

# This is a self-archived version of an original article. This version may differ from the original in pagination and typographic details.

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)

Copyright: © 2022 Cambridge Philosophical Society

Rights: In Copyright

Rights url: http://rightsstatements.org/page/InC/1.0/?language=en

## 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 **Biological Reviews** 



# Cambridge Philosophical Society

# A synthesis of deimatic behaviour

Journal:	Biological Reviews
Manuscript ID	BRV-10-2021-0388.R4
Manuscript Type:	Original Article
Date Submitted by the Author:	17-Jul-2022
Complete List of Authors:	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 Leavell, Brian; Purdue 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, Department of Biology Young, Catherine; Western Sydney University, School of Life and Environmental Sciences Yack, Jayne; Carleton University, Department of Biology Young, Catherine; Western Sydney University, School of Science; Western Sydney University, Hawkesbury Institute for the Environment
Keywords:	Antipredator, defense, predator, prey, competition, cognition, behaviour, aposematism, deimatism, startle

Eleanor Drinkwater<sup>1</sup>, William L. Allen<sup>2</sup>, John A. Endler<sup>3</sup>, Roger T. Hanlon<sup>4</sup>,

Jussi Lehtonen<sup>12,13</sup>, Karl Loeffler-Henry<sup>14</sup>, John Ratcliffe<sup>15</sup>, Candy Rowe<sup>5</sup>,

Graeme D. Ruxton<sup>16</sup>, Tom N. Sherratt<sup>14</sup>, John Skelhorn<sup>5</sup>, Chelsea Skojec<sup>6,7</sup>,

Hannah R. Smart<sup>17</sup>, Thomas E. White<sup>12</sup>, Jayne E. Yack<sup>14</sup>, Catherine M. Young<sup>18</sup>

<sup>1</sup>Department of Animal Science, Writtle University College, Writtle, Chelmsford, CM1 3RR,

<sup>5</sup>Biosciences Institute, Faculty of Medical Sciences, Newcastle University, Newcastle upon

<sup>6</sup>*McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History,* 

<sup>7</sup>Entomology and Nematology Department, University of Florida, Gainesville, Florida

<sup>8</sup>Department of Biosciences, Mokpo National University, Muan, Jeollanamdo, 58554, South

<sup>2</sup>Department of Biosciences, Swansea University, Sketty, Swansea, SA2 8PP, UK

<sup>3</sup>Centre for Integrative Ecology, School of Life & Environmental Sciences, Deakin

<sup>4</sup>Marine Biological Laboratory, Woods Hole, Massachusetts, 02543, USA

University, Waurn Ponds, Victoria, 3216, Australia

University of Florida, Gainesville, Florida, USA 32611, USA

Grace Holmes<sup>5</sup>, Nicholas T. Homziak<sup>6,7</sup>, Changku Kang<sup>8,9,10</sup>, Brian C. Leavell<sup>11</sup>,

1

3	
Δ	
2	
6	
/	
8	
9	
10	
11	
12	
13	
11	
15	
16	
10	
17	
18	
19	
20	
21	
22	
23	
24	
25	
26	
27	
28	
20 20	
∠∀ 2∩	
30	
31	
32	
33	
34	
35	
36	
37	
38	
39	
<u>4</u> 0	
-+U /1 1	
41	
42	
43	
44	
45	
46	
47	
48	
49	
50	
51	
52	
52	
22	
54 57	
55	
56	
57	
58	
59	
60	

1 2

1

2

3

4

5

6

7

8

9

10

11

12

13

14

15

16

17

18

19

20

21

22

23

Tvne, NE2 4HH, UK

32611, USA

Korea

UK

# A synthesis of deimatic behaviour

and Kate D. L. Umbers<sup>17,18,\*</sup>

1 2		
3 4	24	<sup>9</sup> Department of Agricultural Biotechnology, Seoul National University, Seoul, 08826, South
5 6	25	Korea
7 8 9	26	<sup>10</sup> Department of Agriculture and Life Sciences, Seoul National University, Seoul, 08826,
) 10 11	27	South Korea
12 13	28	<sup>11</sup> Department of Biological Sciences, Purdue University, Indiana, 47907, USA
14 15 16	29	<sup>12</sup> Faculty of Science, School of Life and Environmental Sciences, The University of Sydney,
17 18	30	Sydney, NSW, 2006, Australia
19 20	31	<sup>13</sup> Department of Biological and Environmental Science, University of Jyväskylä, Jyväskylä,
21 22 23	32	40014, Finland
23 24 25	33	<sup>14</sup> Department of Biology, Carleton University, Ottawa, Ontario, K1S 5B6, Canada
26 27	34	<sup>15</sup> Department of Biology, University of Toronto Mississauga, Mississauga, L5L 1C6, Canada
28 29	35	<sup>16</sup> School of Biology, University of St Andrews, St Andrews, Fife, KY16 9TH, UK
30 31 32	36	<sup>17</sup> Hawkesbury Institute for the Environment, Western Sydney University, Penrith, NSW, 2751,
33 34	37	Australia
35 36 27	38	<sup>18</sup> School of Science, Western Sydney University, Penrith, NSW, 2751, Australia
37 38 39	39	
40 41	40	
42 43	41	*Author for correspondence (E-mail: k.umbers@westernsydney.edu.au; Tel.: +61 2 4570
44 45 46	42	1603).
47 48	43	
49 50	44	ABSTRACT
51 52	45	Deimatic behaviours, also referred to as startle behaviours, are used against predators and
55 54 55	46	rivals. Although many are spectacular, their proximate and ultimate causes remain unclear. In
56 57	47	this review we aim to synthesise what is known about deimatic behaviour and identify
58 59 60	48	knowledge gaps. We propose a working hypothesis for deimatic behaviour, and discuss the

2					
3 4	49	available evidence for the evolution, ontogeny, causation, and survival value of deimatic			
5	50	behaviour using Tinbergen's Four Questions as a framework. Our overershing aim is to			
6 7	50	benaviour using Tindergen's Four Questions as a framework. Our overarching aim is to			
, 8 9	51	direct future research by suggesting ways to address the most pressing questions in this field.			
10 11	52				
12 13	53	Key words: antipredator, defence, predator, prey, competition, cognition, behaviour,			
14 15 16	54	aposematism, deimatism, startle.			
17 18	55				
19 20	56	CONTENTS			
21 22 23	57	I. Introduction			
24 25	58	II. What is deimatic behaviour?			
26 27	59	(1) Component 1: "A behaviour performed by a target different from fleeing and			
28 29 30	60	retaliation"			
31 32	61	(2) Component 2: "triggered by it perceiving threat from an attacker during approach			
33 34	62	or subjugation"			
35 36 37	63	(3) Component 3: "which can trigger an unlearned avoidance response in the attacker			
38 39	64	" …			
40 41	65	(4) Component 4: "causing it to slow or stop its attack."			
42 43	66	(5) Deliberate exclusions from the hypothesis			
44 45 46	67	(6) Deimatism as a distinct defence			
47 48	68	(7) Mechanisms by which predators respond to initial encounters with deimatic			
49 50	69	behaviour			
51 52 53	70	(a) Startle reflex			
54 55	71	(b) Looming reflex			
56 57	72	(c) Fear responses			
58 59 60	73	(d) Sensory overload			

2		
3 4	74	(e) Confusion effect
5 6	75	III. Deimatic behaviour across taxa
7 8 9	76	(1) Literature search methods
9 10 11	77	(2) Results from literature search
12 13	78	(a) History of describing deimatic behaviour
14 15 16	79	(b) Taxonomic coverage, descriptions, predators and life stages
10 17 18	80	(c) Primary defence associated with deimatic behaviour and stage of predation
19 20	81	sequence deployed
21 22 22	82	(d) Multimodality of deimatic behaviour
25 24 25	83	(e) Speed and duration of deimatic behaviour
26 27	84	(f) Stage of predation sequence in which deimatic behaviour is performed
28 29	85	(3) Potential deimatic behaviours
30 31 32	86	(a) Defensive sprays
33 34	87	(b) Body inflation
35 36	88	(c) Electrical discharge
37 38 39	89	(d) Bioluminescence
40 41	90	(e) Alarm calls and burglar alarms
42 43	91	(f) Vibrations
44 45 46	92	(g) Moth clicks
47 48	93	(h) Rattles
49 50	94	( <i>i</i> ) Facultative flatulence
51 52 53	95	IV. Evolution of deimatic behaviour
55 54 55	96	(1) Evolutionary pathways to deimatism
56 57	97	(2) Modelling the evolution of deimatic behaviour
58 59 60	98	(3) Comparative analyses and the evolution of deimatic behaviour

## **Biological Reviews**

<ul> <li>3 99 (4) Traits associated with the evolution of deimatic behaviour</li> </ul>				
5 6	100	(a) Deimatic behaviour and body size		
7 8 0	101	(b) Deimatic behaviour and prey profitability		
9 10 11	102	(c) Deimatic behaviour and phenology		
12 13	103	V. Ontogeny of deimatic behaviour		
14 15 16	104	VI. Causation of deimatic behaviour		
10 17 18	105	(1) Releasers of deimatic behaviour		
19 20	106	(2) Mechanisms of components of deimatic behaviour		
21 22 23	107	(a) Visual components: colour, movement, and size		
23 24 25	108	(b) Acoustic components: sounds and vibration		
26 27	109	(c) Olfactory/gustatory components: oozing and regurgitating		
28 29 30	110	(3) Changes in deimatic behaviour in response to repeated attack		
30 31 32	111	VII. Survival value of deimatic behaviour		
33 34	112	(1) Does deimatic behaviour increase the probability of prey survival?		
35 36 27	113	(a) Survival value of deimatic behaviour that reveals colour patterns without		
37 38 39	114	chemical defence		
40 41	115	(b) Survival value of deimatic behaviour that reveals colour patterns with chemical		
42 43	116	defence		
44 45 46	117	(c) Survival value of deimatic behaviour that reveals sounds		
47 48	118	(2) Does deimatic behaviour actually deter predators?		
49 50	119	(a) Measures of predator 'startle responses'		
51 52 53	120	(b) Measures of predator hesitation		
53 54 55	121	(c) Measures of predators fleeing		
56 57	122	(3) Do predator responses change across repeat encounters?		
58 59				

1 2		
2 3 4	123	(a) Responses to deimatic behaviour that reveals colour patterns with no chemical
5 6	124	defences
7 8 9	125	(b) Responses to deimatic behaviour that reveals colour patterns with chemical
10 11	126	defences
12 13	127	(c) Responses to deimatic behaviour that reveals sounds
14 15 16	128	VIII. Future directions
17 18	129	(1) Deimatism in the antipredator sequence
19 20	130	(2) Predator responses to deimatic behaviour and prey survival advantage
21 22 23	131	(3) Richer data on prey form and predator response for comparative analyses
23 24 25	132	IX. Conclusions
26 27	133	X. Acknowledgements
28 29 30 31 32	134	XI. Author contributions
	135	XII. References
33 34	136	XIII. Supporting information
35 36 27	137	
37 38 39	138	I. INTRODUCTION
40 41	139	Avoiding predation is essential for prey fitness. Defending against predators can be costly in
42 43	140	terms of time, energy, injury, and death. Therefore, traits that reduce these costs are
44 45 46	141	widespread and diverse. The variety of defensive traits includes: camouflage - concealing
46 47 48 49 50 51 52	142	colours and patterns (Endler, 1978; Stevens & Merilaita, 2011); aposematism - warning
	143	colour patterns and sounds (Mappes, Marples & Endler, 2005); retaliation - expulsion of
	144	blood, toxins, and hot fluids (Eisner, 1970; Sherbrooke, Middendorf & Guyer, 2001); armour
54 55	145	- defensive structures like spines and hard integuments (Speed & Ruxton, 2005); and
56 57	146	mimicry in many forms (Skelhorn et al., 2010; Dell'Aglio et al., 2018). How defensive traits
58 59 60	147	such as visual warning signals work against predators is well understood (Mappes et al.,

2005), while others like deimatic behaviours (Fig. 1), remain poorly understood. Cott (1940, p. 213) commented on deimatic behaviour stating "Indeed, we have here an almost untrodden field for future research". More than 80 years later this statement remains true save for a surge of research in the 1970s, and a more recent second wave. The recent resurgence has precipitated this collaborative review in which we: (1) suggest a hypothesis for deimatism as distinct from other defences; (2) critically evaluate examples of deimatism and their classification; and (3) apply Tinbergen's 'Four Ouestions' framework (Tinbergen, 1963) on evolution, ontogeny, causation, and survival value, to synthesise the literature and identify the critical knowledge gaps we need to fill to understand the evolution of deimatism.

158 II. WHAT IS DEIMATIC BEHAVIOUR?

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

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

Page 9 of 199

### **Biological Reviews**

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

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

#### **Biological Reviews**

Given the overall lack of clarity, but considering the main conceptual points from previous contributions to the field, we suggest the following hypothesis for what constitutes deimatic behaviour: a behaviour performed by a target different from fleeing and retaliation that is triggered by it perceiving threat from an attacker during approach or subjugation, and which can trigger an unlearned avoidance response in the attacker causing it to slow or stop its attack. There are four key components of our hypothesis and we provide rationales for each below plus a summary of our deliberate exclusions. (1) Component 1: "A behaviour performed by a target different from fleeing and retaliation ... " "Behaviour" here is to be interpreted very broadly as something an organism can do including body part movements, the emission of sounds or chemicals, or dynamic changes in colour patterns. The inclusion of the word "performed" is intended to emphasise that it is a discrete state that the prey adopts for a time and to distinguish it from more continuous states, such as constantly exposed aposematic colouration. The behaviour may have been selected to induce the attacker's response or the attacker's response may be an accidental by-product of a prey behaviour. A "target" is the organism or group of organisms that is being attacked, including colonies and other diffuse phenotypes. The target may not always be prey and could be a

competitor (Edmunds, 1974). Deimatic behaviours do not involve the target fleeing from an

attack. They can be performed while fleeing, but their protective value is not in avoiding

capture by increasing physical distance. Deimatic behaviours do not include retaliation (sensu

Edmunds, 1974), in which predators can be physically harmed such as by toxic sprays

(Eisner, 1970).

## **Biological Reviews**

1 2		
2 3 4	223	
5 6	224	(2) Component 2: "triggered by it perceiving threat from an attacker during
7 8 9	225	approach or subjugation"
9 10 11	226	The implication here is that deimatic behaviour evolves in response to attack, and the form
12 13	227	has been influenced by the effect that it has on an attacker, so it is a signal not a cue
14 15 16	228	(Maynard Smith & Harper, 2003). It is triggered by the target perceiving, rightly or wrongly,
17 18	229	that it is threatened; it requires the target to detect the attack. With "perceiving" we intend to
19 20	230	include the most neurologically simple stimulus-response processes. We predict the
21 22 22	231	behaviour will only be performed outside of a threatening context by mistake, for example
25 24 25	232	when targets misidentify an event as a threat (akin to false alarm). We also predict the
26 27 28 29 30 31 32	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,
33 34	236	and micropredators (sensu Lafferty & Kuris, 2002). Display initiation should coincide with
35 36	237	the physical proximity of an attacker within some relevant distance – we suggest the phrase
37 38 39	238	'display initiation distance' (sensu Aguilar-Argüello, Díaz-Fleischer & Rao, 2016) – and it
40 41	239	will cease upon the perceived threat passing, such as when the attacker leaves the scene or
42 43	240	obviously changes its motivation (e.g. from a focused attack to ignoring, or if the prey
44 45 46	241	escapes the predator). The onset of deimatic behaviour may be sudden if it is the result of a
46 47 48	242	threat threshold being breached, but we suggest leaving the time taken to begin performing
49 50	243	the display open because slow transitions may be as effective as fast ones (Holmes et al.,
51 52	244	2018). Deimatic behaviours are performed during predator approach or subjugation – they
53 54 55	245	may function to prevent consumption.
56 57 58	246	

# 247 (3) Component 3: "...which can trigger an unlearned avoidance response in the 248 attacker ..."

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

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

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

## 268 (5) Deliberate exclusions from the hypothesis

Our hypothesis deliberately excludes certain words and phrases to remain inclusive of several
concepts. We have avoided the terms predator and prey because although deimatic displays
are commonly thought of in predator–prey interactions, they also occur in other contexts such

Page 13 of 199

#### **Biological Reviews**

as intraspecific interactions (Edmunds, 1974). We expressly avoid specifying the mechanism
underlying the attacker's response, as several could be exploited. Our hypothesis allows the
target to be 'defended' or 'undefended' because the presence and strength of defences beyond
the behaviour are not needed for it to be deimatic and, equally, their presence does not
preclude deimatism (Fig. 2). The definition also deliberately does not specify the target's
behavioural state at the end of the display which could include the target returning to its
previous state, or fleeing (de-escalation) or retaliation (escalation) (Edmunds, 1972).

280 ((

## 60 (6) Deimatism as a distinct defence

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

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

2	
3	
4	
5	
6	
7	
, 0	
0	
9	
10	
11	
12	
13	
14	
15	
16	
17	
10	
10 10	
19	
20	
21	
22	
23	
24	
25	
26	
20	
27	
28	
29	
30	
31	
32	
33	
34	
35	
36	
30 77	
3/	
38	
39	
40	
41	
42	
43	
44	
45	
16	
40	
4/	
48	
49	
50	
51	
52	
53	
54	
55	
55	
50	
5/ 52	
58	
59	

1

297 Deimatic behaviour can resemble, although is functionally distinct from, fleeing 298 responses like 'flash behaviours' (sensu Edmunds, 1974) which often take the form of 299 repeatedly revealed colour patches and/or sounds by escaping prey (Table S2). These signals 300 are thought to impair the ability of attackers to track a fleeing signaller (Loeffler-Henry et al., 301 2018) whereas deimatic behaviours are not protective *via* disrupting prev tracking or 302 increasing the distance between predator and prey (Edmunds, 1974; Loeffler-Henry et al., 303 2018). Aspects of deimatic behaviour also overlap with retaliatory defences (sensu Edmunds, 304 1974) such as the defensive sprays of bombardier beetles. Such behaviours are also 305 performed when under threat, but differ in that predators are attacked rather than just displayed to. 306

307 Debate and confusion has surrounded whether deimatism is distinct from 308 aposematism (Skelhorn et al., 2016; Umbers & Mappes, 2016). In their most general sense, 309 aposematic signals can be loosely defined as 'go away' signals to predators. Such a broad 310 definition can include many concepts currently considered distinct: warning colouration, 311 flash colouration, types of mimicry and deimatism. This could mean that deimatism is a type 312 of aposematism, in the same way that crypsis and masquerade are both types of camouflage 313 (Skelhorn et al., 2010). But if the term aposematism is used as an umbrella term for all those 314 concepts, classic warning signals need to be given a new name, which could cause 315 unnecessary confusion.

A more useful and biologically precise definition states that aposematism is "...*the* association between the signal and unprofitability...", that "Aposematic signals work best when they are easily detectable and memorable, which facilitates avoidance learning...", and that the benefits of aposematism "...*increase as a function of the density of the similarly signalling individuals*..." (Mappes *et al.*, 2005, p. 598). Deimatism does not fit this definition well. There is preliminary evidence that deimatic behaviours are more effective against naïve Page 15 of 199

## **Biological Reviews**

1	
2 3 4	322
5 6	323
7 8	324
9 10	325
11 12 13	326
13 14 15	327
16 17	328
18 19	329
20 21 22	330
22 23 24	331
25 26	332
27 28	332
29 30	224
31 32 33	225
34 35	335
36 37	336
38 39	337
40 41 42	338
42 43 44	339
45 46	340
47 48	341
49 50	342
51 52 53	343
54 55	344
56 57	345
58 59 60	

322	predators than experienced ones, which is opposite to the expectations of signals that
323	facilitate avoidance learning (Umbers et al., 2019). Deimatic behaviours are not easily
324	detectable; they are temporary and undetectable until they are performed. Learning is not
325	necessary for deimatism to afford protection, which is a major difference from aposematism
326	via learned aversion, although learning might be associated with deimatism after the first
327	encounter (Kang et al., 2016). It is currently unclear whether deimatic behaviours facilitate or
328	impede memorability, and both are possible (Kang et al., 2016). Finally, the benefits of
329	deimatic behaviour can in theory decrease as a function of density, rather than increase, as
330	attackers learn to expect the performance (Sargent, 1990; Ingalls, 1993).
331	Deimatic behaviours can, however, be part of an antipredator strategy that includes an
332	aposematic signal (Umbers et al., 2017) (Fig. 2). If an antipredator strategy includes
333	deimatism and aposematism, deimatic behaviour may cause a predator to break off its attack
334	before directly experiencing any of the prey's other defences. The deimatic function may
335	then hamper development of avoidance learning and reduce the efficacy of, or requirement
336	for, aposematism. Antipredatory strategies that include deimatism can also include Batesian
337	mimicry (for example through revealing markings that mimic a dangerous predator), the use
338	of eyespot signals, or retaliation, and equally, deimatic behaviour can be followed by no
339	further defence (Fig. 2).
340	
341	(7) Mechanisms by which predators respond to initial encounters with deimatic
342	behaviour
343	The sensory and cognitive mechanisms deimatic behaviours exploit in predators are currently
344	unclear. Several non-mutually exclusive hypotheses have been suggested: release of the

startle reflex, the looming reflex, the release of fear in the predator, sensory overload,

346 confusion, and neophobia. Experimentally distinguishing among these mechanisms is an347 important challenge to meet.

*(a) Startle reflex* 

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

The 'startle reflex' is a response that interrupts what an animal is currently doing and produces physiological and behavioural changes that help it evade an immediate threat (Eaton, Bombardieri & Meyer, 1977; Gotz & Janik, 2011; Yilmaz & Meister, 2013; Skelhorn et al., 2016). The startle reflex appears to be triggered by stimuli, whether auditory or visual, that have a high intensity and a rapid onset (Koch & Schnitzler, 1997; Koch, 1999; Deuter et al., 2012). For example, in laboratory experiments where sounds are produced in close proximity to subjects (usually primates and rodents), sounds typically need to be above 80-90 dB with rapid rise times (the time taken for the stimulus to reach its maximum amplitude) of less than 12 ms (Davis, 1984), but sounds of 60 dB can also be effective if they have close 

Page 17 of 199

1

#### **Biological Reviews**

2 3 1	371
4 5 6	372
7 8	373
9 10	374
11 12	375
13 14 15	376
15 16 17	277
17 18 19	3//
20 21	378
22 23	379
24 25	380
26 27	381
28 29	382
30 31 22	383
32 33 34	384
35 36	385
37 38	386
39 40	387
41 42	388
43 44	380
45 46 47	200
47 48 49	390
50 51	391
52 53	392
54 55	393
56 57	394
58 59	395
60	

to instantaneous rise times (Åsli & Flaten, 2012). Caterpillars that make sounds in response to attack can produce them close to instantaneously at 70–90 dB when the predator is at close range, but the limited data available suggest that deimatic behaviours rarely have such intense and rapid onset, at least for auditory signals. Therefore, although the startle reflex is taxonomically widespread, and exploiting it could protect against many enemies, it is unlikely to be the mechanism by which all deimatic behaviours protect.

378 (b) Looming reflex

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

## 396 (c) Fear responses

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

416 (d) Sensory overload

417 Deimatic behaviours could somehow overwhelm a predator's ability to process sensory
418 information by presenting them with more information or noise than they can process at once
419 (Hebets & Papaj, 2004; Low, 2012). This popular idea has been referred to as 'sensory
420 overload' (Hebets & Papaj, 2004; Bro-Jørgensen, 2010). However, this term is often used

Page 19 of 199

1

## **Biological Reviews**

2	
ر ۸	
4	
5	
6	
7	
8	
9	
10	
11	
12	
12	
17	
14	
15	
16	
17	
18	
19	
20	
21	
22	
23	
23	
24	
25	
26	
27	
28	
29	
30	
31	
32	
22	
JJ 2≬	
34 25	
35	
36	
37	
38	
39	
40	
41	
42	
43	
11	
44	
45	
46	
47	
48	
49	
50	
51	
52	
52	
22	
54	
55	
56	
57	
58	
59	
60	

436

421 loosely, and clear conceptual definitions are rare (Schevdt et al., 2017), particularly in the 422 animal signalling literature. From a mechanistic point of view, the behavioural phenomena 423 that appear to be associated with sensory overload (e.g. behavioural immobilization and 424 confusion) may be caused when excessive stimulation from at least two sensory modes 425 blocks the reticular formation; a complex network of brainstem nuclei involved in (amongst 426 other things) perception, attention and maintaining behavioural arousal (Lindsley, 2013). 427 Related concepts probably include visual or auditory distraction, sensory filtering, cognitive 428 overload (Dukas & Kamil, 2000) and breakdown of multimodal/sensory integration. 429 Understanding the mechanisms by which deimatic behaviours protect prey from 430 predators requires directly measuring what the predator is experiencing, which may demand 431 more technically difficult and invasive data collection (Fullard, Dawson & Jacobs, 2003) than 432 measuring predator behaviour and carries important ethical considerations. The difficulty of 433 determining the mechanisms involved increases substantially when attempted in field conditions (Skelhorn et al., 2016; Umbers & Mappes, 2016). Both are worthy goals if we are 434 435 to understand how deimatic behaviours provide survival value.

437 (e) Confusion effect

438 As stated above, deimatic behaviour often involves the exposure of a previously hidden 439 signal that functions to startle a would-be attacker. However, the deployment of hidden 440 signals may also prevent attacks through other mechanisms. Specifically, a cryptic organism revealing a conspicuous signal as it flees may confuse the attacker as to the organism's 441 442 appearance when at rest, hindering subsequent search. This defensive strategy is known as 443 'flash behaviour' and appears to be widespread in nature with putative examples having been 444 described in cephalopods, insects, fish, amphibians, reptiles, birds, and mammals (Edmunds 445 1974; Hanlon & Messenger, 2018). It has been postulated that the confusion effect of flash

behaviour may function in tandem with a startle effect to dissuade attackers (Edmunds, 1974; Cott, 1940). However, a 'proof of concept' experiment demonstrated that the confusion effect of flash behaviour alone is sufficient to prevent attacks (Loeffler-Henry et al., 2018). Moreover, flash displays may be more effective in reducing predation when the signaller flees from a distance, so that the signaller's cryptic resting state is not observed (Loeffler-Henry, Kang & Sherratt, 2021). Since hidden signals are less likely to frighten the observer when exposed from a distance, then deimatic and flash displays are functionally distinct and may often be incompatible.

## 455 III. DEIMATIC BEHAVIOUR ACROSS TAXA

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

## 463 (1) Literature search methods

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

specific terms: 'unken reflex' (amphibians), 'hooding' (cobras) and 'disturbance stridulation' (insects).

#### (2) Results from literature search

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

> (a) History of describing deimatic behaviour

Deimatic behaviour is no doubt known by indigenous people the world over, but to the detriment of this review we found no modern indigenous accounts. However, we found some evidence of ancient knowledge on snakes with putative deimatic behaviours in images and written accounts. A rattlesnake's rattle is prominently depicted in a pictograph dated to approximately 1000 CE at the Pony Hills archaeological site, New Mexico (Schollmeyer, 2020). The Brooklyn Medical Papyrus dated 450 BCE, describes the hooding behaviour of the Egyptian cobra (Naja haja), scale stridulation of saw-scaled vipers (Echis sp.), and 

## **Biological Reviews**

2	
3	
1	
4	
5	
6	
7	
, 0	
0	
9	
1	0
1	1
1	ר
1	2
I	3
1	4
1	5
1	6
1	7
1	, 0
1	0
1	9
2	0
2	1
2	2
2	2
2	с
2	4
2	5
2	6
2	7
2	, 0
2	0
2	9
3	0
3	1
3	2
2	- 2
כ ר	ر ۸
3	4
3	5
3	6
3	7
3	8
2	0
с	9
4	υ
4	1
4	2
4	3
۵	4
4	4 ~
4	2
4	6
4	7
4	8
Δ	9
-	<u>^</u>
כ ר	1
5	1
5	2
5	3
5	4
5	5
с Г	с С
5	ю _
5	7
5	8
5	9
6	٥

1

496	sounds of puff adders (Bitis arietanis) (Golding, 2020). The earliest written description of
497	deimatic behaviour in the scientific literature we could find is that of Goureau (1841) about
498	Mantis religiosa which roughly translates from French to: "she raised her long corselet
499	vertically, carried her forelegs forward, as if to catch her prey, half spread her wings and
500	elytra, and moved her abdomen up and down with a rapid movement; during this movement,
501	the sides of the belly rubbed against the inner edges of the wings and elytra, and produced a
502	noise analogous to that obtained by crumpling parchment" (Goureau, 1841, p. 354). Löhner
503	(1919) described the unken reflex (arched-back posture) in Bombinator igneus toads as
504	potentially hypnotising. Varley (1939) published a comprehensive summation of the
505	literature on mantis 'frightening attitudes' citing 29 publications including Roonwal's (1938)
506	account of the 'frightening display' of the mantis Eremiaphila braueri. After a three-year
507	residence in the jungles of Trinidad, Crane (1952) published her comparative account of the
508	'defensive behaviour' of 15 Trinidad mantis species. Blest (1957a) published a detailed
509	account of 'protective displays' in some Saturnioidea and Sphingidae Lepidoptera.
510	Throughout the 1970s there was a flourish of work on deimatic behaviour. Maldonado
511	described details of the form, habituation and ontogeny of deimatic behaviour in the double
512	eye-spot mantis (Stagmatoptera biocellata) (Maldonado, 1970; Balderrama & Maldonado,
513	1971, 1973).
514	In the early and mid 1970s. Edmunds published two extensive descriptions of the

In the early and mid 1970s, Edmunds published two extensive descriptions of the 'defensive behaviour' of dozens of African mantises (Edmunds, 1972, 1976) and his influential book *Defence in Animals: A Survey of Anti-predator Defences* (Edmunds, 1974), in which he describes 'deimatic behaviour' across species and contexts. Also in the 1970s, Brodie Jr led a series of publications that described the 'defensive posturing' of the newt *Taricha granulosa* and dozens of salamander species (Johnson & Brodie Jr, 1975; Nowak & Brodie, 1978). Since then, the field has progressed steadily including seminal works on the

### **Biological Reviews**

2	
3	
4	
5	
6	
7	
/	
8	
9	
10	
11	
12	
12	
13	
14	
15	
16	
17	
10	
10	
19	
20	
21	
22	
23	
21	
24	
25	
26	
27	
28	
29	
30	
21	
21	
32	
33	
34	
35	
36	
27	
27	
38	
39	
40	
41	
42	
43	
11	
77 1	
45	
46	
47	
48	
49	
50	
50	
51	
52	
53	
54	
55	
56	
57	
57	
58	
59	

underwing moths (*Catocala* spp.) in the 1980s and 1990s (Schlenoff, 1985; Sargent, 1990;
Ingalls, 1993) and peacock butterflies (*Aglais io*) in the 2000s (Vallin *et al.*, 2005; Olofsson,
Jakobsson & Wiklund, 2012*b*).

524

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

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

9 0 537

60

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

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

2 3	546	
4 5 6	547	(d) Multimodality of deimatic behaviour
7 8 9	548	About half the studies suggested that deimatic behaviours target more than one sensory mode
10 11	549	(Higham & Hebets, 2013) (Table S3). However, most studies focused on behaviours
12 13	550	involving movement of large body parts (the wings, body, tail, or head; Table S3, Fig. 3E).
14 15	551	Several visual components were reported: movement and body size increase, colour pattern
16 17 18	552	reveal including eyespots, light production (e.g. bioluminescence), and the revealing or
19 20	553	highlighting of a weapon. Most studies (~ 65%) involved visual components in addition to
21 22	554	movement. We found a few cases of putative Batesian mimicry where posturing alone was
23 24	555	thought to be protective. For example, the stick insect (Oncotophasma martini) curves its
25 26 27	556	abdomen over giving it the appearance of a scorpion (Robinson, 1968b), while the lobster
27 28 29	557	moth (Stauropus fagi) caterpillar adopts a spider-like posture (Poulton, 1890). The most
30 31	558	common incorporation of Batesian mimicry was in the reveal of eyespots [18 Lepidoptera
32 33 24	559	(especially Saturniidae: Automeris), two manitses, one cuttlefish and one frog]. Only about
35 36	560	one quarter of the studies included a focus on auditory, vibrational or olfactory components
37 38	561	and around 40% reported a gustatory or olfactory component (Table S3). It is unclear
39 40	562	whether visual components are more commonly associated with deimatic behaviour or just
41 42 43	563	more often studied (Rowe & Halpin, 2013).
44 45	564	

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

 The movement involved in deimatic behaviour may be important for its protective value (Holmes et al., 2018) but speed and duration were rarely measured. We found no clear information on the speed of state change (rise time) between resting and deimatic behaviours. One exception was for the common octopus (Octopus vulgaris), which initiated changes to its visual appearance in 270 ms and completed a dramatic colour pattern and skin texture change

### **Biological Reviews**

in 2 s using its capacity for rapid neural polyphenism (Hanlon, 2007; Hanlon & Messenger, 2018). The European cuttlefish initiates dramatic changes in appearance over a similar time frame, and varied these responses across three different species of teleost fish predators (Staudinger, Hanlon & Juanes, 2011). In other taxa, display duration varied enormously among species from milliseconds to more than 30 min (Table S3). In the most extreme case a mantis held its pose for 6 h while sharing a cage with a predatory bird (Maldonado, 1970). Deimatic behaviours were described as sustained and/or rhythmical (repeated) (sensu Blest, 1957b), around half the studies report on sustained behaviours, around 30% on rhythmical and 15% on behaviours that have both sustained and rhythmical elements. We found no reports describing movements that were performed only once and thus were neither sustained nor rhythmical.

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

2	
3	595
4	270
5	596
7	
, 8	597
9	
10	598
11	• • •
12	599
13	• • •
14	600
16	
17	601
18	001
19	602
20	002
21	603
22	000
24	604
25	
26	605
27	
28	606
29	000
30	607
32	001
33	608
34	000
35	609
36	
37 38	610
39	
40	611
41	011
42	612
43	
44 45	613
46	
47	614
48	
49	615
50	
51	616
52 53	,
54	617
55	
56	618
57	
58	619
59 60	
0.7	

95 species display during approach. To understand the evolution of deimatic behaviour, it is 96 critical that an ecologically appropriate stimulus is used (see Section VIII.2).

#### 98 (3) Potential deimatic behaviours

99 Confusion as to which behaviours are deimatic became obvious from our survey of the literature. Common sources of ambiguity included defensive spray liquids, body inflation, )0 01 bioluminescent signals, alarm calls, vibrations, and electrical emissions. Given this )2 uncertainty, we briefly discuss these cases below and attempt to clarify the information )3 required to include or exclude them as deimatic, which will mostly depend on the receiver's )4 response.

)6 (a) Defensive spravs

)7 Edmunds (1974) described defensive sprays as retaliatory defences but the posturing before the spray, such as that of a skunk, as deimatic. Skunks (Mephitidae) squirt strong-smelling )8 )9 liquid at their attackers from glands (Medill, Renard & Larivière, 2011; Fisher & 0 Stankowich, 2018) and reflexive bleeders like horned lizards (*Phyrnosoma* spp.) squirt blood 1 at their attackers (Sherbrooke et al., 2001). More harmful sprays include the hot, caustic, 2 liquid sprays of bombardier beetles, stinging peppermint stick insect (*Megacrania batesii*) 3 sprays, and the entangling toxic 'glue' shot by termites (Eisner, 1970; Eisner & Adams, 1975; 4 Eisner, Yack & Aneshansley, 2001b; Eisner et al., 2001a; Dossey, 2011). Interestingly, 5 bombardier beetles and skunks have warning colours as their primary defence, whereas 6 peppermint stick insects and horned lizards use crypsis. We hypothesise that posturing and/or 7 non-harmful sprays are deimatic in that they have an aversive effect when initially 8 encountered and then, on subsequent encounters, have an aposematic effect. The distinction 9 lies in whether the posturing before sprays are employed has a deimatic effect and whether

1

### **Biological Reviews**

2		
3		
4		
ر		
6		
7		
8		
ი ი		
9		
1	0	
1	1	
1	2	
1	2	
I	3	
1	4	
1	5	
1	6	
1	-	
I	/	
1	8	
1	9	
<b>ว</b>	n	
~	1	
2	1	
2	2	
2	3	
	л Л	
2	4	
2	5	
2	6	
2	7	
<u>^</u>	, 0	
2	ð	
2	9	
3	0	
2	1	
2	י ר	
3	2	
3	3	
3	4	
- -	E	
2	2	
3	6	
3	7	
3	8	
2	~	
5	9	
4	0	
4	1	
Δ	2	
т Л	~ >	
4	5	
4	4	
4	5	
4	6	
т л	7	
4	1	
4	8	
4	9	
5	ი	
-	1	
5	I	
5	2	
5	3	
5	۵	
5 7	-T -	
5	5	
5	6	
5	7	
5	Q	
ر -	0	
5	9	

spraying the predator qualifies as retaliation (*sensu* Edmunds, 1974) rather than deimatism,
but no clear line has yet been drawn. Future work could focus on the effect of posturing and
the degree of physical harm done to the attacker during the spraying behaviour to disentangle
these defences.

625 (b) Body inflation

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

640

60

641 (c) Electrical discharge

Electrical signals are surprisingly ubiquitous in nature (England & Robert, 2021). The
electrical discharges generated by numbfishes (Narcinidae), electric rays (Torpedinidae), and
electric eels (*Electrophorus electricus*) could be deimatic behaviours. They are not typically

## **Biological Reviews**

described as deimatic in the literature perhaps because it is mechanism focused (Sheridan, 1965; Mellinger et al., 1978; Macesic & Kajiura, 2009). Electrical signals are, however, known to function in antipredator contexts in some species. Macesic & Kaijura (2009) showed that the lesser electric ray (*Narcine brasiliensis*) generates electric organ discharges against simulated predatory attacks. As there is still limited research into the use of electrical discharges as a defence, it is currently unclear whether this should be considered retaliation to make the prev less profitable, or whether it is a deimatic display. It may be speculated that this could be context dependent, as the same charge could, for example, simply startle a larger predator, whereas it could stun a smaller predator. The mechanism of defence could therefore be related to both the type of predator and the type of prey (for example juvenile lesser electric rays are capable of weaker discharges than adults), however further work is needed to determine whether retaliation and deimatic behaviour can be separated in this example. Behavioural studies on predator responses to electrical discharges are needed to understand how they fit among antipredator defences especially in terms of retaliation and aposematism.

