ORIGINAL ARTICLE

CrossMark

Post-attack defensive displays in three praying mantis species

James C. O'Hanlon[1] [ORCID] · Darshana N. Rathnayake[2] · Katherine L. Barry[2] · Kate D. L. Umbers[3,4]

Abstract

Investigating the stimuli that elicit dynamic defensive displays can indicate when throughout the predation sequence prey are likely to perform them. This is crucial to understanding whether these displays function as classic deimatic 'startle' displays, facultative aposematism or aid in facilitation of predator learning. We investigated the triggers of defensive display in three different praying mantis species found in eastern Australia; *Archimantis latistyla*, *Hierodula majuscula* and *Pseudomantis albofimbriata*. Dynamic displays in praying mantises have been described as 'deimatic' and given the risks inherent in sustaining an attack, especially as mantises are not chemically defended, we predicted that mantises would perform their displays to stimuli that simulate early cues of predation. In a randomised order, we exposed each mantis to five different stimuli simulating a non-specific predator, including tactile and non-tactile stimuli. All species performed their display in response to tactile stimuli however *A. latistyla* and *H. majuscula* were more likely to respond than *P. albofimbriata*. The smallest species, *P. albofimbriata*, did not readily respond to simulated attacks and was the least likely to perform a display. Our results do not meet the prediction that mantises should respond to stimuli that correspond with early stages of the predation sequence. This raises questions surrounding the utilisation of defensive displays in non-chemically defended prey and contributes to our understanding of predator-prey dynamics during the predation sequence.

Significance statement

Startle displays, or deimatic displays, present some of the most charismatic and well-known examples of animal behaviour and colouration. Particularly in animals such as praying mantises, defensive displays are classically cited examples of anti-predator adaptations. It is generally stated that defensive displays in animals function by startling the predator before they have attacked; however, evidence is accumulating that dynamic displays may function in a number of ways including facilitating predator learning, or facultative aposematism. We found that three species of praying mantises only performed dynamic displays in response to simulated predator attacks. This contrasts with predictions that displays should happen before predator attacks, thus fundamentally challenging our understanding of why these strategies have evolved and how they are utilised in nature. This adds to growing evidence that apparent 'deimatic displays' may actually function in other ways such as facilitating predator learning, even in non-chemically defended animals such as praying mantises.

Keywords Predator-prey interactions · Aposematism · Deimatism · Defence · Anti-predator · Mantodea

✉ James C. O'Hanlon
   johanlon@une.edu.au

1   School of Environmental and Rural Sciences, University of New England, Armidale, NSW, Australia

2   Department of Biological Sciences, Macquarie University, North Ryde, NSW, Australia

3   School of Science and Health, Western Sydney University, Richmond, NSW, Australia

4   Hawkesbury Institute for the Environment, Western Sydney University, Richmond, NSW, Australia

Introduction

Successful predation requires animals to encounter, detect, identify, approach, subjugate and consume their prey (Endler 1991). This predatory sequence can be interrupted at any stage by the anti-predator defences of the prey. Defensive adaptations, such as camouflage via crypsis or masquerade, act early in the predation sequence to avoid being detected or correctly identified as prey (Bateman et al. 2014). Later in the prey capture sequence, after being detected and identified, prey can employ evasive escape (flight) or retaliation (fight) behaviours before they can be subjugated or consumed (Ruxton et al. 2004).

Deimatic displays, also known as 'startle displays', are defensive adaptations that have been described as providing protection to prey by startling the predator, either resulting in the predator ceasing pursuit of the prey all together, or pausing the predatory attack for long enough that the prey can escape (Cott 1940; Maldonado 1970; Edmunds 1974, 1976; Endler 1991). A critical feature of deimatic displays is that they have a temporal component. As opposed to classic aposematic signals—those that are displayed conspicuously and constantly to advertise a prey item's unprofitability (Mappes et al. 2005)—deimatic displays involve signals that are usually concealed and only suddenly revealed late in the predation sequence (Umbers and Mappes 2015).

