhythmic signals may be much more effective in stimulating the receiver than
40
41 1159 sustained displays if they avoid sensory adaptation in the predator. Signalling at random time
42
43 1160 intervals may be more effective still if doing so eliminates synchronous sensory adaptation.
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51 1162 *(b) Acoustic components: sounds and vibration*

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53 1163 Sounds (i.e. air and water-borne vibrations) and vibrations (i.e. solid-borne vibrations) are
54
55 1164 widely used in defence across several taxa (Low, Naranjo & Yack, 2021). We discussed
56
57 1165 vibrations in the context of deimatic behaviour in Section III.3*f*, and alarm calls in Section
58
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1
2
3 1166 III.3e. Here we focus on sounds produced during an encounter with a predator which have
4
5 1167 been proposed to function in aposematism, jamming echolocation calls, and as deimatic
6
7 1168 behaviour (see Low *et al.*, 2021). Continuous sound production is presumably too costly in
8
9 1169 terms of conspicuousness or energy (Low *et al.*, 2021). One notable exception occurs in
10
11 1170 cicadas which as a group produce incessant mate-attraction calls *via* tymbalation [the flexing
12
13 1171 of corrugated regions of exoskeleton (tymbals)] that may have a dual function in
14
15 1172 aposematism (Simmons, Wever & Pylka, 1971). Cicadas can drive bird predators out of
16
17 1173 forests both due to the dangerously loud and painful sound, and its disruption to their
18
19 1174 communication (Simmons *et al.*, 1971). Their sound can certainly drive human visitors away
20
21
22
23
24 1175 (K.D.L. Umbers & J.A. Endler, personal observations).

25
26 1176 Sounds used in defence are produced by a huge diversity of body parts or specialised
27
28 1177 organs (Bura *et al.*, 2016; Low *et al.*, 2021) – knocking or rubbing body parts together as in
29
30 1178 stridulation (Bura *et al.*, 2016; Rosi-Denadai *et al.*, 2018), forced air (Bura *et al.*, 2011; Rosi-
31
32 1179 Denadai *et al.*, 2018), percussion, or tymbalation (Ewing, 1989; Dookie *et al.*, 2017).

33
34 1180 Sound created by ‘forced air’ is used across animals. Walnut sphinx (*Amorpha*
35
36 1181 *juglandis*) caterpillars whistle by expelling air *via* muscular contractions through special
37
38 1182 sound-producing spiracles on the A8 abdominal segment (Bura *et al.*, 2011) and can
39
40 1183 successfully deter red-winged blackbirds (*Agelaius phoeniceus*) despite having no further
41
42 1184 defences (Dookie *et al.*, 2017). In the walnut sphinx deimatic sounds are loud, sudden, and of
43
44 1185 longer duration than those produced in other defensive contexts (Low *et al.*, 2021). Other
45
46 1186 caterpillars ‘vocalise’ when attacked, by forcing air out of their gut (Rosi-Denadai *et al.*,
47
48 1187 2018; Bura *et al.*, 2016). Many reptiles including lizards such as the blue-tongued skink
49
50 1188 (*Tiliqua scincoides*) (Badiane *et al.*, 2018) and the frill-necked lizard (*Chlamydosaurus*
51
52 1189 *kingii*) (Perez-Martinez, Riley & Whiting, 2020) also use ‘hissing’ during their deimatic
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3 1190 behaviour by forcing air from their lungs across the glottis, but its effect on predator

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5 1191 behaviour has not been assessed in this context.

6
7 1192 Deimatic behaviour can include stridulation and rasping sounds, for example when

8
9 1193 mantises move their wings and abdomens rhythmically (Hill, 2007; Olofsson *et al.*, 2012b).

10
11 1194 Hill (2007) showed that *Mantis religiosa* have tooth-studded venation on their hindwings and

12
13 1195 denticles on their abdomen and the sound is produced as the former are moved over the latter.

14
15 1196 The peacock butterfly also produces ‘swooshing’ sounds by opening and closing its wings,

16
17 1197 and ultrasonic clicks audible to rodents and bats by a ‘costal clicker’ on the base of the dorsal

18
19 1198 side of the forewing (Møhl & Miller, 1976). Orthoptera also have a wide repertoire of

20
21 1199 defensive stridulatory mechanisms which are performed upon the approach of a predator and

22
23 1200 function to slow or stop its attack (Bedford & Chinnick, 1966; Robinson, 1969; Maldonado,

24
25 1201 1970; Edmunds, 1972). In the katydid *Mygalopsis marki* both adults and nymphs use

26
27 1202 stridulation produced within the head capsule (Bailey & Sandow, 1983). The nymph usually

28
29 1203 attempts to escape by jumping or running but if held in the hand, head stridulation is

30
31 1204 produced.

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33 1205

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35 1206 *(c) Olfactory/gustatory components: oozing and regurgitating*

36
37 1207 Chemical defences are typically associated with aposematism, which predators encounter if

38
39 1208 they dare to attempt consumption. They may, however, also appear as components of

40
41 1209 deimatic behaviour which are released when prey perceive a threat from an attacker during

42
43 1210 approach or subjugation, and which can cause predators to slow or stop their attack (Fig. 2).

44
45 1211 Deimatic chemical defences are those released during the behaviour, not those simply present

46
47 1212 in the organism regardless of an attacker’s proximity. That is, deimatic chemical defences are

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49 1213 produced upon attack.

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3 1214 Chemical defences may be oozed, frothed, or foamed from joints and glands during
4
5 1215 deimatic behaviour, and may have olfactory and/or visual effects on predator behaviour.
6
7
8 1216 Amphibians exude chemical defences from glands during deimatic behaviour (Ferraro, Topa
9
10 1217 & Hermida, 2013) and defensive posturing can enhance the effect (Williams *et al.*, 2000).
11
12 1218 Fire-bellied toads (*Bombina* spp.) can increase the amount of toxin released through physical
13
14 1219 pressure on the glands when the back is arched (Bajger, 1980; Choi, Lee & Ricklefs, 1999).
15
16
17 1220 During their deimatic behaviour four-eyed frogs (*Physalaemus nattereri*) reveal large black
18
19 1221 discs on their rumps where bradykinin peptides and correspondingly strong signals of related
20
21 1222 gene expression are concentrated (Barbosa *et al.*, 2015). Similarly, many salamanders have
22
23 1223 noxious skin secretions and combine their presentation with various postures to orient the
24
25 1224 glands and associated secretions towards the predator (Brodie, 1977). Mountain katydids
26
27 1225 exude droplets of a bitter secretion from the surface of the abdomen when attacked,
28
29 1226 presumably from glands as yet undescribed, with compounds that originate from their
30
31 1227 preferred diet of *Senecio* daisies (Baker, 2019), such as senecionines and sceneciophyllines.
32
33 1228 Some lepidopterans exude noxious chemicals *via* froth which seems to be deimatic behaviour
34
35 1229 rather than retaliation because they are not shot at the attacker. The saturniid moth *Citheronia*
36
37 1230 *brisottii* is a yellow and orange moth with black intersegmental membranes from which
38
39 1231 newly emerged adult males can expel a tar-like substance (Blest, 1957a). Other lepidopteran
40
41 1232 ‘frothers’ include the arctiine moth *Amerila bubo* which emits a ‘sizzling’ sound from the
42
43 1233 thorax as it produces an odorous froth from two large vesicles, as well as its congener *A.*
44
45 1234 *leucoptera* which displays a bright pink body by spreading its wings and expelling a yellow
46
47 1235 froth from the thorax when disturbed (Carpenter, 1938).
48
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50
51 1236 Regurgitation is almost ubiquitous among insects when they are attacked, and in
52
53 1237 lepidopteran larvae is also a common accompaniment to acoustic components of deimatic
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55 1238 behaviour (Bura *et al.*, 2016). Brown, Boettner & Yack (2007) found that defensive
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3 1239 regurgitation often preceded or accompanied the clicking sounds produced by the
4
5 1240 polyphemus moth (*Antheraea polyphemus*) and was an effective deterrent against predators.
6
7 1241 Similarly, caterpillars of the giant peacock moth (*Saturnia pyri*) produce a chemical secretion
8
9 1242 from integumental bristles when attacked repeatedly while ‘chirping’ (Bura, Fleming &
10
11 1243 Yack, 2009). These examples provide some insight into the chemical components of deimatic
12
13 1244 behaviour but leave many questions unanswered about their proximate mechanisms. In
14
15 1245 particular, it is currently unclear whether both the regurgitation and noise function as a
16
17 1246 deimatic defence, or whether the noises produced are deimatic, and the regurgitation consists
18
19 1247 of toxic secondary plant compounds.
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26 1249 **(3) Changes in deimatic behaviour in response to repeated attack**

27
28 1250 Deimatic behaviours can be highly repeatable – performed the same way by the same
29
30 1251 individual every time – or can vary among performances. The limited available evidence
31
32 1252 suggests variability both within and among individuals. For example, over ‘long’ 24-h
33
34 1253 intervals between repeated attacks, consistency in display intensity varied substantially
35
36 1254 among individual mountain katydids and were only somewhat repeatable in the magnitude of
37
38 1255 their displays (De Bona, White & Umbers, 2020). One explanation may be that performing
39
40 1256 deimatic behaviour is condition dependent, but the proximate cause for this variation requires
41
42 1257 future research.
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47 1258 Many species increase the intensity of their deimatic behaviour with repeated
48
49 1259 exposure to stimuli. In simulated sequential, repeated attacks over short intervals (10 s),
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51 1260 mountain katydids increased the intensity of their display (used more components) (F.
52
53 1261 Mourmourakis, S. De Bona & K. D. L. Umbers, unpublished data). Similarly, Brown *et al.*
54
55 1262 (2007) investigated the response of clicking polyphemus moth caterpillars to different
56
57 1263 numbers of simulated repeated attacks and showed that the number of clicks per individual
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2
3 1264 increased with attack number. In a different measure, Vallin *et al.* (2005) showed that the
4
5 1265 second time peacock butterflies were approached by a predator, they displayed when the
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7
8 1266 predator was at a greater distance away than in the first encounter. Increased intensity of
9
10 1267 deimatic behaviour might increase prey survival if displaying maximally upon first stimulus
11
12 1268 carries costs (e.g. conspicuousness) or if the prey are protected from sub-lethal investigative
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14
15 1269 predator behaviour by a tough exterior, and may also depend on their perceived certainty or
16
17 1270 intensity of danger. The degree to which prey are defended may influence their propensity to
18
19 1271 exhibit deimatic behaviour when repeatedly accosted by potential predators. The chemically
20
21 1272 defended cottonmouth snake reduces its expression of deimatic behaviours with repeated
22
23
24 1273 exposure to human model predators (Glaudas, 2004). However, comparatively less-defended
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26 1274 juveniles do so to a lesser degree (Glaudas *et al.*, 2006). Predictions around the mechanisms
27
28 1275 underlying prey responses to repeated attacks is fertile ground for future theory and
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30 1276 experiments.
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33 1277

35 1278 **VII. SURVIVAL VALUE OF DEIMATIC BEHAVIOUR**

37 1279 A limited number of studies have quantified the survival value of deimatic behaviour in the
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39
40 1280 field and the laboratory with respect to prey survival probability (Table S5) and effects on
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42 1281 predators (Table S6).
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47 1283 **(1) Does deimatic behaviour increase the probability of prey survival?**

49 1284 Ten publications have measured the survival value of deimatic behaviour and/or further
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51 1285 signals revealed by them using live prey animals, of which eight were laboratory-based and
52
53 1286 two field-based (Table S5). Some prey were putatively profitable, others putatively
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56 1287 unprofitable (i.e. 'chemically defended'), and most were insects. The efficacy of visual
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58 1288 components, acoustic components, and their combination have all been investigated. Most
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3 1289 studies did not address whether the experimental predators were natural predators thus
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5 1290 leaving questions about the ecological and evolutionary significance of the results.
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10 1292 *(a) Survival value of deimatic behaviour that reveals colour patterns without chemical*
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12 1293 *defence*
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14 1294 Vallin *et al.* (2006) examined the effect of the wing-flicking display with eyespots of the
15
16 1295 peacock butterfly against wild-caught blue tits (*Parus caeruleus*). Peacock butterflies, which
17
18 1296 are seemingly palatable to all their known predators, initiated their deimatic behaviour during
19
20 1297 the predator's approach (average 12 cm distance) and all survived ($N = 10$) (Vallin *et al.*,
21
22 1298 2006). Vallin, Jakobsson & Wiklund (2007) found that peacock butterfly visual displays were
23
24 1299 protective against both blue tits and great tits (*Parus major*), in contrast to those of the larger
25
26 1300 hawkmoth *Smerinthus ocellatus*. Both insects had eyespots which were revealed on the
27
28 1301 approach of a predator, however the type of display was different as the hawkmoth *S.*
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30 1302 *ocellatus* protracted its upper wings to show the eyespots then rocked with its legs, while the
31
32 1303 peacock butterfly continually flicked its wings to hide and reveal its eyespots. Peacock
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34 1304 butterflies survived 12/12 blue tit attacks and 9/12 great tit attacks whereas only 5/13
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36 1305 hawkmoths survived blue tit attacks and 1/14 survived great tit attacks. These findings
37
38 1306 suggest that the type of visual display is more important than the presence of eyespots alone.
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44 1307 Mollusc deimatic behaviour can include a combination of posturing and colour
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46 1308 pattern expression *via* chromatophores without a chemical defence. In a field study, young
47
48 1309 European cuttlefish altered their defensive responses and deimatic behaviour according to
49
50 1310 predator type and avoided attacks (Hanlon & Messenger, 1988). In a laboratory-based study,
51
52 1311 Staudinger *et al.* (2011) showed that longfin squid (*Loligo pealeii*) also alter their defence
53
54 1312 response depending on predator type. Against bluefish (*Pomatomus saltatrix*), a 'pursuit'
55
56 1313 predator, longfin squid primarily used deimatic behaviours, whereas protean behaviours
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3 1314 (erratic escape behaviours, *sensu* Edmunds, 1974) were used against summer flounder
4
5 1315 (*Paralichthys dentatus*), an ambush predator. Overall, while deimatic behaviours saved the
6
7 1316 prey's life in 40–64% of interactions, prey were more likely to survive when confronted with
8
9 1317 predators if they fled rather than performed deimatic behaviours (87–92% survival rate). The
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11 1318 authors suggest that deimatic behaviours are not always the most effective strategy but may
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13 1319 be employed when prey are unlikely to 'outrun' their predators (Staudinger *et al.*, 2011).
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19 1321 *(b) Survival value of deimatic behaviour that reveals colour patterns with chemical defence*

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21 1322 Mountain katydids perform deimatic behaviour: they lift their wings to reveal a brightly
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23 1323 coloured abdomen that exudes a *Senecio*-derived secretion (Umbers & Mappes, 2015; Baker,
24
25 1324 2019; De Bona *et al.*, 2020). Umbers *et al.* (2019) used a field-based experiment to test
26
27 1325 whether the survival value of the katydid's display relates to the prior experience of one of
28
29 1326 their native predators, the Australian magpie (*Gymnorhina tibicen*). In interactions with naïve
30
31 1327 allopatric Australian magpies, katydids survived 70% of encounters, while only 24% of
32
33 1328 katydids survived interactions with sympatric predators. During the experiments katydids
34
35 1329 revealed their display in the subjugation phase of the predation sequence, suggesting that
36
37 1330 camouflage may be their primary defence and that their tough tegmina might help them
38
39 1331 withstand initial predator investigations (Umbers *et al.*, 2019). Katydid were more
40
41 1332 vulnerable to experienced (sympatric) magpies than naïve (allopatric) ones despite the
42
43 1333 katydid's abdominal exudate (Baker, 2019); perhaps they are profitable due to their large size
44
45 1334 (up to 3 g) or perhaps magpies are unaffected by their chemical defence, or both.

46
47 1335 Brodie *et al.* (1984) investigated the survival value of deimatic behaviour in three
48
49 1336 Asian salamander species, *Paramesotriton chinensis* ($N = 15$), *Paramesotriton*
50
51 1337 *caudopunctatus* ($N = 17$) and *Pachytriton brevipes* ($N = 10$), against short-tailed shrews
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53 1338 (*Blarina brevicauda*). All three species displayed and survived 100% of encounters despite
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3 1339 biting and mouthing by shrews (Brodie *et al.*, 1984). Whether shrews were deterred by the
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5 1340 visual component of the behaviour or by the taste or toxic effect of the exudate is unclear,
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8 1341 and more work is required to determine the selective advantage of each component.
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12 1343 *(c) Survival value of deimatic behaviour that reveals sounds*

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14 1344 Two studies have examined the survival value of the auditory component of deimatic
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17 1345 behaviour in the peacock butterfly by studying a population in the wild during its vulnerable
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19 1346 over-wintering period (Olofsson *et al.*, 2011, 2012*b*). Hibernating butterflies were placed in
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21 1347 eight different sites accessible by wild predators and filmed to observe predator–prey
22
23 1348 interactions (Olofsson *et al.*, 2011). Cameras revealed yellow-necked mice (*Apodemus*
24
25 1349 *flavicollis*) and wood mice (*A. sylvaticus*) as the main predators and that the sound of wing-
26
27 1350 flicking displays made predators retreat in 41 out of 52 encounters. Olofsson *et al.* (2012*b*)
28
29 1351 experimentally tested this auditory component against wild-caught mouse predators in a
30
31 1352 laboratory setting. To isolate the auditory component of the display, experiments were
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33 1353 conducted in dark arenas. In 30 min trials in dark arenas mice were presented with either
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35 1354 ‘mute’ butterflies which had both ultrasound and stridulatory sound disabled, and ‘sound’
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37 1355 individuals which were sham-manipulated. 96% of butterflies (23/24) survived the first
38
39 1356 encounter, with no difference in survival between ‘mute’ and ‘sound’ butterflies. However,
40
41 1357 18/24 mice fled when butterflies flicked their wings and fled further from ‘sound’ butterflies
42
43 1358 than from ‘mute’ butterflies. The likelihood of predator-associated wing-flicking behaviour
44
45 1359 varied among individuals. Eight butterflies only required one interaction with mice before
46
47 1360 initiating wing-flicking, while some required up to six interactions or to be physically
48
49 1361 touched. It is not clear whether the sound itself was the deterrent. Olofsson *et al.* (2012*b*)
50
51 1362 suggested that tactile stimulation arising from the sudden movement of air caused by wing-
52
53 1363 flicking or being physically touched by the wings themselves could have deterred the mice.
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3 1364 Further, whether the sound is mimetic of a rodent predator, or simply surprising, is unknown
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5 1365 but would be an interesting avenue for further research.

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7 1366 Vallin *et al.* (2005) tested the effects of the visual and auditory components in the
8
9 1367 peacock butterfly by presenting various combinations of eyespots and sound to blue tits. No
10
11 1368 difference in survival was found between the sound and no-sound treatments, whereas 33/34
12
13 1369 butterflies with intact eyespots survived the trials, and only 7 of 20 butterflies with covered
14
15 1370 eyespots survived. Taking all the peacock butterfly studies together, eyespots seem to be
16
17 1371 effective against blue tits (Vallin *et al.*, 2005) whereas sound seems to be effective against
18
19 1372 rodents (Olofsson *et al.*, 2011, 2012b). A role of airborne chemical signals was not tested.