661 (*d*) Bioluminescence

Bioluminescence, the chemical production of light by living organisms (Kahlke & Umbers, 2016), is used in anti-predatory contexts and can resemble deimatic behaviour (Stanger-Hall & Oakley, 2019). Bioluminescence can be aposematic, as chemically defended adult and larval fireflies elicit avoidance learning in anurans (De Cock & Matthysen, 2003), bats (Leavell et al., 2018), mice (Underwood, Tallamy & Pesek, 1997), and spiders (Long et al., 2012), or it may 'frighten' potential predators (Lloyd, 1973). Esaias & Curl (1972) hypothesised that dinoflagellate (Gonvaulax spp.) bioluminescent flashes function as a protean display "which startles or confuses the copepod" (p. 901) suggesting both fleeing and Page 29 of 199

1

#### **Biological Reviews**

2		
3 4	670	deimatism (Humphries & Driver, 1970; Edmunds, 1974; Driver & Humphries, 1989).
5 6	671	Similarly, lantern fish (Myctophidae) emit bioluminescent flashes in response to their
7 8	672	predators, southern elephant seals (Mirounga leonina), which result in longer prey capture
9 10 11	673	attempts (Goulet et al., 2020). Where feasible, direct tests of predator responses could
12 13	674	identify examples of deimatism in bioluminescent systems.
14 15	675	
16 17 18	676	(e) Alarm calls and burglar alarms
19 20	677	It is currently unclear whether 'alarm calls' (alerting conspecific receivers to a potential
21 22	678	danger), or 'burglar alarms' (attracting the attention of an enemy's enemy) should be
23 24	679	considered as deimatic behaviour (Burkenroad, 1943; Haddock, Moline & Case, 2010;
25 26 27	680	Hanley & Widder, 2017). Vervet monkey (Chlorocebus pygerythrus) predator-specific alar
28 29	681	calls signal the presence of a predator to conspecifics (Cheney & Seyfarth, 1981). However,
30 31	682	it could be speculated that the surprise (or 'startle') caused by an unexpected alarm call may
32 33 34	683	also directly deter predators if the prey's call releases a threat-avoidance response. In
35 36	684	response to copepod (Acartia tonsa) attack some dinoflagellates (Pyrodinium bahamense ar
37 38	685	Lingulodinium polyedrum) use bioluminescent flashes as 'burglar alarms' to draw in copepo
39 40	686	predators, but such flashes may also act to release a rapid threat response in the copepods
41 42 43	687	directly (Hanley & Widder, 2017).
44 45	688	
46 47	689	(f) Vibrations
48 49 50	690	Substrate and airborne signals may constitute vibratory deimatism if they cause a threat-
51 52	691	avoidance response in an attacker. In many species disturbance-induced vibration increases
53 54	692	handling time and decreases predation risk (Bauer, 1976; Smith & Langley, 1978; Masters,
55 56 57	693	1979; Buchler, Wright & Brown, 1981; Lewis & Cane, 1990; Guedes et al., 2012; Low,
58 59	694	2012), although some studies have found no evidence for protection against predation
60		

#### **Biological Reviews**

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

(g) Moth clicks

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

## **Biological Reviews**

3			
4			
5			
5			
7			
8			
9			
1	0		
1	1		
1	2		
1	3		
1	4		
1	5		
1	6		
1	7		
1	8		
1	9		
2	0		
2	1		
2	2		
2	3		
2	4		
2	5		
2	6		
2	7		
2	8		
2	9		
3	0		
3	1		
3	2		
3	3		
3	4		
3	5		
3	6		
3	7		
3	8		
3	9		
4	0		
4	1		
4	2		
4	3		
4	4		
4	5		
4	6		
4	1		
4	8		
4	9		
5	0		
5	1		
5	2		
5	3		
5	4 7		
5 5	5 6		
5 5	0 7		
5	/ c		
5	თ ი		
٦	ч		

60

720 associated with a negative consequence than can a neutral or positive acoustic signal 721 (Guilford & Dawkins, 1991; Ratcliffe & Fullard, 2005; Ter Hofstede & Ratcliffe, 2016). 722

723 (*h*) *Rattles* 

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

732

#### 733 *(i) Facultative flatulence*

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

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

1 ว		
2 3 4	745	
5 6	746	IV. EVOLUTION OF DEIMATIC BEHAVIOUR
7 8 0	747	Understanding the evolution of complex traits like deimatism is challenging, especially
10 11	748	because behaviours are difficult and costly to measure. Evolutionary models are required to
12 13	749	provide explicit hypotheses for experimental testing. Where data are available, comparative
14 15 16	750	approaches also provide important opportunities to generate and test hypotheses on the
17 18	751	evolution of deimatic behaviours. This can be done by establishing when and in what
19 20	752	lineages deimatism has evolved or been lost, and what ecological factors may be associated
21 22 23	753	with its evolution.
23 24 25	754	
26 27	755	(1) Evolutionary pathways to deimatism
28 29	756	Umbers et al. (2017) formally proposed two potential pathways for the evolutionary
30 31 32	757	origins of deimatic behaviour; the 'defence-first' and 'startle-first' hypotheses. The defence-
33 34	758	first hypothesis suggests that the acquisition of some form of chemical defence or weapon
35 36	759	precedes the acquisition of a deimatic behaviour (itself also a defence). Under this
37 38 39	760	hypothesis, the acquired defence facilitates the evolution of, for example, a conspicuous
40 41	761	aposematic colour signal, the costs of which can be offset by concealment, revealing it only
42 43	762	when the prey perceives a threat. The defence-first hypothesis can also include revealing or
44 45 46	763	highlighting weapons, possibly from the ritualisation of counter-attack behaviour (Lieshout,
47 48	764	Elgar & Wilgenburg, 2005). For example, during their deimatic behaviour, many mantises
49 50	765	highlight their large raptorial forelimbs which are used in prey capture and retaliation
51 52	766	(O'Hanlon et al., 2018; Vidal-García et al., 2020). However, unless further defences are lost
53 54 55	767	upon the evolution of deimatic behaviour, the numerous examples of deimatism not
56 57 58 59 60	768	obviously associated with a chemical or weaponry defence require other evolutionary routes.

Page 33 of 199

1

### **Biological Reviews**

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

769 The startle-first hypothesis suggests that the act of performing the behaviour itself has 770 protective value and can allow the evolution of further defences. Given our objections above 771 concerning the use of the word 'startle', perhaps 'behaviour-first hypothesis' is a better name. 772 Vidal-García et al. (2020) found indirect evidence to support this behaviour-first hypothesis, 773 as they reported that wings were used by 29 of 31 displaying mantis species including 11 774 species in relatively basal phylogenetic positions that lacked hidden colours. In a behavioural 775 study, Holmes et al. (2018) showed that movement alone can be protective but that a 776 combination of colour and movement increased survival. Similarly, using a robotic moth and 777 wild black-capped chickadees (Poecile atricapillus), Kang, Zahiri & Sherratt (2017) showed 778 that prey movement alone, without other defensive components like colours, can elicit 779 responses consistent with responses to deimatic behaviour in birds.

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

789

## 790 (2) Modelling the evolution of deimatic behaviour

791 Theoretical models of deimatic behaviour have so far been mostly descriptive, qualitative
792 arguments, although mathematical models of related phenomena have been developed.
793 Theory in this area is necessary to formalise arguments and make testable predictions. Below

we highlight key considerations when developing mathematical models of deimatic behaviour.

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

Deimatic behaviours are typically not primary defences but rather back-up defences deployed at the prey's discretion (Umbers, Lehtonen & Mappes, 2015). This can be formalised in modelling terms by viewing deimatic behaviours as one defence in a sequence of antipredator defences (Fig. 2). If the primary defensive strategy is highly effective in preventing predation, this may impede selection on further defences that are invoked only when the primary defence fails (Britton, Planqué & Franks, 2007; Wang et al., 2019). Such 'strategy blocking' may lead to cross-species associations between primary and subsequent defences (such as deimatism) mediated by factors that affect the upper limit on the primary
Page 35 of 199

## **Biological Reviews**

defence, such as body size (Kang et al., 2017) (for further discussion of body size, see Section IV.4*a*). From an evolutionary perspective, perhaps the most fundamental question is: what is the selective advantage for a predator responding to deimatic behaviour? It is a behavioural response that comes at the cost of energy expenditure and opportunities missed, so what are its benefits? If it is a rapid response to a potential threat (Simons, 1996), it may save the life of the receiver, or prevent injury. Signal detection theory quantifies the optimal trade-off between type I error (such as twigs treated as snakes, 'false alarms') and type II errors (snakes treated as twigs, 'misses') (Leavell & Bernal, 2019). If the costs of mistaking a snake for a twig far outweigh the costs of mistaking a twig for a snake, then a conservative threshold with a high false alarm rate would be optimal, even when the likelihood of the stimulus coming from a true threat is small (Castellano & Cermelli, 2015). While signal detection models identify the optimal response under uncertainty, speed-accuracy trade-offs need to be included (Chittka, Skorupski & Raine, 2009). If the stimulus is sudden, such as that caused by dangerous events like the rush of a potential predator or a tree falling, then quick action will be favoured over careful deliberation. As Janzen et al. (2010, p. 11659), puts it "pause a millisecond to ask whether that eve belongs to acceptable prev or to a predator, you are likely to be—and it takes only once—someone's breakfast". Models that combine signal detection and speed-accuracy trade-offs have been developed and take the form of sequential sampling models in which additional inspections to gain more information come at a cost (e.g. Getty, 1996; Abbott & Sherratt, 2011). Complementary models have separated the two processes almost entirely. For example, motivated by empirical evidence, Trimmer et al. (2008) represented mammalian brains as having two decision-making systems, both Bayesian in nature but acting at different speeds. The first quick-but-inaccurate thalamic decision is assumed to be based on a one-off application of signal-detection theory involving a simple (and conservative) threshold for

## **Biological Reviews**

treating stimuli as threats, whereas the slow-but-accurate cortical decision is based on the
sequential probability ratio test (SPRT) as more evidence governing how to act is gathered
over time (Wald, 1945; Castellano, 2015). Natural selection appears to have favoured an 'act
now, think later' response to certain stimuli because only quick action can save the observer's
life and, like many behaviours, this response can be exploited by potential prey. Modelling
can help clarify why the responses are rapid, and how they continue to be maintained despite
a high propensity for false alarms.

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

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

867 Crane (1952), Edmunds (1972, 1976), Blest (1957*b*), and Brodie (1983) on mantises, moths
868 and salamanders were the first to compare the diversity and systematic patterns of deimatic

Page 37 of 199

### **Biological Reviews**

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

Page 38 of 199

the tree (Fig. 4). These studies all confirm the conclusions of the earlier comparative studies, that deimatic behaviours are frequently gained and lost as a lineage diversifies. The processes driving gains and losses of deimatic behaviour are unclear. In praying mantises there is a hint that deimatic behaviour evolved in response to the evolution of birds, appearing roughly 60 million years ago (Vidal-García et al., 2020). So far, no phylogenetic comparative studies have included the required data to test hypotheses on ecological drivers such as predator diversity, population density, habitat type and activity time, but such analyses would make a valuable contribution to elucidating the evolutionary timing and ecological correlates of deimatic behaviour. 

# 903 (4) Traits associated with the evolution of deimatic behaviour

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

907 (a) Deimatic behaviour and body size

The literature provides mixed support for the hypothesis that larger species are more likely to perform deimatic behaviours. Kang et al. (2017) suggested that hidden colours are more common in large species than in small species of Erebidae moths. In a taxonomically broader study, Loeffler-Henry et al. (2019) also found evidence of a positive correlation between body size and hidden colouration for four insect taxa (Orthoptera, Phasmatidae, Mantidae, Saturniidae) but not for Sphingidae. More nuanced still, particular colours may be correlated with body size. Emberts et al. (2020) studied 26 species of leaf-footed bugs (Coriidae) and found an association between large size and deimatic behaviour only in species with white hidden patches, but not in those with red/orange patches. These studies suggest that certain colours of signals revealed by deimatic behaviour are more common in larger species but do

Page 39 of 199

## **Biological Reviews**

not address whether deimatic behaviour itself is more common in larger species. However, a phylogenetically controlled analysis on 58 praying mantis species that included behaviour, sound production, and hidden colours found no support for the hypothesis that larger species were more likely to exhibit deimatic behaviour (Vidal-García et al., 2020). Discrepancies between this study and that of Loeffler-Henry et al. (2019) are likely due to differences in the sizes of species sampled. Some deimatic species lacked hidden colouration suggesting that a relationship between the presence of hidden colours and size does not extend to deimatic behaviour per se.

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

939 Additionally, larger prey may be more effective at confusing predators or eliciting the
 940 looming reflex in receivers during deimatic behaviour (see Section II.7*b*). Alternatively, an
 941 increase in size could be related to making the prey more challenging to consume,
 942 particularly if the increased size exceeds the maximum gape size of the predator. New theory

2	
3	
4	
5	
6	
7	
/ 0	
ð	
9	
10	
11	
12	
13	
14	
15	
16	
17	
18	
19	
20	
∠∪ 21	
∠ I วว	
22	
23	
24	
25	
26	
27	
28	
29	
30	
31	
32	
22	
21	
24	
30	
36	
37	
38	
39	
40	
41	
42	
43	
44	
45	
46	
47	
-1/ ∆Ω	
-10 10	
49	
50	
51	
52	
53	
54	
55	
56	
57	
58	
59	
60	

and further research are needed to determine how body size and deimatic behaviour interactconsidering trophic level, predator diversity, and other ecological factors.

945

1

# 946 (b) Deimatic behaviour and prey profitability

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

958

## 959 (c) Deimatic behaviour and phenology

960 Kim et al. (2020) compiled data on colour, phenology, and abundance for 1,568 macrolepidopteran species on three continents (Asia, Europe, and North America) and found that 961 962 species with hidden contrasting colours that are putatively used in deimatic behaviour appear 963 later in the season than the species with other colour defences. This finding is interesting as it 964 may be expected that deimatic behaviour would be most effective against naïve predators, 965 and therefore would be most protective earlier in the season. However, it could be that a 966 protective effect against naïve predators may be quickly diluted by predator learning. Thus, 967 the fitness benefit of appearing early in the season may not be significant because this

### **Biological Reviews**

protective effect does not contribute significantly to the survival of adult insects (until they
reproduce). On the other hand, a protective effect through mimicry may remain stable
because predators' avoidance learning remains for longer and more consistently (and perhaps
reinforced continuously through their experience with various aposematic prey).
Some species with deimatic behaviours may gain protection because they reveal a
signal that is a Batesian mimic of defended species. This could be an effective defence if

974 predators generalise signals or if those signals are highly effective against naïve predators. If
975 species with deimatic behaviours derive a selective advantage by delaying their activities

976 until local predators have learned to avoid aposematic signals, it would be interesting to test

977 how this fits into mimic–model systems in Batesian mimicry theory (Waldbauer, Sternburg &

978 Maier, 1977).

## 980 V. ONTOGENY OF DEIMATIC BEHAVIOUR

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

In animals that undergo 'complete' metamorphosis, the differences between juveniles and adults may require different defensive strategies due to differences in mobility, habitat, and diet. Holometabolous insects provide many examples of deimatic behaviour at only one life stage, and we found no descriptions of deimatism for both larval and adult life stages (Table S4). Lepidopteran larvae (caterpillars) provide excellent examples of deimatic behaviour as juveniles but the presence of deimatic behaviours in their adult forms is often unknown. However, in peacock butterflies the reverse is true: adults use deimatic behaviour, whereas we found no evidence of deimatic behaviour in their caterpillars. Ambystomid

## **Biological Reviews**

Page 42 of 199

2	
_	
3	
л	
+	
5	
6	
7	
/	
8	
0	
9	
-	
10	
11	
12	
13	
1 /	
14	
15	
16	
17	
17	
18	
19	
າດ	
20	
21	
<u>د</u> ا	
22	
าา	
23	
24	
27	
25	
20	
26	
27	
21	
28	
29	
20	
50	
31	
5.	
32	
22	
33	
34	
54	
35	
20	
36	
27	
57	
38	
39	
<u>4</u> 0	
-10	
41	
42	
⊿२	
-13	
44	
۸ ۳	
45	
46	
-10	
47	
40	
48	
٥Δ	
77	
50	
51	
50	
52	
53	
54	
<u> </u>	
22	
56	
57	
E 0	
ъγ	
E٥	
~~	
29	

1

993 salamanders also undergo a dramatic metamorphosis, only after which do they exhibit 994 deimatic behaviour. In Anderson's crocodile newt (Echinotriton andersoni), aquatic larvae 995 do not posture, but just one day after they reabsorb their gills terrestrial juveniles can perform 996 an extreme version of the deimatic behaviours seen in mature adults, in which they can bring 997 their ribs forward at an angle of 90° to their spine to pierce the skin (Brodie, Nussbaum & 998 Digiovanni, 1984). The posturing behaviour could be deimatic, with the protrusion of ribs 999 perhaps preparation for retaliation, or a deterrent by exceeding a predator's gape. Such 1000 differences between adult and juvenile defences may reflect adaptations to their different 1001 aquatic and terrestrial habitats. 1002 For animals that undergo relatively gradual changes in morphology over their life

1003 stages, data on changes in deimatic behaviour with ontogeny were available for some 1004 mantises, orthopterans, and squid (Table S4). The double eve-spot mantis (*Stagmatoptera* 1005 *biocellata*) uses crypsis as its sole method of predator defence in the first and second instar, 1006 whereas intermediate instars (3–7) use both crypsis and deimatic behaviours, and adults 1007 primarily use deimatic behaviours (Balderrama & Maldonado, 1973). The authors suggested 1008 that relying on deimatic displays may be too risky when individuals are small and relatively 1009 easy prey, and that their stick-like morphology may allow camouflage. Adults with their 1010 more prominent head may prevent them from mimicking sticks as effectively, reducing their 1011 camouflage and increasing pressure for the evolution of deimatism as a secondary defence. In 1012 the mantis Angela guianensis, adults use deimatic wing displays, while juveniles rely on 1013 running and dropping. In the Texas unicorn mantis (*Phyllovates chlorophaea*) and Peruvian 1014 shield mantis (Choeradodis rhombicollis) juveniles also run and drop in defence. The 1015 deimatic behaviour of adult P. chlorophaea, on the other hand, reveals yellow and black 1016 bands on their dorsal abdomen, while that of adult C. rhombicollis includes rearing up and 1017 posturing towards the attacker. Juveniles also rely on fleeing in several orthopterans. In the

Page 43 of 199

## **Biological Reviews**

katydid Scorpiorinus fragilis (Pseudophyllinae), nymphs rely on escape while adults reveal their vellow dorsal abdomen in response to touch by lifting their wings which produces a stridulatory sound (Robinson, 1969). Adults of the stick insect, Metriotes diocles raise their wings in a deimatic display while nymphs tend to drop and use thanatosis to avoid consumption (Robinson, 1969). Differences during ontogeny have also been reported in the defensive behaviour of two species of squid, Atlantic brief squid (Lolliguncula brevis) and longfin inshore squid (Dorvteuthis pealeii) (York & Bartol, 2016). Paralarvae (hatchlings) of D. pealeii were more likely to use transparency in response to predators whereas juveniles and adults of L. brevis were more likely to perform deimatic behaviours. It is possible that relying on crypsis alone for adults is too costly or risky, or that deimatic behaviour in juveniles is less effective, or perhaps both. By contrast, juvenile cottonmouth snakes (Agkistrodon piscivorus) are more likely than adults to use deimatic behaviour (Glaudas, Winne & Fedewa, 2006). A possible explanation is that adult cottonmouths may face a sufficiently low predation risk that the energetic costs of deimatic behaviour are not justified. Together, these findings suggest a species-specific use of deimatic displays at different life stages.

Changes in deimatic behaviour across development can be more subtle than simple presence or absence. For example, in European cuttlefish, hatchlings, juveniles and adults use different body patterns and postures as deimatic displays (Hanlon & Messenger, 1988). Similar examples of subtle changes in deimatic behaviour during development have been observed in the mountain katvdid (Acripeza reticulata). Subadults have orange and black intersegmental abdominal membranes which are visible when they move (Table S4). Adults, by contrast, have large mottled brown wings which completely hide their red, blue, and black striped abdominal surface. Umbers & Mappes (2015) found that when performing deimatic behaviour, subadult mountain katydids held their position for longer than adults, perhaps

## **Biological Reviews**

because they lack the tough wings of adults. Lacking tough wings may mean juveniles rely more on their deimatic behaviour and the aposematic signal it reveals which could select for longer display times (Baker, 2019). Because subadults lack wings and therefore cannot fly, their extended display may compensate for their reduced opportunity to escape. By contrast, the Western Australian katydid (Mygalopsis marki) develops auditory deimatic behaviour very early in life. Both adults and nymphs stridulate, producing a sound within their head capsule, and this behaviour is maintained throughout ontogeny despite major morphological changes (Bailey & Sandow, 1983), however nymphs are more likely to attempt to escape during the early stages of the predation sequence and stridulate when caught, whereas adults posture while stridulating when faced with a predator. This example may suggest that the constraints on deimatic behaviours involving visual signals and auditory signals may vary. and may arise at different stages across ontogeny.

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

Taken together, the available evidence seems to support the view that deimatic behaviours are more likely to be found in adult animals, but whether this is a research bias or is biologically important is unclear. Body size could be a factor driving the presence and

**Biological Reviews** 

1067	absence of displays at different life stages (see Section IV.4 <i>a</i> ), but this and alternative	
1068	explanations such as differing niches or activity levels remain to be tested.	
1069		
1070	VI. CAUSATION OF DEIMATIC BEHAVIOUR	
1071	Tinbergen (1963) described causation as the physiology of behaviour, encompassing both the	
1072	underlying molecular, physiological and cognitive processes, now more commonly called	
1073	mechanisms. We summarise what is known about triggers that release deimatic behaviour,	
1074	and special mechanisms by which the behaviours are performed. Predator cognition and	
1075	behaviour drive the evolution of deimatic behaviour and we discuss the putative	
1076	psychological mechanisms involved (Fawcett, Marshall & Higginson, 2015).	
1077		
1078	(1) Releasers of deimatic behaviour	
1079	Deimatic behaviours may be released by being touched, hearing a sound, detecting a smell, or	
1080	seeing a visual signal (Table S3). Experimental evidence from studies using ecologically	
1081	relevant predators is rare, with most data coming from experiments where predation is	
1082	simulated by humans. Triggers in some sensory modes may be more likely to release	
1083	deimatic behaviour than others, more likely to release different components of deimatic	
1084	behaviour, and/or release different levels of intensity. In some katydids and mantises most	
1085	individuals perform their deimatic behaviour in response to tactile rather than visual stimuli,	
1086	and more invasive stimuli evoke more intense displays (Umbers & Mappes, 2015; O'Hanlon	
1087	et al., 2018). Maldonado (1970) experimentally investigated the effects of visual and tactile	
1088	triggers on mantises. When visual cues were obliterated by covering the eyes, tactile cues still	
1089	released the full display, however, a visual releaser resulted in a longer display. More work	
1090	needs to be done to determine which cues, signals, and their components are most effective in	
1091	releasing deimatic behaviour. Mechanistic and sensory constraints, including noise, probably	
	1067 1068 1069 1070 1071 1072 1073 1074 1075 1076 1077 1078 1077 1078 1079 1080 1081 1081 1082 1083 1084 1085 1085 1085 1086 1087 1088	

1092 determine the type of stimuli prey respond to and the fitness consequences of their responses1093 (Cooper & Blumstein, 2015).

- 10 1

# 1095 (2) Mechanisms of components of deimatic behaviour

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

# 1103 (a) Visual components: colour, movement, and size

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

Most insect deimatic behaviour includes the movement of legs and/or wings. The mechanisms of movement involved in deimatic behaviour have been directly manipulated in the nervous system of praving mantises. Maldonado (1970) determined that the components of deimatic behaviour performed varied depending on which nerves were severed. A cut between the suboesophageal and prothoracic ganglia resulted in only the head and mouth

## **Biological Reviews**

1116 responding to visual stimuli, and the rest of the body required tactile stimulation to respond1117 (Maldonado, 1970).

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

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

Cephalopods provide a clear exception to movement of large body parts in deimatic behaviour, with their colour patterns displayed and changed by chromatophores (Langridge, 2009). Chromatophore colour change is controlled by the dispersal and concentration of pigments via intracellular innervated radial muscles (Messenger, 2001; Hanlon & Messenger, 2018). The most well-studied cephalopod deimatic behaviour is that of the European cuttlefish, which produce dark rings around the eyes and dark eyespots on the dorsum (Holmes, 1940; Langridge, Broom & Osorio, 2007) (Fig. 11). Their deimatic pattern is 

## **Biological Reviews**

complex, comprising six signalling elements that can be expressed in different combinations:
(1) flattened body posture; (2) paling of the skin; (3) paired mantle spots that look like eyes;
(4) a dark fin line; (5) a dark eye ring; and (6) a dilated pupil. They can also produce
directional displays presenting deimatic patterning only towards the predator and cryptic
patterning away from the predator (Langridge, 2006), indicating that their neural mechanisms
allow targeted responses.

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

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

Page 49 of 199

1

## **Biological Reviews**

2
3
4
5
5
6
7
8
0
9
10
11
12
13
14
14
15
16
17
10
10
19
20
21
22
<u>~~</u> 22
23
24
25
26
27
27
28
29
30
21
51
32
33
34
35
22
30
37
38
39
40
40
41
42
43
44
44
45
46
47
48
40
49
50
51
52
52
22
54
55
56
57
57
20
59
60

	1166	III.3e. Here we focus on sounds produced during an encounter with a predator which have
	1167	been proposed to function in aposematism, jamming echolocation calls, and as deimatic
	1168	behaviour (see Low et al., 2021). Continuous sound production is presumably too costly in
)	1169	terms of conspicuousness or energy (Low et al., 2021). One notable exception occurs in
2	1170	cicadas which as a group produce incessant mate-attraction calls via tymbalation [the flexing
1	1171	of corrugated regions of exoskeleton (tymbals)] that may have a dual function in
2 7 2	1172	aposematism (Simmons, Wever & Pylka, 1971). Cicadas can drive bird predators out of
) )	1173	forests both due to the dangerously loud and painful sound, and its disruption to their
2	1174	communication (Simmons et al., 1971). Their sound can certainly drive human visitors away
3 1 -	1175	(K.D.L. Umbers & J.A. Endler, personal observations).
5	1176	Sounds used in defence are produced by a huge diversity of body parts or specialised
3	1177	organs (Bura et al., 2016; Low et al., 2021) – knocking or rubbing body parts together as in
)	1178	stridulation (Bura et al., 2016; Rosi-Denadai et al., 2018), forced air (Bura et al., 2011; Rosi-
2 3 1	1179	Denadai et al., 2018), percussion, or tymbalation (Ewing, 1989; Dookie et al., 2017).
5	1180	Sound created by 'forced air' is used across animals. Walnut sphinx (Amorpha
7 3	1181	juglandis) caterpillars whistle by expelling air via muscular contractions through special
) ) 	1182	sound-producing spiracles on the A8 abdominal segment (Bura et al., 2011) and can
2	1183	successfully deter red-winged blackbirds (Agelaius phoeniceus) despite having no further
1 5	1184	defences (Dookie et al., 2017). In the walnut sphinx deimatic sounds are loud, sudden, and of
57	1185	longer duration than those produced in other defensive contexts (Low et al., 2021). Other
) )	1186	caterpillars 'vocalise' when attacked, by forcing air out of their gut (Rosi-Denadai et al.,
2	1187	2018; Bura et al., 2016). Many reptiles including lizards such as the blue-tongued skink
3 1 -	1188	(Tiliqua scincoides) (Badiane et al., 2018) and the frill-necked lizard (Chlamydosaurus
5	1189	kingii) (Perez-Martinez, Riley & Whiting, 2020) also use 'hissing' during their deimatic
3		

behaviour by forcing air from their lungs across the glottis, but its effect on predatorbehaviour has not been assessed in this context.

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

, 8 1205

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

1207 Chemical defences are typically associated with aposematism, which predators encounter if 1208 they dare to attempt consumption. They may, however, also appear as components of 1209 deimatic behaviour which are released when prey perceive a threat from an attacker during 1210 approach or subjugation, and which can cause predators to slow or stop their attack (Fig. 2). 1211 Deimatic chemical defences are those released during the behaviour, not those simply present 1212 in the organism regardless of an attacker's proximity. That is, deimatic chemical defences are 1213 produced upon attack. Page 51 of 199

1 2

## **Biological Reviews**

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

60

214 Chemical defences may be oozed, frothed, or foamed from joints and glands during 215 deimatic behaviour, and may have olfactory and/or visual effects on predator behaviour. 216 Amphibians exude chemical defences from glands during deimatic behaviour (Ferraro, Topa 217 & Hermida, 2013) and defensive posturing can enhance the effect (Williams et al., 2000). 218 Fire-bellied toads (Bombina spp.) can increase the amount of toxin released through physical 219 pressure on the glands when the back is arched (Bajger, 1980; Choi, Lee & Ricklefs, 1999). 220 During their deimatic behaviour four-eved frogs (*Physalaemus nattereri*) reveal large black 221 discs on their rumps where bradykinin peptides and correspondingly strong signals of related 222 gene expression are concentrated (Barbosa et al., 2015). Similarly, many salamanders have 223 noxious skin secretions and combine their presentation with various postures to orient the 224 glands and associated secretions towards the predator (Brodie, 1977). Mountain katydids 225 exude droplets of a bitter secretion from the surface of the abdomen when attacked, 226 presumably from glands as yet undescribed, with compounds that originate from their 227 preferred diet of *Senecio* daisies (Baker, 2019), such as senecionines and sceneciophyllines. 228 Some lepidopterans exude noxious chemicals via froth which seems to be deimatic behaviour rather than retaliation because they are not shot at the attacker. The saturniid moth Citheronia 229 230 *brisottii* is a yellow and orange moth with black intersegmental membranes from which 231 newly emerged adult males can expel a tar-like substance (Blest, 1957a). Other lepidopteran 232 'frothers' include the arctiine moth Amerila bubo which emits a 'sizzling' sound from the 233 thorax as it produces an odorous froth from two large vesicles, as well as its congener A. 234 *leucoptera* which displays a bright pink body by spreading its wings and expelling a yellow 235 froth from the thorax when disturbed (Carpenter, 1938). 236 Regurgitation is almost ubiquitous among insects when they are attacked, and in

1237 lepidopteran larvae is also a common accompaniment to acoustic components of deimatic
1238 behaviour (Bura *et al.*, 2016). Brown, Boettner & Yack (2007) found that defensive

/	
- 3 4	1
5 6	]
7 8	1
9 10	1
11 12	1
13 14	1
15 16	]
17 18	]
19 20	]
21 22	1
23 24	1
25 26	]
27	1
29 30 21	1
32 32	-
34 35	
36 37	]
38 39	]
40 41	]
42 43	]
44 45	1
46 47	]
48 49	1
50 51	1
52 53	-
54 55	
56 57	]
58 59	]
OU	

239 regurgitation often preceded or accompanied the clicking sounds produced by the 240 polyphemus moth (Antheraea polyphemus) and was an effective deterrent against predators. 241 Similarly, caterpillars of the giant peacock moth (Saturnia pyri) produce a chemical secretion 242 from integumental bristles when attacked repeatedly while 'chirping' (Bura, Fleming & 243 Yack, 2009). These examples provide some insight into the chemical components of deimatic 244 behaviour but leave many questions unanswered about their proximate mechanisms. In 245 particular, it is currently unclear whether both the regurgitation and noise function as a deimatic defence, or whether the noises produced are deimatic, and the regurgitation consists 246 1247 of toxic secondary plant compounds.

4 1248

1

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

250 Deimatic behaviours can be highly repeatable – performed the same way by the same 251 individual every time – or can vary among performances. The limited available evidence 252 suggests variability both within and among individuals. For example, over 'long' 24-h 253 intervals between repeated attacks, consistency in display intensity varied substantially 254 among individual mountain katydids and were only somewhat repeatable in the magnitude of 255 their displays (De Bona, White & Umbers, 2020). One explanation may be that performing 256 deimatic behaviour is condition dependent, but the proximate cause for this variation requires 1257 future research.

Many species increase the intensity of their deimatic behaviour with repeated
exposure to stimuli. In simulated sequential, repeated attacks over short intervals (10 s),
mountain katydids increased the intensity of their display (used more components) (F.
Mourmourakis, S. De Bona & K. D. L. Umbers, unpublished data). Similarly, Brown *et al.*(2007) investigated the response of clicking polyphemus moth caterpillars to different
numbers of simulated repeated attacks and showed that the number of clicks per individual

Page 53 of 199

## **Biological Reviews**

increased with attack number. In a different measure, Vallin et al. (2005) showed that the second time peacock butterflies were approached by a predator, they displayed when the predator was at a greater distance away than in the first encounter. Increased intensity of deimatic behaviour might increase prey survival if displaying maximally upon first stimulus carries costs (e.g. conspicuousness) or if the prev are protected from sub-lethal investigative predator behaviour by a tough exterior, and may also depend on their perceived certainty or intensity of danger. The degree to which prev are defended may influence their propensity to exhibit deimatic behaviour when repeatedly accosted by potential predators. The chemically defended cottonmouth snake reduces its expression of deimatic behaviours with repeated exposure to human model predators (Glaudas, 2004). However, comparatively less-defended juveniles do so to a lesser degree (Glaudas et al., 2006). Predictions around the mechanisms underlying prev responses to repeated attacks is fertile ground for future theory and experiments.

# 2 1278 VII. SURVIVAL VALUE OF DEIMATIC BEHAVIOUR

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

<sup>4</sup> 1282

## 1283 (1) Does deimatic behaviour increase the probability of prey survival?

Ten publications have measured the survival value of deimatic behaviour and/or further signals revealed by them using live prey animals, of which eight were laboratory-based and two field-based (Table S5). Some prey were putatively profitable, others putatively unprofitable (i.e. 'chemically defended'), and most were insects. The efficacy of visual components, acoustic components, and their combination have all been investigated. Most 1289 studies did not address whether the experimental predators were natural predators thus

1290 leaving questions about the ecological and evolutionary significance of the results.

1292 (a) Survival value of deimatic behaviour that reveals colour patterns without chemical

 $\frac{2}{3}$  1293 defence

Vallin et al. (2006) examined the effect of the wing-flicking display with eyespots of the peacock butterfly against wild-caught blue tits (Parus caeruleus). Peacock butterflies, which are seemingly palatable to all their known predators, initiated their deimatic behaviour during the predator's approach (average 12 cm distance) and all survived (N = 10) (Vallin *et al.*. 2006). Vallin, Jakobsson & Wiklund (2007) found that peacock butterfly visual displays were protective against both blue tits and great tits (*Parus major*), in contrast to those of the larger hawkmoth Smerinthus ocellatus. Both insects had evespots which were revealed on the approach of a predator, however the type of display was different as the hawkmoth S. *ocellatus* protracted its upper wings to show the eyespots then rocked with its legs, while the peacock butterfly continually flicked its wings to hide and reveal its eyespots. Peacock butterflies survived 12/12 blue tit attacks and 9/12 great tit attacks whereas only 5/13hawkmoths survived blue tit attacks and 1/14 survived great tit attacks. These findings suggest that the type of visual display is more important than the presence of eyespots alone. Mollusc deimatic behaviour can include a combination of posturing and colour pattern expression via chromatophores without a chemical defence. In a field study, young European cuttlefish altered their defensive responses and deimatic behaviour according to predator type and avoided attacks (Hanlon & Messenger, 1988). In a laboratory-based study, Staudinger et al. (2011) showed that longfin squid (Loligo pealeii) also alter their defence response depending on predator type. Against bluefish (*Pomatomus saltatrix*), a 'pursuit' 

1313 predator, longfin squid primarily used deimatic behaviours, whereas protean behaviours

#### **Biological Reviews**

(erratic escape behaviours, sensu Edmunds, 1974) were used against summer flounder (Paralichthys dentatus), an ambush predator. Overall, while deimatic behaviours saved the prey's life in 40–64% of interactions, prey were more likely to survive when confronted with predators if they fled rather than performed deimatic behaviours (87–92% survival rate). The authors suggest that deimatic behaviours are not always the most effective strategy but may be employed when prey are unlikely to 'outrun' their predators (Staudinger et al., 2011). 

(b) Survival value of deimatic behaviour that reveals colour patterns with chemical defence Mountain katydids perform deimatic behaviour: they lift their wings to reveal a brightly coloured abdomen that exudes a *Senecio*-derived secretion (Umbers & Mappes, 2015; Baker, 2019; De Bona et al., 2020). Umbers et al. (2019) used a field-based experiment to test whether the survival value of the katydid's display relates to the prior experience of one of their native predators, the Australian magpie (*Gymnorhina tibicen*). In interactions with naïve allopatric Australian magpies, katydids survived 70% of encounters, while only 24% of katydids survived interactions with sympatric predators. During the experiments katydids revealed their display in the subjugation phase of the predation sequence, suggesting that camouflage may be their primary defence and that their tough tegmina might help them withstand initial predator investigations (Umbers et al., 2019). Katydids were more vulnerable to experienced (sympatric) magpies than naïve (allopatric) ones despite the katydid's abdominal exudate (Baker, 2019); perhaps they are profitable due to their large size (up to 3 g) or perhaps magpies are unaffected by their chemical defence, or both. Brodie et al. (1984) investigated the survival value of deimatic behaviour in three Asian salamander species, Paramesotriton chinensis (N = 15), Paramesotriton *caudopunctatus* (N = 17) and *Pachytriton brevipes* (N = 10), against short-tailed shrews (Blarina brevicauda). All three species displayed and survived 100% of encounters despite 

biting and mouthing by shrews (Brodie et al., 1984). Whether shrews were deterred by the visual component of the behaviour or by the taste or toxic effect of the exudate is unclear,

- and more work is required to determine the selective advantage of each component.

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

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

Page 57 of 199

### **Biological Reviews**

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

Vallin et al. (2005) tested the effects of the visual and auditory components in the peacock butterfly by presenting various combinations of eyespots and sound to blue tits. No difference in survival was found between the sound and no-sound treatments, whereas 33/34 butterflies with intact eyespots survived the trials, and only 7 of 20 butterflies with covered evespots survived. Taking all the peacock butterfly studies together, evespots seem to be effective against blue tits (Vallin et al., 2005) whereas sound seems to be effective against rodents (Olofsson et al., 2011, 2012b). A role of airborne chemical signals was not tested. Deimatic behaviour has been studied in detail in a few lepidopteran larvae (Low et al., 2021). Brown et al. (2007) experimentally examined the survival value of mandible clicks in the polyphemus moth which are accompanied by regurgitation when the moth is grasped by forceps or a beak. In experimental trials, domestic chicks (Gallus gallus *domesticus*) induced sound production in 100% and regurgitation in 87.5% of larvae (N = 16) during subjugation and 100% of the caterpillars survived the encounter. Data on long-term survival after attack and any sub-lethal effects are needed. The survival value and function of walnut sphinx whistles and clicks was tested against yellow warblers (Setophaga petechia) (N=3) and showed that when caterpillars produced whistles upon attack, the birds hesitated and even flew away (Bura et al., 2011). All three caterpillars survived with no visible harm to their bodies suggesting potential long-term survival, but to confirm this, a larger sample is needed. In simulated attack trials regurgitation in *A. juglandis* was rare (3% of trials) suggesting that in nature they may rely on the sound alone. Sandow & Bailey (1978) experimentally tested the visual and acoustic components of the deimatic behaviour of the sluggish snout-nosed katydid (Mygalopsis ferruginea (Redtenbacher) syn., *M. pauperculus*) against the salmon-bellied skink, *Ergenia napoleonis*.

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

#### (2) Does deimatic behaviour actually deter predators?

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

## **Biological Reviews**

by the deimatic behaviour from the deimatic behaviour itself. Overall, the ways in which
predator responses have been measured have made direct conclusions about survival value
difficult to draw and fitness implications difficult to assess.

) 1417

1418 (a) Measures of predator 'startle responses'

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

Dookie *et al.* (2017) showed that the whistling sounds of walnut sphinx moth
caterpillars 'startled' red-winged blackbirds. Predators experienced a playback of the
caterpillar's sound in response to contacting a sensor on a feeding dish. The behaviours
recorded included 'shoulder flinch', 'wing flap', 'ruffle feathers', 'body flinch', 'startle hop',
and 'fly away'. The number of behaviours recorded was greater for birds that received a
sound compared to birds that did not (Dookie *et al.*, 2017). An interesting future direction

would be to compare the responses of birds to control sounds to test if aspects of the caterpillar's sounds are especially effective as a deterrent or whether any sound has a similar effect.

#### (b) Measures of predator hesitation

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

Using the same apparatus as Vaughan (1983), Ingalls (1993) tested the latency of naïve hand-raised blue jays (N = 8) to respond to the combined effects of novel colours and patterns. She showed that birds took longer to touch discs with novel colours presented in a striped pattern with black bands than solid novel colours. Despite potentially confounding

Page 61 of 199

1

## **Biological Reviews**

2 3	1464	order effects, these data suggest that the presence of black bands resulted in the greatest
4 5 6	1465	latencies compared to discs without black bands as did colour combinations similar to those
7 8	1466	found naturally in Catocala spp. (Ingalls, 1993). Further, Ingalls (1993) reported interesting
9 10	1467	variation in predator responses, with some birds never habituating to the stimuli and others
11 12 13	1468	habituating relatively quickly, perhaps suggesting that variability within predator species may
14 15	1469	select for variation in prey defences.
16 17	1470	Holmes et al. (2018) tested the protective value of deimatic behaviour using
18 19 20	1471	computer-generated 'moths' with and without colourful hindwings that were revealed
20 21 22	1472	rhythmically at three different speeds to domestic chicks (Gallus gallus domesticus). In a
23 24	1473	laboratory setting they showed that rapid movement alone in the absence of conspicuous
25 26 27	1474	colours delayed a chick's attack, and that the combination of movement and coloured
28 29	1475	hindwings led to longer latencies. These results suggest that movement alone can increase
30 31	1476	latency in predator responses, that this effect can be enhanced by colourful hindwings and, by
32 33 34	1477	extension, that movement could precede colour in the evolution of deimatic behaviour.
35 36	1478	
37 38	1479	(c) Measures of predators fleeing
39 40 41	1480	Predators might flee when they experience deimatic behaviour (De Bona et al., 2015).
42 43	1481	Olofsson et al. (2012b) showed that when field-caught yellow-necked mice and wood mice
44 45	1482	hear the sound of the peacock butterfly's display, the majority flee quickly ( $N = 18/24$ ).
46 47 48	1483	Whether they simply flee or if fleeing is initiated after their startle reflex is released would be
49 50	1484	interesting ground for further testing. Olofsson et al. (2012b) also suggested that mice
51 52	1485	respond as they would to a real predator and hypothesised that the peacock butterfly's sound
53 54 55	1486	may involve Batesian mimicry of snake hisses (Vane-Wright, 1986; Skelhorn et al., 2016).
56 57	1487	
58 59 60	1488	(3) Do predator responses change across repeat encounters?