The timing of the display during the prey capture sequence, or the decision to display at all, is assumed to be critical to the effectiveness of the defence (Lima and Dill 1990; Bateman et al. 2014). As these temporal displays are usually conspicuous signals, they carry the risk of revealing the location of an otherwise camouflaged animal (for discussion see Umbers and Mappes 2015; Umbers et al. 2017). Thus, displaying too early in the prey capture sequence might reveal a prey item's location before the predator has detected them. Where animals are not defended by other means, such as distasteful chemicals, displaying too late in the prey capture sequence puts the prey animal at risk of being eaten, or at least injured, by the predator (Crane 1952; Endler 1991). Therefore, in a simple situation where no other complicating factors are involved, the optimal deimatic strategy for prey should be to avoid deploying their display until they can be certain that they have been detected and correctly identified as a prey by the predator (Edmunds 1974; Endler 1991), and displaying immediately after the risk of injury or death prevails over the costs of conspicuousness.

Some species do not follow these predictions of optimal timing for deimatic dynamic displays. It has been shown that dynamic displays can be utilised after the predator has initiated an attack. For example the Australian mountain katydid *Acripeza reticulata* exhibits a striking dynamic defensive display where dark mottled wings are lifted to reveal conspicuous patterns of alternating red stripes and blue dots (Umbers and

Mappes 2015). This is accompanied by the production of distasteful liquid from the abdomen. Umbers and Mappes (2015) showed that mountain katydids primarily displayed when subjected to tactile simulated predator attacks (being pinched by fingers and dropped) but rarely displayed in response to non-tactile pre-predation stimuli such as looming objects. Similarly, the spotted lanternfly *Lycorma deliculata* exhibits a 'post-attack' display where the mottled brown forewings of adults are lifted to reveal the contrasting red, white and black hindwings (Kang et al. 2016b).

One important similarity between these two examples is that both animals are chemically defended. The spotted lanternfly is known to be distasteful to birds (Kang et al. 2011), and the mountain katydid, during its display, regurgitates its crop contents of *Senecio* plants and secretes a distasteful liquid from its abdomen (Cable and Nocke 1975; Umbers and Mappes 2015). Such findings give support to alternative hypotheses regarding the function of dynamic defensive displays. In these cases, post-attack displays may function to 'facilitate predator learning' (Kang et al. 2016a). Umbers and Mappes (2015) argued that the tough wings of mountain katydids protect them from the initial phase of physical attack, creating an opportunity for the predator to be exposed to the katydid's chemical defences without sustaining serious injuries. It has been shown using artificial prey that post-attack displays can even lead to predators learning to avoid the cryptic form of aposematically defended prey (Kang et al. 2016a). Additionally sudden defensive displays combined with chemical defences may represent a form of 'facultative aposematism', whereby animals may selectively signal their unpalatability to approaching predators thus benefiting from both crypsis and aposematism (Sivinski 1981). These findings have contributed to recent discussions surrounding the utilisation of dynamic components in concert with aposematic signals, and how the best define the term 'deimatic' in order to facilitate progress in this area of behavioural ecology (Skelhorn et al. 2016; Umbers and Mappes 2016; Umbers et al. 2017).

Praying mantises exhibit sudden remarkable defensive displays (Edmunds 1972, 1976; Edmunds and Brunner 1999). When touched, grabbed or persistently chased, some mantises will respond by arching their body upright, and raising their forelimbs and hindwings. Often these behaviours reveal bright colour patches or eyespots on their wings and forelimbs. Early observational research showed that such displays in mantises can sometimes be sufficient to deter attacks from predators such as monkeys and birds (Crane 1952; Maldonado 1970; Edmunds 1972). These defensive displays are often cited as classic examples of deimatism, however mantises have been observed exhibiting post-attack defensive displays (e.g. Edmunds 1976; Liske et al. 1999) and there has been little research into their function and how they are utilised in response to predators. By systematically investigating the

stimuli that elicit defensive displays, we can understand when in the predation sequence these behaviours are utilised. This can help us understand whether these function as classic deimatic displays, or 'startle displays', as is often assumed. Here we investigate the stimuli that elicit defensive displays in three species of Australian praying mantises *Hierodula majuscula*, *Pseudomantis albofimbriata* and *Archimantis latistyla*. We subjected males and females of each species to artificial stimuli simulating a non-specific predator and representing different stages of the predation sequence.