20
21 1373 Deimatic behaviour has been studied in detail in a few lepidopteran larvae (Low *et*
22
23 1374 *al.*, 2021). Brown *et al.* (2007) experimentally examined the survival value of mandible
24
25 1375 clicks in the polyphemus moth which are accompanied by regurgitation when the moth is
26
27 1376 grasped by forceps or a beak. In experimental trials, domestic chicks (*Gallus gallus*
28
29 1377 *domesticus*) induced sound production in 100% and regurgitation in 87.5% of larvae ($N = 16$)
30
31 1378 during subjugation and 100% of the caterpillars survived the encounter. Data on long-term
32
33 1379 survival after attack and any sub-lethal effects are needed. The survival value and function of
34
35 1380 walnut sphinx whistles and clicks was tested against yellow warblers (*Setophaga petechia*)
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37 1381 ($N = 3$) and showed that when caterpillars produced whistles upon attack, the birds hesitated
38
39 1382 and even flew away (Bura *et al.*, 2011). All three caterpillars survived with no visible harm to
40
41 1383 their bodies suggesting potential long-term survival, but to confirm this, a larger sample is
42
43 1384 needed. In simulated attack trials regurgitation in *A. juglandis* was rare (3% of trials)
44
45 1385 suggesting that in nature they may rely on the sound alone.

46
47 1386 Sandow & Bailey (1978) experimentally tested the visual and acoustic components of
48
49 1387 the deimatic behaviour of the sluggish snout-nosed katydid (*Mygalopsis ferruginea*
50
51 1388 (Redtenbacher) syn., *M. pauperculus*) against the salmon-bellied skink, *Ergenia napoleonis*.

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3 1389 Both ‘muted’ katydids ($N = 20$) and intact katydids ($N = 20$) raised their legs, flared their
4
5 1390 mandibles, vibrated their antennae, and attempted stridulation when the predator approached
6
7 1391 (Sandow & Bailey, 1978). Despite both treatments performing stridulation behaviour, only
8
9 1392 intact insects were able to produce a discernible sound. A total of 35 out of 40 katydids
10
11 1393 (87.5%) survived predator encounters and, while there was no difference in survival of
12
13 1394 sound-producing insects compared with muted individuals, the duration of encounters was
14
15 1395 longer for muted katydids (average 4 min) than intact katydids (average 1 min) perhaps
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17 1396 suggesting that sound production saves the katydid energy by reducing interaction time
18
19 1397 (Sandow & Bailey, 1978).
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26 1399 **(2) Does deimatic behaviour actually deter predators?**

28 1400 Prey defences should be categorised by the effect they have on predators and, while
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30 1401 the underlying mechanisms may be unclear, direct measures of predator behaviour can
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32 1402 indicate survival value (Fenton & Licht, 1990; Skelhorn *et al.*, 2016). We found 17 studies on
33
34 1403 predator behavioural responses to deimatic behaviour on 15 species: five species of mammal
35
36 1404 including three bats and two rodents, and 10 species of bird, all passerines except for
37
38 1405 domestic chicks (Galliformes) (Table S6). Experiments tested predator responses to deimatic
39
40 1406 behaviour that revealed colour patterns (including eyespots) both accompanied and
41
42 1407 unaccompanied by chemical defences, and deimatic behaviours with auditory components
43
44 1408 and no further defences. Fifteen of the 17 studies were laboratory-based studies with small
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46 1409 sample sizes, two field-based investigations had larger sample sizes. In all studies, predator
47
48 1410 behaviours were either expressly or implicitly considered proxies for a ‘startle response’.
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50 1411 Qualitative measures of behaviour typically included descriptions of discrete states such as
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52 1412 ‘wing flap’, ‘hesitation’ (latency to attack), or ‘fleeing’ (increasing the distance between
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54 1413 themselves and the prey; Table S6). Most studies did not decouple the visual signals revealed
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3 1414 by the deimatic behaviour from the deimatic behaviour itself. Overall, the ways in which
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5 1415 predator responses have been measured have made direct conclusions about survival value
6
7 1416 difficult to draw and fitness implications difficult to assess.
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12 1418 *(a) Measures of predator 'startle responses'*
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14 1419 The 'startle responses' of predators have typically been measured in response to artificial
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16 1420 prey. Schlenoff (1985) showed that blue jays ($N = 6$) 'startled' in around 50% of their initial
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18 1421 interactions with models featuring *Catocala*-coloured hindwings (red, orange, and yellow),
19
20 1422 which were revealed when cardboard forewings were removed, but never startled in response
21
22 1423 to models with grey hindwings. The startle response was mostly 'low intensity' ("*dropped*
23
24 1424 *prey model, raised crest, moved in a jerky rapid fashion*"; p. 1059), as opposed to 'high
25
26 1425 intensity', which included the low-intensity behaviours plus flying against the side of the
27
28 1426 cage, emitting an alarm call, and wiping beak. Whether these responses correspond to a
29
30 1427 'startle response', whether they constitute 'slowing' their attack, whether they would protect
31
32 1428 real moths, and what the moths might do in response, is mostly unknown. However, Sargent
33
34 1429 (1973) found that blue jays often released *Catocala* moths when their hindwings became
35
36 1430 exposed during prey handling. They left a beak imprint but did not tear the moth's wings,
37
38 1431 thereby suggesting that exposure of *Catocala* hindwings triggered blue jays to release the
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40 1432 moths, perhaps involuntarily.
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46 1433 Dookie *et al.* (2017) showed that the whistling sounds of walnut sphinx moth
47
48 1434 caterpillars 'startled' red-winged blackbirds. Predators experienced a playback of the
49
50 1435 caterpillar's sound in response to contacting a sensor on a feeding dish. The behaviours
51
52 1436 recorded included 'shoulder flinch', 'wing flap', 'ruffle feathers', 'body flinch', 'startle hop',
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54 1437 and 'fly away'. The number of behaviours recorded was greater for birds that received a
55
56 1438 sound compared to birds that did not (Dookie *et al.*, 2017). An interesting future direction
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3 1439 would be to compare the responses of birds to control sounds to test if aspects of the
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5 1440 caterpillar's sounds are especially effective as a deterrent or whether any sound has a similar
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7
8 1441 effect.

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12 1443 *(b) Measures of predator hesitation*

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14 1444 A long-standing hypothesis about deimatic displays is that they cause predators to pause their
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16
17 1445 attack for long enough for prey to escape (Ruxton *et al.*, 2004) and latency to attack seems to
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19 1446 be the response variable most often measured to test this idea. Experiments have usually
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21 1447 presented artificial stimuli such as sound recordings, computer imagery, and abstract models
22
23 1448 (concentric circles) (Table S6). Of the studies that included experiments on live insects
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25 1449 (6/17), prey escape behaviour was not described. Vaughan (1983) tested the effect of model
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27 1450 *Catocala* moth deimatic behaviour on blue jays ($N = 8$) under the hypothesis that the
28
29 1451 anomaly (unexpected), novelty (never previously encountered), and/or rarity (previously
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31 1452 encountered but uncommon) of moth hindwing colours may cause predators to hesitate.
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33 1453 Vaughan (1983) showed that novelty can cause blue jays to hesitate in an experiment where
34
35 1454 they interacted with an experimental apparatus consisting of a series of flaps behind each of
36
37 1455 which was hidden colourful discs resembling *Catocala* hindwing colours and mealworms
38
39 1456 (*Tenebrio molitor* larvae). When the jays encountered discs of a colour they had not
40
41 1457 encountered during training, they took longer to eat the reward mealworm than when they
42
43 1458 encountered colours they had experienced before (Vaughan, 1983), and that hesitancy
44
45 1459 increased with colour rarity.

46
47 1460 Using the same apparatus as Vaughan (1983), Ingalls (1993) tested the latency of
48
49 1461 naïve hand-raised blue jays ($N = 8$) to respond to the combined effects of novel colours and
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51 1462 patterns. She showed that birds took longer to touch discs with novel colours presented in a
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53 1463 striped pattern with black bands than solid novel colours. Despite potentially confounding
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3 1464 order effects, these data suggest that the presence of black bands resulted in the greatest
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5 1465 latencies compared to discs without black bands as did colour combinations similar to those
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8 1466 found naturally in *Catocala* spp. (Ingalls, 1993). Further, Ingalls (1993) reported interesting
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10 1467 variation in predator responses, with some birds never habituating to the stimuli and others
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12 1468 habituating relatively quickly, perhaps suggesting that variability within predator species may
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15 1469 select for variation in prey defences.

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17 1470 Holmes *et al.* (2018) tested the protective value of deimatic behaviour using
18
19 1471 computer-generated ‘moths’ with and without colourful hindwings that were revealed
20
21 1472 rhythmically at three different speeds to domestic chicks (*Gallus gallus domesticus*). In a
22
23 1473 laboratory setting they showed that rapid movement alone in the absence of conspicuous
24
25 1474 colours delayed a chick’s attack, and that the combination of movement and coloured
26
27 1475 hindwings led to longer latencies. These results suggest that movement alone can increase
28
29 1476 latency in predator responses, that this effect can be enhanced by colourful hindwings and, by
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31 1477 extension, that movement could precede colour in the evolution of deimatic behaviour.
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35 1478

36 1479 (c) Measures of predators fleeing

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38 1480 Predators might flee when they experience deimatic behaviour (De Bona *et al.*, 2015).

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40 1481 Olofsson *et al.* (2012b) showed that when field-caught yellow-necked mice and wood mice
41
42 1482 hear the sound of the peacock butterfly’s display, the majority flee quickly ($N = 18/24$).

43
44 1483 Whether they simply flee or if fleeing is initiated after their startle reflex is released would be
45
46 1484 interesting ground for further testing. Olofsson *et al.* (2012b) also suggested that mice
47
48 1485 respond as they would to a real predator and hypothesised that the peacock butterfly’s sound
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50 1486 may involve Batesian mimicry of snake hisses (Vane-Wright, 1986; Skelhorn *et al.*, 2016).

51 1487

52 1488 (3) Do predator responses change across repeat encounters?

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3 1489 Changes in predator behaviour across repeated encounters with prey are central to
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5 1490 understanding the evolution of deimatism. In some environments deimatic prey may be rare
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7 1491 enough for encounter and re-encounter rates to be very low. However, when repeat
8
9 1492 encounters do occur, predator responses may change depending on encounter rate, predator
10
11 1493 age [younger predators may be more neophobic (Lindstrom, Alatalo & Mappes, 1999;
12
13 1494 Marples & Kelly, 1999) or conservative (Thomas *et al.*, 2003)], variability in deimatic
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15 1495 behaviours, and whether or how quickly deimatic behaviours are learned and remembered by
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17 1496 predators.

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23 1498 *(a) Responses to deimatic behaviour that reveals colour patterns with no chemical defences*
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25 1499 In 12 studies that exposed predators to repeated trials (Table S6), four used prey stimuli with
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27 1500 colour patterns and no chemical defence. Of those four, two found evidence that predators
28
29 1501 learn to ignore the signals and attack the prey (Vaughan, 1983; Schlenoff, 1985), one showed
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31 1502 that predators learn to avoid the prey (Ingalls, 1993), and one found no clear pattern (Kang *et*
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33 1503 *al.*, 2017).

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37 1504 Using the *Catocala*-inspired apparatus described above, Vaughan (1983) showed that
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39 1505 blue jays became habituated to the rarity of colours after the first of four experimental days.
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41 1506 Initially the latency to attack a rare colour was >200% of that for a common colour, but after
42
43 1507 one day this dropped to ~110% despite the rarity of the rare colour remaining consistent.
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45 1508 Schlenoff (1985), also using the *Catocala*-inspired apparatus, tested blue jay ($N = 6$)
46
47 1509 responses to different colour patterns. Habituation took 6–25 days for models resembling red-
48
49 1510 banded, yellow-banded and black *Catocala* hindwings and the deterring effect lasted longest
50
51 1511 when trained on two sequential banded patterns rather than a black followed by a banded
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53 1512 pattern. The flight periods of *Catocala* species last for several weeks, which is enough time
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55 1513 for predator habituation to hamper the effectiveness of startle displays. Sargent & Hessel
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3 1514 (1970) observed flight periods exceeding two months for many *Catocala* species in the north-
4
5 1515 eastern USA, and adults can survive for at least 60 days in some species (Gall, 1991).

7 1516 With a further seven wild-caught blue jays, Schlenoff (1985) trained them to two
9
10 1517 different forewing types with corresponding hindwings, and found that a startle response
11
12 1518 could be elicited by swapping hindwing colours. She suggested that the anomalous nature of
13
14 1519 the prey's form combined with the striking colour pattern caused the birds to perform startle
15
16 1520 behaviours, not simply that the hindwings colours were unexpected, and that it is unnecessary
17
18 1521 for the patterns to be unknown to the bird. Schlenoff (1985) also showed that encountering an
19
20 1522 unexpected difference in hindwing colour is not enough to elicit a startle response because
21
22 1523 birds trained on *Catocala* patterns do not startle to unexpected grey hindwings.

26 1524 Ingalls (1993) surmised that *Catocala* hindwings may deter blue jays for several
27
28 1525 reasons: (a) they mimic sympatric aposematic species; (b) they are novel; and/or (c) their
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30 1526 patterns include strong contrasts. She suggested that an optimal number of types of forewings
31
32 1527 must exist. Although an unexpected hindwing colour pattern can deter a predator, if they are
33
34 1528 presented with a new type in every encounter, in theory they could habituate to the rule that
35
36 1529 the hindwing will always be new (Ingalls, 1993). Ingalls' (1993) data suggest that blue jays
37
38 1530 take longer to habituate to startle signals as a function of the diversity of the signals; birds
39
40 1531 presented with a single stimulus colour habituated far more quickly than those presented with
41
42 1532 five colours. However, there was also evidence of consistent individual variation in feeding
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44 1533 strategy. For example, within a group of birds presented with food associated with five
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46 1534 different startle colours, two birds habituated after less than 50 trials, while a third was not
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48 1535 habituated after 149 presentations. This variation in individual predator performance could
49
50 1536 suggest that differences in dietary conservatism (Marples & Kelly, 1999) coupled with
51
52 1537 differences in levels of neophobia could have a significant impact on predator perception of
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54 1538 defences involving multiple stimuli. Overall, this detailed work on *Catocala* and replica
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3 1539 stimuli suggests that colour pattern novelty could be protective but does not provide
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5 1540 information for responses with real prey. The spatial distribution of hindwing colours in
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8 1541 *Catocala* would merit further study.
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11
12 1543 *(b) Responses to deimatic behaviour that reveals colour patterns with chemical defences*

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14 1544 Two studies used prey with colour patterns and chemical defences (Kang *et al.*, 2016;

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16
17 1545 Umbers *et al.*, 2019). Both showed that predators can learn to avoid the prey, while Umbers

18
19 1546 *et al.* (2019) also found that experienced predators can learn to ignore the deimatic behaviour

20
21 1547 and consume the prey. The latter study measured repeated interactions between wild live

22
23 1548 predators and live prey with a deimatic behaviour that reveals a colour pattern and an

24
25 1549 associated chemical defence. Umbers *et al.* (2019) found that Australian magpies naïve

26
27 1550 (allopatric) to mountain katydids learn to avoid them after just one trial, but that experienced

28
29 1551 (sympatric) birds consume katydids at a rate of 50%. This suggests that the initial deterrent

30
31 1552 effect of the display can be lost, perhaps due to the absence of an emetic effect, but the

32
33 1553 conditions that promote repeated sampling of initially repellent prey remain unclear. Using

34
35 1554 chemically defended artificial paper prey, Kang *et al.* (2016) tested whether deimatic

36
37 1555 behaviours facilitate predator avoidance, and in particular whether predators learn to

38
39 1556 associate a cryptic resting appearance with distastefulness. They showed that the speed of

40
41 1557 predator learning was similar between classically aposematic prey and deimatic–aposematic

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43 1558 prey (Kang *et al.*, 2016).
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51 1560 *(c) Responses to deimatic behaviour that reveals sounds*

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53 1561 Three studies investigated predator responses to repeated sound stimuli (Table S6). In two of

54
55 1562 these predators learned to ignore the sound and in the third the result was unclear. Dookie *et*

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57 1563 *al.* (2017) tested for effects of repeated exposure of red-winged blackbirds to the whistle
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3 1564 emitted by the walnut sphinx caterpillar. They found short-term habituation to the sound
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5 1565 within each of their two experimental phases but found no difference in habituation between
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7 1566 phases, indicating that during this two-day period the birds dishabituated despite no changes
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9
10 1567 to the experimental set-up (Dookie *et al.*, 2017).
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14 1569 **VIII. FUTURE DIRECTIONS**

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17 1570 To understand the evolution of deimatic behaviour, further research is required in four broad
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19 1571 areas: (1) deimatism as part of an antipredator sequence and the need to define antipredator
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21 1572 ‘space’; (2) quantifying the underlying mechanisms of predator responses to deimatic
22
23 1573 behaviours and how these change with experience; (3) gathering richer data for comparative
24
25 1574 analyses; and (4) ecological patterns of deimatic behaviour. Collaboration across the breadth
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27
28 1575 of behavioural sciences while conducting laboratory and field-based experiments and
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30 1576 including indigenous knowledge will enable advances in this field.
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35 1578 **(1) Deimatism in the antipredator sequence**

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37 1579 Deimatic behaviour is one part of an antipredator strategy. To understand both the benefits of
38
39 1580 this behaviour and how/when individuals should perform it, we need to establish how it is
40
41 1581 distinct from and interacts with other defensive strategies. The defences that precede and
42
43 1582 follow deimatic behaviour in an antipredator strategy vary among species, among individuals,
44
45 1583 and within individuals. Predators may encounter different sequences of defences when
46
47 1584 encountering different prey (Fig. 2), but equally, prey can, with different degrees of control,
48
49 1585 choose which defences to deploy and when. We predict that the protective value of defences
50
51 1586 can change depending on the combination and order in which they are experienced by
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53 1587 predators and that recognising, quantifying, and analysing this variation is key to
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55 1588 understanding the proximate and ultimate aspects of antipredator strategies in general.
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3 1589 Recognising that antipredator strategies include multiple defences experienced by
4
5 1590 predators in a sequence has profound implications (Endler, 1991). It requires us to reframe
6
7 1591 our view of predator–prey interactions as multi-level escalating interactions rather than a
8
9 1592 simplistic single-level signal and response. Therefore, understanding deimatism is
10
11 1593 complicated by how well other defences are defined and the clarity of the conceptual
12
13 1594 boundaries between them. We therefore encourage mapping the full breadth of antipredator
14
15 1595 defences (i.e. antipredator ‘space’) to define these conceptual boundaries (Fig. 2).
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21 1597 **(2) Predator responses to deimatic behaviour and prey survival advantage**

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23
24 1598 To arrive at a universally accepted definition of deimatism and establish how it differs from
25
26 1599 other defensive strategies, it is crucial to experimentally demonstrate the proximate causes(s)
27
28 1600 by which deimatism deters predators and to test how these differ from other defences within
29
30 1601 and among attacks and predator individuals. This is needed for predator responses to initial
31
32 1602 and repeat encounters as well as for predators over the course of a single deimatic
33
34 1603 performance. Understanding the mechanisms requires working with ecologically relevant
35
36 1604 predators in natural field settings complemented by controlled laboratory experiments or
37
38 1605 well-designed field experiments to disentangle interacting effects. We need to make careful
39
40 1606 choices about how to measure appropriate behaviours for predator species and assumptions
41
42 1607 as to what these measures represent must be made explicit. Measures that allow us to
43
44 1608 distinguish among proposed mechanisms by which deimatism deters predators are needed.
45
46 1609 They include behaviour, physiology, and the stimuli themselves. A coordinated effort to use
47
48 1610 comparable measurements across studies where possible will allow meta-analyses and
49
50 1611 systematic reviews in the future.
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56 1612 Limited evidence suggests that deimatic behaviours are more effective against naïve
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58 1613 predators. If this is true, we predict that they should be more common in areas where their
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3 1614 predators learn slowly, forget quickly, have non-synchronous phenology, or short lifespans
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5 1615 resulting in a lower frequency of experienced predators. In these cases, predators are unlikely
6
7 1616 to learn or habituate so protection could be maintained even if prey possess no additional
8
9 1617 defences. Interestingly, deimatism might also be favoured where predators learn quickly and
10
11 1618 retain memory efficiently if those traits are associated with reluctance to attack, for example
12
13 1619 when attempting to subjugate dangerous prey. Deimatism unaccompanied by subsequent
14
15 1620 defences should be common, even among populations of predators that are good learners, if
16
17 1621 the phenologies of the prey and predator only overlap for a short time, minimising time for
18
19 1622 learning. Similarly, if deimatism is most effective against naïve predators, it may be more
20
21 1623 common in prey species that are only active when young and naïve predators are more
22
23 1624 common than experienced predators. Deimatism may be rare if predators are long-lived and
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25 1625 overlap extensively in time with prey.