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

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

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

# **Biological Reviews**

1		
2 3 4	1514	(1970) observed flight periods exceeding two months for many Catocala species in the north-
5 6	1515	eastern USA, and adults can survive for at least 60 days in some species (Gall, 1991).
7 8 9	1516	With a further seven wild-caught blue jays, Schlenoff (1985) trained them to two
9 10 11	1517	different forewing types with corresponding hindwings, and found that a startle response
12 13	1518	could be elicited by swapping hindwing colours. She suggested that the anomalous nature of
14 15	1519	the prey's form combined with the striking colour pattern caused the birds to perform startle
16 17 18	1520	behaviours, not simply that the hindwings colours were unexpected, and that it is unnecessary
19 20	1521	for the patterns to be unknown to the bird. Schlenoff (1985) also showed that encountering an
21 22	1522	unexpected difference in hindwing colour is not enough to elicit a startle response because
23 24 25	1523	birds trained on Catocala patterns do not startle to unexpected grey hindwings.
26 27	1524	Ingalls (1993) surmised that Catocala hindwings may deter blue jays for several
28 29	1525	reasons: (a) they mimic sympatric aposematic species; (b) they are novel; and/or (c) their
30 31 32	1526	patterns include strong contrasts. She suggested that an optimal number of types of forewings
32 33 34	1527	must exist. Although an unexpected hindwing colour pattern can deter a predator, if they are
35 36	1528	presented with a new type in every encounter, in theory they could habituate to the rule that
37 38	1529	the hindwing will always be new (Ingalls, 1993). Ingalls' (1993) data suggest that blue jays
39 40 41	1530	take longer to habituate to startle signals as a function of the diversity of the signals; birds
42 43	1531	presented with a single stimulus colour habituated far more quickly than those presented with
44 45	1532	five colours. However, there was also evidence of consistent individual variation in feeding
46 47 48	1533	strategy. For example, within a group of birds presented with food associated with five
49 50	1534	different startle colours, two birds habituated after less than 50 trials, while a third was not
51 52	1535	habituated after 149 presentations. This variation in individual predator performance could
53 54 55	1536	suggest that differences in dietary conservativism (Marples & Kelly, 1999) coupled with
56 57	1537	differences in levels of neophobia could have a significant impact on predator perception of
58 59 60	1538	defences involving multiple stimuli. Overall, this detailed work on Catocala and replica

stimuli suggests that colour pattern novelty could be protective but does not provide
information for responses with real prey. The spatial distribution of hindwing colours in *Catocala* would merit further study.

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

<sup>9</sup> 1559

1560 (c) Responses to deimatic behaviour that reveals sounds

Three studies investigated predator responses to repeated sound stimuli (Table S6). In two of
these predators learned to ignore the sound and in the third the result was unclear. Dookie *et al.* (2017) tested for effects of repeated exposure of red-winged blackbirds to the whistle

Page 65 of 199

# **Biological Reviews**

1 2				
3 4	1564	emitted by the walnut sphinx caterpillar. They found short-term habituation to the sound		
5 6	1565	within each of their two experimental phases but found no difference in habituation between		
7 8 0	1566	phases, indicating that during this two-day period the birds dishabituated despite no changes		
9 10 11	1567	to the experimental set-up (Dookie et al., 2017).		
12 13	1568			
14 15 16	1569	VIII. FUTURE DIRECTIONS		
10 17 18	1570	To understand the evolution of deimatic behaviour, further research is required in four broad		
19 20	1571	areas: (1) deimatism as part of an antipredator sequence and the need to define antipredator		
21 22	1572	'space'; (2) quantifying the underlying mechanisms of predator responses to deimatic		
23 24 25	1573	behaviours and how these change with experience; (3) gathering richer data for comparative		
26 27	1574	analyses; and (4) ecological patterns of deimatic behaviour. Collaboration across the breadth		
28 29	1575	of behavioural sciences while conducting laboratory and field-based experiments and		
30 31 32	1576	including indigenous knowledge will enable advances in this field.		
32 33 34	1577			
35 36	1578	(1) Deimatism in the antipredator sequence		
37 38	1579	Deimatic behaviour is one part of an antipredator strategy. To understand both the benefits of		
39 40 41	1580	this behaviour and how/when individuals should perform it, we need to establish how it is		
42 43	1581	distinct from and interacts with other defensive strategies. The defences that precede and		
44 45	1582	follow deimatic behaviour in an antipredator strategy vary among species, among individuals,		
46 47	1583	and within individuals. Predators may encounter different sequences of defences when		
48 49 50	1584	encountering different prey (Fig. 2), but equally, prey can, with different degrees of control,		
51 52	1585	choose which defences to deploy and when. We predict that the protective value of defences		
53 54	1586	can change depending on the combination and order in which they are experienced by		
55 56 57	1587	predators and that recognising, quantifying, and analysing this variation is key to		
58 59 60	1588	understanding the proximate and ultimate aspects of antipredator strategies in general.		

**Biological Reviews** 

2		
2 3 4	1589	Recognising that antipredator strategies include multiple defences experienced by
5 6 7	1590	predators in a sequence has profound implications (Endler, 1991). It requires us to reframe
7 8 9	1591	our view of predator-prey interactions as multi-level escalating interactions rather than a
10 11	1592	simplistic single-level signal and response. Therefore, understanding deimatism is
12 13	1593	complicated by how well other defences are defined and the clarity of the conceptual
14 15 16	1594	boundaries between them. We therefore encourage mapping the full breadth of antipredator
17 18	1595	defences (i.e. antipredator 'space') to define these conceptual boundaries (Fig. 2).
19 20	1596	
21 22 23	1597	(2) Predator responses to deimatic behaviour and prey survival advantage
24 25	1598	To arrive at a universally accepted definition of deimatism and establish how it differs from
26 27	1599	other defensive strategies, it is crucial to experimentally demonstrate the proximate causes(s)
28 29 30	1600	by which deimatism deters predators and to test how these differ from other defences within
31 32	1601	and among attacks and predator individuals. This is needed for predator responses to initial
33 34	1602	and repeat encounters as well as for predators over the course of a single deimatic
35 36 37	1603	performance. Understanding the mechanisms requires working with ecologically relevant
38 39	1604	predators in natural field settings complemented by controlled laboratory experiments or
40 41	1605	well-designed field experiments to disentangle interacting effects. We need to make careful
42 43 44	1606	choices about how to measure appropriate behaviours for predator species and assumptions
45 46	1607	as to what these measures represent must be made explicit. Measures that allow us to
47 48	1608	distinguish among proposed mechanisms by which deimatism deters predators are needed.
49 50 51	1609	They include behaviour, physiology, and the stimuli themselves. A coordinated effort to use
52 53	1610	comparable measurements across studies where possible will allow meta-analyses and
54 55	1611	systematic reviews in the future.
56 57 58	1612	Limited evidence suggests that deimatic behaviours are more effective against naïve
59	1613	predators. If this is true, we predict that they should be more common in areas where their

59 

Page 67 of 199

## **Biological Reviews**

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

11626If it is true that the protective value of deimatism is directly related to predator11627naïvety, it may allow prey to invade new habitats [e.g. lantern bugs (*Lycorma delicatula*) in11628North America]. Prey species with more effective deimatic displays may expand their11629geographic ranges faster than species without or with inefficient deimatic displays and might11630even displace them. This pattern may be stronger when most predators in the new area are11631naïve. If predators are good learners, then the expanding geographic range may stabilise11632quickly.

7 1633

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

1635 To understand the evolutionary pathway(s) *via* which deimatism evolves we need to perform
 1636 comparative analyses. However, comprehensive quantitative descriptions of deimatic
 1637 behaviour are currently too rare, most are missing critical measures such as rise time, speed,
 1638 duration, number of components and sensory modes, the qualities of the components

(colours, frequencies), whether the behaviour is sustained or includes rhythmical elements

(sensu Blest, 1958), and if and when during the predation sequence the behaviour is

performed. Data on how deimatism differs among life stages, between sexes, and among

species and higher taxonomic groups are also required.

> **IX. CONCLUSIONS**

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

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

(3) Multiple non-exclusive hypotheses have been put forward to suggest the mechanism(s) by

which deimatic behaviour is protective including the looming reflex, the startle reflex, fear,

sensory overload, and confusion. Determining whether deimatic behaviours exploit one or

more of these mechanisms is an area of high priority.

(4) Deimatic behaviour can be one defence in an antipredator strategy and therefore the

impact of the display can vary depending on both the predator's physiology and experience. 

and the sequence of defences the prey deploys.

(5) Limited evidence suggests that deimatic behaviours are more effective against naïve

predators, which could have implications for range expansion and inter-individual conflict. 

(6) To develop our understanding of deimatic behaviour, further research is required into: (a)

deimatism as part of an antipredator sequence; (b) quantifying the underlying mechanisms of 

predator responses; (c) comparative analyses; and (d) ecological patterns of deimatic

#### X. ACKNOWLEDGEMENTS

behaviour.

Page 69 of 199

1

## **Biological Reviews**

2	
3	
Δ	
5	
5	
0	
/	
8	
9	
10	
11	
12	
13	
14	
15	
16	
17	
18	
10	
17 20	
20 21	
21	
22	
23	
24	
25	
26	
27	
28	
29	
30	
31	
22	
22 22	
ככ ז∢ר	
34	
35	
36	
37	
38	
39	
40	
41	
42	
43	
44	
45	
46	
47	
<u>1</u> 2	
49	
50	
51	
52	
53	
54	
55	
56	
57	
58	
59	
60	

1664	We thank Melanie Low for comments and discussion, Audrey Manuel, Science Illustrator,
1665	for the salamander images, and Michael Kelly for contributing to data extraction. We are
1666	grateful to the two anonymous reviewers who provided very helpful and insightful
1667	comments. K.D.L.U. and E.D. were funded by a Hermon Slade Grant (HSF 14/3), K.D.L.U.
1668	was funded by an Australian Research Council Discovery Early Career Research Award
1669	(project DE180100026) from the Australian Government, and Western Sydney University's
1670	Women's Fellowship, Carer's Grant and Early Career Grant. G.H. was funded by a BBSRC
1671	Studentship (BB/L017709/1) awarded to J.S. and C.R. C.K. was supported by National
1672	Research Foundation of Korea (NRF-2019R1C1C1002466). B.C.L. was supported by a
1673	National Science Foundation Graduate Research Fellowship (DGE-1842166). J.L. was
1674	funded by an Australian Research Council Discovery Early Career Research Award (project
1675	DE180100526) and by an Academy of Finland grant (340130). J.E.Y. was supported by
1676	Natural Science and Engineering Council of Canada (2020-07056).
1677	
1678	XI. AUTHOR CONTRIBUTIONS
1679	Overall concept and structure – K.D.L.U, E.D. and C.M.Y.; hypothesis and rationales – all
1680	authors; data extraction – E.D., K.D.L.U., C.M.Y. and C.S.; results from literature search –
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.
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.,
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.,

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 –

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.

and K.D.L.U.; intellectual property, ideas, and feedback in meetings – all authors.

<sup>6</sup> 1687

<sup>8</sup> 1688 XII. REFERENCES

2		
3 4	1689	References identified with an asterisk (*) are cited only within the supporting information.
5 6 7	1690	ABBOTT, K.R. & SHERRATT, T.N. (2011). The evolution of superstition through optimal use
7 8 9	1691	of incomplete information. Animal Behaviour 82, 85–92.
10 11	1692	ABRAMS, P.A. (2000). The evolution of predator-prey interactions: Theory and evidence.
12 13	1693	Annual Review of Ecology and Systematics <b>31</b> , 79–105.
14 15 16	1694	*ADAMO, S.A., EHGOETZ, K., SANGSTER, C. & WHITEHORNE, I. (2006). Signaling to the
17 18	1695	enemy? body pattern expression and its response to external cues during hunting in
19 20	1696	the cuttlefish Sepia officinalis (Cephalopoda). The Biological Bulletin 210, 192–200.
21 22	1697	AGUILAR-ARGÜELLO, S., DÍAZ-FLEISCHER, F. & RAO, D. (2016). Motion-triggered defensive
23 24 25	1698	display in a tephritid fly. Journal of Ethology 34, 31–37.
26 27	1699	ÅSLI, O. & FLATEN, M.A. (2012). In the blink of an eye: Investigating the role of awareness
28 29	1700	in fear responding by measuring the latency of startle potentiation. <i>Brain Sciences</i> 2,
30 31 32	1701	61–84.
33 34	1702	BACH, D.R. (2015). A cost minimisation and Bayesian inference model predicts startle reflex
35 36	1703	modulation across species. Journal of Theoretical Biology 370, 53-60.
37 38 20	1704	BADIANE, A., CARAZO, P., PRICE-REES, S.J., FERRANDO-BERNAL, M. & WHITING, M.J.
39 40 41	1705	(2018). Why blue tongue? A potential UV-based deimatic display in a lizard.
42 43	1706	Behavioral Ecology and Sociobiology 72, 104–113.
44 45	1707	BAILEY, W.J. & SANDOW, J.D. (1983). Mechanisms of defensive stridulation in the
46 47 48	1708	bushcricket Mygalopsis marki Bailey (Copiphorini, Tettigoniidae). Acta Zoologica
49 50	1709	<b>64</b> , 117–122.
51 52	1710	BAJGER, J. (1980). Diversity of defensive responses in populations of fire toads (Bombina
53 54 55	1711	bombina and Bombina variegata). Herpetologica <b>36</b> , 133–137.
56 57	1712	BAKER, B. (2019). Antipredator chemical defence in the mountain katydid (Acripeza
58 59 60	1713	reticulata). Masters Thesis, Western Sydney University, Sydney, Australia.
1 2		
--	------	--
3 4	1714	BALDERRAMA, N. & MALDONADO, H. (1971). Habituation of the deimatic response in the
5 6	1715	mantid (Stagmatoptera biocellata). Journal of Comparative and Physiological
7 8 0	1716	<i>Psychology</i> <b>75</b> , 98–106.
9 10 11	1717	BALDERRAMA, N. & MALDONADO, H. (1973). Ontogeny of the behaviour in the praying
12 13	1718	mantis. Journal of Insect Physiology 19, 319–336.
14 15	1719	BARBOSA, E.A., IEMBO, T., MARTINS, G.R., SILVA, L.P., PRATES, M.V., ANDRADE, A.C. &
16 17 18	1720	BLOCH, C. (2015). Skin secretion peptides: the molecular facet of the deimatic
19 20	1721	behavior of the four-eyed frog, Physalaemus nattereri (Anura, Leptodactylidae).
21 22	1722	Rapid Communications in Mass Spectrometry 29, 2061–2068.
23 24 25	1723	BARNETT, C.A., SKELHORN, J., BATESON, M. & ROWE, C. (2012). Educated predators make
25 26 27 28 29 30 31 32 33 34 35 36 37 38	1724	strategic decisions to eat defended prey according to their toxin content. Behavioral
	1725	<i>Ecology</i> <b>23</b> , 418–424.
	1726	*BASTOCK, M. & BLEST, A.D. (1958). An analysis of behaviour sequences in Automeris
	1727	aurantiaca Weym (Lepidoptera). Behaviour 12, 243–284.
	1728	BATEMAN, A.W., VOS, M. & ANHOLT, B.R. (2014). When to defend: antipredator defenses
	1729	and the predation sequence. The American Naturalist 183, 847-855.
39 40 41	1730	BATES, D.L. & FENTON, M.B. (1990). Aposematism or startle? Predators learn their responses
41 42 43	1731	to the defenses of prey. Canadian Journal of Zoology 68, 49-52.
44 45	1732	BAUER, T. (1976). Experimente zur Frage der biologischen Bedeutung des
46 47	1733	Stridulationsverhaltens von Käfern1. Zeitschrift für Tierpsychologie 42, 57-65.
48 49 50	1734	BEDFORD, G.O. & CHINNICK, L.J. (1966). Conspicuous displays in two species of Australian
51 52	1735	stick insects. Animal Behaviour 14, 518-521.
53 54	1736	BLEST, A.D. (1957a). The evolution of protective displays in the Saturnioidea and Sphingidae
55 56 57	1737	(Lepidoptera). Behaviour 11, 257-309.
58 59		
60		

1 2		
2 3 4	1738	BLEST, A.D. (1957b). The function of eyespot patterns in the Lepidoptera. Behaviour 11,
5 6 7	1739	209–256.
7 8 9	1740	BLEST, A.D. (1958). Some interactions between flight, protective display, and oviposition
10 11	1741	behaviour in Callosamia and Rothschildia spp. (Lepidoptera, Saturniidae). Behaviour
12 13	1742	<b>13</b> , 297–317.
14 15 16	1743	BLUMSTEIN, D.T. (2006). The multipredator hypothesis and the evolutionary persistence of
17 18	1744	antipredator behavior. <i>Ethology</i> <b>112</b> , 209–217.
19 20	1745	*BOUWMA, P.E. & HERRNKIND, W.F. (2009). Sound production in Caribbean spiny lobster
21 22 23	1746	Panulirus argus and its role in escape during predatory attack by Octopus briareus.
24 25	1747	New Zealand Journal of Marine and Freshwater Research 43, 3–13.
26 27	1748	BRITTON, N.F., PLANQUÉ, R. & FRANKS, N.R. (2007). Evolution of defence portfolios in
28 29 20	1749	exploiter-victim systems. Bulletin of Mathematical Biology 69, 957–988.
30 31 32	1750	BRODIE, E.D. (1983). Antipredator adaptations of salamanders: evolution and convergence
33 34	1751	among terrestrial species. In Adaptations to Terrestrial Environments (Eds Margaris,
35 36 27	1752	N.S., Arianoutsou-Faraggitaki, M., & Reiter R.J.). pp. 109–133. Springer, New York.
37 38 39	1753	BRODIE, E.D. & HOWARD, R.R. (1972). Behavioral mimicry in the defensive displays of the
40 41	1754	urodele amphibians Nophthalmus viridescens and Pseudotriton ruber. BioScience 22,
42 43	1755	666–667.
44 45 46	1756	BRODIE, E.D., JR. (1977). Salamander antipredator postures. Copeia 1977, 523–535.
47 48	1757	*BRODIE, E.D., JR., WILLIAMS, C.R. & TYLER, M.J. (1998). Evolution of aposematic behavior
49 50	1758	and coloration in the Australian frog genus Uperoleia. Journal of Herpetology 32,
51 52 53	1759	136–139.
54 55	1760	BRODIE, E.D.J., NUSSBAUM, R.A. & DIGIOVANNI, M. (1984). Antipredator adaptations of
56 57 58 59 60	1761	Asian salamanders (Salamandridae). <i>Herpetologica</i> <b>40</b> , 56–68.

1 2		
3 4	1762	BRO-JØRGENSEN, J. (2010). Dynamics of multiple signalling systems: animal communication
5 6	1763	in a world in flux. Trends in Ecology & Evolution 25, 292–300.
7 8 0	1764	BROWN, J.S., KALISH, H.I. & FARBER, I.E. (1951). Conditioned fear as revealed by magnitude
9 10 11	1765	of startle response to an auditory stimulus. Journal of Experimental Psychology 41,
12 13	1766	317–328.
14 15	1767	BROWN, S.G., BOETTNER, G.H. & YACK, J.E. (2007). Clicking caterpillars: acoustic
16 17 18	1768	aposematism in Antheraea polyphemus and other Bombycoidea. Journal of
19 20	1769	Experimental Biology <b>210</b> , 993–1005.
21 22	1770	BUCHLER, E.R., WRIGHT, T.B. & BROWN, E.D. (1981). On the functions of stridulation by the
23 24 25	1771	passalid beetle Odontotaenius disjunctus (Coleoptera: Passalidae). Animal Behaviour
23 26 27	1772	<b>29</b> , 483–486.
28 29	1773	BURA, V.L., FLEMING, A.J. & YACK, J.E. (2009). What's the buzz? Ultrasonic and sonic
30 31	1774	warning signals in caterpillars of the great peacock moth (Saturnia pyri).
32 33 34	1775	Naturwissenschaften 96, 713–718.
35 36	1776	BURA, V.L., KAWAHARA, A.Y. & YACK, J.E. (2016). A Comparative analysis of sonic
37 38	1777	defences in Bombycoidea caterpillars. Scientific Reports 6, 31469.
39 40 41	1778	BURA, V.L., ROHWER, V.G., MARTIN, P.R. & YACK, J.E. (2011). Whistling in caterpillars
42 43	1779	(Amorpha juglandis, Bombycoidea): sound-producing mechanism and function.
44 45	1780	Journal of Experimental Biology 214, 30–37.
46 47 48	1781	BURKENROAD, M.D. (1943). A possible function of bioluminescence. Journal of Marine
40 49 50	1782	<i>Research</i> <b>5</b> , 161–164.
51 52	1783	BURNHAM, R.W. (1939). Repeated auditory stimulation of the startle response in the guinea
53 54	1784	pig. Journal of Psychology 7, 79–89.
55 56 57	1785	*CARPENTER, C.C. (1955). Aposematic behavior in the salamander Ambystoma tigrinum
58 59 60	1786	melanostictum. Copeia 1955, 311–311.

1 2		
2 3 4	1787	CARPENTER, G.D.H. (1938). Audible emission of defensive froth by insects. Proceedings of
5 6	1788	the Zoological Society of London A 108, 243–252.
/ 8 9	1789	*CARTRON, L., SHASHAR, N., DICKEL, L. & DARMAILLACQ, AS. (2013). Effects of stimuli
10 11	1790	shape and polarization in evoking deimatic patterns in the European cuttlefish, Sepia
12 13	1791	officinalis, under varying turbidity conditions. Invertebrate Neuroscience 13, 19–26.
14 15 16	1792	CASTELLANO, S. (2015). Bayes' rule and bias roles in the evolution of decision making.
17 18	1793	Behavioral Ecology 26, 282–292.
19 20	1794	CASTELLANO, S. & CERMELLI, P. (2015). Preys' exploitation of predators' fear: when the
21 22 23	1795	caterpillar plays the Gruffalo. Proceedings of the Royal Society B: Biological
23 24 25	1796	Sciences <b>282</b> , 20151786.
26 27	1797	*CASTNER, J.L. & NICKLE, D.A. (1995). Notes on the biology and ecology of the leaf-
28 29	1798	mimicking katydid Typophyllum bolivari Vignon (Orthoptera: Tettigoniidae:
30 31 32	1799	Pseudophyllinae: Pterochrozini). Journal of Orthoptera Research, 23, 105.
33 34	1800	CHENEY, D.L. & SEYFARTH, R.M. (1981). Selective forces affecting the predator alarm calls
35 36	1801	of vervet monkeys. <i>Behaviour</i> <b>76</b> , 25–60.
37 38 39	1802	CHITTKA, L., SKORUPSKI, P. & RAINE, N.E. (2009). Speed-accuracy tradeoffs in animal
40 41	1803	decision making. Trends in Ecology & Evolution 24, 400-407.
42 43	1804	CHOI, I., LEE, S.H. & RICKLEFS, R.E. (1999). Effectiveness and ecological implications of
44 45 46	1805	anuran defenses against snake predators. Korean Journal of Biological Sciences 3,
40 47 48	1806	247–252.
49 50	1807	*CLARIDGE, M.F. (1974). Stridulation and defensive behaviour in the ground beetle, Cychrus
51 52	1808	caraboides (L.). Journal of Entomology Series A, General Entomology 49, 7–15.
53 54 55	1809	COOPER, W.E. & BLUMSTEIN, D.T. (2015). Escaping from predators: An integrative view of
56 57 58 59 60	1810	escape decisions. Cambridge University Press.

1 2		
2 3 4	1811	CORCORAN, A.J. & HRISTOV, N.I. (2014). Convergent evolution of anti-bat sounds. Journal
5 6 7	1812	of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral
/ 8 9	1813	<i>Physiology</i> <b>200</b> , 811–821.
10 11	1814	COREY, T.B. & HEBETS, E.A. (2020). Testing the hypothesized antipredator defence function
12 13	1815	of stridulation in the spiny orb-weaving spider, Micrathena gracilis. Animal
14 15 16	1816	<i>Behaviour</i> <b>169</b> , 103–117.
17 18	1817	COTT, H.B. (1940). Adaptive coloration in animals. Methuen, London.
19 20	1818	CRANE, J. (1952). A comparative study of innate defensive behavior in Trinidad mantids
21 22 23	1819	(Orthoptera, Mantoidea). Zoologica 37, 259–293.
23 24 25	1820	DAVIS, M. (1984). The Mammalian Startle Response. In Neural Mechanisms of Startle
26 27	1821	Behavior (ed R.C. EATON), pp. 287–351. Springer US, Boston, MA.
28 29 20	1822	DAVIS, M., WALKER, D.L., MILES, L. & GRILLON, C. (2010). Phasic vs sustained fear in rats
30 31 32	1823	and humans: Role of the extended amygdala in fear vs anxiety.
33 34	1824	Neuropsychopharmacology <b>35</b> , 105–135.
35 36	1825	DAWKINS, R. & KREBS, J.R. (1979). Arms races between and within species. Proceedings of
37 38 39	1826	the Royal Society of London. Series B. Biological Sciences 205, 489–511.
40 41	1827	DE BONA, S., VALKONEN, J.K., LÓPEZ-SEPULCRE, A. & MAPPES, J. (2015). Predator mimicry,
42 43	1828	not conspicuousness, explains the efficacy of butterfly eyespots. Proceedings of the
44 45 46	1829	<i>Royal Society B</i> <b>282</b> , 20150202.
40 47 48	1830	DE BONA, S., WHITE, T.E. & UMBERS, K.D.L. (2020). Fight or flight trade-offs and the
49 50	1831	defensive behaviour of the mountain katydid, Acripeza reticulata. Animal Behaviour
51 52	1832	<b>159</b> , 81–87.
55 55	1833	DE COCK, R. & MATTHYSEN, E. (2003). Glow-worm larvae bioluminescence (Coleoptera:
56 57	1834	Lampyridae) operates as an aposematic signal upon toads (Bufo bufo). Behavioral
58 59 60	1835	<i>Ecology</i> <b>14</b> , 103–108.

1 2		
- 3 4	1836	DELL'AGLIO, D.D., TROSCIANKO, J., MCMILLAN, W.O., STEVENS, M. & JIGGINS, C.D.
5 6 7	1837	(2018). The appearance of mimetic Heliconius butterflies to predators and
7 8 9	1838	conspecifics. Evolution; International Journal of Organic Evolution 72, 2156–2166.
10 11	1839	DEUTER, C.E., KUEHL, L.K., BLUMENTHAL, T.D., SCHULZ, A., OITZL, M.S. & SCHACHINGER,
12 13	1840	H. (2012). Effects of cold pressor stress on the human startle response. <i>PloS One</i> 7,
14 15 16	1841	e49866.
17 18	1842	*DIGIOVANNI, M. & BRODIE, E.D., JR. (1981). Efficacy of skin glands in protecting the
19 20	1843	salamander Ambystoma opacum from repeated attacks by the shrew Blarina
21 22	1844	brevicauda. Herpetologica <b>37</b> , 234–237.
23 24 25	1845	DOOKIE, A.L., YOUNG, C.A., LAMOTHE, G., SCHOENLE, L.A. & YACK, J.E. (2017). Why do
26 27	1846	caterpillars whistle at birds? Insect defence sounds startle avian predators.
28 29	1847	Behavioural Processes 138, 58–66.
30 31 32	1848	DOSSEY, A.T. (2011). Chemical Defenses of Insects: A Rich Resource for Chemical Biology
33 34	1849	in the Tropics. In Chemical Biology of the Tropics: An Interdisciplinary Approach
35 36	1850	(eds J.M. VIVANCO & T. WEIR), pp. 27–57. Springer, Berlin, Heidelberg.
37 38 20	1851	DRIVER, P.M. & HUMPHRIES, D.A. (1989). Protean Behaviour: The Biology of
39 40 41	1852	Unpredictability. Clarendon Press, Oxford : New York.
42 43	1853	DUKAS, R. & KAMIL, A.C. (2000). The cost of limited attention in blue jays. Behavioral
44 45	1854	<i>Ecology</i> <b>11</b> , 502–506.
40 47 48	1855	EATON, R.C., BOMBARDIERI, R.A. & MEYER, D.L. (1977). The Mauthner-initiated startle
49 50	1856	response in teleost fish. Journal of Experimental Biology 66, 65-81.
51 52	1857	*EDMUNDS, M. (1968). On the swimming and defensive response of Hexabranchus
53 54 55	1858	marginatus (Mollusca, Nudibranchia). Zoological Journal of the Linnean Society 47,
56 57 58 59 60	1859	425–429.

Page 77 of 199

1 2

3 4	1860	EDMUNDS, M. (1972). Defensive behaviour in Ghanaian praying mantids. Zoological Journal
5 6	1861	of the Linnean Society <b>51</b> , 1–32.
7 8 9	1862	EDMUNDS, M. (1974). Defence in animals: a survey of anti-predator defences. Longman,
9 10 11	1863	California.
12 13	1864	EDMUNDS, M. (1976). The defensive behaviour of Ghanaian praying mantids with a
14 15 16	1865	discussion of territoriality. Zoological Journal of the Linnean Society 58, 1-37.
17 18	1866	EISNER T. (1970). Chemical defense against predation in arthropods, p. 157–217 in E.
19 20	1867	SONDHEIMER, E & SIMEONE, J.B. (eds) Chemical Ecology, Academic Press, New
21 22	1868	York .
23 24 25	1869	EISNER, T. & ADAMS, P.A. (1975). Startle behavior in an ascalaphid (Neuroptera). Psyche: A
26 27	1870	Journal of Entomology <b>82</b> , 304–305.
28 29 20	1871	EISNER, T., ANESHANSLEY, D.J., YACK, J., ATTYGALLE, A.B. & EISNER, M. (2001 <i>a</i> ). Spray
30 31 32	1872	mechanism of crepidogastrine bombardier beetles (Carabidae; Crepidogastrini).
33 34	1873	Chemoecology <b>11</b> , 209–219.
35 36 27	1874	EISNER, T., YACK, J. & ANESHANSLEY, D.J. (2001b). Acoustic concomitants of the defensive
37 38 39	1875	discharges of a primitive bombardier beetle (Metrius contractus). Chemoecology 11,
40 41	1876	221–223.
42 43	1877	EMBERTS, Z., MILLER, C.W., SKOJEC, C., SHEPHERD, R. & MARY, C.M.S. (2020). Leaf-footed
44 45 46	1878	bugs possess multiple hidden contrasting color signals, but only one is associated with
47 48	1879	increased body size. <i>Ecology and Evolution</i> <b>10</b> , 8571–8578.
49 50	1880	ENDLER, J.A. (1978). A Predator's View of Animal Color Patterns. In Evolutionary Biology
51 52 53	1881	pp. 319–364. Springer, Boston, MA.
54 55	1882	ENDLER, J.A. (1986). Defense against predation. In Predator-prey Relationships,
56 57	1883	Perspectives and Approaches from the Study of Lower Vertebrates pp. 109–134.
58 59 60	1884	University of Chicago Press, Chicago.

1 2		
3 4	1885	ENDLER, J.A. (1991). Interactions between predators and prey. In Behavioural Ecology: an
5 6	1886	Evolutionary Approach pp. 169–196. Wiley-Blackwell Publishing.
7 8 9	1887	ENGLAND, S.J. & ROBERT, D. (2022). The ecology of electricity and electroreception.
9 10 11	1888	Biological Reviews 97, 383-413.
12 13	1889	ESAIAS, W.E. & CURL, H.C. (1972). Effect of dinoflagellate bioluminescence on copepod
14 15	1890	ingestion rates. Limnology and Oceanography 17, 901–906.
16 17 18	1891	*EVANS, D.L. (1978). Defensive behavior in Callosamia promethea and Hyalophora
19 20	1892	cecropia (Lepidoptera: Saturniidae). The American Midland Naturalist 100, 475–479.
21 22	1893	EWING, A.W. (1989). Arthropod Bioacoustics: Neurobiology and Behaviour. Comstock
23 24 25	1894	Publishers Associates.
26 27	1895	FAIVOVICH, J., FERRARO, D.P., BASSO, N.G., HADDAD, C.F.B., RODRIGUES, M.T., WHEELER,
28 29	1896	W.C. & LAVILLA, E.O. (2012). A phylogenetic analysis of Pleurodema (Anura:
30 31 32	1897	Leptodactylidae: Leiuperinae) based on mitochondrial and nuclear gene sequences,
33 34	1898	with comments on the evolution of anuran foam nests. Cladistics 28, 460–482.
35 36	1899	FAWCETT, T.W., MARSHALL, J.A.R. & HIGGINSON, A.D. (2015). The evolution of
37 38 20	1900	mechanisms underlying behaviour. Current Zoology 61, 221–225.
39 40 41	1901	FENTON, M.B. & LICHT, L.E. (1990). Why rattle snake? Journal of Herpetology 24, 274–279.
42 43	1902	FERRARO, D.P., TOPA, P.E. & HERMIDA, G.N. (2013). Lumbar glands in the frog genera
44 45	1903	Pleurodema and Somuncuria (Anura: Leiuperidae): histological and histochemical
46 47 48	1904	perspectives. Acta Zoologica 94, 44–57.
49 50	1905	*Ferreira, R.B., Lourenço-de-Moraes, R., Zocca, C., Duca, C., Beard, K.H. & Brodie,
51 52	1906	E.D. (2019). Antipredator mechanisms of post-metamorphic anurans: a global
53 54 55	1907	database and classification system. Behavioral Ecology and Sociobiology 73, 69.
56 57	1908	*FIELD, L.H. & BAILEY, W.J. (1997). Sound production in primitive Orthoptera from
58 59 60	1909	Western Australia: sounds used in defence and social communication in Ametrus sp.

1 2		
2 3 4	1910	and Hadrogryllacris sp. (Gryllacrididae: Orthoptera). Journal of Natural History 31,
5 6	1911	1127–1141.
7 8	1912	FISCHER, C.P., FRANCO, L.A. & ROMERO, L.M. (2016). Are novel objects perceived as
9 10 11	1913	stressful? The effect of novelty on heart rate. <i>Physiology &amp; Behavior</i> <b>161</b> , 7–14.
12 13	1914	FISHER, K.A. & STANKOWICH, T. (2018). Antipredator strategies of striped skunks in
14 15	1915	response to cues of aerial and terrestrial predators. Animal Behaviour 143, 25-34.
16 17 18	1916	FULLARD, J.H., DAWSON, J.W. & JACOBS, D.S. (2003). Auditory encoding during the last
19 20	1917	moment of a moth's life. Journal of Experimental Biology 206, 281–294.
21 22	1918	FULLARD, J.H. & FENTON, M.B. (1977). Acoustic and behavioural analyses of the sounds
23 24 25	1919	produced by some species of Nearctic Arctiidae (Lepidoptera). Canadian Journal of
26 27	1920	Zoology <b>55</b> , 1213–1224.
28 29	1921	GALL, L.F. (1991). Evolutionary ecology of sympatric Catocala moths (Lepidoptera:
30 31 32	1922	Noctuidae). III. Experiments on female oviposition preference. The Journal of
33 34	1923	Research on the Lepidoptera <b>29</b> , 217–233.
35 36	1924	GANS, C. & MADERSON, P.F.A. (1973). Sound producing mechanisms in recent reptiles:
37 38 30	1925	review and comment. American Zoologist 13, 1195–1203.
39 40 41	1926	GETTY, T. (1996). Mate selection by repeated inspection: more on pied flycatchers. Animal
42 43	1927	<i>Behaviour</i> <b>51</b> , 739–745.
44 45	1928	GLAUDAS, X. (2004). Do cottonmouths (Agkistrodon piscivorus) habituate to human
46 47 48	1929	confrontations? Southeastern Naturalist 3, 129–138.
49 50	1930	GLAUDAS, X. & WHINE, C. (2007). Do warning displays predict striking behavior in a viperid
51 52	1931	snake, the cottonmouth (Agkistrodon piscivorus)? Canadian Journal of Zoology 85,
53 54 55	1932	574–578.
56 57	1933	GLAUDAS, X., WINNE, C.T. & FEDEWA, L.A. (2006). Ontogeny of anti-predator behavioral
58 59 60	1934	habituation in cottonmouths (Agkistrodon piscivorus). Ethology <b>112</b> , 608–615.

2		
3 4	1935	GOLDING, W.R.J. (2020). The Brooklyn Papyrus (47.218. 48 and 47.218. 85) and its
5 6	1936	snakebite treatments. University of South Africa.
/ 8 0	1937	GOTCH, W.E. (1997). The behavior of the horned passalus beetle, Odontotaenius disjunctus
9 10 11	1938	(Illiger). Masters Thesis, College of William and Mary in Virginia, Virginia, USA.
12 13	1939	GOTZ, T. & JANIK, V. (2011). Repeated elicitation of the acoustic startle reflex leads to
14 15	1940	sensitisation in subsequent avoidance behaviour and induces fear conditioning. BMC
16 17 18	1941	Neuroscience 12, 1–13.
19 20	1942	GOULET, P., GUINET, C., CAMPAGNA, C., CAMPAGNA, J., TYACK, P.L. & JOHNSON, M. (2020).
21 22	1943	Flash and grab: deep-diving southern elephant seals trigger anti-predator flashes in
23 24 25	1944	bioluminescent prey. Journal of Experimental Biology 223, 1-11.
25 26 27	1945	GOUREAU, P. (1841). Note suivante sur la Mante religieuse. Annales de la Société
28 29	1946	Entomoogique de France France 10, 353–354.
30 31	1947	*GRANDCOLAS, P. & DESUTTER-GRANDCOLAS, L. (1998). Successful use of a deimatic
32 33 34	1948	display by the praying mantid Polyspilota aeruginosa against the yellow-vented
35 36	1949	bulbul. Annales de la Société entomologique de France 34, 335–336.
37 38	1950	GRANT, M. & HAZEL, J. (2004). Who's Who in Classical Mythology. Routledge.
39 40 41	1951	*GREEN, D.M. (1988). Antipredator behaviour and skin glands in the New Zealand native
42 43	1952	frogs, genus Leiopelma. New Zealand Journal of Zoology 15, 39–45.
44 45	1953	GRIFFIN, A.S. (2004). Social learning about predators: a review and prospectus. Learning &
46 47 48	1954	<i>Behavior</i> <b>32</b> , 131–140.
48 49 50	1955	GUEDES, R.N.C., MATHESON, S.M., FREI, B., SMITH, M.L. & YACK, J.E. (2012). Vibration
51 52	1956	detection and discrimination in the masked birch caterpillar (Drepana 79rcuate).
53 54	1957	Journal of Comparative Physiology A 198, 325–335.
55 56 57	1958	GUILFORD, T. (1994). 'Go-slow' signalling and the problem of automimicry. Journal of
58 59 60	1959	Theoretical Biology 170, 311–316.