No praying mantises are known to contain chemical defences and are believed to be generally palatable to predators (Crane 1952; Maldonado 1970). As such, we hypothesise that their displays function to startle the predator rather than providing information about unpalatability and functioning as 'facultative aposematism' or 'facilitation of predator learning'. Given this, we expect that praying mantises should more readily deploy their displays during predator approaches as opposed to chemically defended prey that may utilise post-attack displays. We predicted that mantises would exhibit displays in response to non-tactile stimuli that simulate the approach of a predator, as opposed to waiting until the predator has commenced attacking (i.e. tactile stimuli).

Methods

Study species

The three species chosen for this experiment were based on their availability at the time of the study. *Archimantis latistyla* are slender brown mantises; adult females can grow to over 10 cm in length and males are slightly smaller. Adult males are fully winged and capable of flight whereas females have reduced wings and do not fly. They have a wide range that extends along the eastern coast of Australia. *Hierodula majuscula* are found in the wet tropics region of eastern Australia. They are a charismatic species with bright green colouration on their dorsal side and patches of red and purple along their ventral pronotum and inner forelimbs. Adult females grow to around 10 cm in length and are fully winged yet their large abdomens can limit their flight capacities (*pers. obs.* K.L. Barry). Males are slightly smaller than females and more mobile with wings that extend beyond the tip of the abdomen. *Pseudomantis albofimbriata* are found in temperate regions along the eastern Australian coast and are either green or brown in colour. Adult females can reach around 7 cm in length whereas males reach around 5 cm in length. Adult males are fully winged and capable of flight whereas females have reduced wings and do not fly (Barry et al. 2015).

Collection methods

Juvenile *P. albofimbriata* and *A. latistyla* were collected from Yamble Reserve, Ryde (33° 49′ 0″ S, 151° 6′ 0″ E), Australia in January–February 2014 and 2015. All individuals were found on the leaves and flowers of *Lomandra longifolia* bushes. Juvenile *H. majuscula* were purchased from Minibeast Wildlife, Queensland, Australia, in August 2014.

Husbandry methods

All mantises were housed individually within inverted transparent plastic cups of which the bottom end was replaced by a mesh to improve airflow. They were kept under laboratory conditions with controlled temperatures (25–26 °C), light phase (14 h light: 10 h dark) and humidity (55–60%). Mantises were fed crickets, *Acheta domesticus*, three times per week until maturity, and watered daily. Once mantises had eclosed as adults, our total sample size was 76 mantises—*Archimantis latistyla*: males 6, females 29; *Heirodula majuscula*: males 11, females 9; *Pseudomantis albofimbriata*: males 6, females 19.

Experimental methods

Adult males and females were subjected to five different stimuli and their behavioural response was observed. The stimuli consisted of either (i) the observer gently blowing air towards the mantis using their own breath, from a distance of approximately 50 cm (herein referred to as 'blow'), (ii) the observer moving their hand quickly towards the mantis' head and retracting the hand immediately. The hand would not touch the mantis stopping approx. 1 cm from the mantis' head (looming), (iii) the observer quickly touching the head of the mantis with the tip of a soft paintbrush (poke), (iv) the observer gently pinching the pronotum of the mantis with a set of forceps and then releasing (pinch), or (v) no stimulus presented to the mantis (control). We assume that the observer was visible to the mantises during all treatments including the control treatment. Mantises were placed on an upright stick within an experimental arena (20 cm × 20 cm box) and left to acclimatise for 3 min. After this period, the mantis was subjected to a single stimulus and then observed for 5 min before being returned to their enclosure. The mantises were subjected to a single treatment each day for five consecutive days with the order of stimuli randomised between trials. The behaviour of the mantis immediately following the stimuli was categorised as to whether they performed a defensive display (display), appeared to strike at the stimulus with their forelimbs (strike), attempted to flee by running out of the arena (flee) or did not appear to respond (no response). All experimental stimuli were performed by a single observer (DNR) who took all measures to ensure consistency between trials.