26
27 1626 If it is true that the protective value of deimatism is directly related to predator
28
29 1627 naïvety, it may allow prey to invade new habitats [e.g. lantern bugs (*Lycorma delicatula*) in
30
31 1628 North America]. Prey species with more effective deimatic displays may expand their
32
33 1629 geographic ranges faster than species without or with inefficient deimatic displays and might
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35 1630 even displace them. This pattern may be stronger when most predators in the new area are
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37 1631 naïve. If predators are good learners, then the expanding geographic range may stabilise
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39 1632 quickly.

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48 1634 **(3) Richer data on prey form and predator response for comparative analyses**

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50 1635 To understand the evolutionary pathway(s) *via* which deimatism evolves we need to perform
51
52 1636 comparative analyses. However, comprehensive quantitative descriptions of deimatic
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54 1637 behaviour are currently too rare, most are missing critical measures such as rise time, speed,
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56 1638 duration, number of components and sensory modes, the qualities of the components
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3 1639 (colours, frequencies), whether the behaviour is sustained or includes rhythmical elements
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5 1640 (*sensu* Blest, 1958), and if and when during the predation sequence the behaviour is
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7
8 1641 performed. Data on how deimatism differs among life stages, between sexes, and among
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10 1642 species and higher taxonomic groups are also required.

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12 1643

13 14 1644 **IX. CONCLUSIONS**

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17 1645 (1) Deimatic behaviour has evolved and been lost multiple times and is widespread across a
18
19 1646 diverse range of taxonomic groups.

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21 1647 (2) Deimatic behaviours vary greatly in modality, and may be used singly or in combination
22
23 1648 with other defences triggering one or more of the predator's sensory systems.

24
25 1649 (3) Multiple non-exclusive hypotheses have been put forward to suggest the mechanism(s) by
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27 1650 which deimatic behaviour is protective including the looming reflex, the startle reflex, fear,
28
29 1651 sensory overload, and confusion. Determining whether deimatic behaviours exploit one or
30
31 1652 more of these mechanisms is an area of high priority.

32
33 1653 (4) Deimatic behaviour can be one defence in an antipredator strategy and therefore the
34
35 1654 impact of the display can vary depending on both the predator's physiology and experience,
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37 1655 and the sequence of defences the prey deploys.

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39 1656 (5) Limited evidence suggests that deimatic behaviours are more effective against naïve
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41 1657 predators, which could have implications for range expansion and inter-individual conflict.

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43 1658 (6) To develop our understanding of deimatic behaviour, further research is required into: (a)
44
45 1659 deimatism as part of an antipredator sequence; (b) quantifying the underlying mechanisms of
46
47 1660 predator responses; (c) comparative analyses; and (d) ecological patterns of deimatic
48
49 1661 behaviour.

50
51 1662

52 53 1663 **X. ACKNOWLEDGEMENTS**

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2
3 1664 We thank Melanie Low for comments and discussion, Audrey Manuel, Science Illustrator,
4
5 1665 for the salamander images, and Michael Kelly for contributing to data extraction. We are
6
7 1666 grateful to the two anonymous reviewers who provided very helpful and insightful
8
9
10 1667 comments. K.D.L.U. and E.D. were funded by a Hermon Slade Grant (HSF 14/3), K.D.L.U.
11
12 1668 was funded by an Australian Research Council Discovery Early Career Research Award
13
14 1669 (project DE180100026) from the Australian Government, and Western Sydney University's
15
16
17 1670 Women's Fellowship, Carer's Grant and Early Career Grant. G.H. was funded by a BBSRC
18
19 1671 Studentship (BB/L017709/1) awarded to J.S. and C.R. C.K. was supported by National
20
21 1672 Research Foundation of Korea (NRF-2019R1C1C1002466). B.C.L. was supported by a
22
23 1673 National Science Foundation Graduate Research Fellowship (DGE-1842166). J.L. was
24
25
26 1674 funded by an Australian Research Council Discovery Early Career Research Award (project
27
28 1675 DE180100526) and by an Academy of Finland grant (340130). J.E.Y. was supported by
29
30 1676 Natural Science and Engineering Council of Canada (2020-07056).

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34 35 1678 **XI. AUTHOR CONTRIBUTIONS**

36
37 1679 Overall concept and structure – K.D.L.U, E.D. and C.M.Y.; hypothesis and rationales – all
38
39 1680 authors; data extraction – E.D., K.D.L.U., C.M.Y. and C.S.; results from literature search –
40
41 1681 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.
42
43 1682 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.,
44
45 1683 K.D.L.U. and R.T.H.; causation – J.S., C.R., G.H. and K.D.L.U.; survival value – E.D.,
46
47 1684 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 –
48
49 1685 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.
50
51 1686 and K.D.L.U.; intellectual property, ideas, and feedback in meetings – all authors.

52
53
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55 56 1688 **XII. REFERENCES**

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56 2349 **XIII. SUPPORTING INFORMATION**
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3 2350 Additional supporting information can be found online in the Supporting Information section
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5 2351 at the end of the article.

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8 2352 **Table S1.** Past descriptions of deimatic displays and terms used to describe the concept.

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10 2353 **Table S2.** Deimatic behaviours in the context of other similar antipredator defences adapted
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12 2354 from Umbers *et al.* (2017).

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14 2355 **Table S3.** Descriptions of deimatic behaviour from the literature.

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16 2356 **Table S4.** Comparison of the defensive strategies of juvenile and adult life stages of species
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18 2357 for which both have been studied and at least one stage uses a deimatic display.

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20 2358 **Table S5.** Summary of studies that have assessed the survival value of deimatic displays in
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22 2359 prey.

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24 2360 **Table S6.** Summary of studies that have assessed predator responses to deimatic displays.

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3 2364 **FIGURE LEGENDS**
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5 2365 **Fig. 1.** Examples of deimatic behaviour across three phyla. Icons in the upper right of images
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7 2366 indicate additional non-visual signals: sounds (three curved lines) and chemical defence
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10 2367 (flask shape). (A) Peacock butterfly (*Aglais io*), image: Charles J. Sharp; (B) Io moth
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12 2368 (*Automeris io*), image: Patrick Coin; (C) rosy underwing (*Catocala electa*), image: Yale
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14 2369 Peabody Museum, Entomology Division, Catalog #: YPM ENT 563513; (D) spotted
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16 2370 lanternfly (*Lycorma delicatula*), image: Changku Kang; (E) walnut sphinx (*Amorpha*
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18 2371 *juglandis*) caterpillar, image: Andy Reago & Chrissy McClarren; (F) mountain katydid
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20 2372 (*Acripeza reticulata*), image: Kate Umbers; (G) dead leaf mantis (*Derplatys dessicata*),
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22 2373 image James O’Hanlon; (H) sunbittern (*Eurypyga heilas*), image: Minor Torres Salazar; (I)
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24 2374 European cuttlefish (*Sepia officinalis*), image: Gavan Cooke; (J) Appenine yellow-bellied
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26 2375 toad (*Bombina pachypus*), image: Stefano Canessa; (K) blue-spotted salamander (*Ambystoma*
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28 2376 *laterale*), image: Brock Struecker; (L) rough-skinned newt (*Taricha granulosa*), image: Gary
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30 2377 Nafis.
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37 2379 **Fig. 2.** Five species of insect with their suite of antipredator defences presented together to
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39 2380 highlight the differences and similarities in their sequences. The phrases below the prey
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41 2381 represent the signal sent by different defences: ‘I’m dangerous!’ is aposematic; ‘I’m not
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43 2382 here!’ is camouflage (crypsis or masquerade); ‘Wait!’ is deimatism; ‘I told you so!’ indicates
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45 2383 that the predator has encountered a bad taste or toxin. The dotted rectangle highlights the
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47 2384 deimatic component, the defensive phase refers to the order in which the defences are
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49 2385 deployed or encountered. The predation sequence phase indicates when during the interaction
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51 2386 the predator typically encounters the given defence (Endler, 1991). The seven-spot ladybird
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53 2387 represents what is considered classic aposematism, a conspicuous ever-present signal coupled
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55 2388 with a defence, in this case a chemical defence. Most of the species are camouflaged at rest as
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3 2389 their primary defence. The walnut sphinx caterpillar represents a deimatic sound, a sound that
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5 2390 occurs only when a predator approaches or attempts subjugation; the sound acts as a deterrent
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8 2391 but in this case is not coupled with a chemical defence (the sound would still be deimatic
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10 2392 even if a chemical defence was present; and then would be both deimatic and aposematic).
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12 2393 The peacock butterfly represents deimatic behaviour that includes a sound and a Batesian
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14 2394 defence (eyespot). As far as is currently known mantises also fall into this category, as do
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17 2395 cephalopods. The hash symbol on the peacock butterfly's caption 'I'm dangerous?!#' is
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19 2396 intended to indicate that it is in fact not dangerous; the arrows indicate that the wings open
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21 2397 and close and that this movement is repeated. The mountain katydid reveals its colourful
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23 2398 abdomen as a predator attempts subjugation and then holds this posture and exudes defensive
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25 2399 chemicals from the abdomen in a putative aposematic defence. Finally, the spotted
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28 2400 lanternfly's primary defence is aposematism but it too has a deimatic element with the
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30 2401 opening of its wings to reveal conspicuous colour patterns, followed by a second aposematic
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32 2402 display as the colours are held exposed. If the lanternfly is consumed, the predator will
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34 2403 encounter a bad taste and if the predator continues despite the bad taste and swallows the bug,
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36 2404 the predator may regurgitate. Illustrations: Kate Umbers
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42 2406 **Fig. 3.** Summary of the literature to date on deimatic behaviour showing (A) order of species
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44 2407 studied, (B) components of deimatic behaviour, (C) type of primary defence for species in
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46 2408 study, (D) order of predator species in study, (E) word cloud from the text of all descriptions
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48 2409 of deimatic behaviour highlighting the most common phrases used. Illustration: James
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51 2410 O'Hanlon.
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56 2412 **Fig. 4.** Cladogram adapted from Shen *et al.* (2016), with species lacking data removed from
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58 2413 the original tree, showing the presence and absence of various traits of deimatic displays in
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3 2414 25 species of plethodontid salamanders. 1, Brodie & Howard (1972); 2, Brodie (1977); 3,
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Figure 1

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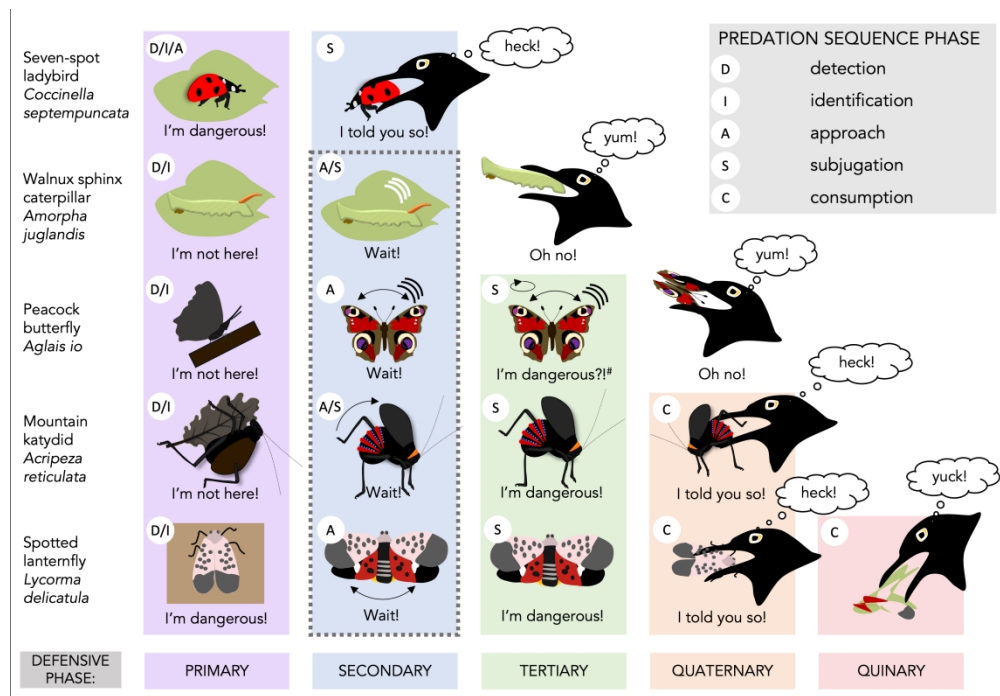


Figure 2

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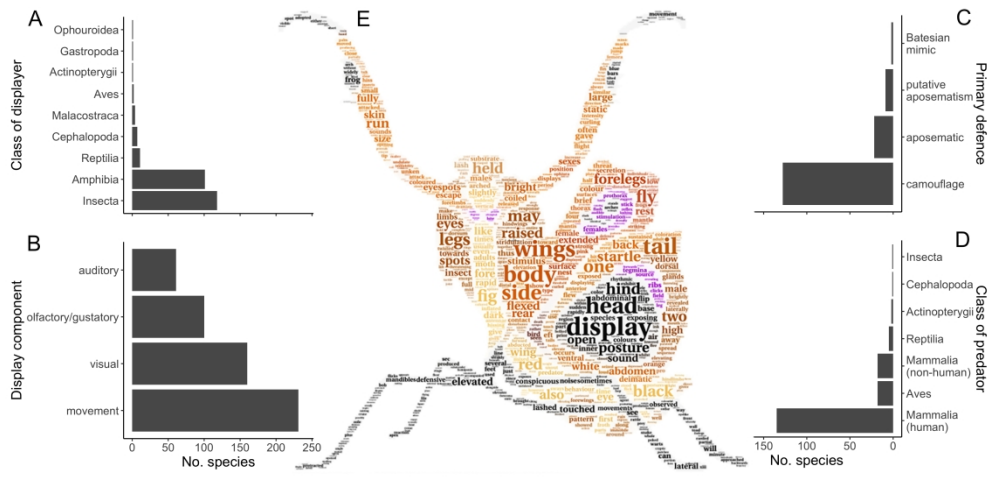


Figure 3

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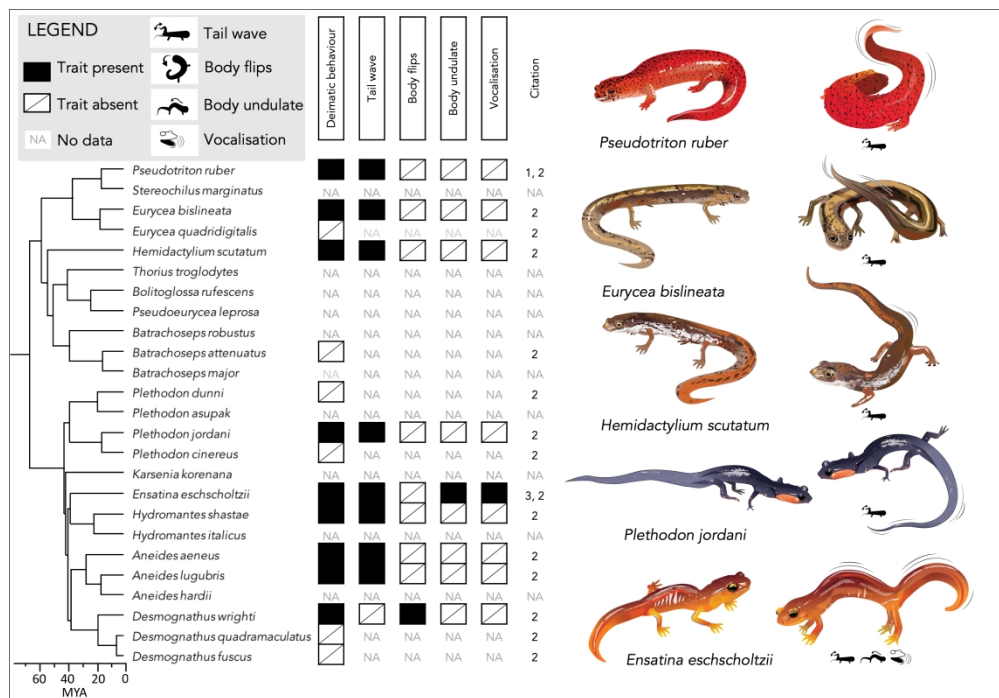


Figure 4

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Table S1. Past descriptions of deimatic displays and terms used to describe the concept. The ‘description’ column provides the relevant passage from the text. The ‘in-text wording’ column provides the name given to the concept as stated by the author.