1 2		
3 4	1960	GUILFORD, T. & DAWKINS, M.S. (1991). Receiver psychology and the evolution of animal
5 6	1961	signals. Animal Behaviour 42, 1–14.
/ 8 9	1962	HADDOCK, S.H.D., MOLINE, M.A. & CASE, J.F. (2010). Bioluminescence in the sea. Annual
) 10 11	1963	Review of Marine Science 2, 443–493.
12 13	1964	HANLEY, K.A. & WIDDER, E.A. (2017). Bioluminescence in dinoflagellates: evidence that the
14 15	1965	adaptive value of bioluminescence in dinoflagellates is concentration dependent.
16 17 19	1966	Photochemistry and Photobiology 93, 519–530.
19 20	1967	HANLON, R.T. (2007). Cephalopod dynamic camouflage. Current Biology 17, R400–R404.
21 22	1968	HANLON, R.T. & MESSENGER, J.B. (1988). Adaptive coloration in young cuttlefish (Sepia
23 24 25	1969	officinalis): the morphology and development of body patterns and their relation to
25 26 27	1970	behaviour. Philosophical Transactions of the Royal Society B 320, 437-487.
27 28 29 30 31 32	1971	HANLON, R.T. & MESSENGER, J.B. (1996). Cephalopod Behaviour. Cambridge University
	1972	Press 1 <sup>st</sup> Ed.
32 33 34	1973	HANLON, R.T. & MESSENGER, J.B. (2018). Cephalopod Behaviour. Cambridge University
35 36	1974	Press, 2 <sup>nd</sup> Ed.
37 38	1975	*HANSON, J.A. & VIAL, J.L. (1956). Defensive behavior and effects of toxins in Bufo
39 40 41	1976	alvarius. Herpetologica 12, 141–149.
42 43	1977	*HAYES, W.A. (1977). Predator response postures of crayfish. I. The genus Procambarus
44 45	1978	(Decapoda, Cambaridae). The Southwestern Naturalist 21, 443-449.
46 47 49	1979	HEBETS, E.A. & PAPAJ, D.R. (2004). Complex signal function: developing a framework of
40 49 50	1980	testable hypotheses. Behavioral Ecology and Sociobiology 57, 197–214.
51 52	1981	HIGHAM, J.P. & HEBETS, E.A. (2013). An introduction to multimodal communication.
53 54	1982	Behavioral Ecology and Sociobiology 67, 1381–1388.
55 56 57	1983	HILL, S.A. (2007). Sound generation in Mantis religiosa (Mantodea: Mantidae): stridulatory
58 59 60	1984	structures and acoustic signal. Journal of Orthoptera Research 16, 35–49.

1 2		
2 3 4	1985	*HINGSTON, R.W.G. (1933). Psychological weapons in animal fight. Journal of Personality
5 6	1986	<b>2</b> , 3–21.
/ 8 9	1987	*HÖDL, W. & GOLLMANN, G. (1986). Distress calls in neotropical frogs. Amphibia-Reptilia 7,
10 11	1988	11–21.
12 13	1989	HOLMES, G.G., DELFERRIÈRE, E., ROWE, C., TROSCIANKO, J. & SKELHORN, J. (2018). Testing
14 15 16	1990	the feasibility of the startle-first route to deimatism. Scientific Reports 8, 10737.
17 18	1991	HOLMES, W. (1940). The colour changes and colour patterns of Sepia officinalis L.
19 20	1992	Proceedings of the Zoological Society of London A110, 17–35.
21 22 23	1993	HOUSTON, A.I. & MCNAMARA, J.M. (2006). John Maynard Smith and the importance of
23 24 25	1994	consistency in evolutionary game theory. Biology and Philosophy 20, 933.
26 27	1995	HRISTOV, N.I. & CONNER, W.E. (2005). Sound strategy: acoustic aposematism in the bat-
28 29	1996	tiger moth arms race. Naturwissenschaften 92, 164–169.
30 31 32	1997	HUBBARD, M.E. (1903). Correlated protective devices in some California salamanders. The
33 34	1998	University Press.
35 36	1999	HUMPHRIES, D.A. & DRIVER, P.M. (1970). Protean defence by prey animals. Oecologia 5,
37 38 39	2000	285–302.
40 41	2001	INGALLS, V. (1993). Startle and habituation responses of blue jays (Cyanocitta cristata) in a
42 43	2002	laboratory simulation of anti-predator defenses of Catocala moths (Lepidoptera:
44 45 46	2003	Noctuidae). Behaviour 126, 77–96.
40 47 48	2004	JANZEN, D.H., HALLWACHS, W. & BURNS, J.M. (2010). A tropical horde of counterfeit
49 50	2005	predator eyes. Proceedings of the National Academy of Sciences 107, 11659–11665.
51 52	2006	JARA, M. & PINCHEIRA-DONOSO, D. (2015). The neck flattening defensive behaviour in
53 54 55	2007	snakes: first record of hooding in the South American colubrid genus Philodryas.
56 57 58 59 60	2008	Animal Biology <b>65</b> , 73–79.

Page 83 of 199

1 2		
3 4	2009	JOHNSON, J.A. & BRODIE JR, E.D. (1975). The selective advantage of the defensive posture of
5 6 7	2010	the newt, Taricha granulosa. American Midland Naturalist 93, 139–148.
7 8 9	2011	KAHLKE, T. & UMBERS, K.D.L. (2016). Bioluminescence. Current Biology 26, R313–R314.
10 11	2012	KANG, C., ZAHIRI, R. & SHERRATT, T.N. (2017). Body size affects the evolution of hidden
12 13	2013	colour signals in moths. Proceedings of the Royal Society B 284, 20171287.
14 15	2014	KANG, CK., CHO, HJ., LEE, SI. & JABLONSKI, P.G. (2016). Post-attack aposematic
16 17 18	2015	display in prey facilitates predator avoidance learning. Frontiers in Ecology and
19 20	2016	Evolution 4, 1–9.
21 22	2017	*KANG, CK., LEE, SI. & JABLONSKI, P.G. (2011). Effect of sex and bright coloration on
23 24 25	2018	survival and predator-induced wing damage in an aposematic lantern fly with startle
26 27	2019	display. Ecological Entomology 36, 709–716.
28 29	2020	KIM, Y., HWANG, Y., BAE, S., SHERRATT, T.N., AN, J., CHOI, SW., MILLER, J.C. & KANG,
30 31 32	2021	C. (2020). Prey with hidden colour defences benefit from their similarity to
33 34	2022	aposematic signals. Proceedings of the Royal Society B: Biological Sciences 287,
35 36	2023	20201894.
37 38 20	2024	KING, A.J. & ADAMO, S.A. (2006). The ventilatory, cardiac and behavioural responses of
39 40 41	2025	resting cuttlefish (Sepia officinalis L.) to sudden visual stimuli. Journal of
42 43	2026	Experimental Biology 209, 1101–1111.
44 45	2027	KOCH, M. (1999). The neurobiology of startle. Progress in Neurobiology 59, 107–128.
46 47 48	2028	KOCH, M. & SCHNITZLER, HU. (1997). The acoustic startle response in rats—circuits
49 50	2029	mediating evocation, inhibition and potentiation. Behavioural Brain Research 89, 35-
51 52	2030	49.
53 54 55	2031	*KOWALSKI, K.N., LAKES-HARLAN, R., LEHMANN, G.U.C. & STRAUB, J. (2014). Acoustic
55 57 58 59 60	2032	defence in an insect: characteristics of defensive stridulation and differences between

1 ว		
2 3 4	2033	the sexes in the tettigoniid Poecilimon ornatus (Schmidt 1850). Zoology 117, 329-
5 6	2034	336.
7 8 9	2035	LAFFERTY, K.D. & KURIS, A.M. (2002). Trophic strategies, animal diversity and body size.
10 11	2036	Trends in Ecology & Evolution 17, 507–513.
12 13	2037	LANGRIDGE, K.V. (2006). Symmetrical crypsis and asymmetrical signalling in the cuttlefish
14 15 16	2038	Sepia officinalis. Proceedings of the Royal Society B: Biological Sciences 273, 959–
17 18	2039	967.
19 20	2040	LANGRIDGE, K.V. (2009). Cuttlefish use startle displays, but not against large predators.
21 22 22	2041	Animal Behaviour 77, 847–856.
23 24 25	2042	LANGRIDGE, K.V., BROOM, M. & OSORIO, D. (2007). Selective signalling by cuttlefish to
26 27	2043	predators. Current Biology 17, R1044–R1045.
28 29	2044	LEAVELL, B.C. & BERNAL, X.E. (2019). The cognitive ecology of stimulus ambiguity: A
30 31 32	2045	predator-prey perspective. Trends in Ecology & Evolution 34, 1048-1060.
33 34	2046	LEAVELL, B.C., RUBIN, J.J., MCCLURE, C.J.W., MINER, K.A., BRANHAM, M.A. & BARBER,
35 36	2047	J.R. (2018). Fireflies thwart bat attack with multisensory warnings. Science Advances
37 38 39	2048	<b>4</b> , eaat6601.
40 41	2049	*Lenzi-Mattos, R., Antoniazzi, M.M., Haddad, C.F.B., Tambourgi, D.V., Rodrigues,
42 43	2050	M.T. & JARED, C. (2005). The inguinal macroglands of the frog Physalaemus
44 45 46	2051	nattereri (Leptodactylidae): structure, toxic secretion and relationship with deimatic
40 47 48	2052	behaviour. Journal of Zoology 266, 385–394.
49 50	2053	LEWIS, E.E. & CANE, J.H. (1990). Stridulation as a primary anti-predator defence of a beetle.
51 52	2054	Animal Behaviour 40, 1003–1004.
55 55	2055	LIDDELL, H.G., SCOTT, R., JONES, S.H.S., MCKENZIE, R., GLARE, P.G.W. & THOMPSON, A.A.
56 57	2056	(1996). A Greek-English Lexicon, 9th edition. Oxford University Press, Oxford, New
58 59 60	2057	York.

1 2		
3 4	2058	LIESHOUT, E. VAN, ELGAR, M.A. & WILGENBURG, E. VAN (2005). Conflict resolution
5 6	2059	strategies in meat ants (Iridomyrmex purpureus): ritualised displays versus lethal
7 8 0	2060	fighting. <i>Behaviour</i> <b>142</b> , 701–716.
) 10 11	2061	LIN, J.Y., MURRAY, S.O. & BOYNTON, G.M. (2009). Capture of attention to threatening
12 13	2062	stimuli without perceptual awareness. Current Biology 19, 1118-1122.
14 15	2063	LINDSLEY, D.B. (2013). Common factors in sensory deprivation, sensory distortion, and
16 17 18	2064	sensory overload. In Sensory Deprivation: A Symposium Held at Harvard Medical
19 20	2065	School pp. 174–194. Harvard University Press.
21 22	2066	LINDSTROM, L., ALATALO, R.V. & MAPPES, J. (1999). Reactions of hand-reared and wild-
23 24 25	2067	caught predators toward warningly colored, gregarious, and conspicuous prey.
26 27	2068	Behavioral Ecology 10, 317–322.
28 29	2069	LLOYD, J.E. (1973). Firefly parasites and predators. The Coleopterists Bulletin 27, 91-106.
30 31 32	2070	LOEFFLER-HENRY, K., KANG, C. & SHERRATT, T.N. (2019). Consistent associations between
32 33 34	2071	body size and hidden contrasting color signals across a range of insect taxa. The
34 35 36	2072	American Naturalist 94, 28-37.
37 38	2073	LOEFFLER-HENRY, K., KANG, C. & SHERRATT, T.N. (2021). The anti-predation benefit of
39 40 41	2074	flash displays is related to the distance at which the prey initiates its escape.
42 43	2075	Proceedings of the Royal Society B: Biological Sciences 288, 20210866.
44 45	2076	LOEFFLER-HENRY, K., KANG, C., YIP, Y., CARO, T. & SHERRATT, T.N. (2018). Flash behavior
46 47 48	2077	increases prey survival. Behavioral Ecology 29, 528-533.
40 49 50	2078	LÖHNER, L. (1919). Über einen eigentümlichen Reflex der Feuerunken nebst Bemerkungen
51 52	2079	über die "tierische Hypnose". Pflüger's Archiv für die gesamte Physiologie des
53 54	2080	Menschen und der Tiere 174, 324–351.
55 56 57	2081	Long, S.M., Lewis, S., Jean-Louis, L., Ramos, G., Richmond, J. & Jakob, E.M. (2012).
58 59 60	2082	Firefly flashing and jumping spider predation. <i>Animal Behaviour</i> <b>83</b> , 81–86.

4	
5 6	208
7 8	208
9 10	208
11 12 13	208
14 15	208
16 17	208
18 19	200
20 21	202
22 23	205
24 25	209
26 27 28	209
20 29 30	209
31 32	209
33 34	209
35 36	209
37 38 20	209
40 41	209
42 43	210
44 45	210
46 47	210
48 49 50	210
50 51 52	210
53 54	210
55 56	210
57 58	
59 60	

2083	Low, C. (2012). An experimental test of the seismic behaviors of Antispila nysaefoliella
2084	(Lepidoptera: Heliozelidae) to vibrational stimuli. Florida Entomologist 95, 16-20.
2085	LOW, M.L., NARANJO, M. & YACK, J.E. (2021). Survival sounds in insects: diversity,
2086	function, and evolution. Frontiers in Ecology and Evolution 9, 641740.
2087	*LYON, B.E. & FOGDEN, M.P.L. (1989). Breeding biology of the sunbittern (Eurypyga helias)
2088	in Costa Rica. The Auk 106, 503-507.
2089	MACESIC, L.J. & KAJIURA, S.M. (2009). Electric organ morphology and function in the lesser
2090	electric ray, Narcine brasiliensis. Zoology 112, 442–450.
2091	MALDONADO, H. (1970). The deimatic reaction in the praying mantis Stagmatoptera
2092	biocellata. Zeitschrift für Vergleichende Physiologie 68, 60–71.
2093	MAPPES, J., MARPLES, N. & ENDLER, J.A. (2005). The complex business of survival by
2094	aposematism. Trends in Ecology & Evolution 20, 598–603.
2095	MARPLES, N.M. & KELLY, D.J. (1999). Neophobia and dietary conservatism: Two distinct
2096	processes? Evolutionary Ecology 13, 641–653.
2097	MARTINS, M. (1989). Deimatic behavior in Pleurodema brachyops. Journal of Herpetology
2098	<b>23</b> , 305.
2099	MASTERS, W.M. (1979). Insect disturbance stridulation: Its defensive role. Behavioral
2100	Ecology and Sociobiology 5, 187–200.
2101	MAYNARD SMITH, J. & HARPER, D. (2003). Animal Signals. Oxford University Press, Oxford.
2102	MEDILL, S.A., RENARD, A. & LARIVIÈRE, S. (2011). Ontogeny of antipredator behaviour in
2103	striped skunks (Mephitis mephitis). Ethology Ecology & Evolution 23, 41-48.
2104	MELLINGER, J., BELBENOIT, P., RAVAILLE, M. & SZABO, T. (1978). Electric organ
2105	development in Torpedo marmorata, Chondrichthyes. Developmental Biology 67,
2106	167–188.

1 2		
- 3 4	2107	MESSENGER, J.B. (2001). Cephalopod chromatophores: neurobiology and natural history.
5 6	2108	Biological Reviews 76, 473–528.
/ 8 9	2109	MILES, L., DAVIS, M. & WALKER, D. (2011). Phasic and sustained fear are pharmacologically
10 11	2110	dissociable in rats. Neuropsychopharmacology 36, 1563–1574.
12 13	2111	MØHL, B. & MILLER, L.A. (1976). Ultrasonic clicks produced by the peacock butterfly: a
14 15 16	2112	possible bat-repellent mechanism. Journal of Experimental Biology 64, 639-644.
17 17 18	2113	MOUGI, A. & IWASA, Y. (2010). Evolution towards oscillation or stability in a predator-prey
19 20	2114	system. Proceedings of the Royal Society B: Biological Sciences 277, 3163–3171.
21 22	2115	*NOBLE, G.K. (1931). The Biology of the Amphibia. 1st edition. McGraw-Hill, New York.
23 24 25	2116	NOWAK, R.T. & BRODIE, E.D., JR. (1978). Rib penetration and associated antipredator
26 27	2117	adaptations in the salamander <i>Pleurodeles waltl</i> (Salamandridae). Copeia 1978, 424-
28 29	2118	429.
30 31 32	2119	O'HANLON, J.C., RATHNAYAKE, D.N., BARRY, K.L. & UMBERS, K.D.L. (2018). Post-attack
33 34	2120	defensive displays in three praying mantis species. Behavioral Ecology and
35 36	2121	Sociobiology <b>72</b> , 176.
37 38 30	2122	*OLOFSSON, M., ERIKSSON, S., JAKOBSSON, S. & WIKLUND, C. (2012a). Deimatic display in
39 40 41	2123	the European swallowtail butterfly as a secondary defence against attacks from great
42 43	2124	tits. PLoS ONE 7, e47092.
44 45	2125	OLOFSSON, M., JAKOBSSON, S. & WIKLUND, C. (2012b). Auditory defence in the peacock
46 47 48	2126	butterfly (Inachis io) against mice (Apodemus flavicollis and A. sylvaticus).
49 50	2127	Behavioral Ecology and Sociobiology 66, 209–215.
51 52	2128	*OLOFSSON, M., LØVLIE, H., TIBBLIN, J., JAKOBSSON, S. & WIKLUND, C. (2013). Eyespot
53 54 55	2129	display in the peacock butterfly triggers antipredator behaviors in naïve adult fowl.
56 57	2130	Behavioral Ecology 24, 305–310.
58 59 60		

3 4	2131	OLOFSSON, M., VALLIN, A., JAKOBSSON, S. & WIKLUND, C. (2011). Winter predation on two
5 6	2132	species of hibernating butterflies: monitoring rodent attacks with infrared cameras.
/ 8 9	2133	Animal Behaviour <b>81</b> , 529–534.
10 11	2134	OTTO, S.P. & DAY, T. (2011). A Biologist's Guide to Mathematical Modeling in Ecology and
12 13	2135	Evolution. Princeton University Press.
14 15	2136	*PACKARD, A. & SANDERS, G. (1971). Body patterns of Octopus vulgaris and maturation of
17 18	2137	the response to disturbance. Animal Behaviour 19, 780-790.
19 20	2138	PEMBURY SMITH, M.Q.R. & RUXTON, G.D. (2021). Size-dependent predation risk in cryptic
21 22 22	2139	prey. Journal of Ethology <b>39</b> , 191–198.
25 24 25	2140	PEREZ-MARTINEZ, C.A., RILEY, J.L. & WHITING, M.J. (2020). Uncovering the function of an
26 27	2141	enigmatic display: antipredator behaviour in the iconic Australian frillneck lizard.
28 29	2142	Biological Journal of the Linnean Society 129, 425–438.
30 31 32	2143	POMEROY, H. & HEPPNER, F. (1977). Laboratory determination of startle reaction time of the
33 34	2144	starling (Sturnus vulgaris). Animal Behaviour 25, 720–725.
35 36	2145	POULTON, E.B. (1890). The colours of animals: their meaning and use, especially considered
37 38 39	2146	in the case of insects. Trench & Trübner, London.
40 41	2147	RAMIREZ-MORENO, D.F. & SEJNOWSKI, T.J. (2012). A computational model for the
42 43	2148	modulation of the prepulse inhibition of the acoustic startle reflex. Biological
44 45 46	2149	<i>Cybernetics</i> <b>106</b> , 169–176.
40 47 48	2150	RATCLIFFE, J.M. & FULLARD, J.H. (2005). The adaptive function of tiger moth clicks against
49 50	2151	echolocating bats: an experimental and synthetic approach. Journal of Experimental
51 52	2152	<i>Biology</i> <b>208</b> , 4689–4698.
54 55	2153	RIND, F.C., SANTER, R.D. & WRIGHT, G.A. (2008). Arousal facilitates collision cvoidance
56 57	2154	mediated by a looming sensitive visual neuron in a flying locust. Journal of
58 59 60	2155	Neurophysiology 100, 670–680.

1 2		
2 3 4	2156	*ROBINSON, M.H. (1968a). The defensive behavior of <i>Pterinoxylus spinulosus</i> Redtenbacher,
5 6	2157	a winged stick insect from Panama (Phasmatodea). Psyche: A Journal of Entomology
7 8 9	2158	<b>75</b> , 195–207.
10 11	2159	*ROBINSON, M.H. (1968b). The defensive behaviour of the stick insect Oncotophasma
12 13	2160	martini (Griffini) (Orthoptera: Phasmatidae). Proceedings of the Royal Entomological
14 15 16	2161	Society of London. Series A, General Entomology 43, 183–187.
10 17 18	2162	ROBINSON, M.H. (1969). The defensive behaviour of some orthopteroid insects from Panama.
19 20	2163	Transactions of the Royal Entomological Society of London 121, 281–303.
21 22	2164	ROONWAL, M.L. (1938). The frightening attitude of a desert mantid, <i>Eremiaphila braueri</i> Kr.
23 24 25	2165	Orthoptera, Mantodea). Proceedings of the Royal Entomological Society of London.
26 27	2166	Series A, General Entomology 13, 71–72.
28 29	2167	ROSI-DENADAI, C.A., SCALLION, M.L., MERRETT, C.G. & YACK, J.E. (2018). Vocalization in
30 31 32	2168	caterpillars: a novel sound-producing mechanism for insects. Journal of Experimental
33 34	2169	<i>Biology</i> <b>221</b> , 169466.
35 36	2170	ROWE, C. & GUILFORD, T. (1999). The evolution of multimodal warning displays.
37 38 20	2171	Evolutionary Ecology 13, 655–671.
39 40 41	2172	ROWE, C. & HALPIN, C. (2013). Why are warning displays multimodal? Behavioral Ecology
42 43	2173	and Sociobiology <b>67</b> , 1425–1439.
44 45	2174	ROWLAND, H.M., RUXTON, G.D. & SKELHORN, J. (2013). Bitter taste enhances predatory
46 47 48	2175	biases against aggregations of prey with warning coloration. Behavioral Ecology 24,
49 50	2176	942–948.
51 52	2177	*RUIZ, J.F., SEPÚLVEDA, R.D. & IBÁÑEZ, C.M. (2012). Behaviour of Robsonella fontaniana
53 54 55	2178	in response to a potential predator. Latin American Journal of Aquatic Research 40,
55 56 57 58 59 60	2179	253–258.

1 2		
3 4	2180	*RUXTON, G.D., ALLEN, W.L., SHERRATT, T.N. & SPEED, M.P. (2019). Avoiding Attack: The
5 6	2181	Evolutionary Ecology of Crypsis, Aposematism, and Mimicry. Oxford University
7 8 0	2182	Press.
9 10 11	2183	RUXTON, G.D., SHERRATT, T.N. & SPEED, M.P. (2004). Avoiding attack: the evolutionary
12 13	2184	ecology of crypsis, warning signals, and mimicry. Oxford University Press.
14 15	2185	SANDOW, J.D. & BAILEY, W.J. (1978). An experimental study of defensive stridulation in
16 17	2186	Mygalopsis ferruginea Redtenbacher (Orthoptera: Tettigoniidae). Animal Behaviour
18 19 20	2187	<b>26</b> , 1004–1011.
21 22	2188	SARGENT, T.D. (1973). Studies on the Catocala (Noctuidae) of southern New England IV. A
23 24 25	2189	preliminary analysis of beak-damaged specimens with discussion of anomalyas a
25 26 27	2190	potential anti-predator function of hindwing diversity. Journal of the Lepidopterists'
28 29	2191	Society 27, 175–192.
30 31 32	2192	SARGENT, T.D. (1990). Startle as an anti-predator mechanism, with special reference to the
32 33 34	2193	underwing moths, (Catocala). In Insect defenses: adaptive mechanisms and strategies
35 36	2194	of prey and predators (eds D. EVANS & J. SCHMIDT), p. SUNY Press.
37 38	2195	SARGENT, T.D. & HESSEL, S.A. (1970). Studies on the Catocala (Noctuidae) of southern New
39 40 41	2196	England. I. Abundance and seasonal occurrence of the species, 1961-1969. Journal of
42 43	2197	the Lepidopterists' Society 24, 105–117.
44 45	2198	SATO, K. & YAMAWAKI, Y. (2014). Role of a looming-sensitive neuron in triggering the
46 47 48	2199	defense behavior of the praying mantis Tenodera aridifolia. Journal of
40 49 50	2200	Neurophysiology 112, 671–682.
51 52	2201	*SCHAL, C., FRASER, J. & BELL, W.J. (1982). Disturbance stridulation and chemical defence
53 54	2202	in nymphs of the tropical cockroach Megaloblatta blaberoides. Journal of Insect
55 56 57 58 59	2203	<i>Physiology</i> <b>28</b> , 541–552.
60		

2 3 4 5 6 7 8	2204	Scheydt, S., Müller Staub, M., Frauenfelder, F., Nielsen, G.H., Behrens, J. &
	2205	NEEDHAM, I. (2017). Sensory overload: a concept analysis. International Journal of
	2206	Mental Health Nursing 26, 110–120.
9 10 11	2207	SCHLENOFF, D.H. (1985). The startle responses of blue jays to Catocala (Lepidoptera:
12 13	2208	Noctuidae) prey models. Animal Behaviour 33, 1057–1067.
14 15 16 17 18 19 20 21 22 23 24 25	2209	SCHOLLMEYER, K. (2020). The archaeology of animals in southwest New Mexico, AD 1000
	2210	- 1130. The Black Range Naturalist <b>3</b> , 7-14.
	2211	*SERAFIM, H. & RIBEIRO DUARTE, M. (2008). Tail mock-strike and hemipenis display in the
	2212	coral snakes, genus Micrurus (Elapidae): epiphenomenon or deimatic behaviour?
	2213	Herpetological Bulletin, 104, 7–8.
26 27	2214	SHEN, X., LIANG, D., CHEN, M., MAO, R., WAKE, D.B., ZHANG, P. (2016). Enlarged multilocus
28 29	2215	data set provides surprisingly younger time of origin for the Plethodontidae, the largest
30 31 32	2216	family of salamanders. Systematic Biology 65, 66–81.
32 33 34 35 36 37 38 39 40 41	2217	SHERBROOKE, W.C., MIDDENDORF III, G.A. & GUYER, C. (2001). Blood-squirting variability
	2218	in horned lizards (Phrynosoma). Copeia 2001, 1114–1122.
	2219	SHERIDAN, M.N. (1965). The fine structure of the electric organ of Torpeda marmorata.
	2220	Journal of Cell Biology 24, 129–141.
42 43	2221	SHRAGAI, T., PING, X., ARAKAKI, C., GARLICK, D., BLUMSTEIN, D.T. & BLAISDELL, A.P.
44 45	2222	(2017). Hermit crab response to a visual threat is sensitive to looming cues. PeerJ 5,
46 47 48 49 50 51 52	2223	e4058.
	2224	SIMMONS, J.A., WEVER, E.G. & PYLKA, J.M. (1971). Periodical cicada: sound production and
	2225	hearing. Science 171, 212–213.
53 54 55	2226	SIMONS, R.C. (1996). Boo!: Culture, Experience, and the Startle Reflex. Oxford University
55 56 57 58 59 60	2227	Press.

1 2		
2 3 4	2228	SKELHORN, J., HOLMES, G.G. & ROWE, C. (2016). Deimatic or aposematic? Animal
5 6 7	2229	<i>Behaviour</i> <b>113</b> , E1–E3.
/ 8 9	2230	SKELHORN, J., ROWLAND, H.M., SPEED, M.P. & RUXTON, G.D. (2010). Masquerade:
10 11	2231	Camouflage without crypsis. Science 327, 51–51.
12 13	2232	*SKÖLD, M. (1998). Escape responses in four epibenthic brittle stars (Ophiuroidea:
14 15 16	2233	Echinodermata). Ophelia 49, 163–179.
17 18	2234	SMITH, R.L. & LANGLEY, W.M. (1978). Cicada stress sound: an assay of its effectiveness as a
19 20	2235	predator defense mechanism. The Southwestern Naturalist 23, 187-195.
21 22 23	2236	SPEED, M.P. & RUXTON, G.D. (2005). Warning displays in spiny animals: one (more)
24 25	2237	evolutionary route to aposematism. Evolution 59, 2499–2508.
26 27	2238	STANGER-HALL, K.F. & OAKLEY, T.H. (2019). Bioluminescent signals. In: Choe, J.C. (Ed.),
28 29	2239	Encyclopedia of Animal Behavior (2nd ed.). vol. 1, pp. 449–461. Elsevier, Academic
30 31 32	2240	Press.
33 34	2241	STAUDINGER, M.D., HANLON, R.T. & JUANES, F. (2011). Primary and secondary defences of
35 36	2242	squid to cruising and ambush fish predators: variable tactics and their survival value.
37 38 39	2243	Animal Behaviour <b>81</b> , 585–594.
40 41	2244	*STEINER, A.L. (1981). Anti-predator strategies II. Grasshoppers (Orthoptera, Acrididae)
42 43	2245	attacked by Prionyx parkeri and some Tachysphex wasps (Hymenoptera, Sphecinae
44 45 46	2246	and Larrinae): A descriptive study. Psyche 88, 1-24.
40 47 48	2247	STEVENS, M. & MERILAITA, S. (2011). Animal Camouflage: Mechanisms and Function.
49 50	2248	Cambridge University Press.
51 52	2249	STEVENS, M. (2013). Sensory Ecology, Behaviour, and Evolution. Oxford University Press.
53 54	2250	STONEMAN, M.G. & FENTON, M.B. (1988). Disrupting foraging bats: The clicks of arctiid
55 56	2251	moths. In Animal Sonar: Processes and Performance (eds P.E. NACHTIGALL &
57 58 59 60	2252	P.W.B. MOORE), pp. 635–638. Springer US, Boston, MA.

Page 93 of 199

1 2		
- 3 4	2253	TEMIZER, I., DONOVAN, J.C., BAIER, H. & SEMMELHACK, J.L. (2015). A visual pathway for
5 6	2254	looming-evoked escape in larval zebrafish. Current Biology 25, 1823–1834.
7 8 0	2255	TER HOFSTEDE, H.M. & RATCLIFFE, J.M. (2016). Evolutionary escalation: the bat-moth arms
9 10 11	2256	race. The Journal of Experimental Biology 219, 1589–1602.
12 13	2257	THOMAS, B.T. & STRAHL, S.D. (1990). Nesting behavior of sunbitterns (Eurypyga helias) in
14 15 16	2258	Venezuela. The Condor 92, 576–581.
17 18	2259	THOMAS, R.J., MARPLES, N.M., CUTHILL, I.C., TAKAHASHI, M. & GIBSON, E.A. (2003).
19 20	2260	Dietary conservatism may facilitate the initial evolution of aposematism. Oikos 101,
21 22	2261	458–466.
23 24 25	2262	TIEN, R.J. & ELLNER, S.P. (2012). Variable cost of prey defense and coevolution in predator-
26 27	2263	prey systems. Ecological Monographs 82, 491–504.
28 29	2264	TINBERGEN, N. (1963). On aims and methods of Ethology. Zeitschrift für Tierpsychologie 20,
30 31 32	2265	410–433.
33 34	2266	*Toledo, L.F., Guimarães, L.D., Lima, L.P., Bastos, R.P. & Haddad, C.F.B. (2004 <i>a</i> ).
35 36	2267	Notes on courtship, egg-laying site, and defensive behavior of <i>Epipedobates</i>
37 38	2268	flavopictus (Anura, Dendrobatidae) from two mountain ranges of central and
39 40 41	2269	southeastern Brazil. Phyllomedusa 3, 145–147.
42 43	2270	*TOLEDO, L.F., TOZETTI, A.M. & ZINA, J. (2004b). Leptodactylus labyrinthicus (pepper
44 45	2271	frog): Repertoire of defensive behaviour. Herpetological Bulletin 90, 29-31.
46 47 48	2272	TOVOTE, P., ESPOSITO, M.S., BOTTA, P., CHAUDUN, F., FADOK, J.P., MARKOVIC, M., WOLFF,
49 50	2273	S.B.E., RAMAKRISHNAN, C., FENNO, L., DEISSEROTH, K., HERRY, C., ARBER, S. &
51 52	2274	LÜTHI, A. (2016). Midbrain circuits for defensive behaviour. Nature 534, 206–212.
53 54	2275	*TOZETTI, A.M., OLIVEIRA, R.B. DE & PONTES, G.M.F. (2009). Defensive repertoire of
55 56 57 58 59	2276	Xenodon dorbignyi (Serpentes, Dipsadidae). Biota Neotropica 9, 157–163.
60		

1 2		
3 4	2277	TRIMMER, P.C., HOUSTON, A.I., MARSHALL, J.A.R., BOGACZ, R., PAUL, E.S., MENDL, M.T. &
5 6	2278	MCNAMARA, J.M. (2008). Mammalian choices: combining fast-but-inaccurate and
/ 8 0	2279	slow-but-accurate decision-making systems. Proceedings of the Royal Society B:
9 10 11	2280	Biological Sciences 275, 2353–2361.
12 13	2281	UMBERS, K.D.L., DE BONA, S., WHITE, T.E., LEHTONEN, J., MAPPES, J. & ENDLER, J.A.
14 15	2282	(2017). Deimatism: a neglected form of antipredator defence. <i>Biology Letters</i> 13, 1–5.
16 17	2283	UMBERS, K.D.L., LEHTONEN, J. & MAPPES, J. (2015). Deimatic displays. Current Biology 25,
18 19 20	2284	R58–R59.
21 22	2285	UMBERS, K.D.L. & MAPPES, J. (2015). Post-attack deimatic display in the mountain katydid
23 24 25	2286	(Acripeza reticulata). Animal Behaviour 100, 68–73.
25 26 27	2287	UMBERS, K.D.L. & MAPPES, J. (2016). Towards a tractable working hypothesis for deimatic
28 29 30 31 32 33 34	2288	displays. Animal Behaviour 113, e5–e7.
	2289	Umbers, K.D.L., White, T.E., De Bona, S., Haff, T., Ryeland, J., Drinkwater, E. &
	2290	MAPPES, J. (2019). The protective value of a defensive display varies with the
35 36	2291	experience of wild predators. Scientific Reports 9, 463.
37 38	2292	UNDERWOOD, T.J., TALLAMY, D.W. & PESEK, J.D. (1997). Bioluminescence in firefly larvae:
39 40 41	2293	a test of the aposematic display hypothesis (Coleoptera: Lampyridae). Journal of
42 43	2294	Insect Behavior 10, 365–370.
44 45	2295	VALLIN, A., JAKOBSSON, S., LIND, J. & WIKLUND, C. (2005). Prey survival by predator
46 47 48	2296	intimidation: an experimental study of peacock butterfly defence against blue tits.
48 49 50	2297	Proceedings of the Royal Society B: Biological Sciences 272, 1203–1207.
51 52	2298	VALLIN, A., JAKOBSSON, S., LIND, J. & WIKLUND, C. (2006). Crypsis versus intimidation —
53 54	2299	anti-predation defence in three closely related butterflies. Behavioral Ecology and
56 57 58	2300	Sociobiology <b>59</b> , 455–459.
59 60		

Page 95 of 199

1 2		
3 4	2301	VALLIN, A., JAKOBSSON, S. & WIKLUND, C. (2007). "An eye for an eye?"— on the generality
5 6	2302	of the intimidating quality of eyespots in a butterfly and a hawkmoth. Behavioral
/ 8 0	2303	Ecology and Sociobiology 61, 1419–1424.
9 10 11	2304	VANE-WRIGHT, R.I. (1986). The snake hiss of hibernating peacocks — audioBatesian
12 13	2305	mimicry. Antenna 10, 5–6.
14 15	2306	VARLEY, G.C. (1939). Frightening attitudes and floral simulation in praying mantids.
16 17	2307	Proceedings of the Royal Entomological Society of London. Series A, General
18 19 20	2308	Entomology 14, 91–96.
21 22	2309	VAUGHAN, F.A. (1983). Startle responses of blue jays to visual stimuli presented during
23 24	2310	feeding. Animal Behaviour 31, 385–396.
25 26 27	2311	*VESTER, H.I., FOLKOW, L.P. & BLIX, A.S. (2004). Click sounds produced by cod (Gadus
28 29	2312	morhua). The Journal of the Acoustical Society of America 115, 914–919.
30 31	2313	VIDAL-GARCÍA, M., O'HANLON, J., SVENSON, G.J. & UMBERS, K.D.L. (2020). The evolution
32 33 34	2314	of startle displays: a case study in praying mantises. Proceedings of the Royal Society
35 36	2315	B 287, 20201016.
37 38	2316	WAHLBERG, M. & WESTERBERG, H. (2003). Sounds produced by herring (Clupea harengus)
39 40	2317	bubble release. Aquatic Living Resources 16, 271–275.
41 42 43	2318	WAINWRIGHT, P.C. & TURINGAN, R.G. (1997). Evolution of pufferfish inflation behavior.
44 45	2319	<i>Evolution</i> <b>51</b> , 506–518.
46 47	2320	WALD, A. (1945). Sequential tests of statistical hypotheses. The Annals of Mathematical
48 49 50	2321	<i>Statistics</i> <b>16</b> , 117–186.
50 51 52	2322	WALDBAUER, G.P., STERNBURG, J.G. & MAIER, C.T. (1977). Phenological relationships of
53 54	2323	wasps, bumblebees, their mimics, and insectivorous birds in an Illinois sand area.
55 56	2324	<i>Ecology</i> <b>58</b> , 583–591.
57 58 59 60	2325	*WALLACE, A.R. (1889). Darwinism. MacMillian and Co, London and New York.

2		
3 4	2326	WANG, L., RUXTON, G.D., CORNELL, S.J., SPEED, M.P. & BROOM, M. (2019). A theory for
5 6	2327	investment across defences triggered at different stages of a predator-prey encounter.
/ 8 0	2328	Journal of Theoretical Biology 473, 9–19.
9 10 11	2329	WANG, LY., HUANG, WS., TANG, HC., HUANG, LC. & LIN, CP. (2018). Too hard to
12 13	2330	swallow: a secret secondary defence of an aposematic insect. Journal of Experimental
14 15 16	2331	<i>Biology</i> <b>221</b> , jeb172486.
17 18	2332	*WHITING, M.J., NOBLE, D.W.A. & SOMAWEERA, R. (2015). Sexual dimorphism in
19 20	2333	conspicuousness and ornamentation in the enigmatic leaf-nosed lizard Ceratophora
21 22 23	2334	tennentii from Sri Lanka. Biological Journal of the Linnean Society 116, 614–625.
23 24 25	2335	WILLIAMS, C.R., BRODIE, E.D., TYLER, M.J. & WALKER, S.J. (2000). Antipredator
26 27	2336	mechanisms of Australian frogs. Journal of Herpetology 34, 431.
28 29	2337	WILSON, B., BATTY, R.S. & DILL, L.M. (2004). Pacific and Atlantic herring produce burst
30 31 32	2338	pulse sounds. Proceedings of the Royal Society B: Biological Sciences 271, S95–S97.
33 34	2339	YAMAWAKI, Y. (2011). Defence behaviours of the praying mantis Tenodera aridifolia in
35 36	2340	response to looming objects. Journal of Insect Physiology 57, 1510–1517.
37 38 30	2341	YILMAZ, M. & MEISTER, M. (2013). Rapid innate defensive responses of mice to looming
40 41	2342	visual stimuli. <i>Current Biology</i> 23, 2011–2015.
42 43	2343	YORK, C.A. & BARTOL, I.K. (2016). Anti-predator behavior of squid throughout ontogeny.
44 45	2344	Journal of Experimental Marine Biology and Ecology 480, 26–35.
40 47 48	2345	YOUNG, B.A. & KARDONG, K.V. (2010). The functional morphology of hooding in cobras.
49 50	2346	Journal of Experimental Biology 213, 1521–1528.
51 52	2347	*YOUNG, J.Z. (1950). Life of Vertebrates. Oxford University Press, Holton, UK.
53 54 55	2348	
55 56 57 58 59 60	2349	XIII. SUPPORTING INFORMATION

2		
- 3 4	2350	Additional supporting information can be found online in the Supporting Information section
5 6	2351	at the end of the article.
7 8 0	2352	Table S1. Past descriptions of deimatic displays and terms used to describe the concept.
9 10 11	2353	Table S2. Deimatic behaviours in the context of other similar antipredator defences adapted
12 13	2354	from Umbers et al. (2017).
14 15	2355	Table S3. Descriptions of deimatic behaviour from the literature.
16 17 18	2356	Table S4. Comparison of the defensive strategies of juvenile and adult life stages of species
19 20	2357	for which both have been studied and at least one stage uses a deimatic display.
21 22	2358	Table S5. Summary of studies that have assessed the survival value of deimatic displays in
23 24 25	2359	prey.
26 27	2360	Table S6. Summary of studies that have assessed predator responses to deimatic displays.
28 29	2361	
30 31 32	2362	
33 34	2363	
35 36		
37 38 30		
39 40 41		
42 43		
44		
46		
47 48		
49		
50		
51 52		
53		
54		
55 56		
50 57		
58		

59 60

#### **FIGURE LEGENDS**

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

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

Page 99 of 199

#### **Biological Reviews**

their primary defence. The walnut sphinx caterpillar represents a deimatic sound, a sound that occurs only when a predator approaches or attempts subjugation; the sound acts as a deterrent but in this case is not coupled with a chemical defence (the sound would still be deimatic even if a chemical defence was present; and then would be both deimatic and aposematic). The peacock butterfly represents deimatic behaviour that includes a sound and a Batesian defence (eyespots). As far as is currently known mantises also fall into this category, as do cephalopods. The hash symbol on the peacock butterfly's caption 'I'm dangerous?!<sup>#</sup>' is intended to indicate that it is in fact not dangerous; the arrows indicate that the wings open and close and that this movement is repeated. The mountain katydid reveals its colourful abdomen as a predator attempts subjugation and then holds this posture and exudes defensive chemicals from the abdomen in a putative aposematic defence. Finally, the spotted lanternfly's primary defence is aposematism but it too has a deimatic element with the opening of its wings to reveal conspicuous colour patterns, followed by a second aposematic display as the colours are held exposed. If the lanternfly is consumed, the predator will encounter a bad taste and if the predator continues despite the bad taste and swallows the bug, the predator may regurgitate. Illustrations: Kate Umbers Fig. 3. Summary of the literature to date on deimatic behaviour showing (A) order of species studied, (B) components of deimatic behaviour, (C) type of primary defence for species in study, (D) order of predator species in study, (E) word cloud from the text of all descriptions of deimatic behaviour highlighting the most common phrases used. Illustration: James O'Hanlon. 

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

1 2		
- 3 4	2414	25 species of plethodontid salamanders. 1, Brodie & Howard (1972); 2, Brodie (1977); 3,
5 6	2415	Hubbard (1903).
7 8		
9 10		
11 12 12		
13 14 15		
16 17		
18 19		
20 21		
22 23 24		
25 26		
27 28		
29 30		
32 33		
34 35		
36 37		
38 39 40		
40 41 42		
43 44		
45 46		
47 48 40		
50 51		
52 53		
54 55		
56 57		
58 59 60		
50		



Figure 1

167x154mm (330 x 330 DPI)



Figure 2

275x190mm (330 x 330 DPI)









Figure 4

275x191mm (330 x 330 DPI)

# **Biological Reviews**

**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,	"Protection by Terrifying Enemies. A considerable number of quite	Terrifying enemies
p. 165)	acquired a resemblance to dangerous animals, or by some threatening or	Threatening or unusual appearance
	unusual appearance. This is obtained either by a modification of shape, of	
	habits, of colour, or of all combined."	
Poulton (1890, pp. 264, 259)	"terrifying attitude", "alarming attitude"	Terrifying attitude
Löhner (1919,	"Die charakteristischen Eigenschaften des Reflexes sind plözlicher Eintritt	Unkenreflex
p. 350)	vollständiger Bewegungslosgkeit in stets konstanter Körperhaltung,	
	Muskeltonussteigerung (bei verschiedenen Muskeln in verschiedenem	
	Grade), Lidschluss, Einstellung bzw. Verflachung des Kahluatspieles und	
	Steigerung der Hautsekretion"	
Noble (1931,	"The typical unken reflex is characterised not only by a distinctive posture	Unken reflex
pp. 380–381)	and immobility but also by a closure of the eyes, a slowing down of the	
	respiratory movements and an increase in the skin secretion"	

Page 106 of 199

Hingston (1933,	"each one has its mechanism for making it look more threatening when	Psychological fighting
p. 3)	face to face with a rival or enemy. It is the making of these gestures that I	
	call psychological fightingThe working of the mechanism makes the	
	animal look more terrible"	
Roonwal (1938,	"The purpose of this peculiar attitude appears to be to frighten away, by	Frightening attitude
p. 71)	suddenly turning at bay, its natural enemies"	
Cott (1940, pp.	"Sudden exhibitions of conspicuous colour." "The sudden appearance of	Intimidating displays
213, 232–233)	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."	
Page 107 of 199

Young (1950,	"Many frogs make a sudden exposure of brightly coloured patches on the	Dymantic
p. 28)	thighs as they jump. This presumably serves to startle the attacker and such	Startling
	colours may be called dymantic or startling	
Crane (1952, p.	""Startle display" or simply "display", covers the type of behavior in which	Startle display
261)	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."	
Blest (1957 <i>a</i> , p.	"Insects of several Orders possess special protective displays which are	Protective displays
257)	elicited by attacking predators, or by stimuli which resemble them"	
Hayes (1977, p.	"If immediate escape is not possible, the crayfish assumes: and intensifies a	Predator response postures
443)	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 orcha and incosta "	

Maldonado	"Mantids present other remarkable pattern of behaviour: a conspicuous	Frightening display
(1970, p. 61)	display when they are faced with a 'threat'. It was called with different	Startle response
	names by different authors: the 'frightening display', the 'startle response', the 'floral simulation'. It will be named the deimatic reaction (DR)	Deimatic reaction
	(G. δειματόω: I frighten)."	
Edmunds	"When discovered by a predator many animals respond by adopting a	Deimatic behaviour
(1974, p. 150)	characteristic posture which appears to be designed to intimidate the	Frightening behaviour
	predator I propose to use the term deimatic behaviour or frightening	6 6
	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".	
Schlenoff	"Startle mechanisms involve sudden conspicuous changes in the appearance	Deimatic displays, startle responses
(1985, p. 1057)	of behavior of prev which serve to confuse or alarm certain predators."	

Page 109 of 199

**Biological Reviews** 

Sargent (1990,	"There does seem to be agreement that startle is a secondary defense,	Startle stimulus / Startle response
p. 230)	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."	
Hanlon &	"Deimatic behaviour is threat, startle, frightening or bluff behaviour and in	Deimatic behaviour
Messenger	most cases it serves to make a predator hesitate during the close approach	
(1996, p. 79)	phase of attack"	
Kang <i>et al</i> .	"sudden movements of conspicuous body parts, which elicit startling	Startle effect
(2011, p. 709)	response in the predator"	
Stevens (2013,	"Startle displays: These are sudden conspicuous changes in appearance that	Startle displays
p. 147)	cause the predator to pause its attack, allowing the prey to escape or conceal	
	itself."	
Umbers <i>et al</i> .	"behaviour in which, when under attack, prey suddenly unleash	Deimatic displays
(2015, p. R58)	unexpected defences to frighten their predators and stop the attack'	

Page 110 of 199

**Biological Reviews** 

Kang et al	" a variety of chemically defended insects are rather cryptic when resting	Post-attack aposematic display / Facultativ
(2016, p, 1)	and only in response to predator attacks (post-attack) they perform displays	aposematic display
(2010, p. 1)	of conspicuous abdomens or hindwings normally hidden under forewings	uposemute display
	The function of those displays in unpalatable insects is not well understood	
	We examined two adaptive hypotheses on this facultative anosematic	
	display.	
	display	
Skelhorn <i>et al</i> .	"We propose that we define a deimatic display as any defensive display that	Deimatic display
(2016, p. e2)	causes a predator to misclassify a prey as a potential threat to its immediate	
· • •	safety'	
Umbers &	"a momentary, transient, conspicuous signal that induces a startle response or	Deimatic display
Mappes (2016,	overloads the senses of an attacking predator, such that the predator pauses,	
p. e7)	slows or stops the attack"	
Umbers <i>et al</i> .	"cause a receiver to recoil reflexively in response to a sudden change in	Deimatic or 'startle' displays
(2017, p. 1)	sensory input', "Crucially, unlike aposematism, reflexive responses to	
	transitory, i.e. deimatic, elements do not require learned or innate aversion."	
Badiane <i>et al</i> .	"Deimatic display theory is based on a fundamental tenet, that the	Deimatic display
(2018, p. 104)	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 "	

Page 111 of 199

**Biological Reviews** 

Holmes <i>et al</i> .	"Deimatic displays, for example, have long been recognised as a discrete	Deimatism
(2018, p. 1)	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	
	,, 	
Ferreira <i>et al</i> .	"Hidden aposematism occur in species that have aposematic color at the	Hidden aposematism
(2019, p. 7)	axila, underside of the body, tongue, thighs, or post-femoral region. These	1
(, r,	through escape or postures such as rear elevation, unken reflex, and death	
	feigning."	
Ruxton et al.	"Startling signals are secondary defences that occur after the focal prey	Startling signals
(2019, p. 179)	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."	
Loeffler-Henry	"Deimatic display involves the sudden exposure of a hidden signal that	Hidden contrasting color signals
<i>et al.</i> (2019, p.	induces a startle response or affects predator psychology/behavior in some	
3)	way to inhibit its attack"	

## **Biological Reviews**

**Table S2.** Deimatic behaviours in the context of other similar antipredator defences adapted from Umbers *et al.* (2017).<sup>1</sup>Not for movement and conspicuous colour pattern; <sup>2</sup>predator must have at least innate aversion of its own predator's eyes; <sup>3</sup>not without its model; <sup>4</sup>predators 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 Oedipoda germanica, black-tailed jackrabbit Lepus californicus	Giant African mantis Sphrodromantis lineola	Io moths (Automeris spp.), stick insect Ocotophasma martini	Mountain katydid (Acripeza reticulata), spotted lanternfly (Lycorma delicatula), caterpillar with regurgitate
Requires learned or innate						waal	
aversion	yes	yes	yes	110	110	yes	110
Requires an evolutionary							
history or environment	no	yes	yes	no	no	yes <sup>2</sup>	no
shared with model species							
Avoidance must be							
learned from the focal prey	yes	no	no	no	no	no	no
species itself							
Avoidance can be learned							
from the focal prey species	yes	yes	no <sup>3</sup>	no	yes	no	yes
itself							
Predators can learn to							
ignore the display	no	no	yes	yes	yes	yes	no <sup>4</sup>

3	Table S3. Descriptions	of deima	tic behaviou	r fro	m the literature	. NA: unclear from te
4 5	Citation	Year	Phylum		Class	Order
6	Carpenter (1938)	1938	Arthropoda		Insecta	Lepidoptera
7	Carpenter (1938)	1938	Arthropoda		Insecta	Lepidoptera
8	Carpenter (1938)	1938	Arthropoda		Insecta	Lepidoptera
9 10	Carpenter (1938)	1938	Arthropoda		Insecta	Lepidoptera
11	Carpenter (1938)	1938	Arthropoda		Insecta	Lepidoptera
12	$\frac{\text{Carpenter}(1938)}{\text{Roonwal}(1938)}$	1038	Arthropoda		Insecta	Mantodea
13 14	Vorlay (1020)	1020	Arthropoda		Insocta	Mantodoa
14	Varley $(1939)$	1939	Arthropoda		Insecta	Mantodea
16	Valley (1959)	1939	Mallugaa		Carbalanada	Samialaida
17	$\frac{1940}{2}$	1940	Arthronodo		Legnalopoda	Septotota Manta das
18 10	Crane (1952)	1952	Arthropoda		Insecta	Mantodea
20	Crane (1952)	1952	Arthropoda		Insecta	Mantodea
21	Crane (1952)	1952	Arthropoda		Insecta	Mantodea
22	Crane (1952)	1952	Arthropoda		Insecta	Mantodea
23 24	Crane (1952)	1952	Arthropoda		Insecta	Mantodea
25	Crane (1952)	1952	Arthropoda		Insecta	Mantodea
26	Crane (1952)	1952	Arthropoda		Insecta	Mantodea
27	Crane (1952)	1952	Arthropoda		Insecta	Mantodea
28 29	Carpenter (1955)	1955	Chordata		Amphibia	Urodela
30	Hanson & Vial (1956)	1956	Chordata		Amphibia	Anura
31	Bastock & Blest (1958	1958	Arthropoda		Insecta	Lepidoptera
32 33	Blest (1958)	1958	Arthropoda		Insecta	Lepidoptera
34	Blest (1958)	1958	Arthropoda		Insecta	Lepidoptera
35	Bedford & Chinnick (	1966	Arthropoda		Insecta	Phasmatodea
36	Bedford & Chinnick (	1966	Arthropoda		Insecta	Phasmatodea
37 38	Edmunds (1968)	1968	Mollusca		Gastropoda	Nudibranchia
39	Robinson (1968b)	1968	Arthropoda		Insecta	Phasmatodea
40	Robinson (1968a)	1968	Arthropoda		Insecta	Phasmatodea
41 42	Robinson (1969)	1969	Arthropoda		Insecta	Orthoptera
43	Robinson (1969)	1969	Arthropoda		Insecta	Mantodea
44	Robinson (1969)	1969	Arthropoda		Insecta	Mantodea
45	Robinson (1969)	1969	Arthropoda		Insecta	Mantodea
40 47	Robinson (1969)	1969	Arthropoda		Insecta	Orthoptera
48	Robinson (1969)	1969	Arthropoda		Insecta	Phasmatodea
49	Maldonado (1970)	1970	Arthropoda		Insecta	Mantodea
50 51	Balderrama & Maldor	1970	Arthropoda		Insecta	Mantodea
52	Dadwird & Sandara (1)	1071	Mollusoo		Conholonodo	Octopoda
53	Fackalu & Salueis $(1)$	19/1	Arthronodo		Inggata	Mantadaa
54 55	Edmunds $(1972)$	1972	Arthronode		Insecta	Mantodaa
55 56	Edmunds $(1972)$	1972			Insecta	Mantolea
57	Edmunds $(19/2)$	19/2	Arthropoda		insecta	Mantodea
58	Edmunds $(19/2)$	1972	Arthropoda		Insecta	Mantodea
59 60	Edmunds $(19/2)$	1972	Artnropoda		insecta	Mantodea

1 2				
3	Edmunds (1972)	1972 Arthropoda	Insecta	Mantodea
4 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 10	Edmunds (1972)	1972 Arthropoda	Insecta	Mantodea
11	Edmunds (1972)	1972 Arthropoda	Insecta	Mantodea
12	Edmunds (1972)	1972 Arthropoda	Insecta	Mantodea
13 14	Claridge (1974)	1974 Arthropoda	Insecta	Coleoptera
15	Johnson & Brodie (19	1975 Chordata	Amphibia	Urodela
16 17	Edmunds (1976)	1976 Arthropoda	Insecta	Mantodea
17	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
23	Edmunds (1976)	1976 Arthropoda	Insecta	Mantodea
24 25	Edmunds (1976)	1976 Arthropoda	Insecta	Mantodea
25 26	Edmunds (1976)	1976 Arthropoda	Insecta	Mantodea
27	Edmunds (1976)	1976 Arthropoda	Insecta	Mantodea
28	Eisner & Adams (197:	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 34	Brodie (1977)	1977 Chordata	Amphibia	Urodela
35	Brodie (1977)	1977 Chordata	Amphibia	Urodela
36	Brodie (1977)	1977 Chordata	Amphibia	Urodela
37 38	Brodie (1977)	1977 Chordata	Amphibia	Urodela
39	Brodie (1977)	1977 Chordata	Amphibia	Urodela
40	Brodie (1977)	1977 Chordata	Amphibia	Urodela
41 42	Brodie (1977)	1977 Chordata	Amphibia	Urodela
43	Brodie (1977)	1977 Chordata	Amphibia	Urodela
44 45	Brodie (1977)	1977 Chordata	Amphibia	Urodela
45 46	Brodie (1977)	1977 Chordata	Amphibia	Urodela
47	Brodie (1977)	1977 Chordata	Amphibia	Urodela
48	Brodie (1977)	1977 Chordata	Amphibia	Urodela
49 50	Brodie (1977)	1977 Chordata	Amphibia	Urodela
51	Brodie (1977)	1977 Chordata	Amphibia	Urodela
52	Brodie (1977)	1977 Chordata	Amphibia	Urodela
53 54	Brodie (1977)	1977 Chordata	Amphibia	Urodela
55	Brodie (1977)	1977 Chordata	Amphibia	Urodela
56	Brodie (1977)	1977 Chordata	Amphibia	Urodela
57 58	Brodie (1977)	1977 Chordata	Amphibia	Urodela
59	Brodie (1977)	1977 Chordata	Amphibia	Urodela
60				

1				
2				
3 4	Brodie (1977)	1977 Chordata	Amphibia	Urodela
4 5	Brodie (1977)	1977 Chordata	Amphibia	Urodela
6	Brodie (1977)	1977 Chordata	Amphibia	Urodela
7	Brodie (1977)	1977 Chordata	Amphibia	Urodela
8	Brodie (1977)	1977 Chordata	Amphibia	Urodela
9 10	Brodie (1977)	1977 Chordata	Amphibia	Urodela
11	Brodie (1977)	1977 Chordata	Amphibia	Urodela
12	Brodie (1977)	1977 Chordata	Amphibia	Urodela
13 14	Brodie (1977)	1977 Chordata	Amphibia	Urodela
15	Brodie (1977)	1977 Chordata	Amphibia	Urodela
16	Brodie $(1977)$	1977 Chordata	Amphibia	Urodela
17	1000000000000000000000000000000000000	1077 Chordata	Amphibia	Urodola
10	Diodic $(1977)$	1977 Chordata	Amphibia	Uradala
20	Drodie (1977)	1977 Chordata	Amphibia	
21	Brodie $(1977)$	1977 Chordata	Amphibia	Urodela
22	Brodie (19/7)	1977 Chordata	Amphibia	Urodela
23	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
29	Brodie (1977)	1977 Chordata	Amphibia	Urodela
30	Brodie (1977)	1977 Chordata	Amphibia	Urodela
31	Brodie (1977)	1977 Chordata	Amphibia	Urodela
32 33	Brodie (1977)	1977 Chordata	Amphibia	Urodela
34	Brodie (1977)	1977 Chordata	Amphibia	Urodela
35	Brodie (1977)	1977 Chordata	Amphibia	Urodela
36 27	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 42	Brodie (1977)	1977 Chordata	Amphibia 🛀	Urodela
43	Brodie (1977)	1977 Chordata	Amphibia	Urodela
44	Brodie (1977)	1977 Chordata	Amphibia	Urodela
45 46	Brodie (1977)	1977 Chordata	Amphibia	Urodela
40	Brodie (1977)	1977 Chordata	Amphibia	Urodela
48	Brodie (1977)	1977 Chordata	Amphibia	Urodela
49	Brodie (1977)	1977 Chordata	Amphibia	Urodela
50 51	Brodie (1977)	1977 Chordata	Amphibia	Urodela
52	Brodie $(1977)$	1977 Chordata	Amphibia	Urodela
53	Diodie $(1977)$ Drodie $(1077)$	1977 Chordata	Amphibia	Urodola
54 55	$U_{\rm avec}(1977)$	1977 Arthropodo	Malagostraga	Decenada
55 56	$\frac{11}{10000} (1977)$	1077 Anthrop 1	Malacostraca	Decapoda
57	Haves(1977)	19// Armropoda	Malacostraca	Decapoda
58	nayes (1977)	19// Arthropoda	Iviaiacostraca	Decapoda
59 60	$Evans(19/\delta)$	1978 Armropoda	msecta	Lepidoptera

2				
3	Evans (1978)	1978 Arthropoda	Insecta	Lepidoptera
4	Nowak & Brodie (197	1978 Chordata	Amphibia	Urodela
6	Sandow & Bailey (19)	1978 Arthropoda	Insecta	Orthoptera
7	Bajger (1980)	1980 Chordata	Amphibia	Anura
8	Bajger (1980)	1980 Chordata	Amphibia	Anura
10	DiGiovanni & Brodie	1981 Chordata	Amphibia	Urodela
11	Steiner (1981)	1981 Arthropoda	Insecta	Orthoptera
12	Schal et al. (1982)	1982 Arthropoda	Insecta	Blattodea
13	Bailey & Sandow (19)	1983 Arthropoda	Insecta	Orthoptera
15	Brodie et al. (1984)	1984 Chordata	Amphibia	Urodela
16	Brodie et al. (1984)	1984 Chordata	Amphibia	Urodela
1/ 18	Brodie et al. (1984)	1984 Chordata	Amphibia	Urodela
19	Brodie et al. $(1984)$	1984 Chordata	Amphibia	Urodela
20	Brodie et al. $(1984)$	1984 Chordata	Amphibia	Urodela
21	$\frac{1904}{1004}$	1984 Chordata	Amphibia	Urodala
22	Hödl & Collmon (109	1964 Chordata	Amphibia	
24	Hödl & Gollman (198	1980 Chordata	Amphibia	Anura
25	Houl & Gollman (198	1980 Chordata	Amphibia	Anura
26 27	Hodi & Goliman (198	1986 Chordata	Amphibia	Anura
28	Hodi & Goliman (198	1986 Chordata	Amphibia	Anura
29	Hödl & Gollman (198	1986 Chordata	Amphibia	Anura
30	Hödl & Gollman (198	1986 Chordata	Amphibia	Anura
31 32	Hödl & Gollman (198	1986 Chordata	Amphibia	Anura
33	Hödl & Gollman (198	1986 Chordata	Amphibia	Anura
34	Hödl & Gollman (198	1986 Chordata	Amphibia	Anura
35	Green (1988)	1988 Chordata	Amphibia	Anura
37	Green (1988)	1988 Chordata	Amphibia	Anura
38	Green (1988)	1988 Chordata	Amphibia	Anura
39	Lyon & Fogden (1989	1989 Chordata	Aves	Eurypygiformes
40 41	Martins (1989)	1989 Chordata	Amphibia	Anura
42	Fenton & Licht (1990)	1990 Chordata	Reptilia 🔪 🥌	Squamata
43	Fenton & Licht (1990)	1990 Chordata	Reptilia	Squamata
44 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	Fenton & Licht (1990)	1990 Chordata	Reptilia	Squamata
49 50	Thomas & Strahl (199	1990 Chordata	Aves	Eurypygiformes
51	Castner & Nickle (199	1995 Arthropoda	Insecta	Orthoptera
52	Field & Bailey (1997)	1997 Arthropoda	Insecta	Orthoptera
53 54	Field & Bailey (1997)	1997 Arthropoda	Insecta	Orthoptera
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 59	Brodie et al. (1998)	1998 Chordata	Amphibia	Anura
60	210410 01 41. (1990)	1770 Chorunn	. mpmon	

Amphibia

Ophuroidea

Amphibia

Amphibia

Amphibia

Amphibia

Amphibia

Amphibia

Amphibia

Amphibia

Insecta

Insecta Insecta

Insecta

Insecta

Reptilia

Reptilia

Insecta

Reptilia

Insecta

Insecta

Insecta

Insecta

Reptilia Insecta

Reptilia

Insecta

Insecta

Insecta

Insecta

Insecta

Insecta Insecta

Insecta Insecta

Insecta

2		
3	Brodie et al. (1998)	1998 Chordata
4 5	Grandcolas & Desutte	1998 Arthropoda
6	Sköld (1998)	1998 Echinodermata
7	Choi et al. (1999)	1999 Chordata
8	Williams et al. (2000)	2000 Chordata
9 10	Williams et al. (2000)	2000 Chordata
10	Williams et al. $(2000)$	2000 Chordata
12	Williams et al. $(2000)$	2000 Chordata
13	Williams et al. $(2000)$	2000 Chordata
14 15	Toledo et al. (2004a)	2004 Chordata
15	Vester et al. (2004)	2004 Chordata
17	Lenzi-Mattos et al. (20	2005 Chordata
18	Toledo et al. (2004b)	2005 Chordata
19 20	Vallin et al. (2005)	2005 Arthropoda
20 21	Adamo et al. (2006)	2006 Mollusca
22	Langridge (2006)	2006 Mollusca
23	Vallin et al. (2006)	2006 Arthropoda
24	Brown et al. (2007)	2007 Arthropoda
25 26	Hill (2007)	2007 Arthropoda
27	Langridge et al. (2007	2007 Mollusca
28	Vallin et al. (2007)	2007 Arthropoda
29	Sorafim & Pibaira Du	2007 Multipodd 2008 Chardata
30 31	Serafim & Ribeiro Du	2008 Chordata
32	Description of the second description of the	2008 Chordata
33	Bouwma & Herrnkind	2009 Arthropoda
34	Bura et al. (2009)	2009 Arthropoda
35 36	Tozetti et al. (2009)	2009 Chordata
37	Olofsson et al. (2012b	2012 Arthropoda
38	Olofsson et al. (2012a)	2012 Arthropoda
39	Ruiz et al. (2012)	2012 Mollusca
40 41	Cartron et al. (2013)	2013 Mollusca
42	Kowalski et al. (2014)	2014 Arthropoda
43	Umbers & Mappes (20	2015 Arthropoda
44	Whiting et al. (2015)	2015 Chordata
45 46	Kang et al. (2016)	2016 Arthropoda
47	Badiane et al. (2018)	2018 Chordata
48	O'Hanlon et al. $(2018)$	2018 Arthropoda
49 50	O'Hanlon et al. $(2018)$	2018 Arthropoda
50 51	O'Hanlon et al. $(2018)$	2018 Arthropoda
52	Umbers at al. (2010)	2010 Arthropoda
53	Direct $(1057h)$	2019 Arthropoda
54	Diest $(193/0)$	1957 Arthropoda
55 56	Blest (195/b)	195/ Arthropoda
57	Blest (1957a)	1957 Arthropoda
58	Blest (1957a)	1957 Arthropoda
59	Blest (1957a)	1957 Arthropoda
60		

Anura Mantodea Ophiurida Anura Anura Anura Anura Anura Anura Actinopterygii Gadiformes Anura Anura Lepidoptera Cephalopoda Sepioloida Cephalopoda Sepioloida Lepidoptera Lepidoptera Mantodea Cephalopoda Sepioloida Lepidoptera Squamata Squamata Malacostraca Decapoda Lepidoptera Squamata Lepidoptera Lepidoptera Cephalopoda Octopoda Cephalopoda Sepioloida Orthoptera Orthoptera Squamata Hemiptera Squamata Mantodea Mantodea Mantodea Orthoptera Lepidoptera Lepidoptera Lepidoptera Lepidoptera Lepidoptera