Citation	Description	In-text wording
Wallace (1889, p. 183)	<i>“Protection by Terrifying Enemies. A considerable number of quite defenceless insects obtains protection from some of their enemies by having acquired a resemblance to dangerous animals, or by some threatening or unusual appearance. This is obtained either by a modification of shape, of habits, of colour, or of all combined.”</i>	Terrifying enemies Threatening or unusual appearance
Poulton (1890, pp. 264, 259)	<i>“terrifying attitude”, “alarming attitude”</i>	Terrifying attitude
Löhner (1919, p. 350)	<i>“Die charakteristischen Eigenschaften des Reflexes sind plötzlicher Eintritt vollständiger Bewegungslosigkeit in stets konstanter Körperhaltung, Muskeltonussteigerung (bei verschiedenen Muskeln in verschiedenem Grade), Lidschluss, Einstellung bzw. Verflachung des Kahluatsspieles und Steigerung der Hautsekretion”</i>	Unkenreflex
Noble (1931, pp. 380–381)	<i>“The typical unken reflex is characterised not only by a distinctive posture and immobility but also by a closure of the eyes, a slowing down of the respiratory movements and an increase in the skin secretion”</i>	Unken reflex

Hingston (1933, p. 3)	<i>“...each one has its mechanism for making it look more threatening when face to face with a rival or enemy. It is the making of these gestures that I call psychological fighting....The working of the mechanism makes the animal look more terrible...”</i>	Psychological fighting
Roonwal (1938, p. 71)	<i>“The purpose of this peculiar attitude ... appears to be to frighten away, by suddenly turning at bay, its natural enemies...”</i>	Frightening attitude
Cott (1940, pp. 213, 232–233)	<i>“Sudden exhibitions of conspicuous colour.” “The sudden appearance of colour previously hidden introduces in itself a new alarming factor which has a psychological effect independent of its mere exhibition.” “The essential character of displays – a sudden and conspicuous exhibition of colour – is achieved by diverse means” “there is essential correlation between the attitude adopted in display and the disposition of the highly pigmented surfaces”, “The conspicuous surfaces are thus normally hidden. Then the changes in appearance ... convert a ... cryptic colour scheme into one that is glaringly conspicuous: the transfiguration is often sudden and rapid; striking and extensive; startling or even terrifying: it occurs typically under special circumstances, namely in times of danger – that is when it is needed; and it is directed in a special manner, namely towards the enemy – that is, where it is needed.”</i>	Intimidating displays

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Young (1950, p. 28)	<i>“Many frogs make a sudden exposure of brightly coloured patches on the thighs as they jump. This presumably serves to startle the attacker and such colours may be called dymantic or startling”</i>	Dymantic Startling
Crane (1952, p. 261)	<i>““Startle display” or simply “display”, covers 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.”</i>	Startle display
Blest (1957a, p. 257)	<i>“Insects of several Orders possess special protective displays which are elicited by attacking predators, or by stimuli which resemble them”</i>	Protective displays
Hayes (1977, p. 443)	<i>“If immediate escape is not possible, the crayfish assumes: and intensifies a species-specific defensive posture-the predator response posture (PRP). This is apparently the same behavior as exhibited in the ‘Aufbaumreflex’ of crabs ... The PRP protects the individual when shelter is unavailable by defensive presentation of chelae. The initial posture acts as a startle display like those of crabs ... and insects ...”</i>	Predator response postures

Maldonado (1970, p. 61)	<i>“Mantids present other remarkable pattern of behaviour: a conspicuous display when they are faced with a ‘threat’. It was called with different names by different authors: the ‘frightening display’ ..., the ‘startle response’ ..., the ‘floral simulation ...’. It will be named the deimatic reaction (DR) (G. δειματώω: I frighten).”</i>	Frightening display Startle response Deimatic reaction
Edmunds (1974, p. 150)	<i>“When discovered by a predator many animals respond by adopting a characteristic posture which appears to be designed to intimidate the predator... I propose to use the term deimatic behaviour or frightening behaviour to include all such displays postures and frightening noises. Deimatic behaviour produces mutually incompatible tendencies in a predator: it stimulates an attacking predator to withdraw and move away. This results in a period of indecision on the part of the predator (even though it may eventually attack), and this gives the displaying animal an increased chance of escaping...”</i>	Deimatic behaviour Frightening behaviour
Schlenoff (1985, p. 1057)	<i>“Startle mechanisms involve sudden conspicuous changes in the appearance of behavior of prey which serve to confuse or alarm certain predators.”</i>	Deimatic displays, startle responses

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Sargent (1990, p. 230)	<i>“There does seem to be agreement that startle is a secondary defense, involving behaviors that a prey organism initiates only after a primary defensive mechanism (usually crypsis) has failed to prevent discovery of disturbance by a predator There also seems to be agreement that the function of a startle display is to interfere in some way with the predator's completion of attack. Beyond this, however, there is considerable confusion as to what constitutes the essential features of a startle display, and why these features are effective in deterring predator attack.”</i>	Startle stimulus / Startle response
Hanlon & Messenger (1996, p. 79)	<i>“Deimatic behaviour is threat, startle, frightening or bluff behaviour and in most cases it serves to make a predator hesitate during the close approach phase of attack”</i>	Deimatic behaviour
Kang <i>et al.</i> (2011, p. 709)	<i>“...sudden movements of conspicuous body parts, which elicit startling response in the predator”</i>	Startle effect
Stevens (2013, p. 147)	<i>“Startle displays: These are sudden conspicuous changes in appearance that cause the predator to pause its attack, allowing the prey to escape or conceal itself.”</i>	Startle displays
Umbers <i>et al.</i> (2015, p. R58)	<i>“...behaviour in which, when under attack, prey suddenly unleash unexpected defences to frighten their predators and stop the attack”</i>	Deimatic displays

Kang <i>et al.</i> (2016, p. 1)	“... a variety of chemically defended insects are rather cryptic when resting, and only in response to predator attacks (post-attack) they perform displays of conspicuous abdomens or hindwings normally hidden under forewings. The function of those displays in unpalatable insects is not well understood. We examined two adaptive hypotheses on this facultative aposematic display...”	Post-attack aposematic display / Facultative aposematic display
Skelhorn <i>et al.</i> (2016, p. e2)	“We propose that we define a deimatic display as any defensive display that causes a predator to misclassify a prey as a potential threat to its immediate safety”	Deimatic display
Umbers & Mappes (2016, p. e7)	“a momentary, transient, conspicuous signal that induces a startle response or overloads the senses of an attacking predator, such that the predator pauses, slows or stops the attack”	Deimatic display
Umbers <i>et al.</i> (2017, p. 1)	“...cause a receiver to recoil reflexively in response to a sudden change in sensory input”, “Crucially, unlike aposematism, reflexive responses to transitory, i.e. deimatic, elements do not require learned or innate aversion.”	Deimatic or ‘startle’ displays
Badiane <i>et al.</i> (2018, p. 104)	“Deimatic display theory is based on a fundamental tenet, that the effectiveness of deimatic displays depends on a sudden transition from an inconspicuous state (e.g. camouflage) to a highly conspicuous display when a predatory attack is imminent, causing a reflexive recoil in the predator ...”	Deimatic display

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Holmes <i>et al.</i> (2018, p. 1)	<i>“Deimatic displays, for example, have long been recognised as a discrete form of defence, and are thought to scare or startle predators, or trigger other reflexive responses that cause predators to delay or abandon their attacks”</i>	Deimatism
Ferreira <i>et al.</i> (2019, p. 7)	<i>“Hidden aposematism occur in species that have aposematic color at the axila, underside of the body, tongue, thighs, or post-femoral region. These species usually exhibit the hidden aposematic or deceptive coloration through escape or postures such as rear elevation, unken reflex, and death feigning.”</i>	Hidden aposematism
Ruxton <i>et al.</i> (2019, p. 179)	<i>“Startling signals are secondary defences that occur after the focal prey individual has been singled out for attack”, “Startling signals involve stimulation of the predator’s senses that cause it to delay or break off an attack.”</i>	Startling signals
Loeffler-Henry <i>et al.</i> (2019, p. 3)	<i>“Deimatic display involves the sudden exposure of a hidden signal that induces a startle response or affects predator psychology/behavior in some way to inhibit its attack..”</i>	Hidden contrasting color signals

Table S2. Deimatic behaviours in the context of other similar antipredator defences adapted from Umbers *et al.* (2017).¹Not for movement and conspicuous colour pattern; ²predator must have at least innate aversion of its own predator's eyes; ³not without its model; ⁴predators can learn to ignore the deimatic component, but not the chemical defences.

	Aposematic			Flee	Deimatic		
Antipredator defence:	Aposematism (non-mimic) (resting state)	Müllerian mimicry (resting state)	Batesian mimicry (resting state)	Flash behaviour / protean behaviour	Deimatic behaviour with no further defence	Deimatic behaviour with Batesian mimicry	Deimatic behaviour with aposematism / Müllerian mimicry
Example	Ladybird, poison frogs	Viceroy and monarch butterflies	Snake head caterpillars, butterfly eyespots	Red winged grasshopper <i>Oedipoda germanica</i> , black-tailed jackrabbit <i>Lepus californicus</i>	Giant African mantis <i>Sphrodromantis lineola</i>	Io moths (<i>Automeris</i> spp.), stick insect <i>Ocotophasma martini</i>	Mountain katydid (<i>Acripeza reticulata</i>), spotted lanternfly (<i>Lycorma delicatula</i>), caterpillar with regurgitate
Requires learned or innate aversion	yes	yes	yes	no	no	yes ¹	no
Requires an evolutionary history or environment shared with model species	no	yes	yes	no	no	yes ²	no
Avoidance must be learned from the focal prey species itself	yes	no	no	no	no	no	no
Avoidance can be learned from the focal prey species itself	yes	yes	no ³	no	yes	no	yes
Predators can learn to ignore the display	no	no	yes	yes	yes	yes	no ⁴

Table S3. Descriptions of deimatic behaviour from the literature. NA: unclear from text

Citation	Year	Phylum	Class	Order
Carpenter (1938)	1938	Arthropoda	Insecta	Lepidoptera
Carpenter (1938)	1938	Arthropoda	Insecta	Lepidoptera
Carpenter (1938)	1938	Arthropoda	Insecta	Lepidoptera
Carpenter (1938)	1938	Arthropoda	Insecta	Lepidoptera
Carpenter (1938)	1938	Arthropoda	Insecta	Lepidoptera
Roonwal (1938)	1938	Arthropoda	Insecta	Mantodea
Varley (1939)	1939	Arthropoda	Insecta	Mantodea
Varley (1939)	1939	Arthropoda	Insecta	Mantodea
Holmes (1940)	1940	Mollusca	Cephalopoda	Sepioloida
Crane (1952)	1952	Arthropoda	Insecta	Mantodea
Crane (1952)	1952	Arthropoda	Insecta	Mantodea
Crane (1952)	1952	Arthropoda	Insecta	Mantodea
Crane (1952)	1952	Arthropoda	Insecta	Mantodea
Crane (1952)	1952	Arthropoda	Insecta	Mantodea
Crane (1952)	1952	Arthropoda	Insecta	Mantodea
Crane (1952)	1952	Arthropoda	Insecta	Mantodea
Crane (1952)	1952	Arthropoda	Insecta	Mantodea
Crane (1952)	1952	Arthropoda	Insecta	Mantodea
Carpenter (1955)	1955	Chordata	Amphibia	Urodela
Hanson & Vial (1956)	1956	Chordata	Amphibia	Anura
Bastock & Blest (1958)	1958	Arthropoda	Insecta	Lepidoptera
Blest (1958)	1958	Arthropoda	Insecta	Lepidoptera
Blest (1958)	1958	Arthropoda	Insecta	Lepidoptera
Bedford & Chinnick (1966)	1966	Arthropoda	Insecta	Phasmatodea
Bedford & Chinnick (1966)	1966	Arthropoda	Insecta	Phasmatodea
Edmunds (1968)	1968	Mollusca	Gastropoda	Nudibranchia
Robinson (1968b)	1968	Arthropoda	Insecta	Phasmatodea
Robinson (1968a)	1968	Arthropoda	Insecta	Phasmatodea
Robinson (1969)	1969	Arthropoda	Insecta	Orthoptera
Robinson (1969)	1969	Arthropoda	Insecta	Mantodea
Robinson (1969)	1969	Arthropoda	Insecta	Mantodea
Robinson (1969)	1969	Arthropoda	Insecta	Mantodea
Robinson (1969)	1969	Arthropoda	Insecta	Orthoptera
Robinson (1969)	1969	Arthropoda	Insecta	Phasmatodea
Maldonado (1970)	1970	Arthropoda	Insecta	Mantodea
Balderrama & Maldonado (1971)	1971	Arthropoda	Insecta	Mantodea
Packard & Sanders (1971)	1971	Mollusca	Cephalopoda	Octopoda
Edmunds (1972)	1972	Arthropoda	Insecta	Mantodea
Edmunds (1972)	1972	Arthropoda	Insecta	Mantodea
Edmunds (1972)	1972	Arthropoda	Insecta	Mantodea
Edmunds (1972)	1972	Arthropoda	Insecta	Mantodea
Edmunds (1972)	1972	Arthropoda	Insecta	Mantodea

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3	Edmunds (1972)	1972 Arthropoda	Insecta	Mantodea
4	Edmunds (1972)	1972 Arthropoda	Insecta	Mantodea
5	Edmunds (1972)	1972 Arthropoda	Insecta	Mantodea
6	Edmunds (1972)	1972 Arthropoda	Insecta	Mantodea
7	Edmunds (1972)	1972 Arthropoda	Insecta	Mantodea
8	Edmunds (1972)	1972 Arthropoda	Insecta	Mantodea
9	Edmunds (1972)	1972 Arthropoda	Insecta	Mantodea
10	Edmunds (1972)	1972 Arthropoda	Insecta	Mantodea
11	Edmunds (1972)	1972 Arthropoda	Insecta	Mantodea
12	Edmunds (1972)	1972 Arthropoda	Insecta	Mantodea
13	Edmunds (1972)	1972 Arthropoda	Insecta	Mantodea
14	Claridge (1974)	1974 Arthropoda	Insecta	Coleoptera
15	Johnson & Brodie (1975)	1975 Chordata	Amphibia	Urodela
16	Edmunds (1976)	1976 Arthropoda	Insecta	Mantodea
17	Edmunds (1976)	1976 Arthropoda	Insecta	Mantodea
18	Edmunds (1976)	1976 Arthropoda	Insecta	Mantodea
19	Edmunds (1976)	1976 Arthropoda	Insecta	Mantodea
20	Edmunds (1976)	1976 Arthropoda	Insecta	Mantodea
21	Edmunds (1976)	1976 Arthropoda	Insecta	Mantodea
22	Edmunds (1976)	1976 Arthropoda	Insecta	Mantodea
23	Edmunds (1976)	1976 Arthropoda	Insecta	Mantodea
24	Edmunds (1976)	1976 Arthropoda	Insecta	Mantodea
25	Edmunds (1976)	1976 Arthropoda	Insecta	Mantodea
26	Edmunds (1976)	1976 Arthropoda	Insecta	Mantodea
27	Edmunds (1976)	1976 Arthropoda	Insecta	Mantodea
28	Eisner & Adams (1976)	1976 Arthropoda	Insecta	Neuroptera
29				
30	Brodie (1977)	1977 Chordata	Amphibia	Urodela
31	Brodie (1977)	1977 Chordata	Amphibia	Urodela
32	Brodie (1977)	1977 Chordata	Amphibia	Urodela
33	Brodie (1977)	1977 Chordata	Amphibia	Urodela
34	Brodie (1977)	1977 Chordata	Amphibia	Urodela
35	Brodie (1977)	1977 Chordata	Amphibia	Urodela
36	Brodie (1977)	1977 Chordata	Amphibia	Urodela
37	Brodie (1977)	1977 Chordata	Amphibia	Urodela
38	Brodie (1977)	1977 Chordata	Amphibia	Urodela
39	Brodie (1977)	1977 Chordata	Amphibia	Urodela
40	Brodie (1977)	1977 Chordata	Amphibia	Urodela
41	Brodie (1977)	1977 Chordata	Amphibia	Urodela
42	Brodie (1977)	1977 Chordata	Amphibia	Urodela
43	Brodie (1977)	1977 Chordata	Amphibia	Urodela
44	Brodie (1977)	1977 Chordata	Amphibia	Urodela
45	Brodie (1977)	1977 Chordata	Amphibia	Urodela
46	Brodie (1977)	1977 Chordata	Amphibia	Urodela
47	Brodie (1977)	1977 Chordata	Amphibia	Urodela
48	Brodie (1977)	1977 Chordata	Amphibia	Urodela
49	Brodie (1977)	1977 Chordata	Amphibia	Urodela
50	Brodie (1977)	1977 Chordata	Amphibia	Urodela
51	Brodie (1977)	1977 Chordata	Amphibia	Urodela
52	Brodie (1977)	1977 Chordata	Amphibia	Urodela
53	Brodie (1977)	1977 Chordata	Amphibia	Urodela
54	Brodie (1977)	1977 Chordata	Amphibia	Urodela
55	Brodie (1977)	1977 Chordata	Amphibia	Urodela
56	Brodie (1977)	1977 Chordata	Amphibia	Urodela
57	Brodie (1977)	1977 Chordata	Amphibia	Urodela
58	Brodie (1977)	1977 Chordata	Amphibia	Urodela
59	Brodie (1977)	1977 Chordata	Amphibia	Urodela
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3	Brodie (1977)	1977 Chordata	Amphibia	Urodela
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6	Brodie (1977)	1977 Chordata	Amphibia	Urodela
7	Brodie (1977)	1977 Chordata	Amphibia	Urodela
8	Brodie (1977)	1977 Chordata	Amphibia	Urodela
9	Brodie (1977)	1977 Chordata	Amphibia	Urodela
10	Brodie (1977)	1977 Chordata	Amphibia	Urodela
11	Brodie (1977)	1977 Chordata	Amphibia	Urodela
12	Brodie (1977)	1977 Chordata	Amphibia	Urodela
13	Brodie (1977)	1977 Chordata	Amphibia	Urodela
14	Brodie (1977)	1977 Chordata	Amphibia	Urodela
15	Brodie (1977)	1977 Chordata	Amphibia	Urodela
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17	Brodie (1977)	1977 Chordata	Amphibia	Urodela
18	Brodie (1977)	1977 Chordata	Amphibia	Urodela
19	Brodie (1977)	1977 Chordata	Amphibia	Urodela
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21	Brodie (1977)	1977 Chordata	Amphibia	Urodela
22	Brodie (1977)	1977 Chordata	Amphibia	Urodela
23	Brodie (1977)	1977 Chordata	Amphibia	Urodela
24	Brodie (1977)	1977 Chordata	Amphibia	Urodela
25	Brodie (1977)	1977 Chordata	Amphibia	Urodela
26	Brodie (1977)	1977 Chordata	Amphibia	Urodela
27	Brodie (1977)	1977 Chordata	Amphibia	Urodela
28	Brodie (1977)	1977 Chordata	Amphibia	Urodela
29	Brodie (1977)	1977 Chordata	Amphibia	Urodela
30	Brodie (1977)	1977 Chordata	Amphibia	Urodela
31	Brodie (1977)	1977 Chordata	Amphibia	Urodela
32	Brodie (1977)	1977 Chordata	Amphibia	Urodela
33	Brodie (1977)	1977 Chordata	Amphibia	Urodela
34	Brodie (1977)	1977 Chordata	Amphibia	Urodela
35	Brodie (1977)	1977 Chordata	Amphibia	Urodela
36	Brodie (1977)	1977 Chordata	Amphibia	Urodela
37	Brodie (1977)	1977 Chordata	Amphibia	Urodela
38	Brodie (1977)	1977 Chordata	Amphibia	Urodela
39	Brodie (1977)	1977 Chordata	Amphibia	Urodela
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42	Brodie (1977)	1977 Chordata	Amphibia	Urodela
43	Brodie (1977)	1977 Chordata	Amphibia	Urodela
44	Brodie (1977)	1977 Chordata	Amphibia	Urodela
45	Brodie (1977)	1977 Chordata	Amphibia	Urodela
46	Brodie (1977)	1977 Chordata	Amphibia	Urodela
47	Brodie (1977)	1977 Chordata	Amphibia	Urodela
48	Brodie (1977)	1977 Chordata	Amphibia	Urodela
49	Brodie (1977)	1977 Chordata	Amphibia	Urodela
50	Brodie (1977)	1977 Chordata	Amphibia	Urodela
51	Brodie (1977)	1977 Chordata	Amphibia	Urodela
52	Brodie (1977)	1977 Chordata	Amphibia	Urodela
53	Brodie (1977)	1977 Chordata	Amphibia	Urodela
54	Brodie (1977)	1977 Chordata	Amphibia	Urodela
55	Hayes (1977)	1977 Arthropoda	Malacostraca	Decapoda
56	Hayes (1977)	1977 Arthropoda	Malacostraca	Decapoda
57	Hayes (1977)	1977 Arthropoda	Malacostraca	Decapoda
58	Hayes (1977)	1977 Arthropoda	Malacostraca	Decapoda
59	Evans (1978)	1978 Arthropoda	Insecta	Lepidoptera
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3	Evans (1978)	1978 Arthropoda	Insecta	Lepidoptera
4	Nowak & Brodie (1978)	1978 Chordata	Amphibia	Urodela
5	Sandow & Bailey (1978)	1978 Arthropoda	Insecta	Orthoptera
6	Bajger (1980)	1980 Chordata	Amphibia	Anura
7	Bajger (1980)	1980 Chordata	Amphibia	Anura
8	DiGiovanni & Brodie (1981)	1981 Chordata	Amphibia	Urodela
9	Steiner (1981)	1981 Arthropoda	Insecta	Orthoptera
10	Schal et al. (1982)	1982 Arthropoda	Insecta	Blattodea
11	Bailey & Sandow (1983)	1983 Arthropoda	Insecta	Orthoptera
12	Brodie et al. (1984)	1984 Chordata	Amphibia	Urodela
13	Brodie et al. (1984)	1984 Chordata	Amphibia	Urodela
14	Brodie et al. (1984)	1984 Chordata	Amphibia	Urodela
15	Brodie et al. (1984)	1984 Chordata	Amphibia	Urodela
16	Brodie et al. (1984)	1984 Chordata	Amphibia	Urodela
17	Brodie et al. (1984)	1984 Chordata	Amphibia	Urodela
18	Brodie et al. (1984)	1984 Chordata	Amphibia	Urodela
19	Hödl & Gollman (1986)	1986 Chordata	Amphibia	Anura
20	Hödl & Gollman (1986)	1986 Chordata	Amphibia	Anura
21	Hödl & Gollman (1986)	1986 Chordata	Amphibia	Anura
22	Hödl & Gollman (1986)	1986 Chordata	Amphibia	Anura
23	Hödl & Gollman (1986)	1986 Chordata	Amphibia	Anura
24	Hödl & Gollman (1986)	1986 Chordata	Amphibia	Anura
25	Hödl & Gollman (1986)	1986 Chordata	Amphibia	Anura
26	Hödl & Gollman (1986)	1986 Chordata	Amphibia	Anura
27	Hödl & Gollman (1986)	1986 Chordata	Amphibia	Anura
28	Hödl & Gollman (1986)	1986 Chordata	Amphibia	Anura
29	Hödl & Gollman (1986)	1986 Chordata	Amphibia	Anura
30	Hödl & Gollman (1986)	1986 Chordata	Amphibia	Anura
31	Hödl & Gollman (1986)	1986 Chordata	Amphibia	Anura
32	Hödl & Gollman (1986)	1986 Chordata	Amphibia	Anura
33	Hödl & Gollman (1986)	1986 Chordata	Amphibia	Anura
34	Green (1988)	1988 Chordata	Amphibia	Anura
35	Green (1988)	1988 Chordata	Amphibia	Anura
36	Green (1988)	1988 Chordata	Amphibia	Anura
37	Green (1988)	1988 Chordata	Amphibia	Anura
38	Lyon & Fogden (1989)	1989 Chordata	Aves	Eurypygiformes
39	Martins (1989)	1989 Chordata	Amphibia	Anura
40	Fenton & Licht (1990)	1990 Chordata	Reptilia	Squamata
41	Fenton & Licht (1990)	1990 Chordata	Reptilia	Squamata
42	Fenton & Licht (1990)	1990 Chordata	Reptilia	Squamata
43	Fenton & Licht (1990)	1990 Chordata	Reptilia	Squamata
44	Fenton & Licht (1990)	1990 Chordata	Reptilia	Squamata
45	Fenton & Licht (1990)	1990 Chordata	Reptilia	Squamata
46	Fenton & Licht (1990)	1990 Chordata	Reptilia	Squamata
47	Fenton & Licht (1990)	1990 Chordata	Reptilia	Squamata
48	Thomas & Strahl (1990)	1990 Chordata	Aves	Eurypygiformes
49	Castner & Nickle (1995)	1995 Arthropoda	Insecta	Orthoptera
50	Field & Bailey (1997)	1997 Arthropoda	Insecta	Orthoptera
51	Field & Bailey (1997)	1997 Arthropoda	Insecta	Orthoptera
52	Brodie et al. (1998)	1998 Chordata	Amphibia	Anura
53	Brodie et al. (1998)	1998 Chordata	Amphibia	Anura
54	Brodie et al. (1998)	1998 Chordata	Amphibia	Anura
55	Brodie et al. (1998)	1998 Chordata	Amphibia	Anura
56	Brodie et al. (1998)	1998 Chordata	Amphibia	Anura
57	Brodie et al. (1998)	1998 Chordata	Amphibia	Anura
58	Brodie et al. (1998)	1998 Chordata	Amphibia	Anura
59	Brodie et al. (1998)	1998 Chordata	Amphibia	Anura
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Brodie et al. (1998)	1998 Chordata	Amphibia	Anura
Grandcolas & Desuttes	1998 Arthropoda	Insecta	Mantodea
Sköld (1998)	1998 Echinodermata	Ophuroidea	Ophiurida
Choi et al. (1999)	1999 Chordata	Amphibia	Anura
Williams et al. (2000)	2000 Chordata	Amphibia	Anura
Williams et al. (2000)	2000 Chordata	Amphibia	Anura
Williams et al. (2000)	2000 Chordata	Amphibia	Anura
Williams et al. (2000)	2000 Chordata	Amphibia	Anura
Toledo et al. (2004a)	2004 Chordata	Amphibia	Anura
Vester et al. (2004)	2004 Chordata	Actinopterygii	Gadiformes
Lenzi-Mattos et al. (2005)	2005 Chordata	Amphibia	Anura
Toledo et al. (2004b)	2005 Chordata	Amphibia	Anura
Vallin et al. (2005)	2005 Arthropoda	Insecta	Lepidoptera
Adamo et al. (2006)	2006 Mollusca	Cephalopoda	Sepioloida
Langridge (2006)	2006 Mollusca	Cephalopoda	Sepioloida
Vallin et al. (2006)	2006 Arthropoda	Insecta	Lepidoptera
Brown et al. (2007)	2007 Arthropoda	Insecta	Lepidoptera
Hill (2007)	2007 Arthropoda	Insecta	Mantodea
Langridge et al. (2007)	2007 Mollusca	Cephalopoda	Sepioloida
Vallin et al. (2007)	2007 Arthropoda	Insecta	Lepidoptera
Serafim & Ribeiro Du	2008 Chordata	Reptilia	Squamata
Serafim & Ribeiro Du	2008 Chordata	Reptilia	Squamata
Bouwma & Herrnkind	2009 Arthropoda	Malacostraca	Decapoda
Bura et al. (2009)	2009 Arthropoda	Insecta	Lepidoptera
Tozetti et al. (2009)	2009 Chordata	Reptilia	Squamata
Olofsson et al. (2012b)	2012 Arthropoda	Insecta	Lepidoptera
Olofsson et al. (2012a)	2012 Arthropoda	Insecta	Lepidoptera
Ruiz et al. (2012)	2012 Mollusca	Cephalopoda	Octopoda
Cartron et al. (2013)	2013 Mollusca	Cephalopoda	Sepioloida
Kowalski et al. (2014)	2014 Arthropoda	Insecta	Orthoptera
Umbers & Mappes (2015)	2015 Arthropoda	Insecta	Orthoptera
Whiting et al. (2015)	2015 Chordata	Reptilia	Squamata
Kang et al. (2016)	2016 Arthropoda	Insecta	Hemiptera
Badiane et al. (2018)	2018 Chordata	Reptilia	Squamata
O'Hanlon et al. (2018)	2018 Arthropoda	Insecta	Mantodea
O'Hanlon et al. (2018)	2018 Arthropoda	Insecta	Mantodea
O'Hanlon et al. (2018)	2018 Arthropoda	Insecta	Mantodea
Umbers et al. (2019)	2019 Arthropoda	Insecta	Orthoptera
Blest (1957b)	1957 Arthropoda	Insecta	Lepidoptera
Blest (1957b)	1957 Arthropoda	Insecta	Lepidoptera
Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera

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3	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
4	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
5	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
6	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
7	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
8	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
9	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
10	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
11	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
12	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
13	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
14	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
15	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
16	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
17	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
18	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
19	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
20	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
21	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
22	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
23	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
24	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
25	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
26	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
27	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
28	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
29	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
30	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
31	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
32	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
33	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
34	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
35	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
36	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
37	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
38	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
39	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
40	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
41	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
42	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
43	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
44	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
45	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
46	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
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ext or not included in study, varied: too many different approaches to mention.]

Family	Species	Study type
Erebidae	<i>Pseudohypsa speciosa</i>	descriptive
Erebidae	<i>Rhodogastria bubo</i>	descriptive
Erebidae	<i>Rhodogastria leucoptera</i>	descriptive
Erebidae	<i>Amphicallier pactolicus</i>	descriptive
Erebidae	<i>Rhodogastria lupia</i>	descriptive
Eremiaphilidae	<i>Eremiaphila braueri</i>	descriptive
Hymenopodidae	<i>Hestiasula sarawaka</i>	descriptive
Mantidae	<i>Stagmomantis</i> sp.	descriptive
Sepiidae	<i>Sepia officinalis</i>	descriptive
Acanthopidae	<i>Acanthops falcata</i>	descriptive
Acanthopidae	<i>Acontiothespis multicolor</i>	descriptive
Liturgusidae	<i>Liturgusa</i> sp.	descriptive
Thespidae	<i>Musonia surinama</i>	descriptive
Mantidae	<i>Stagmatoptera septentrionalis</i>	descriptive
Mantidae	<i>Stagmomantis carolina</i>	descriptive
Mantidae	<i>Thesprotia filum</i>	descriptive
Acanthopidae	<i>Tithrone roseipennis</i>	descriptive
Ambystomatidae	<i>Ambystoma tigrinum melanostictum</i>	descriptive
Bufo	<i>Bufo alvarius</i>	manipulative
Saturniidae	<i>Automeris aurantiaca</i>	descriptive
Saturniidae	<i>Callosamia promethea</i>	descriptive
Saturniidae	<i>Rothschildia jacobaeae</i>	descriptive
Phasmatidae	<i>Eurycnema goliath</i>	descriptive
Phasmatidae	<i>Tropidoderus childrenii</i>	descriptive
Hexabanchidae	<i>Hexabanchus marginatus</i>	descriptive
Pseudophasmatidae	<i>Pterinoxylus spinulosus</i>	descriptive
Diapheromeridae	<i>Oncotophasma martini</i>	descriptive
Tettigoniidae	<i>Acanthodis curvidens</i>	descriptive
Angelida	<i>Angela guianensis</i>	descriptive
Mantidae	<i>Choerododis rhombicollis</i>	descriptive
Mantidae	<i>Phyllovates chlorophaea</i>	descriptive
Tettigoniidae	<i>Scorpiorinus fragilis</i>	descriptive
Pseudophasmatidae	<i>Metriotes diocles</i>	descriptive
Mantidae	<i>Stagmatoptera biocellata</i>	manipulative
Mantidae	<i>Stagmatoptera biocellata</i>	manipulative
Octopodidae	<i>Octopus vulgaris</i>	descriptive
Mantidae	<i>Danuria buchholzi</i>	descriptive
Tarachodidae	<i>Galepsus toganus</i>	descriptive
Empusidae	<i>Hemiempusa capensis</i>	descriptive
Empusidae	<i>Idolomorpha lateralis</i>	descriptive
Mantidae	<i>Mantis religiosa</i>	descriptive

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3	Mantidae	<i>Miomantis aurea</i>	descriptive
4	Mantidae	<i>Plistospilota guineensis</i>	descriptive
5	Mantidae	<i>Polyspilota aeruginosa</i>	descriptive
6	Mantidae	<i>Pseudocreobotra ocellata</i>	descriptive
7	Hymenopodidae	<i>Sphodromantis lineola</i>	descriptive
8	Mantidae	<i>Stenovates strachani</i>	descriptive
9	Mantidae	<i>Tarachodes afzelii</i>	descriptive
10	Eremiaphilidae	<i>Tenodera superstitiosa</i>	descriptive
11	Mantidae	<i>Cychnus caraboides</i>	manipulative
12	Carabidae	<i>Taricha granulosa</i>	manipulative
13	Salamandridae	<i>Cataspilota misana</i>	descriptive
14	Mantidae	<i>Chilonoptera lestoni</i>	descriptive
15	Hymenopodidae	<i>Chloroharpax modesta</i>	descriptive
16	Hymenopodidae	<i>Panurgica compressicollis</i>	descriptive
17	Hymenopodidae	<i>Paramantis togana</i>	descriptive
18	Mantidae	<i>Popa undata</i>	descriptive
19	Deroplatyidae	<i>Prohierodula ornatipennis</i>	descriptive
20	Mantidae	<i>Sphodromantis aurea</i>	descriptive
21	Mantidae	<i>Statilia apicalis</i>	descriptive
22	Mantidae	<i>Haploglenius luteus</i>	descriptive
23	Ascalaphidae	<i>Ambystoma annulatum</i>	descriptive
24	Ascalaphidae	<i>Ambystoma cingulatum</i>	descriptive
25	Ambystomatidae	<i>Ambystoma gracile</i>	descriptive
26	Ambystomatidae	<i>Ambystoma jeffersonianum</i>	descriptive
27	Ambystomatidae	<i>Ambystoma lacustris</i>	descriptive
28	Ambystomatidae	<i>Ambystoma laterale</i>	descriptive
29	Ambystomatidae	<i>Ambystoma mabeei</i>	descriptive
30	Ambystomatidae	<i>Ambystoma macrodactylum</i>	descriptive
31	Ambystomatidae	<i>Ambystoma maculatum</i>	descriptive
32	Ambystomatidae	<i>Ambystoma mexicanum</i>	descriptive
33	Ambystomatidae	<i>Ambystoma opacum</i>	descriptive
34	Ambystomatidae	<i>Ambystoma ordinarium</i>	descriptive
35	Ambystomatidae	<i>Ambystoma talpoideum</i>	descriptive
36	Ambystomatidae	<i>Ambystoma texanum</i>	descriptive
37	Ambystomatidae	<i>Ambystoma tigrinum</i>	descriptive
38	Ambystomatidae	<i>Pseudotriton montanus</i>	descriptive
39	Plethodontidae	<i>Pseudotriton ruber</i>	descriptive
40	Plethodontidae	<i>Cynops pyrrhogaster</i>	descriptive
41	Salamandridae	<i>Desmognathus wrighti</i>	descriptive
42	Plethodontidae	<i>Notophthalmus perstriatus</i>	descriptive
43	Salamandridae	<i>Paramesotriton hongkongensis</i>	descriptive
44	Salamandridae	<i>Taricha rivularis</i>	descriptive
45	Salamandridae	<i>Taricha rivularis</i>	descriptive
46	Salamandridae		
47	Salamandridae		
48	Salamandridae		
49	Salamandridae		
50	Salamandridae		
51	Salamandridae		
52	Salamandridae		
53	Salamandridae		
54	Salamandridae		
55	Salamandridae		
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57	Salamandridae		
58	Salamandridae		
59	Salamandridae		
60	Salamandridae		

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2			
3	Salamandridae	<i>Taricha torosa</i>	descriptive
4	Salamandridae	<i>Taricha torosa</i>	descriptive
5	Salamandridae	<i>Triturus alpestris</i>	descriptive
6	Salamandridae	<i>Triturus alpestris</i>	descriptive
7	Salamandridae	<i>Triturus alpestris</i>	descriptive
8	Salamandridae	<i>Triturus cristatus</i>	descriptive
9	Salamandridae	<i>Triturus cristatus</i>	descriptive
10	Salamandridae	<i>Triturus helveticus</i>	descriptive
11	Salamandridae	<i>Triturus marmoratus</i>	descriptive
12	Salamandridae	<i>Triturus vulgaris</i>	descriptive
13	Salamandridae	<i>Triturus vulgaris</i>	descriptive
14	Salamandridae	<i>Notophthalmus viridescens</i>	descriptive
15	Ambystomatidae	<i>Rhyacotriton olympicus</i>	descriptive
16	Salamandridae	<i>Taricha granulosa</i>	descriptive
17	Salamandridae	<i>Taricha granulosa</i>	descriptive
18	Plethodontidae	<i>Aneides aeneus</i>	descriptive
19	Plethodontidae	<i>Aneides ferreus</i>	descriptive
20	Plethodontidae	<i>Aneides ferreus</i>	descriptive
21	Plethodontidae	<i>Aneides lugubris</i>	descriptive
22	Ambystomatidae	<i>Dicamptodon ensatus</i>	descriptive
23	Plethodontidae	<i>Ensatina eschscholtzii</i>	descriptive
24	Plethodontidae	<i>Eurycea bislineata</i>	descriptive
25	Plethodontidae	<i>Eurycea bislineata</i>	descriptive
26	Plethodontidae	<i>Eurycea longicauda guttolineata</i>	descriptive
27	Plethodontidae	<i>Eurycea lucifuga</i>	descriptive
28	Plethodontidae	<i>Eurycea lucifuga</i>	descriptive
29	Plethodontidae	<i>Gyrinophilus porphyriticus</i>	descriptive
30	Plethodontidae	<i>Hydromantes genei</i>	descriptive
31	Plethodontidae	<i>Hydromantes genei</i>	descriptive
32	Plethodontidae	<i>Hydromantes shastae</i>	descriptive
33	Hynobiidae	<i>Hynobius dunni</i>	descriptive
34	Hynobiidae	<i>Hynobius leechi</i>	descriptive
35	Hynobiidae	<i>Hynobius leechi</i>	descriptive
36	Hynobiidae	<i>Hynobius nebulosus</i>	descriptive
37	Hynobiidae	<i>Hynobius tsuensis</i>	descriptive
38	Plethodontidae	<i>Leurognathus marmoratus</i>	descriptive
39	Plethodontidae	<i>Plethodon caddoensis</i>	descriptive
40	Plethodontidae	<i>Plethodon glutinosus</i>	descriptive
41	Plethodontidae	<i>Plethodon glutinosus</i>	descriptive
42	Plethodontidae	<i>Plethodon jordani</i>	descriptive
43	Plethodontidae	<i>Plethodon larselli</i>	descriptive
44	Plethodontidae	<i>Plethodon larselli</i>	descriptive
45	Plethodontidae	<i>Plethodon nettingi hubrichti</i>	descriptive
46	Salamandridae	<i>Pleurodeles waltl</i>	descriptive
47	Ambystomatidae	<i>Rhyacosiredon altamirani</i>	descriptive
48	Ambystomatidae	<i>Rhyacosiredon rivularis</i>	descriptive
49	Ambystomatidae	<i>Rhyacosiredon rivularis</i>	descriptive
50	Salamandridae	<i>Salamandra atra</i>	descriptive
51	Salamandridae	<i>Salamandra atra</i>	descriptive
52	Salamandridae	<i>Salamandra atra</i>	descriptive
53	Plethodontidae	<i>Typhlotriton spelaeus</i>	descriptive
54	Plethodontidae	<i>Typhlotriton spelaeus</i>	descriptive
55	Plethodontidae	<i>Hemidactylium scutatum</i>	descriptive
56	Cambaridae	<i>Procambrus acutus acutus</i>	descriptive
57	Cambaridae	<i>Procambrus acutus acutus</i>	descriptive
58	Cambaridae	<i>Procambrus gracilis</i>	descriptive
59	Cambaridae	<i>Procambrus simulans simulans</i>	descriptive
60	Saturniidae	<i>Callosamia promethea</i>	manipulative