3Blest (1957a)1957 ArthropodaInsectaLepidoptera5Blest (1957a)1957 ArthropodaInsectaLepidoptera6Blest (1957a)1957 ArthropodaInsectaLepidoptera7Blest (1957a)1957 ArthropodaInsectaLepidoptera9Blest (1957a)1957 ArthropodaInsectaLepidoptera10Blest (1957a)1957 ArthropodaInsectaLepidoptera11Blest (1957a)1957 ArthropodaInsectaLepidoptera12Blest (1957a)1957 ArthropodaInsectaLepidoptera13Blest (1957a)1957 ArthropodaInsectaLepidoptera14Blest (1957a)1957 ArthropodaInsectaLepidoptera15Blest (1957a)1957 ArthropodaInsectaLepidoptera16Blest (1957a)1957 ArthropodaInsectaLepidoptera17Blest (1957a)1957 ArthropodaInsectaLepidoptera18Blest (1957a)1957 ArthropodaInsectaLepidoptera20Blest (1957a)1957 ArthropodaInsectaLepidoptera21Blest (1957a)1957 ArthropodaInsectaLepidoptera22Blest (1957a)1957 ArthropodaInsectaLepidoptera23Blest (1957a)1957 ArthropodaInsectaLepidoptera24Blest (1957a)1957 ArthropodaInsectaLepidoptera25Blest (1957a)1957 ArthropodaInsectaLepidoptera <tr< th=""><th>1</th><th></th><th></th><th></th><th></th></tr<>	1				
4Blest (1957a)1957 ArthropodaInsectaLepidoptera5Blest (1957a)1957 ArthropodaInsectaLepidoptera7Blest (1957a)1957 ArthropodaInsectaLepidoptera9Blest (1957a)1957 ArthropodaInsectaLepidoptera10Blest (1957a)1957 ArthropodaInsectaLepidoptera11Blest (1957a)1957 ArthropodaInsectaLepidoptera12Blest (1957a)1957 ArthropodaInsectaLepidoptera13Blest (1957a)1957 ArthropodaInsectaLepidoptera14Blest (1957a)1957 ArthropodaInsectaLepidoptera15Blest (1957a)1957 ArthropodaInsectaLepidoptera16Blest (1957a)1957 ArthropodaInsectaLepidoptera17Blest (1957a)1957 ArthropodaInsectaLepidoptera18Blest (1957a)1957 ArthropodaInsectaLepidoptera20Blest (1957a)1957 ArthropodaInsectaLepidoptera21Blest (1957a)1957 ArthropodaInsectaLepidoptera22Blest (1957a)1957 ArthropodaInsectaLepidoptera23Blest (1957a)1957 ArthropodaInsectaLepidoptera24Blest (1957a)1957 ArthropodaInsectaLepidoptera25Blest (1957a)1957 ArthropodaInsectaLepidoptera26Blest (1957a)1957 ArthropodaInsectaLepidoptera <t< td=""><td>2</td><td><math>\mathbf{D}_{1}</math> (1057.)</td><td></td><td>T /</td><td><b>T 1</b></td></t<>	2	$\mathbf{D}_{1}$ (1057.)		T /	<b>T 1</b>
5Blest (1957a)1957ArthropodaInsectaLepidoptera6Blest (1957a)1957ArthropodaInsectaLepidoptera7Blest (1957a)1957ArthropodaInsectaLepidoptera9Blest (1957a)1957ArthropodaInsectaLepidoptera10Blest (1957a)1957ArthropodaInsectaLepidoptera11Blest (1957a)1957ArthropodaInsectaLepidoptera12Blest (1957a)1957ArthropodaInsectaLepidoptera13Blest (1957a)1957ArthropodaInsectaLepidoptera14Blest (1957a)1957ArthropodaInsectaLepidoptera15Blest (1957a)1957ArthropodaInsectaLepidoptera16Blest (1957a)1957ArthropodaInsectaLepidoptera17Blest (1957a)1957ArthropodaInsectaLepidoptera18Blest (1957a)1957ArthropodaInsectaLepidoptera20Blest (1957a)1957ArthropodaInsectaLepidoptera21Blest (1957a)1957ArthropodaInsectaLepidoptera22Blest (1957a)1957ArthropodaInsectaLepidoptera23Blest (1957a)1957ArthropodaInsectaLepidoptera24Blest (1957a)1957ArthropodaInsectaLepidoptera25Blest (1957a)1957Arthropo	4	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
6Blest (1957a)1957 ArthropodaInsectaLepidoptera7Blest (1957a)1957 ArthropodaInsectaLepidoptera9Blest (1957a)1957 ArthropodaInsectaLepidoptera10Blest (1957a)1957 ArthropodaInsectaLepidoptera11Blest (1957a)1957 ArthropodaInsectaLepidoptera12Blest (1957a)1957 ArthropodaInsectaLepidoptera13Blest (1957a)1957 ArthropodaInsectaLepidoptera14Blest (1957a)1957 ArthropodaInsectaLepidoptera15Blest (1957a)1957 ArthropodaInsectaLepidoptera16Blest (1957a)1957 ArthropodaInsectaLepidoptera17Blest (1957a)1957 ArthropodaInsectaLepidoptera18Blest (1957a)1957 ArthropodaInsectaLepidoptera20Blest (1957a)1957 ArthropodaInsectaLepidoptera23Blest (1957a)1957 ArthropodaInsectaLepidoptera24Blest (1957a)1957 ArthropodaInsectaLepidoptera25Blest (1957a)1957 ArthropodaInsectaLepidoptera26Blest (1957a)1957 ArthropodaInsectaLepidoptera27Blest (1957a)1957 ArthropodaInsectaLepidoptera28Blest (1957a)1957 ArthropodaInsectaLepidoptera29Blest (1957a)1957 ArthropodaInsectaLepidoptera<	5	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
9Blest (1957a)1957 ArthropodaInsectaLepidoptera9Blest (1957a)1957 ArthropodaInsectaLepidoptera10Blest (1957a)1957 ArthropodaInsectaLepidoptera11Blest (1957a)1957 ArthropodaInsectaLepidoptera12Blest (1957a)1957 ArthropodaInsectaLepidoptera13Blest (1957a)1957 ArthropodaInsectaLepidoptera14Blest (1957a)1957 ArthropodaInsectaLepidoptera15Blest (1957a)1957 ArthropodaInsectaLepidoptera18Blest (1957a)1957 ArthropodaInsectaLepidoptera19Blest (1957a)1957 ArthropodaInsectaLepidoptera20Blest (1957a)1957 ArthropodaInsectaLepidoptera21Blest (1957a)1957 ArthropodaInsectaLepidoptera22Blest (1957a)1957 ArthropodaInsectaLepidoptera23Blest (1957a)1957 ArthropodaInsectaLepidoptera24Blest (1957a)1957 ArthropodaInsectaLepidoptera25Blest (1957a)1957 ArthropodaInsectaLepidoptera26Blest (1957a)1957 ArthropodaInsectaLepidoptera27Blest (1957a)1957 ArthropodaInsectaLepidoptera28Blest (1957a)1957 ArthropodaInsectaLepidoptera29Blest (1957a)1957 ArthropodaInsectaLepidoptera	6	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
9Blest (1957a)1957 ArthropodaInsectaLepidoptera10Blest (1957a)1957 ArthropodaInsectaLepidoptera11Blest (1957a)1957 ArthropodaInsectaLepidoptera12Blest (1957a)1957 ArthropodaInsectaLepidoptera13Blest (1957a)1957 ArthropodaInsectaLepidoptera14Blest (1957a)1957 ArthropodaInsectaLepidoptera15Blest (1957a)1957 ArthropodaInsectaLepidoptera16Blest (1957a)1957 ArthropodaInsectaLepidoptera17Blest (1957a)1957 ArthropodaInsectaLepidoptera18Blest (1957a)1957 ArthropodaInsectaLepidoptera20Blest (1957a)1957 ArthropodaInsectaLepidoptera21Blest (1957a)1957 ArthropodaInsectaLepidoptera22Blest (1957a)1957 ArthropodaInsectaLepidoptera23Blest (1957a)1957 ArthropodaInsectaLepidoptera24Blest (1957a)1957 ArthropodaInsectaLepidoptera25Blest (1957a)1957 ArthropodaInsectaLepidoptera26Blest (1957a)1957 ArthropodaInsectaLepidoptera27Blest (1957a)1957 ArthropodaInsectaLepidoptera28Blest (1957a)1957 ArthropodaInsectaLepidoptera29Blest (1957a)1957 ArthropodaInsectaLepidoptera <td>/ 8</td> <td>Blest (1957a)</td> <td>1957 Arthropoda</td> <td>Insecta</td> <td>Lepidoptera</td>	/ 8	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
10Blest (1957a)1957 ArthropodaInsectaLepidoptera11Blest (1957a)1957 ArthropodaInsectaLepidoptera12Blest (1957a)1957 ArthropodaInsectaLepidoptera13Blest (1957a)1957 ArthropodaInsectaLepidoptera14Blest (1957a)1957 ArthropodaInsectaLepidoptera15Blest (1957a)1957 ArthropodaInsectaLepidoptera16Blest (1957a)1957 ArthropodaInsectaLepidoptera17Blest (1957a)1957 ArthropodaInsectaLepidoptera19Blest (1957a)1957 ArthropodaInsectaLepidoptera20Blest (1957a)1957 ArthropodaInsectaLepidoptera21Blest (1957a)1957 ArthropodaInsectaLepidoptera22Blest (1957a)1957 ArthropodaInsectaLepidoptera23Blest (1957a)1957 ArthropodaInsectaLepidoptera24Blest (1957a)1957 ArthropodaInsectaLepidoptera25Blest (1957a)1957 ArthropodaInsectaLepidoptera26Blest (1957a)1957 ArthropodaInsectaLepidoptera27Blest (1957a)1957 ArthropodaInsectaLepidoptera28Blest (1957a)1957 ArthropodaInsectaLepidoptera30Blest (1957a)1957 ArthropodaInsectaLepidoptera31Blest (1957a)1957 ArthropodaInsectaLepidoptera <td>9</td> <td>Blest (1957a)</td> <td>1957 Arthropoda</td> <td>Insecta</td> <td>Lepidoptera</td>	9	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
11 12 13Blest (1957a)1957 ArthropodaInsectaLepidoptera13 14 	10	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
12Blest (1957a)1957 ArthropodaInsectaLepidoptera14Blest (1957a)1957 ArthropodaInsectaLepidoptera15Blest (1957a)1957 ArthropodaInsectaLepidoptera16Blest (1957a)1957 ArthropodaInsectaLepidoptera17Blest (1957a)1957 ArthropodaInsectaLepidoptera18Blest (1957a)1957 ArthropodaInsectaLepidoptera20Blest (1957a)1957 ArthropodaInsectaLepidoptera21Blest (1957a)1957 ArthropodaInsectaLepidoptera22Blest (1957a)1957 ArthropodaInsectaLepidoptera23Blest (1957a)1957 ArthropodaInsectaLepidoptera24Blest (1957a)1957 ArthropodaInsectaLepidoptera25Blest (1957a)1957 ArthropodaInsectaLepidoptera26Blest (1957a)1957 ArthropodaInsectaLepidoptera27Blest (1957a)1957 ArthropodaInsectaLepidoptera28Blest (1957a)1957 ArthropodaInsectaLepidoptera29Blest (1957a)1957 ArthropodaInsectaLepidoptera31Blest (1957a)1957 ArthropodaInsectaLepidoptera32Blest (1957a)1957 ArthropodaInsectaLepidoptera33Blest (1957a)1957 ArthropodaInsectaLepidoptera34Blest (1957a)1957 ArthropodaInsectaLepidoptera <td>11 12</td> <td>Blest (1957a)</td> <td>1957 Arthropoda</td> <td>Insecta</td> <td>Lepidoptera</td>	11 12	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
14Blest (1957a)1957 ArthropodaInsectaLepidoptera15Blest (1957a)1957 ArthropodaInsectaLepidoptera16Blest (1957a)1957 ArthropodaInsectaLepidoptera17Blest (1957a)1957 ArthropodaInsectaLepidoptera18Blest (1957a)1957 ArthropodaInsectaLepidoptera20Blest (1957a)1957 ArthropodaInsectaLepidoptera21Blest (1957a)1957 ArthropodaInsectaLepidoptera22Blest (1957a)1957 ArthropodaInsectaLepidoptera23Blest (1957a)1957 ArthropodaInsectaLepidoptera24Blest (1957a)1957 ArthropodaInsectaLepidoptera25Blest (1957a)1957 ArthropodaInsectaLepidoptera26Blest (1957a)1957 ArthropodaInsectaLepidoptera27Blest (1957a)1957 ArthropodaInsectaLepidoptera28Blest (1957a)1957 ArthropodaInsectaLepidoptera29Blest (1957a)1957 ArthropodaInsectaLepidoptera31Blest (1957a)1957 ArthropodaInsectaLepidoptera32Blest (1957a)1957 ArthropodaInsectaLepidoptera33Blest (1957a)1957 ArthropodaInsectaLepidoptera34Blest (1957a)1957 ArthropodaInsectaLepidoptera35Blest (1957a)1957 ArthropodaInsectaLepidoptera <td>12</td> <td>Blest (1957a)</td> <td>1957 Arthropoda</td> <td>Insecta</td> <td>Lepidoptera</td>	12	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
15 16 17Blest (1957a)1957 ArthropodaInsectaLepidoptera17 18 	14	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
16Blest (1957a)1957 ArthropodaInsectaLepidoptera17Blest (1957a)1957 ArthropodaInsectaLepidoptera19Blest (1957a)1957 ArthropodaInsectaLepidoptera20Blest (1957a)1957 ArthropodaInsectaLepidoptera21Blest (1957a)1957 ArthropodaInsectaLepidoptera22Blest (1957a)1957 ArthropodaInsectaLepidoptera23Blest (1957a)1957 ArthropodaInsectaLepidoptera24Blest (1957a)1957 ArthropodaInsectaLepidoptera25Blest (1957a)1957 ArthropodaInsectaLepidoptera26Blest (1957a)1957 ArthropodaInsectaLepidoptera27Blest (1957a)1957 ArthropodaInsectaLepidoptera28Blest (1957a)1957 ArthropodaInsectaLepidoptera29Blest (1957a)1957 ArthropodaInsectaLepidoptera31Blest (1957a)1957 ArthropodaInsectaLepidoptera32Blest (1957a)1957 ArthropodaInsectaLepidoptera33Blest (1957a)1957 ArthropodaInsectaLepidoptera34Blest (1957a)1957 ArthropodaInsectaLepidoptera35Blest (1957a)1957 ArthropodaInsectaLepidoptera36Blest (1957a)1957 ArthropodaInsectaLepidoptera37Blest (1957a)1957 ArthropodaInsectaLepidoptera <td>15</td> <td>Blest (1957a)</td> <td>1957 Arthropoda</td> <td>Insecta</td> <td>Lepidoptera</td>	15	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
18Blest (1957a)1957 ArthropodaInsectaLepidoptera19Blest (1957a)1957 ArthropodaInsectaLepidoptera20Blest (1957a)1957 ArthropodaInsectaLepidoptera21Blest (1957a)1957 ArthropodaInsectaLepidoptera22Blest (1957a)1957 ArthropodaInsectaLepidoptera23Blest (1957a)1957 ArthropodaInsectaLepidoptera24Blest (1957a)1957 ArthropodaInsectaLepidoptera25Blest (1957a)1957 ArthropodaInsectaLepidoptera26Blest (1957a)1957 ArthropodaInsectaLepidoptera27Blest (1957a)1957 ArthropodaInsectaLepidoptera28Blest (1957a)1957 ArthropodaInsectaLepidoptera30Blest (1957a)1957 ArthropodaInsectaLepidoptera31Blest (1957a)1957 ArthropodaInsectaLepidoptera32Blest (1957a)1957 ArthropodaInsectaLepidoptera33Blest (1957a)1957 ArthropodaInsectaLepidoptera34Blest (1957a)1957 ArthropodaInsectaLepidoptera35Blest (1957a)1957 ArthropodaInsectaLepidoptera36Blest (1957a)1957 ArthropodaInsectaLepidoptera37Blest (1957a)1957 ArthropodaInsectaLepidoptera38Blest (1957a)1957 ArthropodaInsectaLepidoptera <td>16 17</td> <td>Blest (1957a)</td> <td>1957 Arthropoda</td> <td>Insecta</td> <td>Lepidoptera</td>	16 17	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
19 20 21Blest (1957a)1957 ArthropodaInsectaLepidoptera21 22 	18	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
20 21Blest (1957a)1957 ArthropodaInsectaLepidoptera22 22 23Blest (1957a)1957 ArthropodaInsectaLepidoptera23 24 25 26Blest (1957a)1957 ArthropodaInsectaLepidoptera24 25 26 27 28 28 29 30Blest (1957a)1957 ArthropodaInsectaLepidoptera26 27 28 29 30 30Blest (1957a)1957 ArthropodaInsectaLepidoptera27 29 30 31 31 31 31 32 32 32 32 33 32 34 35 36 36 36 36 36 36 36 37 31 310 310 32 32 33 33 34 34 34 34 34 34 34 35 34 <td>19</td> <td>Blest (1957a)</td> <td>1957 Arthropoda</td> <td>Insecta</td> <td>Lepidoptera</td>	19	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
21Blest (1957a)1957 ArthropodaInsectaLepidoptera23Blest (1957a)1957 ArthropodaInsectaLepidoptera24Blest (1957a)1957 ArthropodaInsectaLepidoptera25Blest (1957a)1957 ArthropodaInsectaLepidoptera26Blest (1957a)1957 ArthropodaInsectaLepidoptera27Blest (1957a)1957 ArthropodaInsectaLepidoptera28Blest (1957a)1957 ArthropodaInsectaLepidoptera29Blest (1957a)1957 ArthropodaInsectaLepidoptera30Blest (1957a)1957 ArthropodaInsectaLepidoptera31Blest (1957a)1957 ArthropodaInsectaLepidoptera32Blest (1957a)1957 ArthropodaInsectaLepidoptera33Blest (1957a)1957 ArthropodaInsectaLepidoptera34Blest (1957a)1957 ArthropodaInsectaLepidoptera35Blest (1957a)1957 ArthropodaInsectaLepidoptera36Blest (1957a)1957 ArthropodaInsectaLepidoptera37Blest (1957a)1957 ArthropodaInsectaLepidoptera38Blest (1957a)1957 ArthropodaInsectaLepidoptera39Blest (1957a)1957 ArthropodaInsectaLepidoptera40Blest (1957a)1957 ArthropodaInsectaLepidoptera41Blest (1957a)1957 ArthropodaInsectaLepidoptera <td>20</td> <td>Blest (1957a)</td> <td>1957 Arthropoda</td> <td>Insecta</td> <td>Lepidoptera</td>	20	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
23Blest (1957a)1957 ArthropodaInsectaLepidoptera24Blest (1957a)1957 ArthropodaInsectaLepidoptera26Blest (1957a)1957 ArthropodaInsectaLepidoptera27Blest (1957a)1957 ArthropodaInsectaLepidoptera28Blest (1957a)1957 ArthropodaInsectaLepidoptera29Blest (1957a)1957 ArthropodaInsectaLepidoptera30Blest (1957a)1957 ArthropodaInsectaLepidoptera31Blest (1957a)1957 ArthropodaInsectaLepidoptera32Blest (1957a)1957 ArthropodaInsectaLepidoptera33Blest (1957a)1957 ArthropodaInsectaLepidoptera34Blest (1957a)1957 ArthropodaInsectaLepidoptera35Blest (1957a)1957 ArthropodaInsectaLepidoptera36Blest (1957a)1957 ArthropodaInsectaLepidoptera37Blest (1957a)1957 ArthropodaInsectaLepidoptera38Blest (1957a)1957 ArthropodaInsectaLepidoptera39Blest (1957a)1957 ArthropodaInsectaLepidoptera41Blest (1957a)1957 ArthropodaInsectaLepidoptera42Blest (1957a)1957 ArthropodaInsectaLepidoptera43Blest (1957a)1957 ArthropodaInsectaLepidoptera44Blest (1957a)1957 ArthropodaInsectaLepidoptera <td>22</td> <td>Blest (1957a)</td> <td>1957 Arthropoda</td> <td>Insecta</td> <td>Lepidoptera</td>	22	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
24Blest (1957a)1957 ArthropodaInsectaLepidoptera26Blest (1957a)1957 ArthropodaInsectaLepidoptera27Blest (1957a)1957 ArthropodaInsectaLepidoptera28Blest (1957a)1957 ArthropodaInsectaLepidoptera29Blest (1957a)1957 ArthropodaInsectaLepidoptera30Blest (1957a)1957 ArthropodaInsectaLepidoptera31Blest (1957a)1957 ArthropodaInsectaLepidoptera32Blest (1957a)1957 ArthropodaInsectaLepidoptera33Blest (1957a)1957 ArthropodaInsectaLepidoptera34Blest (1957a)1957 ArthropodaInsectaLepidoptera35Blest (1957a)1957 ArthropodaInsectaLepidoptera36Blest (1957a)1957 ArthropodaInsectaLepidoptera37Blest (1957a)1957 ArthropodaInsectaLepidoptera38Blest (1957a)1957 ArthropodaInsectaLepidoptera39Blest (1957a)1957 ArthropodaInsectaLepidoptera41Blest (1957a)1957 ArthropodaInsectaLepidoptera42Blest (1957a)1957 ArthropodaInsectaLepidoptera43Blest (1957a)1957 ArthropodaInsectaLepidoptera44Blest (1957a)1957 ArthropodaInsectaLepidoptera45Blest (1957a)1957 ArthropodaInsectaLepidoptera <td>23</td> <td>Blest (1957a)</td> <td>1957 Arthropoda</td> <td>Insecta</td> <td>Lepidoptera</td>	23	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
25Blest (1957a)1957 ArthropodaInsectaLepidoptera27Blest (1957a)1957 ArthropodaInsectaLepidoptera28Blest (1957a)1957 ArthropodaInsectaLepidoptera29Blest (1957a)1957 ArthropodaInsectaLepidoptera30Blest (1957a)1957 ArthropodaInsectaLepidoptera31Blest (1957a)1957 ArthropodaInsectaLepidoptera32Blest (1957a)1957 ArthropodaInsectaLepidoptera33Blest (1957a)1957 ArthropodaInsectaLepidoptera34Blest (1957a)1957 ArthropodaInsectaLepidoptera35Blest (1957a)1957 ArthropodaInsectaLepidoptera36Blest (1957a)1957 ArthropodaInsectaLepidoptera37Blest (1957a)1957 ArthropodaInsectaLepidoptera38Blest (1957a)1957 ArthropodaInsectaLepidoptera39Blest (1957a)1957 ArthropodaInsectaLepidoptera40Blest (1957a)1957 ArthropodaInsectaLepidoptera41Blest (1957a)1957 ArthropodaInsectaLepidoptera42Blest (1957a)1957 ArthropodaInsectaLepidoptera43Blest (1957a)1957 ArthropodaInsectaLepidoptera44Blest (1957a)1957 ArthropodaInsectaLepidoptera45Blest (1957a)1957 ArthropodaInsectaLepidoptera <td>24 25</td> <td>Blest (1957a)</td> <td>1957 Arthropoda</td> <td>Insecta</td> <td>Lepidoptera</td>	24 25	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
27Blest (1957a)1957 ArthropodaInsectaLepidoptera28Blest (1957a)1957 ArthropodaInsectaLepidoptera29Blest (1957a)1957 ArthropodaInsectaLepidoptera30Blest (1957a)1957 ArthropodaInsectaLepidoptera31Blest (1957a)1957 ArthropodaInsectaLepidoptera32Blest (1957a)1957 ArthropodaInsectaLepidoptera33Blest (1957a)1957 ArthropodaInsectaLepidoptera34Blest (1957a)1957 ArthropodaInsectaLepidoptera35Blest (1957a)1957 ArthropodaInsectaLepidoptera36Blest (1957a)1957 ArthropodaInsectaLepidoptera37Blest (1957a)1957 ArthropodaInsectaLepidoptera38Blest (1957a)1957 ArthropodaInsectaLepidoptera39Blest (1957a)1957 ArthropodaInsectaLepidoptera41Blest (1957a)1957 ArthropodaInsectaLepidoptera42Blest (1957a)1957 ArthropodaInsectaLepidoptera43Blest (1957a)1957 ArthropodaInsectaLepidoptera44Blest (1957a)1957 ArthropodaInsectaLepidoptera45Blest (1957a)1957 ArthropodaInsectaLepidoptera46Blest (1957a)1957 ArthropodaInsectaLepidoptera47Blest (1957a)1957 ArthropodaInsectaLepidoptera <td>25</td> <td>Blest (1957a)</td> <td>1957 Arthropoda</td> <td>Insecta</td> <td>Lepidoptera</td>	25	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
28 29Blest (1957a)1957 ArthropodaInsectaLepidoptera30Blest (1957a)1957 ArthropodaInsectaLepidoptera31Blest (1957a)1957 ArthropodaInsectaLepidoptera32Blest (1957a)1957 ArthropodaInsectaLepidoptera33Blest (1957a)1957 ArthropodaInsectaLepidoptera34Blest (1957a)1957 ArthropodaInsectaLepidoptera35Blest (1957a)1957 ArthropodaInsectaLepidoptera36Blest (1957a)1957 ArthropodaInsectaLepidoptera37Blest (1957a)1957 ArthropodaInsectaLepidoptera38Blest (1957a)1957 ArthropodaInsectaLepidoptera39Blest (1957a)1957 ArthropodaInsectaLepidoptera40Blest (1957a)1957 ArthropodaInsectaLepidoptera41Blest (1957a)1957 ArthropodaInsectaLepidoptera42Blest (1957a)1957 ArthropodaInsectaLepidoptera43Blest (1957a)1957 ArthropodaInsectaLepidoptera44Blest (1957a)1957 ArthropodaInsectaLepidoptera45Blest (1957a)1957 ArthropodaInsectaLepidoptera46Blest (1957a)1957 ArthropodaInsectaLepidoptera47Hepidoptera1957 ArthropodaInsectaLepidoptera	27	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
29Blest (1957a)1957 ArthropodaInsectaLepidoptera31Blest (1957a)1957 ArthropodaInsectaLepidoptera32Blest (1957a)1957 ArthropodaInsectaLepidoptera33Blest (1957a)1957 ArthropodaInsectaLepidoptera34Blest (1957a)1957 ArthropodaInsectaLepidoptera35Blest (1957a)1957 ArthropodaInsectaLepidoptera36Blest (1957a)1957 ArthropodaInsectaLepidoptera37Blest (1957a)1957 ArthropodaInsectaLepidoptera39Blest (1957a)1957 ArthropodaInsectaLepidoptera40Blest (1957a)1957 ArthropodaInsectaLepidoptera41Blest (1957a)1957 ArthropodaInsectaLepidoptera42Blest (1957a)1957 ArthropodaInsectaLepidoptera43Blest (1957a)1957 ArthropodaInsectaLepidoptera44Blest (1957a)1957 ArthropodaInsectaLepidoptera45Blest (1957a)1957 ArthropodaInsectaLepidoptera46Blest (1957a)1957 ArthropodaInsectaLepidoptera46Blest (1957a)1957 ArthropodaInsectaLepidoptera474747474747	28	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
31Blest (1957a)1957 ArthropodaInsectaLepidoptera32Blest (1957a)1957 ArthropodaInsectaLepidoptera33Blest (1957a)1957 ArthropodaInsectaLepidoptera34Blest (1957a)1957 ArthropodaInsectaLepidoptera35Blest (1957a)1957 ArthropodaInsectaLepidoptera36Blest (1957a)1957 ArthropodaInsectaLepidoptera37Blest (1957a)1957 ArthropodaInsectaLepidoptera38Blest (1957a)1957 ArthropodaInsectaLepidoptera39Blest (1957a)1957 ArthropodaInsectaLepidoptera40Blest (1957a)1957 ArthropodaInsectaLepidoptera41Blest (1957a)1957 ArthropodaInsectaLepidoptera42Blest (1957a)1957 ArthropodaInsectaLepidoptera43Blest (1957a)1957 ArthropodaInsectaLepidoptera44Blest (1957a)1957 ArthropodaInsectaLepidoptera45Blest (1957a)1957 ArthropodaInsectaLepidoptera46Blest (1957a)1957 ArthropodaInsectaLepidoptera471957a1957 ArthropodaInsectaLepidoptera	29 30	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
32 33Blest (1957a)1957 ArthropodaInsectaLepidoptera34Blest (1957a)1957 ArthropodaInsectaLepidoptera35Blest (1957a)1957 ArthropodaInsectaLepidoptera36Blest (1957a)1957 ArthropodaInsectaLepidoptera37Blest (1957a)1957 ArthropodaInsectaLepidoptera38Blest (1957a)1957 ArthropodaInsectaLepidoptera39Blest (1957a)1957 ArthropodaInsectaLepidoptera40Blest (1957a)1957 ArthropodaInsectaLepidoptera41Blest (1957a)1957 ArthropodaInsectaLepidoptera42Blest (1957a)1957 ArthropodaInsectaLepidoptera43Blest (1957a)1957 ArthropodaInsectaLepidoptera44Blest (1957a)1957 ArthropodaInsectaLepidoptera45Blest (1957a)1957 ArthropodaInsectaLepidoptera46Blest (1957a)1957 ArthropodaInsectaLepidoptera471957 ArthropodaInsectaLepidoptera	31	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
33Blest (1957a)1957 ArthropodaInsectaLepidoptera35Blest (1957a)1957 ArthropodaInsectaLepidoptera36Blest (1957a)1957 ArthropodaInsectaLepidoptera37Blest (1957a)1957 ArthropodaInsectaLepidoptera38Blest (1957a)1957 ArthropodaInsectaLepidoptera39Blest (1957a)1957 ArthropodaInsectaLepidoptera40Blest (1957a)1957 ArthropodaInsectaLepidoptera41Blest (1957a)1957 ArthropodaInsectaLepidoptera42Blest (1957a)1957 ArthropodaInsectaLepidoptera43Blest (1957a)1957 ArthropodaInsectaLepidoptera44Blest (1957a)1957 ArthropodaInsectaLepidoptera45Blest (1957a)1957 ArthropodaInsectaLepidoptera46Blest (1957a)1957 ArthropodaInsectaLepidoptera4719571957 ArthropodaInsectaLepidoptera	32	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
35Blest (1957a)1957 ArthropodaInsectaLepidoptera36Blest (1957a)1957 ArthropodaInsectaLepidoptera37Blest (1957a)1957 ArthropodaInsectaLepidoptera38Blest (1957a)1957 ArthropodaInsectaLepidoptera39Blest (1957a)1957 ArthropodaInsectaLepidoptera40Blest (1957a)1957 ArthropodaInsectaLepidoptera41Blest (1957a)1957 ArthropodaInsectaLepidoptera42Blest (1957a)1957 ArthropodaInsectaLepidoptera43Blest (1957a)1957 ArthropodaInsectaLepidoptera44Blest (1957a)1957 ArthropodaInsectaLepidoptera45Blest (1957a)1957 ArthropodaInsectaLepidoptera46Blest (1957a)1957 ArthropodaInsectaLepidoptera47471957 ArthropodaInsectaLepidoptera	33 34	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
36 37Blest (1957a)1957 ArthropodaInsectaLepidoptera38Blest (1957a)1957 ArthropodaInsectaLepidoptera39Blest (1957a)1957 ArthropodaInsectaLepidoptera40Blest (1957a)1957 ArthropodaInsectaLepidoptera41Blest (1957a)1957 ArthropodaInsectaLepidoptera42Blest (1957a)1957 ArthropodaInsectaLepidoptera43Blest (1957a)1957 ArthropodaInsectaLepidoptera44Blest (1957a)1957 ArthropodaInsectaLepidoptera45Blest (1957a)1957 ArthropodaInsectaLepidoptera46Blest (1957a)1957 ArthropodaInsectaLepidoptera47471957 ArthropodaInsectaLepidoptera	35	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
37Blest (1957a)1957 ArthropodaInsectaLepidoptera39Blest (1957a)1957 ArthropodaInsectaLepidoptera40Blest (1957a)1957 ArthropodaInsectaLepidoptera41Blest (1957a)1957 ArthropodaInsectaLepidoptera42Blest (1957a)1957 ArthropodaInsectaLepidoptera43Blest (1957a)1957 ArthropodaInsectaLepidoptera44Blest (1957a)1957 ArthropodaInsectaLepidoptera45Blest (1957a)1957 ArthropodaInsectaLepidoptera46Blest (1957a)1957 ArthropodaInsectaLepidoptera47471957 ArthropodaInsectaLepidoptera	36	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
39Blest (1957a)1957 ArthropodaInsectaLepidoptera40Blest (1957a)1957 ArthropodaInsectaLepidoptera41Blest (1957a)1957 ArthropodaInsectaLepidoptera42Blest (1957a)1957 ArthropodaInsectaLepidoptera43Blest (1957a)1957 ArthropodaInsectaLepidoptera44Blest (1957a)1957 ArthropodaInsectaLepidoptera45Blest (1957a)1957 ArthropodaInsectaLepidoptera46Blest (1957a)1957 ArthropodaInsectaLepidoptera474747474848	37 38	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
40Blest (1957a)1957 ArthropodaInsectaLepidoptera41Blest (1957a)1957 ArthropodaInsectaLepidoptera42Blest (1957a)1957 ArthropodaInsectaLepidoptera43Blest (1957a)1957 ArthropodaInsectaLepidoptera44Blest (1957a)1957 ArthropodaInsectaLepidoptera45Blest (1957a)1957 ArthropodaInsectaLepidoptera46Blest (1957a)1957 ArthropodaInsectaLepidoptera474747474848	39	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
411000 (1957a)1957 ArthropodaInsecta1000 (1900)42Blest (1957a)1957 ArthropodaInsectaLepidoptera43Blest (1957a)1957 ArthropodaInsectaLepidoptera44Blest (1957a)1957 ArthropodaInsectaLepidoptera45Blest (1957a)1957 ArthropodaInsectaLepidoptera46Blest (1957a)1957 ArthropodaInsectaLepidoptera47	40	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
42Diest (1957a)1957 ArthropodaInsectaDepidoptera43Blest (1957a)1957 ArthropodaInsectaLepidoptera44Blest (1957a)1957 ArthropodaInsectaLepidoptera45Blest (1957a)1957 ArthropodaInsectaLepidoptera46Blest (1957a)1957 ArthropodaInsectaLepidoptera47	41 42	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
44 45 46Blest (1957a)1957 ArthropodaInsectaLepidoptera46 47Blest (1957a)1957 ArthropodaInsectaLepidoptera	42 43	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
45Blest (1957a)1957 ArthropodaInsectaLepidoptera46Blest (1957a)1957 ArthropodaInsectaLepidoptera47	44	Blest (1957a)	1957 Arthropoda	Insecta	Lepidontera
$\frac{46}{47}$	45	Blest (1957a)	1957 Arthropoda	Insecta	Lepidoptera
	46 47	Dicst (1757a)	1997 / 1100000	moota	Depidopiera

2 3			1 / / 1
4	ext or not included in	study, varied: too many different appro	Study type
5	Family	Species Desude human an estimat	Study type
7		P seudonypsa speciosa	
8	Erebidae	Rhodogastria bubo	descriptive
9	Erebidae	Rhodogastria leucoptera	descriptive
10	Erebidae	Amphicallier pactolicus	descriptive
12	Erebidae	Rhodogastria lupia	descriptive
13	Eremiaphilidae	Eremiaphila braueri	descriptive
14	Hymenopodidae	Hestiasula sarawaka	descriptive
15 16	Mantidae	Stagmomantis sp.	descriptive
17	Sepiidae	Sepia officinalis	descriptive
18	Acanthopidae	Acanthops falcata	descriptive
19	Acanthopidae	Acontiothespis multicolor	descriptive
20 21	Liturgusidae	Liturgusa sp.	descriptive
22	Thespidae	Musonia surinama	descriptive
23	Mantidae	Stagmatoptera septentrionalis	descriptive
24 25	Mantidae	Stagmomantis carolina	descriptive
26	Mantidae	Thesprotia filum	descriptive
27	Acanthopidae	Tithrone roseipennis	descriptive
28	Ambystomatidae	Ambystoma tigrinum melanostictum	descriptive
29 30	Bufonidae	Bufo alvarius	manipulative
31	Saturniidae	Automeris aurantiaca	descriptive
32	Saturniidae	Callosamia promethea	descriptive
33 34	Saturniidae	Rothschildia jacobaeae	descriptive
35	Phasmatidae	Eurvcnema goliath	descriptive
36	Phasmatidae	Tropidoderus childrenii	descriptive
37	Hexabranchidae	Hexabranchus marginatus	descriptive
39	Pseudophasmatidae	Pterinoxylus spinulosus	descriptive
40	Diapheromeridae	Oncotophasma martini	descriptive
41 42	Tettigoniidae	Acanthodis curvidens	descriptive
42	Angelida	Angela guianensis	descriptive
44	Mantidae	Choerododis rhombicollis	descriptive
45	Mantidae	Phyllovates chlorophaea	descriptive
46 47	Tettigoniidae	Scorniorinus fragilis	descriptive
48	Pseudonhasmatidae	Matriotas dioclas	descriptive
49	Mantidae	Stagmatontara biocallata	manipulative
50 51	Mantidae	Stagmatoptera biocellata	manipulative
52	Datanadidaa	Ostorus milogris	degorintivo
53	Mantidaa	Decopus vulgaris	descriptive
54			descriptive
55 56		Galepsus toganus	descriptive
57	Empusidae	Hemiempusa capensis	descriptive
58	Empusidae	Idolomorpha lateralis	descriptive
59 60	Mantidae	Mantis religiosa	descriptive

2	
3	
4	
5	
6	
7	
/ 0	
0	
9	
10	
11	
12	
13	
14	
15	
16	
17	
18	
19	
20	
21	
22	
23	
24	
25	
26	
27	
28	
29	
30	
31	
37	
32	
37	
25	
36	
30	
20	
20	
40	
40	
41	
42	
43	
44	
45	
46	
4/	
48	
49	
50	
51	
52	
53	
54	
55	
56	
57	
58	
59	
60	

Mantidae

Mantidae

Mantidae

Mantidae

Mantidae

Mantidae

Carabidae

Mantidae

Mantidae

Mantidae

Mantidae

Mantidae

Ascalaphidae

Deroplatyidae

Miomantis aurea *Plistospilota guineensis* Polyspilota aeruginosa Hymenopodidae Pseudocreobotra ocellata Sphodromantis lineola Stenovates strachani Eremiaphilidae Tarachodes afzelii Tenodera superstitiosa Cychrus caraboides Salamandridae Taricha granulosa Cataspilota misana Hymenopodidae *Childonoptera lestoni* Hymenopodidae Chloroharpax modesta Hymenopodidae Panurgica compressicollis Paramantis togana Popa undata Prohierodula ornatipennis Sphodromantis aurea Statilia apicalis Haploglenius luteus Ambystomatidae Ambystoma annulatum Ambystomatidae Ambystoma cingulatum Ambystomatidae Ambystoma gracile Ambystomatidae Ambystoma jeffersonianum Ambystomatidae Ambystoma lacustris Ambystomatidae Ambystoma laterale Ambystomatidae Ambystoma mabeei Ambystomatidae Ambystoma macrodactylum Ambystomatidae Ambystoma maculatum Ambystomatidae Ambystoma mexicanum Ambystomatidae Ambystoma opacum Ambystomatidae Ambystoma ordinarium Ambystomatidae Ambystoma talpoideum Ambystomatidae Ambystoma texanum Ambystomatidae Ambystoma tigrinum Plethodontidae *Pseudotriton montanus* Plethodontidae Pseudotriton ruber Salamandridae *Cynops pyrrhogaster* Plethodontidae Desmognathus wrighti Salamandridae Notophthalmus perstriatus Salamandridae Paramesotriton hongkongensis Salamandridae Taricha rivularis Salamandridae Taricha rivularis

descriptive descriptive descriptive descriptive descriptive descriptive descriptive descriptive manipulative manipulative descriptive descriptive

2	
3	Salamandridae
4	Salamandridae
5	Salamandridaa
7	
8	Salamandridae
9	Salamandridae
10	Salamandridae
11	Salamandridae
12	Salamandridae
14	Salamandridae
15	Ambystomatidae
16	Salamandridaa
17	
18	Plethodontidae
20	Plethodontidae
21	Plethodontidae
22	Ambystomatidae
23	Plethodontidae
24	Plethodontidae
25	Plethodontidae
20 27	Plathadantidaa
28	
29	Plethodontidae
30	Plethodontidae
31	Plethodontidae
32	Hynobiidae
34	Hynobiidae
35	Hynobiidae
36	Hynobiidae
37	Disthadantidaa
38	Plethodontidae
39 40	Plethodontidae
41	Plethodontidae
42	Plethodontidae
43	Plethodontidae
44	Plethodontidae
45 46	Salamandridae
40 47	Ambystomatidae
48	Ambystomatidae
49	Amoystomatidae
50	Salamandridae
51	Salamandridae
52	Plethodontidae
55	Plethodontidae
55	Cambaridae
56	Cambaridae
57	Cambaridae
58	Californiidaa
59 60	Saturnitae

Taricha torosa Taricha torosa Triturus alpestris Triturus alpestris Triturus cristatus Triturus helveticus Triturus marmoratus Triturus vulgaris Notophthalmus viridescens Rhyacotriton olympicus Taricha granulosa Aneides aeneus Aneides ferreus Aneides lugubris Dicamptodon ensatus Ensatina eschscholtzii *Eurycea bislineata* Eurycea longicauda guttolineata Eurycea lucifuga *Gyrinophilus porphyriticus* Hydromantes genei Hydromantes shastae Hynobius dunni Hynobius leechi Hynobius nebulosus Hynobius tsuensis Leurognathus marmoratus Plethodon caddoensis Plethodon glutinosus Plethodon jordani Plethodon larselli Plethodon nettingi hubrichti Pleurodeles waltl *Rhyacosiredon altamirani* Rhvacosiredon rivularis Salamandra atra Salamandra salamandra Typhlotriton spelaeus Hemidactylium scutatum Procambrus acutus acutus Procambrus gracilis Procambrus simulans simulans Callosamia promethea

descriptive manipulative

3	G ( <sup>11</sup> 1
4	Saturniidae
5	Salamandridae
6	Tettigoniidae
7	Bombinatoridae
8	Bombinatoridae
9 10	Ambystomatidaa
10	
12	Acrididae
13	Ectobildae
14	Tettigoniidae
15	Salamandridae
10 17	Salamandridae
18	Salamandridae
19	Salamandridae
20	Salamandridae
21	Salamandridae
22	Salamandridae
23	Leptodactylidae
24 25	Leptodactylidae
26	Hylidae
27	Hylidae
28	Hylidae
29	Lantadaatulidaa
30	Lepiodactylidae
31 32	Leptodactylidae
33	Leptodactylidae
34	Leptodactylidae
35	Leiopelmatidae
36	Leiopelmatidae
37	Leionelmatidae
30	Europennatidaa
40	Eurypygidae
41	Leptodactylidae
42	Viperidae
43	Viperidae
44	Viperidae
45 46	Viperidae
47	Vineridae
48	Viperidae
49	
50	Eurypygidae
51	Tettigoniidae
52 53	Gryllacrididae
55	Gryllacrididae
55	Myobatrachidae
56	Myobatrachidae
57	Myobatrachidaa
58	March atra -1.: 1
59 60	wyooatrachidae

*Hyalophora cecropia* Pleurodeles waltl Mygalopsis ferruginea Bombina bombina *Bombina variegata* Ambystoma opacum Mestobregma plattei rubripeme Megaloblatta blaberoides Mygalopsis marki Tylototriton verrucosus Echinotriton andersoni Mertensiella caucasica Pachytriton brevipes Paramesotriton caudopunctatus Paramesotriton chinensis Adenomera hylaedactyla Hydrolaetare schmidti Hyla boans Hyla lanciformis Hyla raniceps Leptodactylus fuscus Leptodactylus ocellatus Leptodactylus pentadactylus Leptodactylus rhodomystax Leiopelma archeyi Leiopelma hamiltoni Leiopelma hochstetteri Eurypyga helias Pleurodema brachyops Crotalus adamanteus Crotalus atrox Crotalus cerastes Crotalus horridus Crotalus viridis Sistrurus catenatus Eurypyga helias Pterochroza ocellata Ametrus sp. Hadrogryllacris sp. Uperoleia aspera Uperoleia borealis Uperoleia lithomoda Uperoleia mjobergi

manipulative manipulative manipulative manipulative manipulative manipulative descriptive descriptive descriptive manipulative manipulative manipulative manipulative manipulative manipulative descriptive manipulative manipulative manipulative manipulative manipulative manipulative descriptive descriptive descriptive descriptive descriptive descriptive descriptive descriptive

2	
3	Myobatrachidae
4 5	Mantidae
6	Ophiuridae
7	Bombinatoridaa
8	
9	Myobatrachidae
10	Myobatrachidae
 12	Myobatrachidae
12	Myobatrachidae
14	Dendrobatidae
15	Gadidae
16	Leptodactylidae
17	Leptodaetylidae
18 10	Lepiodactyndae
20	Nymphalidae
21	Sepiidae
22	Sepiidae
23	Sphingidae
24	Saturniidae
25 26	Mantidae
27	Sanjidaa
28	Nemebalidaa
29	Nymphalidae
30	Elapidae
31	Elapidae
32 33	Palinuridae
34	Saturniidae
35	Colubridae
36	Nymphalidae
37	Panilionidae
38	
40	Octopodidae
41	Sepudae
42	Tettigoniidae
43	Tettigoniidae
44	Agamidae
45 46	Fulgoridae
40	Scincidae
48	Montidae
49	Manudae
50	Mantidae
51	Mantidae
52 53	Tettigoniidae
55	Nymphalidae
55	Nymphalidae
56	Saturniidae
57	Saturniidaa
58	Saturniida
59 60	Saturmuae
~~	

Uperoleia talpa Polyspilota aeruginosa Ophiura ophiura Bombina orientalis Pseudophryne bibronii Pseudophryne semimarmorata Uperoleia altissima *Uperoleia littlejohni* Epipedobates flavopictus Gadus morhua Physalaemus nattereri *Leptodactylus labyrinthicus* Aglais io Sepia officinalis Sepia officinalis *Smerinthus ocellatus* Antheraea polyphemus Mantis religiosa Sepia officinalis Aglais io Micrurus altirostris *Micrurus frontalis* Panulirus argus Saturnia pyri Xenodon dorbignyi Aglais io Papilio machaon Robsonella fontaniana Sepia officinalis Poecilimon ornatus Acripeza reticulata Ceratophora tennentii Lycorma delicatula Tiliqua scincoides intermedia Archimantis latistyla Hierodula majuscula Pseudomantis albofimbriata Acripeza reticulata Aglais utrticae Aglais io Aglia tau Antherea paphia Antherina suraka

descriptive descriptive manipulative manipulative descriptive descriptive descriptive descriptive descriptive manipulative descriptive descriptive manipulative manipulative manipulative manipulative manipulative descriptive manipulative manipulative descriptive descriptive manipulative manipulative descriptive manipulative manipulative manipulative manipulative descriptive manipulative descriptive manipulative manipulative manipulative manipulative manipulative manipulative manipulative descriptive descriptive descriptive descriptive

3	Saturniidae	Attacus edwardsi	descriptive	
4 5	Saturniidae	Automeris aurantiaca	descriptive	
6	Saturniidae	Automeris coresus	descriptive	
7	Saturniidae	Automeris illustris	descriptive	
8 9	Saturniidae	Automeris io	descriptive	
10	Saturniidae	Automeris janus	descriptive	
11	Saturniidae	Automeris memusae	descriptive	
12	Saturniidae	Automeris nvctimane	descriptive	
13	Saturniidae	Automeris saturata	descriptive	
15	Saturniidae	Callosamia promethea	descriptive	
16	Sphingidae	Celerio euphorbiae	descriptive	
17	Saturniidae	Citheronia bristottii	descriptive	
19	Saturniidae	Copaxa lavendera	descriptive	
20	Saturniidae	Dictvonloca cachara	descriptive	
21	Saturniidae	Enithora atharina sudanica	descriptive	
23	Saturniidae	Eudia navonia	descriptive	
24	Saturniidae	Fudvaria venata	descriptive	
25 26	Saturniidae	Gynanisa maja	descriptive	
20	Saturniidae	Hylesia nigricans	descriptive	
28	Saturniidae	Imbrasia macrothyris	descriptive	
29	Sphingidae	I gothog populi	descriptive	
30 31	Saturniidaa	Luoinoe populi Lobohungag apithyrang	descriptive	
32	Saturniidaa	Lobobunded epiinyrend	descriptive	
33	Saturniidaa	Loopa katinka	descriptive	
34 35	Saturnidae		descriptive	
36	Saturniidae	Nudaurella arala	descriptive	
37	Saturniidae	Nuaaurella alone	descriptive	
38	Saturniidae	Philosamia cynthia cynthia	descriptive	
39 40	Saturniidae	Philosamia cynthia ricini	descriptive	
41	Saturniidae	Rothschildia orizaba	descriptive	
42	Saturniidae	Samia cecropia	descriptive	
43	Sphingidae	Smerinthus ocellatus	descriptive	
44 45	Sphingidae	Sphinx ligustri	descriptive	
46	Saturniidae	Telea polyphemus	descriptive	
47				
4X				

1 2			
3 ⊿	For the five display m	ode columns, $0 = absent$ , $1 = pres$	ent.
5	Life stage studied	Primary defence reported	Predator in study
6	adult	NA	human
7	adult	NA	human
8 9	adult	NA	human
10	adult	NA	human
11	adult	NA	human
12	NA	camouflage	human
15 14	NA	camouflage	NA
15	NA	NA	human
16	adult	camouflage	human
17 18	adult	camouflage	human
19	adult	camouflage	many
20	adult	camouflage	human
21	adult	camouflago	human
22 23	auun NIA	camouflage	human
24	NA - 114	camounage	numan
25		camouflage	numan
26 27	adult	camouflage	many
27	adult	camouflage	many
29	NA	NA	human
30	adult	NA	mammal
31 22	adult	NA	human
33	adult	NA	human
34	adult	NA	human
35	adult	camouflage	human
30 37	adult	camouflage	human
38	adult	NA	human
39	adult	camouflage	human
40 41	NA	camouflage	human
42	adult	camouflage	human
43	juvenile, adult	camouflage	human
44	juvenile, adult	camouflage	many
45 46	juvenile, adult	camouflage	human
47	juvenile, adult	camouflage	human
48	iuvenile, adult	NA	NA
49 50	NA	NA	bird
50 51	adult	NA	bird
52	iuvenile adult	camouflage	human
53	adult	camouflage	NA
54 55	adult	camouflage	NΛ
56	adult	camouflage	ΝA
57	adult	camouflage	NA NA
58	adult	announlage	mammal rantila
59 60	auun	Cambunage	mammai, repute

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

2			
3	adult	camouflage	NA
4	adult	camouflage	NA
6	adult	camouflage	NA
7	adult	camouflage	NA
8	adult	camouflage	NA
9 10	adult	camouflage	NA
11	adult	camouflage	NA
12	adult	camouflage	NΔ
13 14	adult	camouflage	NA
14	adult	camouflage	NA
16			
17	adult	camouflage	bird
18	adult	NA	NA
20	adult	NA	NA
21	adult	NA	NA
22	adult	NA	NA
23	adult	NA	NA
24 25	adult	NA	bird, mammal
26	adult	NA	bird, mammal
27	adult	NA	NA
28 20	adult	NA	NA
30	adult	NA	NA
31	adult	NA	NA
32	adult	NA	NA
33 34	adult	NA	NA
35	adult	NA	NA
36	adult	NA	NA
37	adult	NA	NA
39	adult	NA	NA
40	adult	NΔ	mammal
41	adult		mammal
42	adult		N A
44			NA
45			NA
46	adult	NA	NA
4/	adult	NA	NA
49	adult	NA	NA
50	adult	NA	NA
51	adult	NA	NA
52	adult	NA	NA
55	adult	NA	NA
55	adult	camouflage	human
56	adult	camouflage	human
57 58	adult	camouflage	human
59	adult	camouflage	human
60		5	-

2			
3	adult	camouflage	human
5	NA	NA	human, mammal
6	NA	camouflage	reptile
7	adult	camouflage	human
8	adult	camouflage	human
9 10	NΔ	NΔ	mammal
11	adult	aamouflago	incost
12		califounage	have a
13	juvenile	aposematic	numan
14 15	juvenile, adult	camouflage	reptile
16	NA	aposematic	mammal
17	juvenile, adult	NA	human
18	NA	NA	human
19	NA	NA	mammal
20 21	NA	NA	mammal
22	NA	NA	mammal
23	adult	NA	human
24 25	adult	NA	human
26	adult	NA	human
27	adult	NA	human
28	adult	NA	human
30	adult	NA	human
31	adult	NA	human
32	adult	NA	human
34	adult	NA	human
35	adult	camouflage	human
36	adult	camouflage	human
37 38	adult	camouflage	human
39	iuvenile adult	NA	human
40	NA	camouflage	human
41	adult	NA	human
42 43	adult	NA NA	human
44	adult		human
45		NA	numan
46	juvenile, adult	NA	human
47	adult	NA	human
40 49	adult	NA	human
50	juvenile, adult	NA	bird
51	adult	camouflage	human
52	adult	NA	human
53 54	adult	NA	human
55	adult	camouflage	human
56	adult	camouflage	human
57	adult	camouflage	human
58 50	adult	camouflage	human
60	adun	camounage	numan

Page 129 of 199

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

2			
3	adult	putative aposematism	human
4 5	adult	camouflage	human
6	adult	camouflage	human
7	adult	camouflage	human
8 9	adult	camouflage	human
10	adult	camouflage	human
11	adult	camouflage	human
12 13	adult	camouflage	human
14	adult	camouflage	human
15	adult	putative aposematism	human
16 17	adult	camouflage	human
18	adult	putative aposematism	human
19	adult	camouflage	human
20 21	adult	camouflage	human
22	adult	putative aposematism	human
23	adult	camouflage	human
24 25	adult	aposematic	human
26	adult	NA	human
27	adult	aposematic	human
28 29	adult	camouflage	human
30	adult	camouflage	human
31	adult	camouflage	human
32	adult	camouflage	human
34	adult	putative aposematism	human
35	adult	camouflage	human
36 27	adult	camouflage	human
38	adult	putative aposematism	human
39	adult	putative aposematism	human
40 41	adult	putative aposematism	human
41	adult	putative aposematism	human
43	adult	camouflage	human
44 45	adult	camouflage	human
45 46	adult	camouflage	human
17			

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

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

2		
3	varied	approach, subjugation
4	varied	subiugation
6	varied	subjugation
7	varied	NA
8	varied	subiligation
9 10	varied	subjugation
10	varied	subjugation
12		subjugation
13	varied	subjugation
14	varied	subjugation
15	varied	subjugation
17	varied	subjugation
18	varied	subjugation
19	varied	approach, subjugation
20	varied	NA
21	varied	subjugation
23	varied	NA
24 25	varied	approach, subjugation
26	varied	approach, subjugation
27	varied	approach, subjugation
28 29	varied	NA
30	varied	NA
31	varied	NA
32	varied	NA
34	varied	NA
35	varied	NA
36	varied	NA
37	varied	NA
39	varied	approach
40	varied	approach subjugation
41	varied	approach subjugation
42	varied	approach
44	varied	approach
45	varied	approach subjugation
46		approach, subjugation
47 48	varied	NA
49	varied	NA
50	varied	subjugation
51	varied	subjugation
52	varied	approach, subjugation
53 54	NA	NA
55	visual	approach
56	vienal	annroach
57	visual	approach
58	visual	approach
59 60	tactile, vibration	approach, subjugation
00		

2		
3	tactile, vibration	approach, subjugation
4 5	tactile	subjugation
6	NA	approach
7	tactile	subjugation
8	tactile	subjugation
9 10	tactile visual auditory alfactory	NA
10	tactile, visual, auditory, offactory	
12	tactile	subjugation
13	tactile, visual, vibration	approach
14	NA	NA
15 16	tactile, visual	subjugation
10	tactile	subjugation
18	tactile	subjugation
19	tactile	subjugation
20	tactile	subjugation
21	tactile, visual, auditory, olfactory	subjugation
23	tactile	subjugation
24	tactile	subjugation
25	tactile	subjugation
20 27	tactile	subjugation
28		subjugation
29	tactile	subjugation
30	tactile	subjugation
31	tactile	subjugation
33	tactile	subjugation
34	tactile	subjugation
35	tactile	subjugation
36	tactile	subjugation
37 38	tactile	subjugation
39	visual	approach
40	tactile	approach subjugation
41	visual	approach
42 43	visual	approach
44	visual	approach
45	visual	approach
46	visual	approach
47	visual	approach
40 49	visual	approach
50	visual	approach
51	tactile, vibration	subjugation
52	NA	subjugation
53 54	NA	subjugation
55	tactile	subjugation
56	tactile	subiugation
57	tactile	subjugation
58	tactilo	subjugation
60 60		suojuganon

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

1		
2		
3 4	visual	approach
5	tactile	subjugation
6	tactile	subjugation
7 8	tactile	subjugation
9	tactile	subjugation
10	tactile	subjugation
11 12	tactile	subjugation
12	tactile	subjugation
14	tactile	subjugation
15	visual	approach
16 17	visual	approach
18	tactile	subjugation
19	visual	approach
20 21	visual	approach
22	tactile	subjugation
23	tactile	subjugation
24 25	tactile	subjugation
26	tactile	subjugation
27	tactile	subjugation
28 29	tactile	subjugation
30	tactile	subjugation
31	tactile	subjugation
32	tactile	subjugation
34	tactile	subjugation
35	tactile	subjugation
36 27	tactile	subjugation
38	visual	approach
39	visual	approach
40	visual	approach
41	visual	approach
43	tactile	subjugation
44 45	visual	approach
45 46	tactile	subjugation
47		

1	
2	
3	
4	Display duration description
5	NA
7	
8	
9	NA
10	NA
11	NA
13	NA
14	NA
15	NA
16 17	colours displayed for a few seconds, posture not specified
17	NA
19	NA
20	
21	
22	up to a few seconds
23 24	NA
25	NA
26	NA
27	up to a few seconds
28	NA
29 30	NA
31	<330
32	NA NA
33	
34 25	NA 000 1000
36	900-1200
37	NA
38	NA
39	more than 1 min
40 41	NA
42	NA
43	NA
44	NA
45	NA
46 47	NA
48	
49	
50	between a few seconds to 45 mins. In one case kept presenting to a bird for 6h
51	150-490
52 53	NA
55 54	NA
55	NA
56	NA
57 59	NA
50 59	NA
60	

1		
2		
3	NA	
4	NA	
5	NA	
7	NA	
8	NA NA	
9	NA	
10	NA	
12	NA	
13	NA	
14 15	NA	
15 16	NA	
17	NA	
18	NA	
19 20	NA	
20	NA	
22	NA	
23	NA	
24 25	NA	
25	NA	
27	NA	
28	NA	
29	NA	
31	NA	
32	NA	
33	NA	
34 35	NA	
36	NA NA	
37	NA NA	
38 30	INA NA	
40	NA	
41	NA	
42	NA Contraction of the second s	
43 44	NA	
45	NA	
46	NA	
47	NA	
48 49	NA	
50	NA	
51	NA	
52	NA	
53 54	NA	
55		
	NA	
56	NA NA	
56 57	NA NA NA	
56 57 58 59	NA NA NA	

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

2	
3	NA
4 5	NA
5	NA
7	12+
8	12+
9	
10 11	NA
12	NA
13	NA
14	NA
15 16	NA
10	NA
18	NA
19	NA
20	NA
21	NA
23	23 milliseconds
24	312 milliseconds
25	615 - 756 milliseconds
26 27	280 1001 millissoonds
28	
29	
30	265 milliseconds
31	808 milliseconds
33	213-312 milliseconds
34	NA
35	NA
36 37	NA
38	NA
39	NA
40	a few sec
41 42	recorded for 500 ms
43	recorded for 500 ms
44	recorded for 500 ms
45	recorded for 500 ms
46 47	recorded for 500 ms
48	recorded for 500 ms
49	recorded for 500 ms
50	NA 25.102
51 52	25-183
5∠ 53	NA
54	NA
55	NA
56	NA
57 58	NA
59	NA
60	

2	
3	NA
4	during attack - several seconds, after attack - 1 minute
5	NA
7	
8	
9	NA
10	NA
11	NA
12	NA
14	NA
15	NA
16	NA
17	
18	NA
20	between 1 and 22 flicks per minute
20	NA
22	up to 30 sec
23	NA
24	>60
25 26	NA
20	NA
28	
29	NA NA
30	NA
31	NA
32	NA
34	0.05-4.65
35	NA
36	about 5 wing flicks per 5 seconds
37	NA
38 30	
40	NA NA
41	NA
42	continued for a few seconds after stimulation had ended
43	up to 300 sec, and longer
44	NA
45 46	up to 192 seconds
47	NA
48	NA
49	
50	NA
51	NA
52 53	NA
54	NA
55	NA
56	short
57	NΔ
58	
59 60	INA
00	

2			
3	NA		
4	ΝΔ		
5	austained static display up to 5 minutes		
7	sustained static display up to 5 minutes		
8	sustained static display up to 5 minutes		
9	NA		
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		
15	NA		
16	NA		
17			
18 10			
20	1-4 seconds repeated		
21	1-4 seconds repeated		
22	sustained static display up to 5 minutes		
23	short		
24 25	short		
26	NA		
27	NA		
28	sustained static display up to 5 minutes		
29	NA		
31	NA		
32			
33	NA		
34	NA		
35	NA		
37	NA		
38	NA		
39	NA		
40	NA		
41 42	NA		
43	1-4 seconds repeated		
44	1-4 seconds repeated		
45	sustained static display up to 5 minutes		
46 47	sustained state display up to 5 minutes		
47 48			
49			
50			
Jisplay duration (sec) (max if range given)           NA	1		
--	----------	--------------------------------	--------------
Jisplay duration (sec) (max if range given)         NA         NA     <	2		
Jisplay duration (see) (max if range given)           NA	3		
3       Expansion (us) (us) (us) (us) (us) (us) (us) (us)	4 5	Display duration (sec) (max if	range given)
7       NA         8       NA         9       NA         10       NA         11       NA         12       NA         13       NA         14       NA         15       NA         16       3         17       3         18       NA         20       3         21       NA         22       3         23       NA         24       NA         25       NA         26       NA         27       3         38       NA         39       NA         30       NA         311       330         32       NA         330       NA         34       NA         35       1200         36       NA         37       1200         38       NA         39       NA         41       NA         42       NA         43       NA         44       NA         450       2700 <th>5</th> <th>NA</th> <th></th>	5	NA	
8       NA         9       NA         10       NA         11       NA         12       NA         13       NA         14       NA         15       NA         16       3         17       3         18       NA         19       NA         21       NA         22       3         10       3         23       NA         24       NA         25       NA         26       NA         27       3         28       NA         300       NA         330       330         331       330         332       NA         3330       330         334       NA         35       1200         36       1200         37       NA         38       NA         39       NA         41       NA         42       NA         43       NA         44       NA         45       NA	7	NA	
9       NA         10       NA         11       NA         12       NA         13       NA         14       NA         15       NA         16       NA         17       3         18       NA         20       3         21       NA         22       3         23       NA         24       NA         25       NA         26       NA         27       3         28       NA         29       NA         300       NA         31       330         32       NA         33       NA         34       NA         35       1200         36       1200         37       NA         38       NA         39       NA         40       NA         41       NA         42       NA         43       NA         44       NA         45       NA         46       NA <th>8</th> <th></th> <th></th>	8		
10       NA         11       NA         12       NA         13       NA         14       NA         15       NA         16       3         17       3         18       NA         19       NA         20       3         21       NA         22       3         23       NA         24       NA         25       NA         26       NA         27       3         28       NA         29       NA         30       NA         31       330         32       NA         330       330         331       330         332       NA         330       330         331       330         332       NA         330       330         331       330         332       NA         34       NA         35       NA         36       NA         37       NA         38       NA <th>9</th> <th>NA</th> <th></th>	9	NA	
12       NA         13       NA         14       NA         15       NA         16       NA         17       3         18       NA         19       NA         20       3         21       NA         22       3         23       NA         24       NA         25       NA         26       NA         27       3         28       NA         29       NA         30       NA         31       330         32       NA         330       NA         34       NA         35       I200         36       NA         37       NA         38       NA         39       NA         39       NA         41       NA         42       NA         43       NA         44       NA         45       NA         46       NA         57       NA         58       NA	10	NA	
13       NA         14       NA         15       NA         16       3         17       3         18       NA         19       NA         20       NA         21       NA         22       3         23       NA         24       NA         25       NA         26       NA         27       3         28       NA         29       NA         20       NA         21       NA         22       3         23       NA         24       NA         25       NA         30       NA         31       330         32       NA         330       NA         34       NA         35       NA         36       1200         37       NA         38       NA         39       NA         44       NA         45       NA         46       NA         47       NA	12	NA	
14       NA         15       NA         16       3         17       3         18       NA         20       NA         21       NA         22       3         23       NA         24       NA         25       NA         26       NA         27       3         28       NA         29       NA         300       NA         31       330         32       NA         331       330         332       NA         333       NA         34       NA         35       1200         36       NA         37       NA         38       NA         39       NA         40       NA         41       NA         42       NA         43       NA         44       NA         45       NA         46       NA         47       NA         48       NA         59       NA     <	13	NA	
15       NA       3         18       NA       3         19       NA       3         20       NA       3         21       NA       3         22       3       3         23       NA       3         24       NA       3         25       NA       3         26       NA       3         27       3       3         28       NA       3         29       NA       330         30       NA       330         33       NA       330         33       NA       330         33       NA       330         33       NA       34         34       NA       1200         35       NA       1200         36       NA       44         NA       44       NA         35       NA       490         36       NA       490         37       NA       490         38       NA       490         39       NA       490         30       NA       490	14	NA	
16       3         18       NA         19       NA         20       NA         21       3         22       3         23       NA         24       NA         25       NA         26       NA         27       3         28       NA         29       NA         30       NA         31       330         32       NA         330       330         331       NA         30       NA         31       330         32       NA         330       330         331       NA         330       330         331       NA         330       330         331       NA         34       NA         35       NA         36       NA         37       NA         38       NA         39       NA         300       2700         301       490         31       700         32       N	15	NA	
NA	16 17		3
10       NA         20       NA         21       NA         22       3         23       NA         24       NA         25       NA         26       NA         27       3         28       NA         29       NA         30       NA         31       330         32       NA         330       NA         34       NA         35       1200         36       NA         37       NA         38       NA         39       NA         40       NA         41       NA         42       NA         43       NA         44       NA         45       NA         46       NA         47       NA         48       NA         50       NA         51       NA         53       NA         54       NA         55       NA         56       NA         57       NA <th>17</th> <th>NA</th> <th>-</th>	17	NA	-
20       NA         21       NA         22       3         23       NA         24       NA         25       NA         26       NA         27       3         28       NA         29       NA         30       NA         31       330         32       NA         33       330         34       NA         35       1200         36       NA         37       NA         38       NA         39       NA         40       NA         41       NA         42       NA         43       NA         44       NA         45       NA         46       NA         47       NA         48       NA         490       2700         53       NA         54       NA         55       NA         56       NA         57       NA         58       NA         59       NA	19	NA	
21       NA       3         22       3         23       NA         24       NA         25       NA         26       NA         27       3         28       NA         30       NA         31       330         32       NA         33       NA         34       NA         35       1200         36       NA         37       NA         38       NA         39       NA         40       NA         41       NA         42       NA         43       NA         44       NA         45       NA         46       NA         47       NA         48       NA         50       2700         51       2700         52       NA         53       NA         54       NA         55       NA         56       NA         57       NA         58       NA         59	20		
22       3         23       NA         24       NA         25       NA         26       NA         27       3         28       NA         30       NA         31       330         32       NA         330       NA         331       NA         332       NA         333       NA         330       NA         331       NA         332       NA         333       NA         330       330         331       NA         332       NA         333       NA         34       NA         35       NA         36       NA         37       NA         38       NA         39       NA         44       NA         45       NA         50       2700         51       2700         52       NA         53       NA         54       NA         55       NA         56       N	21	INA	
13       NA         14       NA         15       NA         16       NA         17       3         18       NA         19       NA         10       NA         11       330         1200       330         11       1200         12       NA         12       NA         1200       1200         1200       1200         1200       1200         1200       1200         12       NA         12       NA         12       NA         12       NA         12       NA         12       NA         13       NA         14       NA         15       NA         16       NA         17       NA         18       NA         19       NA         10       1200         10       1200         11       1200         12       1200         13       1200         14       14         15 </th <th>22</th> <th></th> <th>3</th>	22		3
25       NA         26       NA         27       3         28       NA         30       NA         31       330         32       NA         33       NA         34       NA         35       1200         36       NA         37       NA         38       NA         39       NA         40       NA         41       NA         42       NA         43       NA         44       NA         45       NA         46       NA         47       NA         48       NA         50       2700         51       2700         52       NA         54       NA         55       NA         56       NA         57       NA         58       NA         59       NA	23	NA	
26       NA         27       3         28       NA         30       NA         31       330         32       NA         33       NA         34       NA         35       1200         36       NA         37       NA         38       NA         39       NA         40       NA         41       NA         42       NA         43       NA         44       NA         45       NA         46       NA         47       NA         48       NA         490       1         50       2700         51       2700         52       NA         53       NA         54       NA         55       NA         56       NA         57       NA         58       NA         59       NA	24	NA	
27       3         28       NA         30       NA         31       330         32       NA         33       NA         34       NA         35       1200         36       NA         37       NA         38       NA         39       NA         40       NA         41       NA         42       NA         43       NA         44       NA         45       NA         46       NA         47       NA         48       NA         490       1         50       2700         51       2700         52       NA         53       NA         54       NA         55       NA         56       NA         57       NA         58       NA         59       NA	26	NA	
28       NA         30       NA         31       330         32       NA         33       NA         34       NA         35       1200         36       NA         37       NA         38       NA         39       NA         40       NA         41       NA         42       NA         43       NA         44       NA         45       NA         46       NA         47       NA         48       NA         50       2700         51       2700         52       NA         53       NA         54       NA         55       NA         56       NA         57       NA         58       NA         59       NA	27		3
29       NA       330         31       330         32       NA         33       NA         34       NA         35       1200         36       NA         37       NA         38       NA         39       NA         40       NA         41       NA         42       NA         43       NA         44       NA         45       NA         46       NA         47       NA         48       NA         50       2700         51       2700         52       NA         53       NA         54       NA         55       NA         56       NA         57       NA         58       NA         59       NA	28	NA	
30       NA         33       NA         34       NA         35       1200         36       NA         37       NA         38       NA         39       NA         40       NA         41       NA         42       NA         43       NA         44       NA         45       NA         46       NA         47       NA         48       NA         50       2700         51       490         52       NA         53       NA         54       NA         55       NA         56       NA         57       NA         58       NA         59       NA	29 30	NA	
32     NA       33     NA       34     NA       35     1200       36     NA       37     NA       38     NA       39     NA       40     NA       41     NA       42     NA       43     NA       44     NA       45     NA       46     NA       47     NA       48     NA       50     2700       51     490       52     NA       53     NA       54     NA       55     NA       56     NA       57     NA       58     NA       59     NA	31		330
33       INA         34       NA         35       1200         36       NA         38       NA         39       NA         40       NA         41       NA         42       NA         43       NA         44       NA         45       NA         46       NA         47       NA         48       NA         50       2700         51       490         52       NA         53       NA         54       NA         55       NA         56       NA         57       NA         58       NA         59       NA	32	NIA	330
34       NA         35       1200         36       NA         37       NA         38       NA         39       NA         40       NA         41       NA         42       NA         43       NA         44       NA         45       NA         46       NA         47       NA         48       NA         50       2700         51       2700         53       NA         54       NA         55       NA         56       NA         57       NA         58       NA         59       NA	33		
35       1200         36       NA         37       NA         38       NA         39       NA         40       NA         41       NA         42       NA         43       NA         44       NA         45       NA         46       NA         47       NA         48       NA         50       2700         51       490         52       NA         53       NA         54       NA         55       NA         56       NA         57       NA         58       NA         59       NA	34	NA	
37       NA         38       NA         39       NA         40       NA         41       NA         42       NA         43       NA         44       NA         45       NA         46       NA         47       NA         48       NA         50       2700         51       2700         52       NA         53       NA         54       NA         55       NA         56       NA         57       NA         58       NA         59       NA	35 36		1200
38       NA         39       NA         40       NA         41       NA         42       NA         43       NA         44       NA         45       NA         46       NA         47       NA         48       NA         50       2700         51       2700         53       NA         54       NA         55       NA         56       NA         57       NA         58       NA         59       NA	37	NA	
39       NA         40       NA         41       NA         42       NA         43       NA         44       NA         45       NA         46       NA         47       NA         48       NA         50       2700         51       2700         52       NA         53       NA         54       NA         55       NA         56       NA         57       NA         58       NA         59       NA	38	NA	
40       NA         41       NA         42       NA         43       NA         44       NA         45       NA         46       NA         47       NA         48       NA         50       2700         51       2700         51       490         52       NA         53       NA         54       NA         55       NA         56       NA         57       NA         58       NA         59       NA	39	NA	
41       42       NA         42       NA         43       NA         44       NA         45       NA         46       NA         47       NA         48       NA         50       2700         51       2700         52       NA         53       NA         54       NA         55       NA         56       NA         57       NA         58       NA         60       NA	40	NA	
43       NA         44       NA         45       NA         46       NA         47       NA         48       NA         50       2700         51       490         52       NA         53       NA         54       NA         55       NA         56       NA         57       NA         58       NA         60       60	41 42	NA	
44       NA         45       NA         46       NA         47       NA         48       NA         50       2700         51       490         52       NA         53       NA         54       NA         55       NA         56       NA         57       NA         58       NA         59       NA	43	NA	
45       NA         46       NA         47       NA         48       NA         50       2700         51       2700         52       NA         53       NA         54       NA         55       NA         56       NA         57       NA         58       NA         59       NA	44	NA	
46       NA         47       NA         48       NA         49       2700         50       2700         51       490         52       NA         53       NA         54       NA         55       NA         56       NA         57       NA         58       NA         59       NA	45	N A	
47       NA         48       NA         49       2700         50       2700         51       490         52       NA         53       NA         54       NA         55       NA         56       NA         57       NA         58       NA         59       NA	46		
10       NA         49       2700         50       490         51       490         52       NA         53       NA         54       NA         55       NA         56       NA         57       NA         58       NA         59       NA	47 48	NA	
50     2700       51     490       52     NA       53     NA       54     NA       55     NA       56     NA       57     NA       58     NA       59     NA	49	NA	
51     490       52     NA       53     NA       54     NA       55     NA       56     NA       57     NA       58     NA       59     NA	50		2700
52       NA         53       NA         54       NA         55       NA         56       NA         57       NA         58       NA         59       NA	51		490
53       NA         54       NA         55       NA         56       NA         57       NA         58       NA         59       NA	52 52	NA	
55 NA 56 NA 57 NA 58 NA 59 NA	53 54	NA	
56         NA           57         NA           58         NA           59         NA	55	NA	
57 NA 58 NA 59 NA	56	NA	
58 NA 59 NA	57	ΝΔ	
59 INA 60	58		
	59 60	INA	

1		
2		
3 1	NA	
5	NA	
6	NA	
7	NA	
8 9	NA	
10	NA	
11	NA	
12	NA	
13	NA	
15	NA	
16	NA	
17	NA	
19	NA	
20	NA	
21 22	NA	
23	NA	
24	NA	
25 26	NA	
20	NA	
28	NA	
29	NA	
30	NA	
32	NA	
33	NA	
34 35	NA	
36	NA	
37	NA	
38 39	NA	
40	NA	
41	NA	
42 43	NA	
44	NA	
45	NA	
46 47	NA	
48	NA	
49	N A	
50 51	NA	
52	NA	
53	NA	
54 55	NΔ	
56	ΝΛ	
57	NA NA	
58		
50	NΔ	

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

1		
2		
3	NA	
4 5	NA	
6	NA	
7		12
8		12
9	NIA	12
10	NA	
12	NA	
13	NA	
14	NA	
15 16	NA	
17	NA	
18	NA	
19	NA	
20	NA	
21	NA	
23	1 11 1	
24		0
25		
26		
27		
29		0
30		0
31		
32 33		0
34	NA	
35	NA	
36	NA	
37 38	NA	
39	NA	
40	1,111	3
41	NA	J
42		
44	INA	
45	NA	
46	NA	
47 49	NA	
40 49	NA	
50	NA	
51		183
52	NA	
53 54	NA	
55	NA	
56	NA	
57	NA	
58 50	NA NA	
60	INA	

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

2		
3	NA	
4		
5	NA	
6		300
7		300
8	NI A	
9	NA	
10		300
11		300
12		300
13		200
14		300
15	NA	
10	NA	
1/ 10	NA	
10	NA	
20		4
20		4
21		300
22	NIA	
23	NA	
25	NA	
26	NA	
27	NA	
28	NA	
29		300
30	NA	
31	NA	
32		
33	INA	
34	NA	
35	NA	
36	NA	
37		
38	NA	
39	NA	
40	NA	
41	NA	
4Z 42		4
45 11		4
44		4
46		300
47		
48		
49		
50		
51		
52		
53		
54		
55		
56		
57		
58		

1

1	
2	
3	
4	Movement of large body parts to perform display
5	0
7	0
8	0
9	1
10	1
11	0
12	1
14	1
15	1
16	
17	0
18	1
19	1
20 21	1
22	1
23	
24	1
25	
26 27	
27	
29	1
30	• 1
31	1
32	
33 34	4
35	
36	
37	
38	
39 40	I
41	1
42	1
43	1
44	1
45 46	1
40 47	1
48	1
49	l
50	1
51	1
52	0
55 54	1
55	1
56	- 1
57	1
58	
59 60	1
00	



$ \begin{array}{c} 1\\2\\3\\4\\5\\6\\7\\8\\9\\10\\11\\12\\13\\14\\15\\16\\17\\18\\19\\20\\21\\22\\23\\24\\25\\26\\27\end{array} $		1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1
28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43	NA	1 0 1 1 1 1 1 1 1 1 1 1 1
<ol> <li>44</li> <li>45</li> <li>46</li> <li>47</li> <li>48</li> <li>49</li> <li>50</li> <li>51</li> <li>52</li> <li>53</li> <li>54</li> <li>55</li> <li>56</li> <li>57</li> <li>58</li> <li>59</li> <li>60</li> </ol>	NA	1 1 1 1 1 1 1 1 1 1 1



1		
2		
2		
3	1	
4	1	
5	1	
6	1	
7	1	
8	l	
0	1	
10	1	
10	1	
11	1	
12	1	
13	1	
14	1	
15	0	
16	Ū	
17	1	
18	1	
10	1	
19	1	
20	0	
21		
22	0	
23		
24		
25	l	
26		
27	0	
28		
20	1	
29	1	
30	I	
31	1	
32	0	
33		
34	I	
35	1	
36		
37	1	
38	1	
39	1	
40	1	
41	0	
41	1	
42	I	
43	1	
44	1	
45	- 1	
46	1	
47	1	
48	- 1	
49	1	
50	1	
51	1	
ר ב בי	1	
52	1	
53	1	
54	1	
55	1	
56	1	
57	1	
58	1	
59	1	
60	1	
00		



6	
7	
8	
9	
10	
11	
12	
13	
14	
15	
16	
17	
10	
10	
20	
20	
21	
22	
23	
24	
25	
26	
27	
28	
29	
30	
31	
32	
33	
34	
35	
36	
37	
38	
39	
40	
41	
42	
42	
44	
77 15	
45	
40	
47	
4ð	
49	
50	
51	
52	
53	
54	
55	
56	

58	
59	

22	
60	

4 5	Visual aside from movement (colour patch, eyespot, spine, etc.)	Eyespots	
6		1	0
7		1	0
8		1	0
9 10		1	0
11		1	0
12		1	0
13		1	0
14 15		l	0
15		1	0
17		1	0
18		1	0
19		1	0
20		1	0
22		1	0
23		1	0
24		1	0
25		1	0
26 27		1	0
28		l	0
29		0	0
30		0	0
31		1	1
32 33		0	0
34		0	0
35		1	0
36 27		1	0
37 38		1	0
39		1	0
40		1	0
41		1	0
42 43		1	0
44		1	0
45		1	0
46		1	0
4/ 48		l	0
49		1	0
50		1	0
51		1	0
52 53		1	0
55 54		1	0
55		1	0
56		1	0
57		1	0
со 59		-	0
60		I	0

**Biological Reviews** 

1		
2		0
4	l	0
5	l	0
6 7	l	0
8	l	l
9	l	0
10 11	1	0
12	1	0
13	1	0
14	1	0
16	1	0
17	1	0
18 19	1	1
20	1	0
21	1	0
22 23	1	0
24	1	0
25	1	0
26	1	0
28	1	0
29	l	0
30	0	0
32		0
33	0	0
34	0	0
36		0
37	0	0
38	0	0
40	0	0
41	0	0
42	0	0
44	0	0
45	0	0
46 47	0	0
48	0	0
49	0	0
50 51	0	0
52	U 1	0
53		0
54 55	1	0
56	1	0
57	1	0
58	1	0
60	1	U

1			
2 3		1	0
4		1	0
5		1	0
7		1	0
8		1	0
9 10		1	0
11		1	0
12 13		1	0
13		1	0
15		1	0
16 17		1	0
18		0	0
19 20		0	0
20 21		0	0
22		0	0
23		1	0
24		0	0
26		0	0
27 28		0	0
29	NA		0
30		0	0
31 32		0	0
33		0	0
34		0	0
35 36		0	0
37		0	0
38	NA	0	0
40		0	0
41		0	0
42 43		1	0
44		0	0
45		1	0
46 47		0	0
48		0	0
49 50		0	0
50		0	0
52		0	0
53 54	NA		0
55		0	0
56		0	0
57 58		0	0
59		1	0
60			

**Biological Reviews** 

1 2			
3 ⊿		1	0
5		1	0
6		1	0
7		1	0
8		1	0
9 10		0	0 0
10		1	0
12		1	0
13		1	0
14 15		0	0
15		1	0
17		1	0
18		1	0
19 20		1	0
20 21		1	0
22		1	0
23	NA		0
24 25	NA		0
25 26	NA		0
27	NA		0
28	NA		ů 0
29	NA		0
30 31	NA NA		0
32			0
33	NA		0
34 25	NA	0	0
35 36		0	0
37		0	0
38		0	0
39		1	0
40 41		1	1
42	NA		0
43	NA		0
44 45	NA		0
45 46	NA		0
47	NA		0
48	NA		0
49		1	Õ
50 51		1	0
52		1	0
53		1	U
54		1	0
55 56		l	0
57		1	0
58		1	0
59		0	0
60			

1		
2		
3	0	0
5	1	0
6	0	0
7	1	Û.
8	1	0
9	1	0
10	1	0
12	1	0
13	1	0
14	1	0
15	0	0
17	1	0
18	1	0
19	1	1
20	1	0
21	1	1
22 23	1	1
24	1	1
25	0	0
26	1	0
27	1	1
29	1	0
30	1	0
31	1	0
32	0	0
33	1	0
35	1	Û.
36	1	1
37	1	1
38		0
40		0
41	1	0
42	0	0
43	1	0
44	1	0
46	1	0
47	1	0
48	1	0
49	1	0
50	1	0
52	1	0
53	1	U
54	1	0
55	1	1
50 57	1	1
58	1	1
59	1	1
60		

**Biological Reviews** 

1				
2				
3			0	0
4 5			1	0
6			1	1
7			1	1
8			1	0
9			1	1
10			1	1
12			1	1
13			l	l
14			1	1
15 16			0	0
17			0	0
18			1	0
19			1	0
20			1	0
21			1	1
23			1	1
24			1	0
25	NΛ		1	0
20			1	0
28			1	0
29			l	1
30			0	0
31			1	1
33			1	1
34			1	0
35			1	0
36 37			1	0
38			0	0
39			0	0
40			0	0
41			1	0
43			1	0
44			0	ů 0
45			1	1
46 47			1	1
48				
49				
50				
51 52				
52 53				
54				
55				
56				

1			
2			
3			
4	Auditory	Olfactory or Gustatory	Elements of display repeated or sustained
5	j	1	1 sustained
7		1	1 sustained
8		1	
9		0	1 sustained
10		0	1 sustained
11		0	1 sustained
12		0	0 NA
14		1	0 repeated
15		1	0 NA
16		0	0 sustained
17		0	0 substanted
18 10		0	
20		0	0 sustained
21		0	0 sustained
22		0	0 sustained
23		0	0 repeated
24		0	0 repeated
25 26		0	0 sustained
20			0 repeated
28			
29	NA	NA	sustained, repeated
30		1	1 sustained
31		0	0 sustained
32 33		0	0 repeated
34		0	0 repeated
35		1	0 repeated
36		1	0 repeated
37			orepeated
38			sustained
39 40		1	0 repeated
41		0	0 repeated
42		0	0 sustained
43		1	0 NA
44		1	0 NA
45		0	0 NA
40 47		1	ΟΝΔ
48		0	0 systems d
49		0	
50		l	0 sustained, repeated
51		1	0 sustained
52 53		0	0 sustained
54		0	0 sustained
55		0	0 sustained
56		0	0 sustained
57		0	0 sustained
58		1	0 repeated
60		ı	0 Tepeateu

2			
3		0	0 repeated
4 5		0	0 sustained
5 6		0	0 sustained
7		1	
8		1	0 repeated
9		0	0 NA
10		1	0 NA
11		0	0 NA
12		1	0 NA
14		1	1 repeated
15		0	1 sustained
16		1	0 NA
17			
18 19		0	
20		0	0 NA
21		0	0 NA
22		0	0 NA
23		0	0 NA
24 25		0	0 NA
25 26		0	0 NA
27		1	0 NA
28			0 sustained
29		0	
30	NA		I sustained, repeated
31 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
3/	NA		1 sustained repeated
39	ΝΔ		1 sustained, repeated
40	NA		1 sustained, repeated
41			1 sustained, repeated
42	INA		I sustained, repeated
43 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 50	NA		0 sustained
50 51	NA		0 sustained
52	NIA		1 sustained
53			1 sustained
54	NA		0 sustained
55 56	NA		1 sustained
50 57	NA		1 sustained
58	NA		1 sustained
59	NA		1 sustained
60			

1				
2				
3	NA		1	sustained
4	NA		1	sustained
6	NA		1	sustained
7	NA		1	sustained reneated
8	NA		1	sustained, repeated
9			1	sustained
10	NA		1	sustained
12	NA		1	sustained, repeated
13	NA		1	sustained
14	NA		1	sustained
15	NA		1	sustained
10	NA		1	sustained
18	NA		1	sustained
19	NA		1	sustained
20	NA		1	sustained
21	NΛ		1	sustained
22	1 1 1 2	1	1	sustained repeated
24	NT A	1	1	sustained, repeated
25	NA		I	sustained
26	NA		$\mathbf{N}$	sustained
2/	NA		1	sustained
20 29	NA	NA		NA
30	NA		1	sustained
31	NA		1	sustained
32	NA		1	sustained, repeated
33 34	NA		1	sustained repeated
35	NΔ		1	sustained, repeated
36	NA		1	sustained, repeated
37			1	sustanieu, repeateu
38	NA	NA	1	NA
39 40	NA		1	sustained, repeated
41	NA		1	sustained, repeated
42	NA		1	sustained, repeated
43	NA		1	sustained, repeated
44 45	NA		1	sustained, repeated
45		1	1	sustained
47	NA		1	sustained
48	NA		1	sustained
49	NA		1	sustained
50 51	NA		1	sustained
52			1	sustained
53	NA		1	sustained
54	INA	NA	-	NA
55		1	0	sustained
סט 57		0	0	sustained
58		1	0	sustained
59		0	0	sustained, repeated
60				· •

2			
3	0	1	sustained, repeated
4	1	1	sustained
5	1	1	sustained
7	1	0	sustained
8	0	1	sustained
9	0	1	sustained
10	0	1	sustained
11	0	1	repeated
12	1	1	NA
14	1	0	repeated
15	0	1	sustained
16	0	1	sustained
17	0	1	sustained, repeated
18	0	1	sustained, repeated
19	0	1	sustained, repeated
20	0	0	sustained
22	0	0	sustained
23	1 NA		sustained
24	1 NA		sustained
25			sustained
26	I NA		sustained
27	1 NA		sustained
28	1 NA		sustained
30	1 NA		sustained
31	1 NA		sustained
32	1 NA		sustained
33	1 NA		sustained
34	I NA	1	sustailled
36	1	1	repeated
37	1	1	repeated
38	1	1	repeated
39	1	0	sustained
40	0 NA		sustained
41	1	1	repeated
42	1	1	repeated
44	1	1	Tepeated
45	1	1	repeated
46	1	1	repeated
47	1	1	repeated
48	1	1	repeated
49 50	1	0	repeated
50	0	0	sustained
52	1	0	sustained repeated
53	1	0	sustained, repeated
54	1	0	sustained, repeated
55	0	1	sustained
56 57	0	1	sustained
57 58	0	1	sustained
59	0	1	sustained
60	-	1	

1			
2			
3	0	1	sustained
4 5	0	0	sustained
5	0	0	sustained
7	0	0	sustailled
8	0	1	sustained
9	0	1	sustained
10	0	1	sustained
11	0	1	sustained
12	0	1	sustained
13	0 NA	1	sustained
14	0 NA	0	Sustained
16	1	0	NA
17	0	1	sustained
18	1 NA		sustained
19	1	0	repeated
20	0	0	sustained
21	0	0	sustained
22	0		sustained
25	0	0	NA
25	1	1	repeated
26	1	0	sustained, repeated
27	0	0	sustained
28	0	Ő	repeated
29	0	0	
30	0	0	repeated
31 22	0	0	repeated
32	1	0	repeated
34	1	1	repeated
35	0	0	sustained
36	1	ů 0	repeated
37	1	0	
38	0	0	sustained
39	0	0	NA
40 41	0	0	sustained
42	1	1	sustained, repeated
43	0 NA		sustained
44	0	0	sustained
45	0	1	sustained
46	0	1	sustained
47	1	0	sustained
40 49	0	0	sustained
50	0	0	sustained
51	0	0	sustained
52	ΟΝΔ		sustained
53	0	0	sustained
54	0	0	Sustaineu
55	1	0	repeated
50 57	0	0	sustained
57 58	0	0	sustained
59	0	0	sustained
60	-	Ŭ	

0	0 repeated
0	0 sustained
0	0 repeated
0	0 repeated
0	1 sustained
0	0 repeated
0	0 repeated
0	0 sustained
0	0 repeated
0	0 NA
0	0 NA
0	0 repeated
0	0 sustained
0	0 sustained
0	0 repeated
0	0 NA
0	0 repeated
0	0 sustained

1	
2	
3	
4	Sum of modes (visual modes combined here)
5	sum of modes (visual modes combined here)
0 7	3
7 8	3
9	2
10	2
11	2
12	2
13	1
14	2
15	2
16	1
1/	1
1ð 10	1
20	
20	1
22	
23	
24	
25	
26	
27	1
28	1
29	3
30	1
32	
33	
34	1
35	2
36	2
37	
38	
39 40	2
40 41	1
42	1
43	2
44	2
45	2
46	1
47	2
48	1
49 50	2
50	2
52	1
53	1
54	1
55	1
56	1
57	1
58	1
59	2
60	



$\begin{array}{c}1\\2\\3\\4\\5\\6\\7\\8\\9\\10\\11\\2\\13\\14\\15\\16\\7\\8\\9\\10\\12\\23\\24\\5\\26\\7\\8\\9\\0\\1\\2\\3\\3\\4\\5\\36\\7\\8\\9\\0\\41\\2\\3\\4\\4\\5\\6\\7\\8\\9\\0\\41\\2\\3\\4\\4\\5\\6\\7\\8\\9\\0\\41\\2\\3\\4\\4\\5\\6\\7\\8\\9\\0\\41\\2\\3\\4\\5\\6\\7\\8\\9\\0\\41\\2\\3\\4\\5\\6\\7\\8\\9\\0\\41\\2\\3\\4\\5\\6\\7\\8\\9\\0\\41\\2\\3\\4\\5\\6\\7\\8\\9\\0\\41\\2\\3\\4\\5\\6\\7\\8\\9\\0\\41\\2\\3\\4\\5\\6\\7\\8\\9\\0\\41\\2\\3\\4\\5\\6\\7\\8\\9\\0\\41\\2\\3\\4\\5\\6\\7\\8\\9\\0\\41\\2\\3\\4\\5\\6\\7\\8\\9\\0\\41\\2\\3\\4\\5\\6\\7\\8\\9\\0\\41\\2\\3\\4\\5\\6\\7\\8\\9\\0\\41\\2\\3\\4\\5\\6\\7\\8\\9\\0\\41\\2\\3\\4\\5\\6\\7\\8\\9\\0\\41\\2\\3\\8\\9\\0\\41\\2\\3\\4\\5\\6\\7\\8\\9\\0\\41\\2\\3\\4\\5\\6\\7\\8\\9\\0\\41\\2\\3\\4\\5\\6\\7\\8\\9\\0\\41\\2\\3\\4\\5\\6\\7\\8\\9\\0\\41\\2\\3\\4\\5\\6\\7\\8\\9\\0\\41\\2\\3\\8\\9\\0\\41\\2\\3\\4\\5\\6\\7\\8\\9\\0\\41\\2\\3\\4\\5\\6\\7\\8\\9\\0\\41\\2\\3\\4\\5\\6\\7\\8\\9\\0\\41\\2\\3\\4\\5\\6\\7\\8\\9\\0\\41\\2\\3\\4\\5\\6\\7\\8\\9\\0\\41\\2\\3\\4\\5\\6\\7\\8\\9\\0\\41\\2\\3\\4\\5\\6\\7\\8\\9\\0\\41\\2\\3\\4\\5\\6\\7\\8\\9\\0\\41\\2\\3\\4\\5\\6\\7\\8\\9\\0\\41\\2\\3\\4\\5\\6\\7\\8\\9\\0\\1\\2\\3\\4\\5\\6\\7\\8\\9\\0\\41\\2\\3\\4\\5\\6\\6\\7\\8\\9\\0\\1\\2\\3\\4\\5\\6\\6\\7\\8\\9\\0\\1\\2\\3\\4\\5\\6\\6\\7\\8\\9\\0\\1\\2\\3\\4\\5\\6\\6\\7\\8\\9\\0\\1\\2\\3\\4\\5\\6\\6\\7\\8\\9\\0\\1\\2\\3\\4\\5\\6\\6\\6\\6\\8\\6\\6\\6\\6\\6\\6\\6\\6\\6\\6\\6\\6\\6\\6$	$ \begin{array}{c} 2\\2\\2\\2\\2\\2\\2\\2\\2\\2\\2\\2\\2\\2\\2\\2\\2\\2\\2\\$
40 41	2 2 2
42 43	2
44 ⊿5	2
45 46	3
47 48	2
49	2
50 51	2
52	2
53 54	1
55	2
56 57	1
58	2
59 60	1