1			
2			
3	Saturniidae	<i>Hyalophora cecropia</i>	manipulative
4	Salamandridae	<i>Pleurodeles waltl</i>	manipulative
5	Tettigoniidae	<i>Mygalopsis ferruginea</i>	manipulative
6	Bombinatoridae	<i>Bombina bombina</i>	manipulative
7	Bombinatoridae	<i>Bombina variegata</i>	manipulative
8	Bombinatoridae	<i>Bombina variegata</i>	manipulative
9	Bombinatoridae	<i>Bombina variegata</i>	manipulative
10	Ambystomatidae	<i>Ambystoma opacum</i>	manipulative
11	Acrididae	<i>Mestobregma plattei rubripeme</i>	descriptive
12	Ectobiidae	<i>Megaloblatta blaberoides</i>	descriptive
13	Ectobiidae	<i>Megaloblatta blaberoides</i>	descriptive
14	Tettigoniidae	<i>Mygalopsis marki</i>	descriptive
15	Salamandridae	<i>Tylotriton verrucosus</i>	manipulative
16	Salamandridae	<i>Echinotriton andersoni</i>	manipulative
17	Salamandridae	<i>Echinotriton andersoni</i>	manipulative
18	Salamandridae	<i>Mertensiella caucasica</i>	manipulative
19	Salamandridae	<i>Pachytriton brevipes</i>	manipulative
20	Salamandridae	<i>Paramesotriton caudopunctatus</i>	manipulative
21	Salamandridae	<i>Paramesotriton caudopunctatus</i>	manipulative
22	Salamandridae	<i>Paramesotriton chinensis</i>	manipulative
23	Leptodactylidae	<i>Adenomera hylaedactyla</i>	descriptive
24	Leptodactylidae	<i>Hydrotaetare schmidtii</i>	descriptive
25	Leptodactylidae	<i>Hydrotaetare schmidtii</i>	descriptive
26	Hylidae	<i>Hyla boans</i>	descriptive
27	Hylidae	<i>Hyla lanciformis</i>	descriptive
28	Hylidae	<i>Hyla lanciformis</i>	descriptive
29	Hylidae	<i>Hyla raniceps</i>	descriptive
30	Leptodactylidae	<i>Leptodactylus fuscus</i>	descriptive
31	Leptodactylidae	<i>Leptodactylus ocellatus</i>	descriptive
32	Leptodactylidae	<i>Leptodactylus ocellatus</i>	descriptive
33	Leptodactylidae	<i>Leptodactylus pentadactylus</i>	descriptive
34	Leptodactylidae	<i>Leptodactylus rhodomystax</i>	descriptive
35	Leiopelmatidae	<i>Leiopelma archeyi</i>	descriptive
36	Leiopelmatidae	<i>Leiopelma archeyi</i>	descriptive
37	Leiopelmatidae	<i>Leiopelma hamiltoni</i>	descriptive
38	Leiopelmatidae	<i>Leiopelma hochstetteri</i>	descriptive
39	Eurypygidae	<i>Eurypyga helias</i>	descriptive
40	Leptodactylidae	<i>Pleurodema brachyops</i>	descriptive
41	Leptodactylidae	<i>Pleurodema brachyops</i>	descriptive
42	Viperidae	<i>Crotalus adamanteus</i>	manipulative
43	Viperidae	<i>Crotalus atrox</i>	manipulative
44	Viperidae	<i>Crotalus atrox</i>	manipulative
45	Viperidae	<i>Crotalus cerastes</i>	manipulative
46	Viperidae	<i>Crotalus horridus</i>	manipulative
47	Viperidae	<i>Crotalus horridus</i>	manipulative
48	Viperidae	<i>Crotalus viridis</i>	manipulative
49	Viperidae	<i>Sistrurus catenatus</i>	manipulative
50	Eurypygidae	<i>Eurypyga helias</i>	descriptive
51	Tettigoniidae	<i>Pterochroza ocellata</i>	descriptive
52	Gryllacrididae	<i>Ametrus</i> sp.	descriptive
53	Gryllacrididae	<i>Ametrus</i> sp.	descriptive
54	Gryllacrididae	<i>Hadrogryllacris</i> sp.	descriptive
55	Myobatrachidae	<i>Uperoleia aspera</i>	descriptive
56	Myobatrachidae	<i>Uperoleia borealis</i>	descriptive
57	Myobatrachidae	<i>Uperoleia borealis</i>	descriptive
58	Myobatrachidae	<i>Uperoleia lithomoda</i>	descriptive
59	Myobatrachidae	<i>Uperoleia lithomoda</i>	descriptive
60	Myobatrachidae	<i>Uperoleia mjobergi</i>	descriptive

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3	Myobatrachidae	<i>Uperoleia talpa</i>	descriptive
4	Mantidae	<i>Polyspilota aeruginosa</i>	descriptive
5	Ophiuridae	<i>Ophiura ophiura</i>	manipulative
6	Bombinatoridae	<i>Bombina orientalis</i>	manipulative
7	Myobatrachidae	<i>Pseudophryne bibronii</i>	descriptive
8	Myobatrachidae	<i>Pseudophryne semimarmorata</i>	descriptive
9	Myobatrachidae	<i>Uperoleia altissima</i>	descriptive
10	Myobatrachidae	<i>Uperoleia littlejohni</i>	descriptive
11	Dendrobatidae	<i>Epipedobates flavopictus</i>	descriptive
12	Gadidae	<i>Gadus morhua</i>	manipulative
13	Leptodactylidae	<i>Physalaemus nattereri</i>	descriptive
14	Leptodactylidae	<i>Leptodactylus labyrinthicus</i>	descriptive
15	Nymphalidae	<i>Aglais io</i>	manipulative
16	Sepiidae	<i>Sepia officinalis</i>	manipulative
17	Sepiidae	<i>Sepia officinalis</i>	manipulative
18	Sphingidae	<i>Smerinthus ocellatus</i>	manipulative
19	Saturniidae	<i>Antheraea polyphemus</i>	manipulative
20	Mantidae	<i>Mantis religiosa</i>	descriptive
21	Sepiidae	<i>Sepia officinalis</i>	manipulative
22	Nymphalidae	<i>Aglais io</i>	manipulative
23	Elapidae	<i>Micrurus altirostris</i>	descriptive
24	Elapidae	<i>Micrurus frontalis</i>	descriptive
25	Palinuridae	<i>Panulirus argus</i>	manipulative
26	Saturniidae	<i>Saturnia pyri</i>	manipulative
27	Colubridae	<i>Xenodon dorbignyi</i>	descriptive
28	Nymphalidae	<i>Aglais io</i>	manipulative
29	Papilionidae	<i>Papilio machaon</i>	manipulative
30	Octopodidae	<i>Robsonella fontaniana</i>	manipulative
31	Sepiidae	<i>Sepia officinalis</i>	manipulative
32	Tettigoniidae	<i>Poecilimon ornatus</i>	descriptive
33	Tettigoniidae	<i>Acripeza reticulata</i>	manipulative
34	Agamidae	<i>Ceratophora tennentii</i>	descriptive
35	Fulgoridae	<i>Lycorma delicatula</i>	manipulative
36	Scincidae	<i>Tiliqua scincoides intermedia</i>	manipulative
37	Mantidae	<i>Archimantis latistyla</i>	manipulative
38	Mantidae	<i>Hierodula majuscula</i>	manipulative
39	Mantidae	<i>Pseudomantis albofimbriata</i>	manipulative
40	Tettigoniidae	<i>Acripeza reticulata</i>	manipulative
41	Nymphalidae	<i>Aglais urticae</i>	manipulative
42	Nymphalidae	<i>Aglais io</i>	descriptive
43	Saturniidae	<i>Aglia tau</i>	descriptive
44	Saturniidae	<i>Antherea paphia</i>	descriptive
45	Saturniidae	<i>Antherina suraka</i>	descriptive
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58			
59			
60			

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2			
3	Saturniidae	<i>Attacus edwardsi</i>	descriptive
4	Saturniidae	<i>Automeris aurantiaca</i>	descriptive
5	Saturniidae	<i>Automeris coeresus</i>	descriptive
6	Saturniidae	<i>Automeris illustris</i>	descriptive
7	Saturniidae	<i>Automeris io</i>	descriptive
8	Saturniidae	<i>Automeris janus</i>	descriptive
9	Saturniidae	<i>Automeris memusae</i>	descriptive
10	Saturniidae	<i>Automeris nyctimane</i>	descriptive
11	Saturniidae	<i>Automeris saturata</i>	descriptive
12	Saturniidae	<i>Callosamia promethea</i>	descriptive
13	Saturniidae	<i>Celerio euphorbiae</i>	descriptive
14	Saturniidae	<i>Citheronia bristottii</i>	descriptive
15	Saturniidae	<i>Copaxa lavendera</i>	descriptive
16	Saturniidae	<i>Dictyoploca cachara</i>	descriptive
17	Saturniidae	<i>Epithora atbarina sudanica</i>	descriptive
18	Saturniidae	<i>Eudia pavonia</i>	descriptive
19	Saturniidae	<i>Eudyarina venata</i>	descriptive
20	Saturniidae	<i>Gynanisa maia</i>	descriptive
21	Saturniidae	<i>Hylesia nigricans</i>	descriptive
22	Saturniidae	<i>Imbrasia macrothyris</i>	descriptive
23	Saturniidae	<i>Laothoe populi</i>	descriptive
24	Saturniidae	<i>Lobobunaea epithyrena</i>	descriptive
25	Saturniidae	<i>Lobobunaea phaedusa</i>	descriptive
26	Saturniidae	<i>Loepa katinka</i>	descriptive
27	Saturniidae	<i>Nudaurelia arata</i>	descriptive
28	Saturniidae	<i>Nudaurelia dione</i>	descriptive
29	Saturniidae	<i>Philosamia cynthia cynthia</i>	descriptive
30	Saturniidae	<i>Philosamia cynthia ricini</i>	descriptive
31	Saturniidae	<i>Rothschildia orizaba</i>	descriptive
32	Saturniidae	<i>Samia cecropia</i>	descriptive
33	Saturniidae	<i>Smerinthus ocellatus</i>	descriptive
34	Saturniidae	<i>Sphinx ligustri</i>	descriptive
35	Saturniidae	<i>Telea polyphemus</i>	descriptive
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For the five display mode columns, 0 = absent, 1 = present.

Life stage studied	Primary defence reported	Predator in study
adult	NA	human
adult	NA	human
adult	NA	human
adult	NA	human
adult	NA	human
NA	camouflage	human
NA	camouflage	NA
NA	NA	human
adult	camouflage	human
adult	camouflage	human
adult	camouflage	many
adult	camouflage	human
adult	camouflage	human
NA	camouflage	human
adult	camouflage	human
adult	camouflage	many
adult	camouflage	many
NA	NA	human
adult	NA	mammal
adult	NA	human
adult	NA	human
adult	NA	human
adult	camouflage	human
adult	camouflage	human
adult	NA	human
adult	camouflage	human
NA	camouflage	human
adult	camouflage	human
juvenile, adult	camouflage	human
juvenile, adult	camouflage	many
juvenile, adult	camouflage	human
juvenile, adult	camouflage	human
juvenile, adult	NA	NA
NA	NA	bird
adult	NA	bird
juvenile, adult	camouflage	human
adult	camouflage	NA
adult	camouflage	NA
adult	camouflage	NA
adult	camouflage	NA
adult	camouflage	mammal, reptile

1			
2			
3	adult	camouflage	human
4	adult	camouflage	human
5	adult	camouflage	NA
6	adult	camouflage	NA
7	adult	camouflage	NA
8	adult	camouflage	mammal, reptile
9	adult	camouflage	NA
10	adult	camouflage	NA
11	adult	camouflage	human
12	adult	camouflage	human
13	adult	NA	human
14	adult	NA	human
15	NA	NA	bird
16	adult	camouflage	human
17	adult	camouflage	human
18	adult	camouflage	human
19	adult	camouflage	human
20	juvenile, adult	camouflage	NA
21	adult	camouflage	human
22	adult	camouflage	NA
23	adult	camouflage	human
24	adult	camouflage	human
25	adult	camouflage	human
26	adult	camouflage	human
27	adult	camouflage	human
28	adult	NA	human
29	adult	aposematic	NA
30	adult	aposematic	NA
31	adult	aposematic	NA
32	adult	aposematic	NA
33	adult	aposematic	NA
34	adult	aposematic	NA
35	adult	aposematic	NA
36	adult	aposematic	NA
37	adult	aposematic	NA
38	adult	aposematic	NA
39	adult	aposematic	NA
40	adult	aposematic	NA
41	adult	aposematic	NA
42	adult	aposematic	NA
43	adult	aposematic	NA
44	adult	aposematic	NA
45	adult	aposematic	NA
46	adult	aposematic	NA
47	adult	aposematic	NA
48	adult	aposematic	NA
49	adult	Batesian mimic	mammal
50	adult	Batesian mimic	mammal
51	adult	camouflage	NA
52	adult	camouflage	NA
53	adult	camouflage	NA
54	adult	camouflage	NA
55	adult	camouflage	NA
56	adult	camouflage	NA
57	adult	camouflage	NA
58	adult	camouflage	NA
59	adult	camouflage	NA
60			

1			
2			
3	adult	camouflage	NA
4	adult	camouflage	NA
5	adult	camouflage	NA
6	adult	camouflage	NA
7	adult	camouflage	NA
8	adult	camouflage	NA
9	adult	camouflage	NA
10	adult	camouflage	NA
11	adult	camouflage	NA
12	adult	camouflage	NA
13	adult	camouflage	NA
14	adult	camouflage	NA
15	adult	camouflage	NA
16	adult	camouflage	bird
17	adult	NA	NA
18	adult	NA	NA
19	adult	NA	NA
20	adult	NA	NA
21	adult	NA	NA
22	adult	NA	NA
23	adult	NA	NA
24	adult	NA	bird, mammal
25	adult	NA	bird, mammal
26	adult	NA	NA
27	adult	NA	NA
28	adult	NA	NA
29	adult	NA	NA
30	adult	NA	NA
31	adult	NA	NA
32	adult	NA	NA
33	adult	NA	NA
34	adult	NA	NA
35	adult	NA	NA
36	adult	NA	NA
37	adult	NA	NA
38	adult	NA	NA
39	adult	NA	NA
40	adult	NA	mammal
41	adult	NA	mammal
42	adult	NA	NA
43	adult	NA	NA
44	adult	NA	NA
45	adult	NA	NA
46	adult	NA	NA
47	adult	NA	NA
48	adult	NA	NA
49	adult	NA	NA
50	adult	NA	NA
51	adult	NA	NA
52	adult	NA	NA
53	adult	NA	NA
54	adult	camouflage	human
55	adult	camouflage	human
56	adult	camouflage	human
57	adult	camouflage	human
58	adult	camouflage	human
59	adult	camouflage	human
60			

1			
2			
3	adult	camouflage	human
4	NA	NA	human, mammal
5	NA	camouflage	reptile
6	adult	camouflage	human
7	adult	camouflage	human
8	adult	camouflage	human
9	adult	camouflage	human
10	NA	NA	mammal
11	adult	camouflage	insect
12	juvenile	aposematic	human
13	juvenile, adult	camouflage	reptile
14	NA	aposematic	mammal
15	juvenile, adult	NA	human
16	NA	NA	human
17	NA	NA	mammal
18	NA	NA	mammal
19	NA	NA	mammal
20	NA	NA	mammal
21	NA	NA	mammal
22	adult	NA	human
23	adult	NA	human
24	adult	NA	human
25	adult	NA	human
26	adult	NA	human
27	adult	NA	human
28	adult	NA	human
29	adult	NA	human
30	adult	NA	human
31	adult	NA	human
32	adult	NA	human
33	adult	NA	human
34	adult	camouflage	human
35	adult	camouflage	human
36	adult	camouflage	human
37	adult	camouflage	human
38	juvenile, adult	NA	human
39	NA	camouflage	human
40	adult	NA	human
41	adult	NA	human
42	adult	NA	human
43	adult	NA	human
44	adult	NA	human
45	juvenile, adult	NA	human
46	adult	NA	human
47	adult	NA	human
48	adult	NA	human
49	juvenile, adult	NA	bird
50	adult	camouflage	human
51	adult	NA	human
52	adult	NA	human
53	adult	camouflage	human
54	adult	camouflage	human
55	adult	camouflage	human
56	adult	camouflage	human
57	adult	camouflage	human
58	adult	camouflage	human
59	adult	camouflage	human
60			

1			
2			
3	adult	camouflage	human
4	adult	NA	bird
5	adult	NA	bird
6	NA	camouflage	human
7	adult	aposematic	reptile
8	NA	NA	human
9	NA	NA	human
10	NA	NA	human
11	NA	NA	human
12	NA	NA	human
13	NA	NA	human
14	adult	NA	human
15	juvenile	NA	mammal
16	adult	NA	human
17	adult	camouflage	human
18	adult	camouflage	bird
19	adult	camouflage	bird
20	juvenile	camouflage	bird
21	NA	camouflage	human
22	adult	camouflage	bird
23	adult	camouflage	bird, human
24	juvenile	camouflage	NA
25	adult	camouflage	many
26	adult	camouflage	bird
27	NA	aposematic	human
28	NA	aposematic	human
29	adult	camouflage	cephalopod
30	juvenile	camouflage	human
31	adult	camouflage	bird
32	adult	camouflage	mammal
33	adult	NA	bird
34	NA	NA	fish
35	juvenile	camouflage	fish
36	adult	NA	human
37	juvenile, adult	camouflage	human
38	adult	NA	human
39	adult	camouflage	human
40	adult	camouflage	bird, reptile, mammal
41	adult	camouflage	human
42	adult	camouflage	human
43	adult	camouflage	human
44	adult	camouflage	human
45	adult	camouflage	human
46	adult	camouflage	human
47	adult	camouflage	human
48	adult	camouflage	human
49	adult	camouflage	human
50	adult	camouflage	human
51	adult	camouflage	human
52	NA	camouflage	bird
53	adult	camouflage	bird
54	adult	camouflage	human
55	adult	camouflage	human
56	adult	camouflage	human
57	adult	camouflage	human
58	adult	camouflage	human
59	adult	camouflage	human
60			

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adult	putative aposematism	human
adult	camouflage	human
adult	camouflage	human
adult	camouflage	human
adult	camouflage	human
adult	camouflage	human
adult	camouflage	human
adult	camouflage	human
adult	putative aposematism	human
adult	camouflage	human
adult	putative aposematism	human
adult	camouflage	human
adult	camouflage	human
adult	putative aposematism	human
adult	camouflage	human
adult	aposematic	human
adult	NA	human
adult	aposematic	human
adult	camouflage	human
adult	camouflage	human
adult	camouflage	human
adult	camouflage	human
adult	putative aposematism	human
adult	camouflage	human
adult	camouflage	human
adult	putative aposematism	human
adult	putative aposematism	human
adult	putative aposematism	human
adult	putative aposematism	human
adult	camouflage	human
adult	camouflage	human
adult	camouflage	human

	Trigger sensory mode	Predation sequence stage
1		
2		
3		
4		
5	Trigger sensory mode	Predation sequence stage
6	NA	NA
7	tactile	subjugation
8	NA	NA
9	NA	NA
10	tactile	subjugation
11	NA	NA
12	tactile, visual	approach
13	NA	NA
14	tactile	subjugation
15	tactile, visual	approach, subjugation
16	NA	approach
17	visual	approach
18	tactile, visual	NA
19	tactile	subjugation
20	tactile, visual	approach, subjugation
21	tactile, visual	approach, subjugation
22	tactile, visual	approach
23	NA	approach
24	NA	approach
25	NA	approach
26	tactile	subjugation
27	tactile	subjugation
28	tactile	subjugation
29	tactile	subjugation
30	tactile	subjugation
31	tactile	subjugation
32	tactile	subjugation
33	tactile	subjugation
34	tactile	subjugation
35	tactile	subjugation
36	tactile	subjugation
37	tactile	subjugation
38	tactile	subjugation
39	tactile	subjugation
40	tactile	subjugation
41	tactile	subjugation
42	tactile	subjugation
43	tactile	subjugation
44	visual	approach
45	NA	NA
46	tactile	subjugation
47	tactile	NA
48	tactile, visual	approach
49	visual	approach
50	visual	approach
51	NA	NA
52	NA	subjugation
53	NA	NA
54	NA	subjugation
55	NA	NA
56	NA	subjugation
57	NA	NA
58	NA	subjugation
59	NA	NA
60		

1		
2		
3	tactile	subjugation
4	tactile	subjugation
5	tactile	subjugation
6	NA	NA
7	NA	NA
8	visual	approach
9	NA	subjugation
10	NA	subjugation
11	tactile	subjugation
12	tactile	subjugation
13	tactile	subjugation
14	tactile	approach, subjugation
15	tactile, visual	approach, subjugation
16	tactile	subjugation
17	tactile	subjugation
18	tactile	subjugation
19	tactile	subjugation
20	NA	NA
21	NA	NA
22	tactile	subjugation
23	NA	NA
24	tactile	subjugation
25	tactile	subjugation
26	tactile	subjugation
27	tactile	subjugation
28	tactile	subjugation
29	tactile	subjugation
30	NA	NA
31	varied	subjugation
32	varied	subjugation
33	varied	subjugation
34	varied	subjugation
35	varied	subjugation
36	varied	subjugation
37	varied	subjugation
38	varied	subjugation
39	varied	subjugation
40	varied	approach, subjugation
41	varied	subjugation
42	varied	subjugation
43	varied	approach, subjugation
44	varied	subjugation
45	varied	subjugation
46	varied	subjugation
47	varied	subjugation
48	varied	subjugation
49	varied	subjugation
50	tactile	subjugation
51	varied	NA
52	varied	approach, subjugation
53	varied	subjugation
54	varied	subjugation
55	varied	approach, subjugation
56	varied	subjugation
57	varied	subjugation
58	varied	subjugation
59	varied	subjugation
60		