1	
2	
3	1
4 F	1
5	1
7	1
8	1
9	1
10	1
11	1
12	1
13	1
14	l
15	1
17	1
18	2
19	1
20	1
21	
22	
23	1
24	1
25	
27	1
28	
29	1
30	• 1
31	1
32	1
33 34	47
35	
36	
37	
38	1
39	1
40	1
41	1
42	1
43	1
45	l
46	1
47	
48	
49	
50	
51	
<i>32</i> 53	
54	
51	

1	
2	Key to Table S3.
3	Column heading
4 5	Citation
6	Year
7	Phylum
8	Class
9 10	Order
11	Family
12	Species
13	Species
14	Study type
15 16	Life stage studied
17	Primary defence reported
18	Predator in study
19	Trigger sensory mode
20	Predation sequence stage
21	Display duration description
23	Display duration (sec) (max if range given)
24	Movement of large body parts to perform display
25	Visual aside from movement (colour patch evespot spine etc.)
20 27	Evesnots
28	Auditory
29	Additory
30	
31 20	Elements of display repeated or sustained
33	Sum of modes (visual modes combined here)
34	
35	
36 27	
37 38	
39	
40	
41	
42 43	
44	
45	
46	
4/	
40 49	
50	
51	
52	
53 54	
55	
56	
57	
58 50	
60	

## Definition

1 2 3

- 4 Source of information
- 6 Year of publication
- 7 Phylum of displaying animal
- <sup>8</sup> 9 Class of displaying animal
- 10 Order of displaying animal
- <sup>11</sup> Family of displaying animal
- <sup>12</sup> 13 Species of displaying animal
- 14 Study types categorised into manipulative or description
- <sup>15</sup> Stage classified as adult or juvenile
- <sup>16</sup> Whether the study described any primary defences (e.g. camouflage)
- 18 Species used to trigger display
- 19 Method to trigger display
- 20 21 Stage in predation sequence display triggered
- Description of display duration
- 23 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
- 27 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
- 31 Whether there were repeated or sustained elements of the display; 1 = Yes, 0 = No32 Sum of concerv modes the display operates in (movement, visual, and everyots are
- <sup>32</sup> 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

3	Citation	Order	Species
4 5	Bailey & Sandow (1983)	Orthoptera	Mygalopsis marki
6	Brodie et al. (1984)	Urodela	Echinotriton andersoni
7	Lyon & Fogden (1989)	Aves	Eurypyga helias
8	Robinson (1969)	Orthoptera	Scorpiorinus fragilis
9 10	Robinson (1969)	Phasmatodea	Metriotes diocles
11	Robinson (1969)	Mantodea	Angela guianensis
12	Robinson (1969)	Mantodea	Phyllovates chlorophaea
13 14	Robinson (1969)	Mantodea	Choeradodis rhombicollis
15	Thomas & Strahl (1990)	Aves	Eurvnyga helias
16	Umbers & Mannes (2015)	Orthoptera	Acrineza reticulata
17	Balderrama & Maldonado (1973)	Mantodea	Stagmatontera hiocellata
18 19	Vork & Bartol (2016)	Muonsida	I olliguncula bravis
20	Honlon & Mossonger (1088)	Sopiido	Sonia officinalis
21	Claudes et al. (200()	Septida	
22	Glaudas et al. (2006)	Squamata	Agkistrodon piscivorus
23 24			
25			
26			
27			
28			
30			
31			
32			
33			
34			
35			
30 27			
37 38			
39			
40			
41			
42			
43			
ΔΔ			

1	as of succies for which h	ath have have studi
2	es of species for which b	both have been studi
5 4	Juvenile strategy	Adult strategy
5	flee	display
6	display	display
7	display	display
8	flee	display
9 10	flee	display
11	flee	display
12	flee	flee and display
13	flee	display
14 15	1. 1	
15	display	display
17	display	display
18	cryptic posture and limit	te display
19	display	display
20	limited display	display
21	display	display
23	1 5	
24		
25		
26		
27 28		
29		
30		
31		
32		
34		
35		
36		
37		
38 39		
40		
41		
42		
43		
44 45		
46		
47		
48		
49 50		
51		
52		
53		
54		
55 56		
57		
58		
59		
60		

1 2	ied and at least one stage uses a deimatic display
3	
4 5	
6	
7	
8	
9 10	
11	
12 13	
13	
15	
16 17	
17	
19	
20 21	
∠ı 22	
23	
24 25	
26	
27	
28 29	
30	
31	
32 33	
34	
35	
36 37	
38	
39 40	
40	
42	
43 44	
45	
46	
47 48	
49	
50	
51 52	
53	
54	
55 56	
57	
58	
59 60	

1	
2	Table S5. Summary of studie
3	Citation
4 5	Brodie et al. 1984
6	Brodie et al. 1984
7	Brodie et al. 1984
8	Brown et al. 2007
9	Olofsson et al. $2011$
10 11	Olofsson et al. 2012b
12	Sandara & Dailar 1079
13	Sandow & Balley 1978
14	Staudinger et al. 2011
15 16	Umbers et al. 2019
10	Umbers et al. 2019
18	Vallin et al. 2005
19	Vallin et al. 2006
20	Vallin et al. 2007
21	Vallin et al. 2007
23	Vallin et al 2007
24	Vallin et al. 2007
25	
26 27	
27 28	
29	
30	
31	
32 33	
34	
35	
36	
37	
38 39	
40	
41	
42	
43 11	
44	
46	
47	
48	
49 50	
51	
52	
53	
54	
55 56	
57	
58	
## **Biological Reviews**

s that have assessed the survival value of deimatic displays in prev

Aim To present data on the defence strategies of four genera of salamanders (previously unstudied) and pro-To present data on the defence strategies of four genera of salamanders (previously unstudied) and pro-To present data on the defence strategies of four genera of salamanders (previously unstudied) and pro-To explore the mechanisms and function behind caterpillar clicks. Is clicking an acoustic aposematic si

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

To investigate winter predation on hibernating butterflies - are rodents responsible for winter predation To describe the defensive behaviours in the Western Australian katydid and assess the survival value o To evaluate predator-prev interactions between longfin squid, bluefish and flounder: investigate intial To test the efficiency of a generally accepted deimatic display in a natural setting

To test the efficiency of a generally accepted deimatic display in an environment in which predators are To investigate the relative importance of evespots and sound for defence and the survival value when a To test the hypothesis that different species of butterflies with different defence strategies (e.g. relying To test whether large evespots on lepidopterans are effective for preventing attacks from small birds ar To test whether large eyespots on lepidopterans are effective for preventing attacks from small birds ar To test whether large evespots on lepidopterans are effective for preventing attacks from small birds ar 

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

ισμ..

Prey order       Prey common name       Prey taxonomic name         Urodela       Spot-tailed warty newt       Paramesotriton chinensis         Urodela       Spot-tailed warty newt       Paramesotriton chinensis         Lepidoptera       Common silkmoth       Antheraea polyphemus         Lepidoptera       Peacock butterfly       Aglais io         12       Orthoptera       Western Australian katydid       Mygalopsis ferruginea         13       Orthoptera       Mountain katydid       Acripeza reticulata         14       Cephalopoda       Longfin squid       Loligo pealeii         15       Orthoptera       Mountain katydid       Acripeza reticulata         16       Orthoptera       Peacock butterfly       Aglais io         17       Lepidoptera       Peacock butterfly       Aglais io         18       Lepidoptera       Peacock butterfly       Aglais io         19       Lepidoptera       Peacock butterfly       Aglais io         21       Lepidoptera       Peacock butterfly       Aglais io         22       Lepidoptera       Peacock butterfly       Aglais io         23       Lepidoptera       Fyed hawkmoth       Smerinthus ocellatus         24       Lepidoptera       Fyed hawkmoth <th>1</th> <th></th> <th></th> <th></th>	1			
4       Urodela       Spot-tailed warty newt       Paramesotrition chinensis         6       Urodela       Spot-tailed warty newt       Paramesotrition chinensis         7       Urodela       Spoted paddle-tail newt       Paramesotrition chinensis         8       Lepidoptera       Common silkmoth       Antheraea polyphemus         9       Lepidoptera       Peacock butterfly       Aglais io         11       Lepidoptera       Peacock butterfly       Aglais io         12       Orthoptera       Western Australian katydid       Acripeza reticulata         14       Cephalopoda       Longfin squid       Loligo pealeii         15       Orthoptera       Mountain katydid       Acripeza reticulata         16       Orthoptera       Peacock butterfly       Aglais io         12       Lepidoptera       Peacock butterfly       Aglais io         13       Lepidoptera       Peacock butterfly       Aglais io         14       Lepidoptera       Peacock butterfly       Aglais io         15       Lepidoptera       Peacock butterfly       Aglais io         16       Lepidoptera       Eyed hawkmoth       Smerinthus ocellatus         17       Lepidoptera       Eyed hawkmoth       Smerinthus ocellatus </th <th>2 3</th> <th>Prey order</th> <th>Prey common name</th> <th>Prey taxonomic name</th>	2 3	Prey order	Prey common name	Prey taxonomic name
6       Urodela       Spotted paddle-tail newt       Paramesotriton caudopunctatus         7       Urodela       Spotted paddle-tail newt       Pachyrition brevipes         8       Lepidoptera       Common silkmoth       Antheraea polyphemus         9       Lepidoptera       Peacock butterfly       Aglais io         11       Lepidoptera       Peacock butterfly       Aglais io         12       Orthoptera       Western Australian katydid       Mrgalopsis ferruginea         13       Orthoptera       Mountain katydid       Acripeza reticulata         14       Cephalopoda       Longifn squid       Acripeza reticulata         15       Orthoptera       Mountain katydid       Acripeza reticulata         16       Lepidoptera       Peacock butterfly       Aglais io         17       Lepidoptera       Peacock butterfly       Aglais io         18       Lepidoptera       Peacock butterfly       Aglais io         19       Lepidoptera       Peacock butterfly       Aglais io         20       Lepidoptera       Eyed hawkmoth       Smerinthus ocellatus         21       Lepidoptera       Eyed hawkmoth       Smerinthus ocellatus         22       Lepidoptera       Eyed hawkmoth       Smerinthusoce	4	Urodela	Chinese warty newt	Paramesotriton chinensis
Urodela       Spotted paddle-tail newt       Pachytrition brevipes         Lepidoptera       Common silkmoth       Antheraea polyphemus         12       Lepidoptera       Peacock butterfly       Aglais io         12       Orthoptera       Westem Australian katydid       Mygalopsis ferruginea         14       Cephalopoda       Longfin squid       Loligo pealeii         15       Orthoptera       Mountain katydid       Acripeza reticulata         16       Orthoptera       Peacock butterfly       Aglais io         17       Orthoptera       Mountain katydid       Acripeza reticulata         18       Lepidoptera       Peacock butterfly       Aglais io         19       Lepidoptera       Peacock butterfly       Aglais io         10       Lepidoptera       Peacock butterfly       Aglais io         12       Lepidoptera       Peacock butterfly       Aglais io         12       Lepidoptera       Peacock butterfly       Aglais io         13       Lepidoptera       Eyed hawkmoth       Smerinthus ocellatus         14       Lepidoptera       Eyed hawkmoth       Smerinthus ocellatus         15       Pridoptera       Eyed hawkmoth       Smerinthus ocellatus         16       Pr	6	Urodela	Spot-tailed warty newt	Paramesotriton caudopunctatus
Image: second	7	Urodela	Spotted paddle-tail newt	Pachytriton brevipes
9       Lepidoptera       Peacock butterfly       Aglais io         11       Lepidoptera       Peacock butterfly       Aglais io         12       Orthoptera       Western Australian katydid       Mygalopsis ferruginea         13       Orthoptera       Wountain katydid       Acripeza reticulata         14       Cephalopoda       Longfin squid       Acripeza reticulata         15       Orthoptera       Mountain katydid       Acripeza reticulata         16       Lepidoptera       Peacock butterfly       Aglais io         17       Orthoptera       Peacock butterfly       Aglais io         18       Lepidoptera       Peacock butterfly       Aglais io         19       Lepidoptera       Peacock butterfly       Aglais io         10       Lepidoptera       Peacock butterfly       Aglais io         12       Lepidoptera       Peacock butterfly       Aglais io         12       Lepidoptera       Eyed hawkmoth       Smerinthus ocellatus         13       Lepidoptera       Eyed hawkmoth       Smerinthus ocellatus         14       Image: State in the state i	8	Lepidoptera	Common silkmoth	Antheraea polyphemus
10       Lepidoptera       Peacock butterfly       Aglais io         12       Orthoptera       Western Australian katydid       Mygalopsis ferruginea         13       Orthoptera       Western Australian katydid       Acripeza reticulata         14       Cephalopoda       Longfin squid       Acripeza reticulata         15       Orthoptera       Mountain katydid       Acripeza reticulata         16       Orthoptera       Peacock butterfly       Aglais io         17       Lepidoptera       Peacock butterfly       Aglais io         18       Lepidoptera       Peacock butterfly       Aglais io         19       Lepidoptera       Peacock butterfly       Aglais io         21       Lepidoptera       Peacock butterfly       Aglais io         22       Lepidoptera       Peacock butterfly       Aglais io         23       Lepidoptera       Eyed hawkmoth       Smerinthus ocellatus         24       Lepidoptera       Eyed hawkmoth       Smerinthus ocellatus         25       Peacock butterfly       Aglais io       Peacock butterfly         26       Lepidoptera       Eyed hawkmoth       Smerinthus ocellatus         27       Peacock butterfly       Aglais io       Peacock butterfly <td>9 10</td> <td>Lepidoptera</td> <td>Peacock butterfly</td> <td>Aglais in</td>	9 10	Lepidoptera	Peacock butterfly	Aglais in
12       Dependent       Fraction of the second solution of the s	11	Lepidoptera	Peacock butterfly	Aglais io
13       Orthopera       Integration National Katyon       Integration of the second	12	Orthontera	Western Australian katydid	Myalonsis ferruginea
14       Cephaloptea       Longin squud       Longo peterin         15       Orthoptera       Mountain katydid       Acripeza reticulata         16       Orthoptera       Peacock butterfly       Aglais io         19       Lepidoptera       Peacock butterfly       Aglais io         21       Lepidoptera       Peacock butterfly       Aglais io         22       Lepidoptera       Peacock butterfly       Aglais io         23       Lepidoptera       Peacock butterfly       Aglais io         24       Lepidoptera       Eyed hawkmoth       Smerinthus ocellatus         25       Lepidoptera       Eyed hawkmoth       Smerinthus ocellatus         26       Smerinthus ocellatus       Smerinthus ocellatus         27       Smerinthus ocellatus       Smerinthus ocellatus         28       Smerinthus ocellatus       Smerinthus ocellatus         29       Smerinthus ocellatus       Smerinthus ocellatus         20       Smerinthus ocellatus       Smerinthus ocellatus         23       Smerinthus ocellatus       Smerinthus ocellatus         24       Smerinthus ocellatus       Smerinthus ocellatus         25       Smerinthus ocellatus       Smerinthus ocellatus         26       Smerint	13	Canhalanada	Longfin squid	I oligo pogloji
Orthoptera       Mountain katydid       Acripeza reticulata         Orthoptera       Mountain katydid       Acripeza reticulata         Lepidoptera       Peacock butterfly       Aglais io         Lepidoptera       Exoch butterfly       Aglais io         Lepidoptera       Exoch butterfly       Aglais io         Lepidoptera       Eyed hawkmoth       Smerinthus ocellatus         Lepidoptera       Eyed hawkmoth       Smerinthus ocellatus         Paceock       Smerinthus ocellatus       Paceock         Paceock       Smerinthus ocellatus       Paceock         Paceock       Smerinthus ocellatus       Paceock         Paceock       Smerinthus ocellatus       Paceock         Paceock       Paceock       Paceock         Paceock       Paceock       Paceock         Paceock       Paceock       Paceock         Paceock       Paceock       Paceock	14 15	Orthontoro	Mountain katudid	Longo pedien
17       Orthopera       Montain Ratydu       Actriges in cludud         18       Lepidoptera       Peacock butterfly       Aglais io         20       Lepidoptera       Peacock butterfly       Aglais io         21       Lepidoptera       Peacock butterfly       Aglais io         22       Lepidoptera       Peacock butterfly       Aglais io         23       Lepidoptera       Peacock butterfly       Aglais io         24       Lepidoptera       Eyed hawkmoth       Smerinthus ocellatus         25       Lepidoptera       Eyed hawkmoth       Smerinthus ocellatus         26       Image: State	16	Orthoptera	Mountain katydid	Acripeza reliculata
18       Lepidoptera       Peacock butterfly       Aglais io         20       Lepidoptera       Peacock butterfly       Aglais io         21       Lepidoptera       Peacock butterfly       Aglais io         22       Lepidoptera       Peacock butterfly       Aglais io         23       Lepidoptera       Peacock butterfly       Aglais io         24       Lepidoptera       Eyed hawkmoth       Smerinthus ocellatus         25       Lepidoptera       Eyed hawkmoth       Smerinthus ocellatus         26       .       .       .         27       .       .       .       .         28       .       .       .       .         29       .       .       .       .         29       .       .       .       .         20       .       .       .       .         21       .       .       .       .         22       .       .       .       .         23       .       .       .       .         24       .       .       .       .         23       .       .       .       .         24	17	Unidentena		
19       Lepidoptera       Peacock butterfly       Aglais to         21       Lepidoptera       Peacock butterfly       Aglais io         22       Lepidoptera       Peacock butterfly       Aglais io         23       Lepidoptera       Eyed hawkmoth       Smerinthus ocellatus         24       Lepidoptera       Eyed hawkmoth       Smerinthus ocellatus         25       Lepidoptera       Eyed hawkmoth       Smerinthus ocellatus         26       Icpidoptera       Eyed hawkmoth       Smerinthus ocellatus         27       Icpidoptera       Eyed hawkmoth       Smerinthus ocellatus         28       Icpidoptera       Icpidoptera       Icpidoptera         29       Icpidoptera       Icpidoptera       Icpidoptera         29       Icpidoptera       Icpidoptera       Icpidoptera         29       Icpidoptera       Icpidoptera       Icpidoptera         29       Icpidoptera       Icpidoptera       Icpidoptera         30       Icpidoptera       Icpidoptera       Icpidoptera         31       Icpidoptera       Icpidoptera       Icpidoptera         32       Icpidoptera       Icpidoptera       Icpidoptera         33       Icpidoptera       Icpidoptera <td>18</td> <td>Lepidoptera</td> <td>Peacock butterily</td> <td>Agiais io</td>	18	Lepidoptera	Peacock butterily	Agiais io
1       Lepidoptera       Peacock butterfly       Aglais to         22       Lepidoptera       Eyed hawkmoth       Smerinthus ocellatus         23       Lepidoptera       Eyed hawkmoth       Smerinthus ocellatus         24       Lepidoptera       Eyed hawkmoth       Smerinthus ocellatus         25       Lepidoptera       Eyed hawkmoth       Smerinthus ocellatus         26	19 20	Lepidoptera	Peacock butterfly	Aglais 10
22       Lepidoptera       Peacock butterfly       Aglais io         23       Lepidoptera       Eyed hawkmoth       Smerinthus ocellatus         24       Lepidoptera       Eyed hawkmoth       Smerinthus ocellatus         25       Lepidoptera       Eyed hawkmoth       Smerinthus ocellatus         26	21	Lepidoptera	Peacock butterfly	Aglais io
Lepidoptera Eyed hawkmoth Smerinthus ocellatus Lepidoptera Eyed hawkmoth Smerinthus ocellatus	22	Lepidoptera	Peacock butterfly	Aglais io
Lepidoptera         Eyed hawkmoth         Smerinthus ocellatus           26         27         28           29         30         31           31         32         33           33         34         35           36         37         38           39         40         41           41         42         43           42         43         44           43         44         44           44         44         45           45         46         47           46         47         48           47         48         49           50         51         52           51         52         53           53         54         55           56         56         56           57         58         56           56         56         56           57         58         56           58         59         50           56         56         56           57         58         56           56         57         56           57	23	Lepidoptera	Eyed hawkmoth	Smerinthus ocellatus
26         27         28         29         30         31         32         33         34         35         36         37         38         39         40         41         42         43         44         45         46         47         48         49         50         51         52         53         54         55         56         57         58         59         60	24 25	Lepidoptera	Eyed hawkmoth	Smerinthus ocellatus
27         28         29         30         31         32         33         34         35         36         37         38         39         40         41         42         43         44         45         46         47         48         49         50         51         52         53         54         55         56         57         58         59         60	26			
28       29         30       31         31       32         33       34         34       35         36       37         38       39         40       41         41       42         42       43         43       44         44       45         50       51         51       52         53       54         56       57         58       56         57       58         59       60	27			
29       29         30       31         31       32         33       34         34       35         36       9         37       9         40       9         41       42         43       44         44       45         45       46         46       47         48       49         50       51         52       53         54       55         55       56         56       57         58       59         60       60	28			
31         32         33         34         35         36         37         38         39         40         41         42         43         44         45         46         47         48         49         50         51         52         53         54         55         56         57         58         59         60	29 30			
32         33         34         35         36         37         38         39         40         41         42         43         44         45         46         47         48         49         50         51         52         53         54         55         56         57         58         59         60	31			
33	32			
34         35         36         37         38         39         40         41         42         43         44         45         46         47         48         49         50         51         52         53         54         55         56         57         58         59         60	33			
36         37         38         39         40         41         42         43         44         45         46         47         48         49         50         51         52         53         54         55         56         57         58         59         60	34 35			
37         38         39         40         41         42         43         44         45         46         47         48         49         50         51         52         53         54         55         56         57         58         59         60	36			
38         39         40         41         42         43         44         45         46         47         48         49         50         51         52         53         54         55         56         57         58         59         60	37			
39         40         41         42         43         44         45         46         47         48         49         50         51         52         53         54         55         56         57         58         59         60	38			
41         42         43         44         45         46         47         48         49         50         51         52         53         54         55         56         57         58         59         60	39 40			
42         43         44         45         46         47         48         49         50         51         52         53         54         55         56         57         58         59         60	41			
<ul> <li>43</li> <li>44</li> <li>45</li> <li>46</li> <li>47</li> <li>48</li> <li>49</li> <li>50</li> <li>51</li> <li>52</li> <li>53</li> <li>54</li> <li>55</li> <li>56</li> <li>57</li> <li>58</li> <li>59</li> <li>60</li> </ul>	42			
44         45         46         47         48         49         50         51         52         53         54         55         56         57         58         59         60	43 44			
46         47         48         49         50         51         52         53         54         55         56         57         58         59         60	44			
47 48 49 50 51 52 53 54 55 56 57 58 59 60	46			
<ul> <li>48</li> <li>49</li> <li>50</li> <li>51</li> <li>52</li> <li>53</li> <li>54</li> <li>55</li> <li>56</li> <li>57</li> <li>58</li> <li>59</li> <li>60</li> </ul>	47			
49         50         51         52         53         54         55         56         57         58         59         60	48			
51 52 53 54 55 56 57 58 59 60	49 50			
52 53 54 55 56 57 58 59 60	51			
53 54 55 56 57 58 59 60	52			
55 56 57 58 59 60	53 54			
56 57 58 59 60	55			
57 58 59 60	56			
58 59 60	57			
60	58 59			
	60			

1			
2 3	Predator order	Predator common name	Predator taxonomic name
4	Mammalia	Northern short-tailed shrew	Blarina brevicauda
5	Mammalia	Northern short-tailed shrew	Blarina brevicauda
7	Mammalia	Northern short-tailed shrew	Blarina brevicauda
8	Aves	Domestic chick	Gallus gallus domesticus
9 10	Mammalia	Yellow-necked mouse and wood mouse	Apodemus flavicollis and A. svlvc
11	Mammalia	Yellow-necked mouse and wood mouse	Apodemus flavicollis and A. svlvc
12	Reptilia	Salmon-bellied skink	Egernia napoleonis
13 14	Actinoptervgii	Bluefish and summer flounder	<i>Pomatomus saltatrix</i> and <i>Paralic</i>
15	Aves	Australian magnie	Gymnorhina tihicen
16	Aves	Australian magpie	Gymnorhina tibicen
17 18	Aves	Blue tit	Parus caeruleus
19	Aves	Blue tit	Parus caeruleus
20	Aves	Blue tit	Parus caeruleus
21	Aves	Great tit	Parus major
22	Aves	Blue tit	Parus caeruleus
24	Aves	Great tit	Parus major
25 26	11,05		
26 27			
28			
29			
30 31			
32			
33			
34 25			
35			
37			
38			
39 40			
41			
42			
43			

2	Constant	C 4	44 <b>* T</b> 4	
л Л	Country	Study se	ttin I reatm	ent Description of display
5	USA	lab	none	display posture
6	USA	lab	none	display posture
7	USA	lab	none	no display posture
8 9	Nth America	lab	none	sound and regurgitation
10	Sweden	field	none	display
11	Sweden	lab	sound ar	nd 1 display
12 13	Australia	lab	sound ar	nd 1 sound and posture
14	USA	lab	none	display, protean behaviour, inking
15	Australia	field	none	display with colour
16 17	Australia	field	none	display with colour
18	Sweden	lab	with and	l widisplay with eyespots
19	Sweden	lab	none	display
20 21	Sweden	lab	none	display
22	Sweden	lab	none	display
23	Sweden	lab	none	display
24 25	Sweden	lab	none	display

none dispira,

2				
3	Stage display deployed	Sample size	Number survived	Survival percentage
4 5	subjugation	15	15	100
5 6	subjugation	17	17	100
7	subjugation	10	10	100
8	subjugation	10	16	100
9	subjugation	10	10	100
10	approach	21	10	48
11	subjugation	24	23	96
13	approach	40	35	88
14	NA	18	11	61
15	subjugation	29	7	24
16	subjugation	37	26	70
1/ 18	approach subjugation	34	33	97
10	approach	10	10	100
20	subjugation	10	10	100
21		12	12	100
22	subjugation		9	/5
23	subjugation	13	5	38
24 25	subjugation	14	1	7
26				
27				
28				
29				
30 31				
32				
33				
34				
35				
30 37				
38				
39				
40				
41				
42				
43 44				
45				

2	
3	Predator response
4	NA
5	
6	NA
7	distaste reaction
8	withdrawal and return
9	
10	retreat and escape
11	flee or retreat after first encounter
12	NA
13	
14	caused bluensh to startle
15	NA
16	NA
17	ratraat
18	Tetteat
19	retreat
20	flee and return or not
21	flee and return or not
22	
23	riee and return or not
24	flee and return or not
25	
20	
27	
20	
29	
30	
37	
33	
34	
35	
36	
37	
38	
39	
40	
41	
42	
43	
44	
45	
46	
47	
48	
49	
50	
51	
52	
53	
54	
55	
56	
57	
58	
59	
60	

1	
2	
3	Table S6 Summary of studies
4	Citation
5	
6 7	Bates & Fenton (1990)
/ 8	Blest (1957b)
9	Blest (1957b)
10	
11	
12	De Bona et al. (2015)
13	Dookie et al. (2017)
14 15	Holmes et al. (2018)
16	Ingalls (1993)
17	Kang et al. (2016)
18	Kang et al. $(2017)$
19	Olofician et al. (2017)
20	Oloisson et al. $(2012a)$
21	Olofsson et al. (2012b)
22	Olofsson et al. (2013)
24	Schlenoff (1985)
25	Stoneman & Fenton (1988)
26	Umbers et al. (2019)
27	Vallin et al. (2005)
28	
29	Vaughan (1983)
30 31	
32	
33	
34	
35	
36	
37	
38	
39 40	
41	
42	
43	
44	
45	

2	
3	that have assessed predator responses to deimatic displays
4	Aim
5	
6	Do moth clicks function as deimatic displays?
/ 8	Do predators respond differently to butterflies with eyespots compared to the
9	How do predators respond to different suddenly presented patterns?
10	now do producors respond to anterent suddenly presented patients.
11	
12	Do eye spots mimic eyes?
13	Do caterpillar whistles funcation as deimatic displays?
14	Does movement and/or colour patch influence predator response?
15	(1) Describe and/or colour paten influence predator response:
16	(1) Does the presence of a banding pattern enhance the startie reaction to no
17	Does facultative aposematism differ from crypsis and aposematism?
18	Does size and/or hindwing colour influence predator startle response?
20	Does wing-flicking protect the butterfly from bird or is just conspicuous cold
20	Do sounds datar mice?
22	
23	Does the presence of eyespots in the startle display influence predator behav
24	Does novelty and/or oddity influence predator startle response?
25	How do moth clicks disrupt bat attack?
26	Does predator familiarity influence the efficacy of startle displays?
27	Is the combination of every and sound more effective than the component
28	The combination of cyclopols and sound more effective than the component
29	Do hind wing patterns deter birds?, Is novelty important?
30 21	
37	
33	
34	
35	
36	
37	
38	
39	
40	
41	
4Z 42	
43 44	
45	
46	
47	
48	
49	
50	
51	
52	

1		
2		
3		
4 5	Predator order	Predator common name
6	Mammalia: Chiroptera	Big brown bat
7 8	Aves	Yellow bunting and great tit
9	Aves	Chaffinch, yellow bunting and
10 11		
12	Aves	Great tit
13	Aves	Red-winged blackbird
14 15	Aves	Chicken
16	Aves	Blue jay
17	Aves	Oriental tit
18 10	Aves	Black-capped chickadee
20	Aves	Great tit
21	Mammalia: Chiroptera	Wood mouse and yellow-neck
22	Aves	Chicken
23 24	Aves	Blue jay
25	Mammalia: Chiroptera	Greater false vampire bat and
26 27	Aves	Australian magpie
27 28	Aves	Blue tit
29	Aves	Blue jay
30		
31		
32 33		
34		
35		
36		
37		
38		
39		
40		
41		
42		
43		
44		

Predator taxonomic name	Sample size
Eptisicus fuscus	4
Emberiza sulphurata and Parus major	8 and 4
Fringilla coelebs, Emberiza sulphurata, and Parus major	unclear
Parus major	97
Agelaius phoeniceus	12
Gallus gallus domesticus	56
Cyanocitta cristata	8
Parus minor	36
Poecile atricapillus	36 flocks
Parus major	27
Apodemus sylvaticus and A. flavicollis	18 and 8
Gallus gallus domesticus	40
Cvanocitta cristata	6
Megaderma lyra and Macrotus californicus	3 and 7
Cracticus tibicen	163
Parus caeruleus	54
Cvanocitta cristata	8
	0

1		
2		
3		
4	Stimulus type simple	Stimulus type category
5	sound	sound
7	live insect	evecnots
8	live liiseet	cycspots
9	image	eyespots - abstract
10 11		
12	image	eyespots
13	sound	sound
14	image	
15	model	colour pattern
10 17	model	colour pattern
18		1
19	model	colour pattern
20	live insect	
21	live insect	
22	live insect	
24	model	colour pattern
25	sound	sound
26	live insect	
27	live insect	
20	model	colour pattern
30		
31		
32		
33 34		
35		
36		
37		
38 30		
40		
41		
42		
43		
45		
46		
47		
48		
49 50		
51		
52		
53		
54 55		
56		
57		
58		
59 60		
00		

2	
3 4	
5	Stimulus
6	Sound - acousite recording of insect
/ 8	Insects - live
9	Images of prev - back-projected onto a screen
10	See r j in r jinner
11	Images of prove enimeted photographs of Lenidenters with everyons and evel ever
12 13	Sound accousite recording of insect
14	Sound - acoustic recording of insect
15	Images of prey - computer generated images
16	Model prey - holes covered with flaps
17 18	Model prey - paper models of abstract prey
10	Model prey - robomoth
20	Insects - live and dead
21	Insects - live
22	Insects - live
23 24	Model prey - cardboard and plastic mechanical moth models
25	Sound - acousite recording of insect
26	Insects - live
27	Insects - live
28 20	Model prov. holes accored with flaps
30	woder prey - noies covered with haps
31	
32	
33	
34 35	
36	
37	
38	
39 40	
41	
42	
43	
44 45	
45 46	
47	
48	
49 50	
50 51	
52	
53	
54	
55 56	
57	
58	
59	
60	

2 3		
4 5	Stimulus order	Stimulus model
6	Lepidoptera	Dogbane tiger moth (Cycnia tenera)
7 8	Lepidoptera	Peacock butterfly (Aglais io)
9 10	Lepidoptera	Painted models
11	Lepidoptera & Aves	Owled eyed butterfly (Caligo martia) and Eurasian pyg
13	Lepidoptera	Walnut sphinx caterpillar (Amorpha juglandis)
14 15	Lepidoptera	loosely based on Catocala sp.
16	Lepidoptera	loosely based on Catocala sp.
17	Lepidoptera	paper models with hidden colours
18 10	Lepidoptera	paper models with hidden colours
20	Lepidoptera	European swallowtail (Papilio machaon)
21	Lepidoptera	Peacock butterfly (Aglais io)
22	Lepidoptera	Peacock butterfly (Aglais io)
25 24	Lepidoptera	loosely based on Catocala sp.
25	Lepidoptera	Dogbane tiger moth ( <i>Cycnia tenera</i> ), milkweed tussock
26	Orthoptera	Mountain katydid (Acripeza reticulata)
27 28	Lepidoptera	Peacock butterfly (Aglais io)
29 30 31	Lepidoptera	loosely based on Catocala sp.

2 3		
4	D	
5	Prey 'defended'	Study setting
6 7	no	
8	no	180
9 10	no	lab
10		
12	no	lab
13	no	lab
14 15	no	lab
16	no	lab
17	yes	lab
18 10	no	field
20		lab
21	no	lab
22 23	no	lab
23 24	no	lab
25	no	lab
26 27	yes	field
27 28	no	lab
29	no	lab
30		
31		
33		
34		
35 36		
37		
38		
39 40		
41		
42		
43 44		
45		
46		
47 48		
48 49		
50		
51 52		
52 53		
54		
55 56		
50 57		
58		
59		
60		

## Treatments

- (1) recorded clicks of an arctiid moth, (2) synthetic clicks (white noise temporally matched to arctiid
- (1) butterflies with eyespots, (2) butterfles without eyespots
- (1) an equals symbol: '=', (2) a large thin plus symbol: '+', (3) a small thick plus symbol: '+', (4) a sing
- (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
- 3 (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
- 6 (1) solid-coloured discs, (2) banded discs;
- 7 (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 v
- (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) butterfles without eyespots
- (1) uniform, pale grey; (2) red and black bands with a narrow white border (redbanded), such as found
- (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 greyplasticine ball
  - (1) eyespots intact, (2) eyespots obliterated, (3) sound-producers intact, (4) sound producers obliterate
  - (1) trained on one colour (2) presented a novel colour

<b>Trigger</b>	<b>Timing</b>	<b>Response measures</b>
Bat foraging behaviour - cross	Predator approach	Whether or not bat landed e
Bird foraging behaviour	Predator subjugation	Escape responses
Bird foraging behaviour	Predator subjugation	Escape responses
Operator, based on bird behav Bird foraging behaviour trigge Operator, based on bird behav Bird foraging behaviour Bird foraging behaviour Operator, based on bird behav Prey behaviour Operator stimulating butterfly Prey behaviour Bird foraging behaviour	Predator approach Predator subjugation Predator approach Predator subjugation Predator subjugation Predator approach Prey's choice Prey's choice Prey's choice Prey's choice	No response, stare, explore No reaction, shoulder flinc Latency to attack Latency to touch artifical p Prey eaten or rejected Stayed, left but returned, le Flew or hopped away Escape trajectories Flinching, ceasing foraging
Bird foraging behaviour	Predator subjugation	Initial reaction (high and lc
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' as

Predator subjugation Defined statute response

1	
2	
2	
1	
-+ C	
5	
6	
7	
8	
9	
10	
11	
12	
13	
14	
15	
16	
17	
18	
10	
י 20	
20 21	
21	
22	
23	
24	
25	
26	
27	
28	
29	
30	
31	
37	
JZ 22	
22	
34	
35	
36	
37	
38	
39	
40	
41	
42	
43	
44	
45	
46	
47	
47 70	
40 40	
49 50	
50	
51	
52	
53	
54	
55	
56	
57	
58	
59	

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 d	listNA	yes
yes	yes	yes

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

<b>Repeated trials</b>	Learned avoid simplified sco
yes	no
yes	no
yes	no
yes	NA
yes	yes
10	NA
/es	yes
es	yes
/es	NA
10	NA
10	NA
10	NA
yes	no
yes	NA
yes	yes
10	NA
'es	no

1	
2	
3	
4	Learned eveld
5	Learneu avoiu
6	no
7	inverse of 'learned ignore' column
8	
9 10	no
10	
12	unclear
13	Vec
14	yes
15	NA
16	yes, more hestiant in future trials when experienced with banded stimuli
17	yes, in fewer trials than cryptic prey, but similar to conspicuous prey
18	unclear
19	NA
20	
21 22	NA
∠∠ 23	NA
25 74	habituated
25	unclear
26	vag hyt only a gingle report
27	yes, out only a single repeat
28	NA
29	unclear
30	
31	
32	
33	
34 25	
36	
37	
38	
39	
40	
41	
42	
43	
44	
45	
46	
4/	
48 40	
49 50	
51	
52	
53	
54	
55	
56	
57	
58	
59	
60	

Learned ignore s	simplified sc Learned ignore	Result
yes	yes	Bats initally startled but then h
yes	yes, for 6 yellow buntings, no	More escape responses to butt
yes	yes, waning was rapid	Circular patterns released esca
NA	unclear	Mimetic eyespots as effective
yes	yes, some evidence of habituation	alBirds flew away on first encou
NA	NA	Conspicuousness effective, slo
no	no	Banded patterns increased star
no	no, but that was not expected	Facultative display as effective
NA	unclear	Startle response stronger to lar
NA	NA	Birds were more likely to attac
NA	NA	Mice fled further from butterfl
NA	NA	Birds reacted to both treatmen
ves	ves, but slower when prev ap	Novelty alone did not release a
NA	unclear	Reject jamming hypothesis, su
ves	ves for experienced birds no	Display is more protective aga
NA	NA	Birds spent more time close to
Ves	Ves	"rarity tends to reduce the r
yes	yes	fairty tends to reduce the f

1	
2	
3	
4	
5	applituated to sound
7	
8	ertiles with eyespots intact than to those with eyespots obliterated
9 10	pe responses more readily than non-circular patterns, of the circular patterns, those most like eyes
11	
12	as own cycs
13	inter with sound
15	ow and fast both effective, medium not
16	rtle response and future avoidance compared to solid colours
17	e as aposematic display
18	rger moth model
19	ck the dead butterfly treatment. Live butterfly's display resulted in birds visitng more times before a
20	lies that produced sound
22	to but these that viewed evenets were clewer to recume foreging
23	its, but mose that viewed eyespois were slower to resume foraging
24	a startle display, the colours themselves matter. Startle on first encounter with coloured hindwing n
25	apport startle hypothesis
20 27	ainst naïve than familiar birds
27	) the butterflies with no eyespots, no difference was found between the sound treatments. No synge
29	risk of predation"
30	
31	
32	
33 34	
35	
36	
37	
38	
39 40	
40	
42	
43	
44	
45	
40 47	
48	
49	
50	
51	
52	
53 54	
55	
56	
57	
58	
59 60	
00	

attacking

nodels but not grey models

rgistic effect of eyespots and sound was supported