1		
2		
3	varied	approach, subjugation
4	varied	subjugation
5	varied	subjugation
6	varied	subjugation
7	varied	NA
8	varied	subjugation
9	varied	subjugation
10	varied	subjugation
11	varied	subjugation
12	varied	subjugation
13	varied	subjugation
14	varied	subjugation
15	varied	subjugation
16	varied	subjugation
17	varied	subjugation
18	varied	subjugation
19	varied	approach, subjugation
20	varied	NA
21	varied	subjugation
22	varied	NA
23	varied	approach, subjugation
24	varied	approach, subjugation
25	varied	approach, subjugation
26	varied	approach, subjugation
27	varied	NA
28	varied	NA
29	varied	NA
30	varied	NA
31	varied	NA
32	varied	NA
33	varied	NA
34	varied	NA
35	varied	NA
36	varied	NA
37	varied	NA
38	varied	approach
39	varied	approach, subjugation
40	varied	approach, subjugation
41	varied	approach
42	varied	approach
43	varied	approach, subjugation
44	varied	NA
45	varied	NA
46	varied	subjugation
47	varied	subjugation
48	varied	approach, subjugation
49	varied	NA
50	varied	NA
51	visual	approach
52	visual	approach
53	visual	approach
54	tactile, vibration	approach, subjugation
55		
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1		
2		
3	tactile, vibration	approach, subjugation
4	tactile	subjugation
5	NA	approach
6	tactile	subjugation
7	tactile	subjugation
8	tactile, visual, auditory, olfactory	NA
9	tactile	subjugation
10	tactile, visual, vibration	approach
11	NA	NA
12	tactile, visual	subjugation
13	tactile	subjugation
14	tactile	subjugation
15	tactile	subjugation
16	tactile	subjugation
17	tactile	subjugation
18	tactile	subjugation
19	tactile	subjugation
20	tactile	subjugation
21	tactile, visual, auditory, olfactory	subjugation
22	tactile	subjugation
23	tactile	subjugation
24	tactile	subjugation
25	tactile	subjugation
26	tactile	subjugation
27	tactile	subjugation
28	tactile	subjugation
29	tactile	subjugation
30	tactile	subjugation
31	tactile	subjugation
32	tactile	subjugation
33	tactile	subjugation
34	tactile	subjugation
35	tactile	subjugation
36	tactile	subjugation
37	tactile	subjugation
38	visual	approach
39	tactile	approach, subjugation
40	visual	approach
41	visual	approach
42	visual	approach
43	visual	approach
44	visual	approach
45	visual	approach
46	visual	approach
47	visual	approach
48	visual	approach
49	visual	approach
50	tactile, vibration	subjugation
51	NA	subjugation
52	NA	subjugation
53	tactile	subjugation
54	tactile	subjugation
55	tactile	subjugation
56	tactile	subjugation
57	tactile	subjugation
58	tactile	subjugation
59		
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1		
2		
3	tactile	subjugation
4	visual	approach
5	tactile, visual	subjugation
6	NA	NA
7	tactile	subjugation
8	tactile	subjugation
9	tactile	subjugation
10	tactile	subjugation
11	tactile	subjugation
12	tactile	subjugation
13	tactile	subjugation
14	tactile	subjugation
15	visual	approach
16	tactile	subjugation
17	tactile, visual	approach, subjugation
18	tactile	subjugation
19	visual	approach
20	NA	approach
21	NA	subjugation
22	tactile	subjugation
23	NA	NA
24	NA	approach, subjugation
25	NA	subjugation
26	NA	approach
27	NA	approach
28	NA	subjugation
29	NA	approach
30	NA	approach
31	tactile	subjugation
32	tactile	subjugation
33	NA	approach, subjugation
34	tactile	subjugation
35	NA	approach
36	visual	approach
37	NA	approach
38	visual	approach
39	tactile	subjugation
40	tactile	subjugation
41	tactile	subjugation
42	tactile	subjugation
43	tactile	subjugation
44	tactile	subjugation
45	visual	approach
46	tactile, visual	approach, subjugation
47	tactile	subjugation
48	tactile	subjugation
49	tactile	subjugation
50	tactile, visual	approach, subjugation
51	tactile, visual, vibration	approach, subjugation
52	tactile	subjugation
53	tactile	subjugation
54	tactile	subjugation
55	tactile	subjugation
56	tactile	subjugation
57	tactile	subjugation
58	tactile	subjugation
59	tactile	subjugation
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visual	approach
tactile	subjugation
tactile	subjugation
tactile	subjugation
tactile	subjugation
tactile	subjugation
tactile	subjugation
tactile	subjugation
tactile	subjugation
tactile	subjugation
visual	approach
visual	approach
tactile	subjugation
visual	approach
visual	approach
tactile	subjugation
tactile	subjugation
tactile	subjugation
tactile	subjugation
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tactile	subjugation
tactile	subjugation
tactile	subjugation
tactile	subjugation
tactile	subjugation
tactile	subjugation
visual	approach
visual	approach
visual	approach
visual	approach
tactile	subjugation
visual	approach
tactile	subjugation

For Review Only

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Display duration description

NA

NA

NA

NA

NA

NA

NA

NA

colours displayed for a few seconds, posture not specified

NA

NA

NA

up to a few seconds

NA

NA

NA

up to a few seconds

NA

NA

<330

NA

NA

900-1200

NA

NA

more than 1 min

NA

NA

NA

NA

NA

NA

NA

between a few seconds to 45 mins. In one case kept presenting to a bird for 6h

150-490

NA

NA

NA

NA

NA

NA

NA

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1
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3 NA
4 NA
5 NA
6 NA
7 NA
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9 NA
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For Review Only

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55 NA
56 NA
57 NA
58 NA
59 NA
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For Review Only

1
2
3 NA
4 NA
5 NA
6 NA
7 12+
8 12+
9
10 NA
11 NA
12 NA
13 NA
14 NA
15 NA
16 NA
17 NA
18 NA
19 NA
20 NA
21 NA
22 NA
23 23 milliseconds
24 312 milliseconds
25 615 - 756 milliseconds
26 380-1091 milliseconds
27 191 milliseconds
28 265 milliseconds
29 808 milliseconds
30 213-312 milliseconds
31 NA
32 NA
33 NA
34 NA
35 NA
36 NA
37 NA
38 NA
39 NA
40 a few sec
41 recorded for 500 ms
42 recorded for 500 ms
43 recorded for 500 ms
44 recorded for 500 ms
45 recorded for 500 ms
46 recorded for 500 ms
47 recorded for 500 ms
48 recorded for 500 ms
49 NA
50 25-183
51 NA
52 NA
53 NA
54 NA
55 NA
56 NA
57 NA
58 NA
59 NA
60

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1
2
3 NA
4 during attack - several seconds, after attack - 1 minute
5
6 NA
7 NA
8 NA
9 NA
10 NA
11 NA
12 NA
13 NA
14 NA
15 NA
16 NA
17 NA
18 NA
19 between 1 and 22 flicks per minute
20 NA
21 up to 30 sec
22 NA
23 >60
24 NA
25 NA
26 NA
27 NA
28 NA
29 NA
30 NA
31 NA
32 NA
33 0.05-4.65
34 NA
35 about 5 wing flicks per 5 seconds
36 NA
37 NA
38 NA
39 continued for a few seconds after stimulation had ended
40 up to 300 sec, and longer
41 NA
42 up to 192 seconds
43 NA
44 NA
45 NA
46 NA
47 NA
48 NA
49 NA
50 NA
51 NA
52 NA
53 NA
54 NA
55 NA
56 short
57 NA
58 NA
59 NA
60

1
2
3 NA

4 NA

5
6 sustained static display up to 5 minutes

7 sustained static display up to 5 minutes

8 NA

9
10 sustained static display up to 5 minutes

11 sustained static display up to 5 minutes

12 sustained static display up to 5 minutes

13 sustained static display up to 5 minutes

14
15 NA

16 NA

17 NA

18
19 1-4 seconds repeated

20 1-4 seconds repeated

21 sustained static display up to 5 minutes

22 short

23 short

24 NA

25 NA

26 sustained static display up to 5 minutes

27 NA

28 NA

29 NA

30 NA

31 NA

32 NA

33 NA

34 NA

35 NA

36 NA

37 NA

38 NA

39 NA

40 NA

41 NA

42 NA

43 1-4 seconds repeated

44 1-4 seconds repeated

45 sustained static display up to 5 minutes

46

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1
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3 NA
4 NA
5 NA
6 NA
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For Review Only

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59 NA
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For Review Only

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3	NA	
4	NA	
5	NA	
6	NA	
7		12
8		12
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10	NA	
11	NA	
12	NA	
13	NA	
14	NA	
15	NA	
16	NA	
17	NA	
18	NA	
19	NA	
20	NA	
21	NA	
22	NA	
23		0
24		0
25		1
26		1
27		1
28		0
29		0
30		0
31		1
32		0
33		
34	NA	
35	NA	
36	NA	
37	NA	
38	NA	
39	NA	
40		3
41		
42	NA	
43	NA	
44	NA	
45	NA	
46	NA	
47	NA	
48	NA	
49	NA	
50		
51		183
52	NA	
53	NA	
54	NA	
55	NA	
56	NA	
57	NA	
58	NA	
59	NA	
60		

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1		
2		
3	NA	
4		
5		60
6	NA	
7	NA	
8	NA	
9	NA	
10	NA	
11	NA	
12	NA	
13	NA	
14	NA	
15	NA	
16	NA	
17	NA	
18	NA	
19	NA	
20	NA	
21	NA	
22		30
23	NA	
24		60
25		
26	NA	
27	NA	
28	NA	
29	NA	
30	NA	
31	NA	
32	NA	
33		
34		5
35	NA	
36	NA	
37	NA	
38	NA	
39	NA	
40	NA	
41		
42		3
43		300
44	NA	
45		
46		192
47	NA	
48	NA	
49	NA	
50	NA	
51	NA	
52	NA	
53	NA	
54	NA	
55		300
56	NA	
57	NA	
58	NA	
59	NA	
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For Review Only

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NA

NA

300

300

NA

300

300

300

300

NA

NA

NA

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300

NA

NA

NA

NA

300

NA

NA

NA

NA

NA

NA

NA

NA

NA

NA

4

4

300

1			
2			
3			
4		1	0
5		1	0
6		1	0
7		1	0
8		1	0
9		1	0
10		1	0
11		1	0
12		1	0
13		1	0
14		1	0
15		1	0
16		1	0
17		1	0
18		0	0
19		0	0
20		0	0
21		0	0
22		0	0
23		1	0
24		0	0
25		0	0
26		0	0
27		0	0
28	NA		0
29			0
30		0	0
31		0	0
32		0	0
33		0	0
34		0	0
35		0	0
36		0	0
37	NA		0
38			0
39		0	0
40		0	0
41			
42		1	0
43		0	0
44		0	0
45			
46		1	0
47		0	0
48		0	0
49		0	0
50		0	0
51		0	0
52		0	0
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54	NA		0
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Auditory	Olfactory or Gustatory	Elements of display repeated or sustained
	1	1 sustained
	1	1 sustained
	0	1 sustained
	0	1 sustained
	0	1 sustained
	0	0 NA
	1	0 repeated
	1	0 NA
	0	0 sustained
	0	0 repeated
	0	0 sustained
	0	0 sustained
	0	0 sustained
	0	0 repeated
	0	0 repeated
	0	0 sustained
	0	0 repeated
NA	NA	sustained, repeated
	1	1 sustained
	0	0 sustained
	0	0 repeated
	0	0 repeated
	1	0 repeated
	1	0 repeated
	0 NA	sustained
	1	0 repeated
	0	0 repeated
	0	0 sustained
	1	0 NA
	1	0 NA
	0	0 NA
	1	0 NA
	0	0 sustained
	1	0 sustained, repeated
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	0	0 sustained
	0	0 sustained
	0	0 sustained
	0	0 sustained
	0	0 sustained
	0	0 sustained
	1	0 repeated

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3		0 repeated
4		0 sustained
5		0 sustained
6		0 sustained
7		1 repeated
8		0 NA
9		0 NA
10		1 NA
11		0 NA
12		0 NA
13		1 NA
14		1 repeated
15		0 sustained
16		1 sustained
17		0 NA
18		0 NA
19		0 NA
20		0 NA
21		0 NA
22		0 NA
23		0 NA
24		0 NA
25		0 NA
26		0 NA
27		1 NA
28		0 sustained
29		
30	NA	1 sustained, repeated
31	NA	1 sustained, repeated
32	NA	1 sustained, repeated
33	NA	1 sustained, repeated
34	NA	1 sustained, repeated
35	NA	1 sustained, repeated
36	NA	1 sustained, repeated
37	NA	1 sustained, repeated
38	NA	1 sustained, repeated
39	NA	1 sustained, repeated
40	NA	1 sustained, repeated
41	NA	1 sustained, repeated
42	NA	1 sustained, repeated
43	NA	1 sustained, repeated
44	NA	1 sustained, repeated
45	NA	1 sustained, repeated
46	NA	1 sustained, repeated
47	NA	1 sustained, repeated
48	NA	1 sustained, repeated
49	NA	0 sustained
50	NA	0 sustained
51	NA	0 sustained
52	NA	1 sustained
53	NA	0 sustained
54	NA	0 sustained
55	NA	1 sustained
56	NA	1 sustained
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58	NA	1 sustained
59	NA	1 sustained
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3	NA		1 sustained
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6	NA		1 sustained
7	NA		1 sustained, repeated
8	NA		1 sustained
9	NA		1 sustained
10	NA		1 sustained
11	NA		1 sustained, repeated
12	NA		1 sustained
13	NA		1 sustained
14	NA		1 sustained
15	NA		1 sustained
16	NA		1 sustained
17	NA		1 sustained
18	NA		1 sustained
19	NA		1 sustained
20	NA		1 sustained
21	NA		1 sustained
22	NA		1 sustained
23		1	1 sustained, repeated
24	NA		1 sustained
25	NA		1 sustained
26	NA		1 sustained
27	NA		1 sustained
28	NA	NA	NA
29	NA		1 sustained
30	NA		1 sustained
31	NA		1 sustained, repeated
32	NA		1 sustained, repeated
33	NA		1 sustained, repeated
34	NA		1 sustained, repeated
35	NA		1 sustained, repeated
36	NA		1 sustained, repeated
37	NA	NA	NA
38	NA		1 sustained, repeated
39	NA		1 sustained, repeated
40	NA		1 sustained, repeated
41	NA		1 sustained, repeated
42	NA		1 sustained, repeated
43	NA		1 sustained, repeated
44	NA		1 sustained, repeated
45		1	1 sustained
46	NA		1 sustained
47	NA		1 sustained
48	NA		1 sustained
49	NA		1 sustained
50	NA		1 sustained
51	NA		1 sustained
52	NA		1 sustained
53	NA	NA	NA
54		1	0 sustained
55		0	0 sustained
56		1	0 sustained
57		0	0 sustained, repeated
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3	0	1 sustained, repeated
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6	0	1 sustained
7	0	1 sustained
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9	0	1 sustained
10	0	1 sustained
11	0	1 repeated
12	1	1 NA
13	1	0 repeated
14	0	1 sustained
15	0	1 sustained, repeated
16	0	1 sustained, repeated
17	0	1 sustained, repeated
18	0	0 sustained
19	0	0 sustained
20	1 NA	sustained
21	1 NA	sustained
22	1 NA	sustained
23	1 NA	sustained
24	1 NA	sustained
25	1 NA	sustained
26	1 NA	sustained
27	1 NA	sustained
28	1 NA	sustained
29	1 NA	sustained
30	1 NA	sustained
31	1 NA	sustained
32	1 NA	sustained
33	1 NA	sustained
34	1	1 repeated
35	1	1 repeated
36	1	1 repeated
37	1	0 sustained
38	0 NA	sustained
39	1	1 repeated
40	1	1 repeated
41	1	1 repeated
42	1	1 repeated
43	1	1 repeated
44	1	1 repeated
45	1	1 repeated
46	1	1 repeated
47	1	1 repeated
48	1	1 repeated
49	1	0 repeated
50	0	0 sustained
51	1	0 sustained, repeated
52	1	0 sustained, repeated
53	0	1 sustained
54	0	1 sustained
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3	0	1 sustained
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6	0	0 sustained
7	0	1 sustained
8	0	1 sustained
9	0	1 sustained
10	0	1 sustained
11	0	1 sustained
12	0	1 sustained
13	0	1 sustained
14	0 NA	sustained
15	1	0 NA
16	0	1 sustained
17	1 NA	sustained
18	1	0 repeated
19	0	0 sustained
20	0	0 sustained
21	0	0 NA
22	1	1 repeated
23	1	0 sustained, repeated
24	0	0 sustained
25	0	0 repeated
26	0	0 repeated
27	0	0 repeated
28	0	0 repeated
29	0	0 repeated
30	0	0 repeated
31	0	0 repeated
32	1	0 repeated
33	1	1 repeated
34	0	0 sustained
35	1	0 repeated
36	0	0 sustained
37	0	0 NA
38	0	0 sustained
39	0	0 NA
40	0	0 sustained
41	1	1 sustained, repeated
42	0 NA	sustained
43	0	0 sustained
44	0	1 sustained
45	1	0 sustained
46	0	0 sustained
47	0	0 sustained
48	0	0 sustained
49	0	0 sustained
50	0	0 sustained
51	0	0 sustained
52	0 NA	sustained
53	0	0 sustained
54	1	0 repeated
55	0	0 sustained
56	0	0 sustained
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9	0	0 sustained
10	0	0 sustained
11	0	0 sustained
12	0	0 sustained
13	0	0 sustained
14	0	0 sustained
15	0	0 repeated
16	0	0 repeated
17	0	0 repeated
18	0	1 sustained
19	0	0 repeated
20	0	0 repeated
21	0	0 sustained
22	0	0 sustained
23	0	0 sustained
24	0	0 sustained
25	0	0 sustained
26	0	0 sustained
27	0	0 sustained
28	0	0 sustained
29	0	0 sustained
30	0	0 repeated
31	0	0 NA
32	0	0 NA
33	0	0 repeated
34	0	0 repeated
35	0	0 sustained
36	0	0 sustained
37	0	0 repeated
38	0	0 repeated
39	0	0 NA
40	0	0 repeated
41	0	0 repeated
42	0	0 repeated
43	0	0 repeated
44	0	0 repeated
45	0	0 repeated
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Key to Table S3.

Column heading

Citation

Year

Phylum

Class

Order

Family

Species

Study type

Life stage studied

Primary defence reported

Predator in study

Trigger sensory mode

Predation sequence stage

Display duration description

Display duration (sec) (max if range given)

Movement of large body parts to perform display

Visual aside from movement (colour patch, eyespot, spine, etc.)

Eyespots

Auditory

Olfactory or Gustatory

Elements of display repeated or sustained

Sum of modes (visual modes combined here)

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Definition

Source of information

Year of publication

Phylum of displaying animal

Class of displaying animal

Order of displaying animal

Family of displaying animal

Species of displaying animal

Study types categorised into manipulative or description

Stage classified as adult or juvenile

Whether the study described any primary defences (e.g. camouflage)

Species used to trigger display

Method to trigger display

Stage in predation sequence display triggered

Description of display duration

How long the display was held

Whether there was a movement of large body parts to display; 1 = Yes, 0 = No

Whether there was a visual stimulus (except movement); 1 = Yes, 0 = No

Whether eyespots were shown in the display; 1 = Yes, 0 = No

Whether there was an auditory component of the display; 1 = Yes, 0 = No

Whether there as an olfactory or gustatory element to the display; 1 = Yes, 0 = No

Whether there were repeated or sustained elements of the display; 1 = Yes, 0 = No

Sum of sensory modes the display operates in (movement, visual, and eyespots are categorised as on

Table S4. Comparison of the defensive strategies of juvenile and adult life stage

Citation	Order	Species
Bailey & Sandow (1983)	Orthoptera	<i>Mygalopsis marki</i>
Brodie et al. (1984)	Urodela	<i>Echinotriton andersoni</i>
Lyon & Fogden (1989)	Aves	<i>Eurypyga helias</i>
Robinson (1969)	Orthoptera	<i>Scorpiorinus fragilis</i>
Robinson (1969)	Phasmatodea	<i>Metriotes diocles</i>
Robinson (1969)	Mantodea	<i>Angela guianensis</i>
Robinson (1969)	Mantodea	<i>Phyllovates chlorophaea</i>
Robinson (1969)	Mantodea	<i>Choeradodis rhombicollis</i>
Thomas & Strahl (1990)	Aves	<i>Eurypyga helias</i>
Umbers & Mappes (2015)	Orthoptera	<i>Acripeza reticulata</i>
Balderrama & Maldonado (1973)	Mantodea	<i>Stagmatoptera biocellata</i>
York & Bartol (2016)	Myopsida	<i>Lolliguncula brevis</i>
Hanlon & Messenger (1988)	Sepiida	<i>Sepia officinalis</i>
Glaudas et al. (2006)	Squamata	<i>Agkistrodon piscivorus</i>

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2 es of species for which both have been studi

3 Juvenile strategy	4 Adult strategy
5 flee	6 display
7 display	8 display
9 display	10 display
11 flee	12 display
13 flee	14 display
15 flee	16 flee and display
17 flee	18 display
19 display	20 display
21 display	22 display
23 cryptic posture and limited	24 display
25 display	26 display
27 limited display	28 display
29 display	30 display

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2 ied and at least one stage uses a deimatic display
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2 Table S5. Summary of studie

3 **Citation**

4 Brodie et al. 1984

5 Brodie et al. 1984

6 Brodie et al. 1984

7 Brown et al. 2007

8 Olofsson et al. 2011

9 Olofsson et al. 2012b

10 Sandow & Bailey 1978

11 Staudinger et al. 2011

12 Umbers et al. 2019

13 Umbers et al. 2019

14 Vallin et al. 2005

15 Vallin et al. 2006

16 Vallin et al. 2007

17 Vallin et al. 2007

18 Vallin et al. 2007

19 Vallin et al. 2007

20 Vallin et al. 2007

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2 s that have assessed the survival value of deimatic displays in prey

3 **Aim**

4 To present data on the defence strategies of four genera of salamanders (previously unstudied) and pro

5 To present data on the defence strategies of four genera of salamanders (previously unstudied) and pro

6 To present data on the defence strategies of four genera of salamanders (previously unstudied) and pro

7 To explore the mechanisms and function behind caterpillar clicks. Is clicking an acoustic aposematic si

8 To test whether sound production on its own is enough to induce escape behaviours in predators.

9 To investigate winter predation on hibernating butterflies - are rodents responsible for winter predation

10 To describe the defensive behaviours in the Western Australian katydid and assess the survival value o

11 To evaluate predator-prey interactions between longfin squid, bluefish and flounder: investigate initial

12 To test the efficiency of a generally accepted deimatic display in a natural setting

13 To test the efficiency of a generally accepted deimatic display in an environment in which predators ar

14 To investigate the relative importance of eyespots and sound for defence and the survival value when a

15 To test the hypothesis that different species of butterflies with different defence strategies (e.g. relying

16 To test whether large eyespots on lepidopterans are effective for preventing attacks from small birds ar

17 To test whether large eyespots on lepidopterans are effective for preventing attacks from small birds ar

18 To test whether large eyespots on lepidopterans are effective for preventing attacks from small birds ar

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Prey order	Prey common name	Prey taxonomic name
Urodela	Chinese warty newt	<i>Paramesotriton chinensis</i>
Urodela	Spot-tailed warty newt	<i>Paramesotriton caudopunctatus</i>
Urodela	Spotted paddle-tail newt	<i>Pachytriton brevipes</i>
Lepidoptera	Common silkworm	<i>Antheraea polyphemus</i>
Lepidoptera	Peacock butterfly	<i>Aglais io</i>
Lepidoptera	Peacock butterfly	<i>Aglais io</i>
Orthoptera	Western Australian katydid	<i>Mygalopsis ferruginea</i>
Cephalopoda	Longfin squid	<i>Loligo pealeii</i>
Orthoptera	Mountain katydid	<i>Acripeza reticulata</i>
Orthoptera	Mountain katydid	<i>Acripeza reticulata</i>
Lepidoptera	Peacock butterfly	<i>Aglais io</i>
Lepidoptera	Peacock butterfly	<i>Aglais io</i>
Lepidoptera	Peacock butterfly	<i>Aglais io</i>
Lepidoptera	Peacock butterfly	<i>Aglais io</i>
Lepidoptera	Eyed hawkmoth	<i>Smerinthus ocellatus</i>
Lepidoptera	Eyed hawkmoth	<i>Smerinthus ocellatus</i>

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Predator order	Predator common name	Predator taxonomic name
Mammalia	Northern short-tailed shrew	<i>Blarina brevicauda</i>
Mammalia	Northern short-tailed shrew	<i>Blarina brevicauda</i>
Mammalia	Northern short-tailed shrew	<i>Blarina brevicauda</i>
Aves	Domestic chick	<i>Gallus gallus domesticus</i>
Mammalia	Yellow-necked mouse and wood mouse	<i>Apodemus flavicollis</i> and <i>A. sylvaticus</i>
Mammalia	Yellow-necked mouse and wood mouse	<i>Apodemus flavicollis</i> and <i>A. sylvaticus</i>
Reptilia	Salmon-bellied skink	<i>Egernia napoleonis</i>
Actinopterygii	Bluefish and summer flounder	<i>Pomatomus saltatrix</i> and <i>Paralichthys oblongus</i>
Aves	Australian magpie	<i>Gymnorhina tibicen</i>
Aves	Australian magpie	<i>Gymnorhina tibicen</i>
Aves	Blue tit	<i>Parus caeruleus</i>
Aves	Blue tit	<i>Parus caeruleus</i>
Aves	Blue tit	<i>Parus caeruleus</i>
Aves	Great tit	<i>Parus major</i>
Aves	Blue tit	<i>Parus caeruleus</i>
Aves	Great tit	<i>Parus major</i>

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Country	Study setting	Treatment	Description of display
USA	lab	none	display posture
USA	lab	none	display posture
USA	lab	none	no display posture
Nth America	lab	none	sound and regurgitation
Sweden	field	none	display
Sweden	lab	sound and i	display
Australia	lab	sound and i	sound and posture
USA	lab	none	display, protean behaviour, inking
Australia	field	none	display with colour
Australia	field	none	display with colour
Sweden	lab	with and wi	display with eyespots
Sweden	lab	none	display
Sweden	lab	none	display
Sweden	lab	none	display
Sweden	lab	none	display

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Stage display deployed	Sample size	Number survived	Survival percentage
subjugation	15	15	100
subjugation	17	17	100
subjugation	10	10	100
subjugation	16	16	100
approach	21	10	48
subjugation	24	23	96
approach	40	35	88
NA	18	11	61
subjugation	29	7	24
subjugation	37	26	70
approach, subjugation	34	33	97
approach	10	10	100
subjugation	12	12	100
subjugation	12	9	75
subjugation	13	5	38
subjugation	14	1	7

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Predator response

NA

NA

distaste reaction

withdrawal and return

retreat and escape

flee or retreat after first encounter

NA

caused bluefish to startle

NA

NA

retreat

retreat

flee and return or not

flee and return or not

flee and return or not

flee and return or not

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Table S6. Summary of studies

Citation

Bates & Fenton (1990)

Blest (1957b)

Blest (1957b)

De Bona et al. (2015)

Dookie et al. (2017)

Holmes et al. (2018)

Ingalls (1993)

Kang et al. (2016)

Kang et al. (2017)

Olofsson et al. (2012a)

Olofsson et al. (2012b)

Olofsson et al. (2013)

Schlenoff (1985)

Stoneman & Fenton (1988)

Umbers et al. (2019)

Vallin et al. (2005)

Vaughan (1983)

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1
2
3 that have assessed predator responses to deimatic displays

4 **Aim**

5 Do moth clicks function as deimatic displays?

6 Do predators respond differently to butterflies with eyespots compared to the

7
8 How do predators respond to different suddenly presented patterns?

9
10
11 Do eye spots mimic eyes?

12 Do caterpillar whistles function as deimatic displays?

13 Does movement and/or colour patch influence predator response?

14 (1) Does the presence of a banding pattern enhance the startle reaction to noise?

15 Does facultative aposematism differ from crypsis and aposematism?

16 Does size and/or hindwing colour influence predator startle response?

17 Does wing-flicking protect the butterfly from bird or is just conspicuous coloration?

18 Do sounds deter mice?

19 Does the presence of eyespots in the startle display influence predator behavior?

20 Does novelty and/or oddity influence predator startle response?

21 How do moth clicks disrupt bat attack?

22 Does predator familiarity influence the efficacy of startle displays?

23 Is the combination of eyespots and sound more effective than the components alone?

24 Do hind wing patterns deter birds?, Is novelty important?
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Predator order	Predator common name
Mammalia: Chiroptera	Big brown bat
Aves	Yellow bunting and great tit
Aves	Chaffinch, yellow bunting and
Aves	Great tit
Aves	Red-winged blackbird
Aves	Chicken
Aves	Blue jay
Aves	Oriental tit
Aves	Black-capped chickadee
Aves	Great tit
Mammalia: Chiroptera	Wood mouse and yellow-neck
Aves	Chicken
Aves	Blue jay
Mammalia: Chiroptera	Greater false vampire bat and
Aves	Australian magpie
Aves	Blue tit
Aves	Blue jay

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Predator taxonomic name	Sample size
<i>Eptisicus fuscus</i>	4
<i>Emberiza sulphurata</i> and <i>Parus major</i>	8 and 4
<i>Fringilla coelebs</i> , <i>Emberiza sulphurata</i> , and <i>Parus major</i>	unclear
<i>Parus major</i>	97
<i>Agelaius phoeniceus</i>	12
<i>Gallus gallus domesticus</i>	56
<i>Cyanocitta cristata</i>	8
<i>Parus minor</i>	36
<i>Poecile atricapillus</i>	36 flocks
<i>Parus major</i>	27
<i>Apodemus sylvaticus</i> and <i>A. flavicollis</i>	18 and 8
<i>Gallus gallus domesticus</i>	40
<i>Cyanocitta cristata</i>	6
<i>Megaderma lyra</i> and <i>Macrotus californicus</i>	3 and 7
<i>Cracticus tibicen</i>	163
<i>Parus caeruleus</i>	54
<i>Cyanocitta cristata</i>	8

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Stimulus type simple**Stimulus type category**

sound

sound

live insect

eyespot

image

eyespot - abstract

image

eyespot

sound

sound

image

model

colour pattern

model

model

colour pattern

live insect

live insect

live insect

model

colour pattern

sound

sound

live insect

live insect

model

colour pattern

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Stimulus

Sound - acoustic recording of insect

Insects - live

Images of prey - back-projected onto a screen

Images of prey - animated photographs of Lepidoptera with eyespots and owl eyes

Sound - acoustic recording of insect

Images of prey - computer generated images

Model prey - holes covered with flaps

Model prey - paper models of abstract prey

Model prey - robomoth

Insects - live and dead

Insects - live

Insects - live

Model prey - cardboard and plastic mechanical moth models

Sound - acoustic recording of insect

Insects - live

Insects - live

Model prey - holes covered with flaps

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Stimulus order**Stimulus model**

Lepidoptera	Dogbane tiger moth (<i>Cycnia tenera</i>)
Lepidoptera	Peacock butterfly (<i>Aglaia io</i>)
Lepidoptera	Painted models
Lepidoptera & Aves	Owled eyed butterfly (<i>Caligo martia</i>) and Eurasian pyg
Lepidoptera	Walnut sphinx caterpillar (<i>Amorpha juglandis</i>)
Lepidoptera	loosely based on <i>Catocala</i> sp.
Lepidoptera	loosely based on <i>Catocala</i> sp.
Lepidoptera	paper models with hidden colours
Lepidoptera	paper models with hidden colours
Lepidoptera	European swallowtail (<i>Papilio machaon</i>)
Lepidoptera	Peacock butterfly (<i>Aglaia io</i>)
Lepidoptera	Peacock butterfly (<i>Aglaia io</i>)
Lepidoptera	loosely based on <i>Catocala</i> sp.
Lepidoptera	Dogbane tiger moth (<i>Cycnia tenera</i>), milkweed tussock
Orthoptera	Mountain katydid (<i>Acripeza reticulata</i>)
Lepidoptera	Peacock butterfly (<i>Aglaia io</i>)
Lepidoptera	loosely based on <i>Catocala</i> sp.

	Prey 'defended'	Study setting
6	no	lab
7	no	lab
9	no	lab
12	no	lab
13	no	lab
14	no	lab
15	no	lab
16	no	lab
17	yes	lab
18	no	field
20		lab
21	no	lab
22	no	lab
23	no	lab
24	no	lab
25	no	lab
26	yes	field
27	no	lab
28	no	lab
29	no	lab

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Treatments

- (1) recorded clicks of an arctiid moth, (2) synthetic clicks (white noise temporally matched to arctiid clicks)
- (1) butterflies with eyespots, (2) butterflies without eyespots
- (1) an equals symbol: '=', (2) a large thin plus symbol: '+', (3) a small thick plus symbol: '+', (4) a single dot: '.'
- (1) an owl with open eyes, (2) an owl with eyes closed, (3) a butterfly with mimetic (real) eyespots, (4) a butterfly with modified (reversed) eyespots, (5) and a butterfly without eyespots
- (1) without sound, (2) with 70 dB sound, (3) with 60 dB sound
- (1) stationary cryptic, (2a, b, c) slow medium and fast dynamic with conspicuous hindwings, (3a, b, c) dynamic with conspicuous hindwings
- (1) solid-coloured discs, (2) banded discs;
- (1) continuously conspicuous prey, (2) facultatively conspicuous prey, (3) non-conspicuous prey
- (1) large with red hindwings, (2) small with red hindwings, (3) large with grey hindwings, (4) small with grey hindwings
- (1) dead butterflies showing colours, (2) live butterflies cryptic at rest
- (1) butterflies with sound-producers intact, (2) butterflies with sound-producers obliterated
- (1) butterflies with eyespots, (2) butterflies without eyespots
- (1) uniform, pale grey; (2) red and black bands with a narrow white border (redbanded), such as found in nature
- (1) amplifier turned off, (2) amplifier on receiving tape noise, (3) amplifier with recorded moth clicks
- (1) a mountain katydid (2) a palatable orthopteran (3) an inedible grey plasticine ball
- (1) eyespots intact, (2) eyespots obliterated, (3) sound-producers intact, (4) sound producers obliterated
- (1) trained on one colour (2) presented a novel colour

Trigger	Timing	Response measures
Bat foraging behaviour - cross	Predator approach	Whether or not bat landed
Bird foraging behaviour	Predator subjugation	Escape responses
Bird foraging behaviour	Predator subjugation	Escape responses
Operator, based on bird behav	Predator approach	No response, stare, explore
Bird foraging behaviour trigge	Predator subjugation	No reaction, shoulder flinch
Operator, based on bird behav	Predator approach	Latency to attack
Bird foraging behaviour	Predator subjugation	Latency to touch artificial p
Bird foraging behaviour	Predator subjugation	Prey eaten or rejected
Operator, based on bird behav	Predator approach	Stayed, left but returned, le
Prey behaviour	Prey's choice	Flew or hopped away
Operator stimulating butterfly	Prey's choice	Escape trajectories
Prey behaviour	Prey's choice	Flinching, ceasing foraging
Bird foraging behaviour	Predator subjugation	Initial reaction (high and lo
Bat foraging behaviour - cross	Predator approach	Change in approach to feed
Prey behaviour	Prey's choice	Where in the predation seq
Prey behaviour	Prey's choice	Time birds remained within
Bird foraging behaviour	Predator subjugation	Defined 'startle response' a

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Startle observed	Startle observed simple	Predator deterred
yes	yes	yes
unclear	NA	yes
not mentioned	NA	yes
yes	yes	yes
yes	yes	yes
not mentioned	NA	yes
yes	yes	yes
no	no	yes
yes	yes	yes
yes	yes	yes
unclear - "sudden evasion"	NA	yes
yes	yes	yes
yes	yes	yes
yes	yes	yes
no	no	yes
unclear - "bird was visibly dis	NA	yes
yes	yes	yes

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	Repeated trials	Learned avoid simplified sco
6	yes	no
7	yes	no
9	yes	no
12	yes	NA
13	yes	yes
14	no	NA
16	yes	yes
17	yes	yes
18	yes	NA
19	no	NA
20	no	NA
21	no	NA
22	no	NA
23	yes	no
25	yes	NA
26	yes	yes
27	no	NA
29	yes	no

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Learned avoid

no

inverse of 'learned ignore' column

no

unclear

yes

NA

yes, more hestiant in future trials when experienced with banded stimuli

yes, in fewer trials than cryptic prey, but similar to conspicuous prey

unclear

NA

NA

NA

habituated

unclear

yes, but only a single repeat

NA

unclear

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	Learned ignore simplified	Learned ignore	Result
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6	yes	yes	Bats initially startled but then h
7	yes	yes, for 6 yellow buntings, no	More escape responses to butte
8			
9	yes	yes, waning was rapid	Circular patterns released esca
10			
11			
12	NA	unclear	Mimetic eyespots as effective
13	yes	yes, some evidence of habituat	Birds flew away on first encou
14	NA	NA	Conspicuousness effective, slo
15			
16	no	no	Banded patterns increased star
17	no	no, but that was not expected t	Facultative display as effective
18	NA	unclear	Startle response stronger to lar
19			
20	NA	NA	Birds were more likely to attac
21	NA	NA	Mice fled further from butterfl
22	NA	NA	Birds reacted to both treatment
23			
24	yes	yes, but slower when prey app	Novelty alone did not release e
25	NA	unclear	Reject jamming hypothesis, su
26	yes	yes, for experienced birds, no	Display is more protective aga
27			
28	NA	NA	Birds spent more time close to
29	yes	yes	"rarity ... tends to reduce the r
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6 habituated to sound

7 butterflies with eyespots intact than to those with eyespots obliterated

8
9 type responses more readily than non-circular patterns, of the circular patterns, those most like eyes

10
11 as owl eyes

12 inter with sound

13 slow and fast both effective, medium not

14 startle response and future avoidance compared to solid colours

15 as aposematic display

16 larger moth model

17
18 check the dead butterfly treatment. Live butterfly's display resulted in birds visiting more times before a

19 flies that produced sound

20 starts, but those that viewed eyespots were slower to resume foraging

21 a startle display, the colours themselves matter. Startle on first encounter with coloured hindwing n

22 support startle hypothesis

23 against naïve than familiar birds

24 to the butterflies with no eyespots, no difference was found between the sound treatments. No synge

25 risk of predation"

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9 were most effective
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19 attacking
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23 nodels but not grey models
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28 rgistic effect of eyespots and sound was supported
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