Fig. 1 Frequency of behavioural responses of *Archimantis latistyla* males (**a**; $n = 6$) and females (**b**; $n = 29$) to different stimuli simulating a predatory approach. Numbers on bars indicate the tally of individual mantises exhibiting this behaviour. The frequency of mantises that exhibited 'no response' are not plotted here
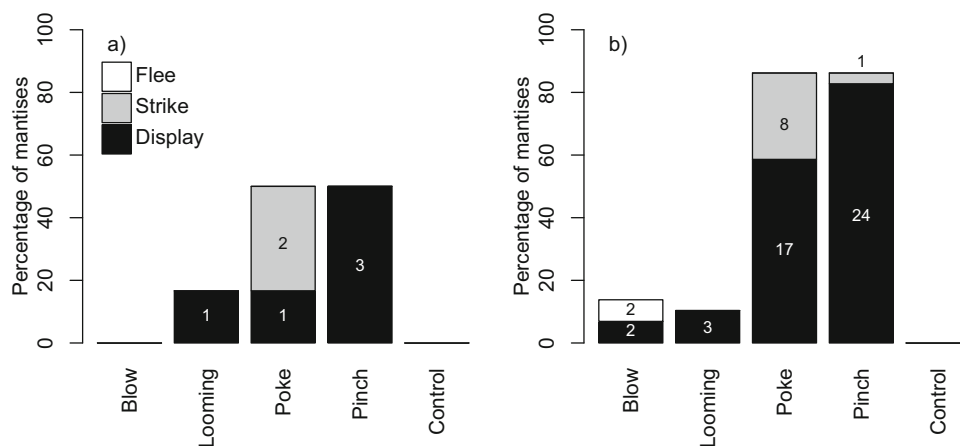
Results

Our results and sample sizes precluded multinomial statistics and the calculation of interaction effects, due to complete separation of data between treatments leading to inflated estimates of significance. We tested the effect of experimental treatment on the likelihood that mantises exhibited a defensive display expressed as a binomial outcome (see supplementary data). Other responses (flee, strike) were not counted as a defensive display, these are presented in Figs. 1, 2 and 3 and discussed below. To account for quasi-separation of results in analyses, we used Firth's Bias-Reduced Logistic Regressions, using the R package *logistf* (Heinze and Ploner 2016). Separate models were conducted for each species, including sex as a factor and accounting for repeated measures by including individual mantises as a random factor. All analyses were conducted using R version 3.3.0 (R Development Core Team 2011).

Data availability statement All data generated or analysed during this study are included in this published article and its supplementary information files.

Across all species and both sexes, mantises rarely responded to non-tactile stimuli such as 'looming' and 'blow' and no responses were noted during control treatments (no stimulus) (Figs. 1, 2 and 3). *Archimantis latistyla* were most likely to perform displays in response to the 'pinch' stimulus compared to other stimuli (Likelihood ratio test; $\chi^2_6 = 82.28$, $p < 0.001$; Table 1). There was a significant effect of sex ($\chi^2 = 4.577$, $p = 0.032$) and males appeared less likely to exhibit any behavioural response across all stimuli. The 'poke' stimulus elicited displays in *A. latistyla*—again particularly in females—but also elicited 'strike' behaviours (Fig. 1). Similarly, *Hierodula majuscula* performed displays in response to tactile stimuli ('poke' and 'pinch') more than non-tactile stimuli ('blow', 'looming') ($\chi^2_6 = 55.72$, $p < 0.001$; Fig. 2; Table 1). There was no significant effect of sex on the frequency to display ($\chi^2 = 2.157$, $p = 0.142$).

Pseudomantis albofimbriata appeared to respond differently to the stimuli in comparison to the other species. Only a small number of females displayed in response to 'pinch' stimuli (Fig. 3; Table 1). Instead, *P. albofimbriata* were more

Fig. 2 Frequency of behavioural responses of *Hierodula majuscula* males (**a**; $n = 11$) and females (**b**; $n = 9$) to different stimuli simulating a predatory approach. Numbers on bars indicate the tally of individual mantises exhibiting this behaviour. The frequency of mantises that exhibited 'no response' are not plotted here
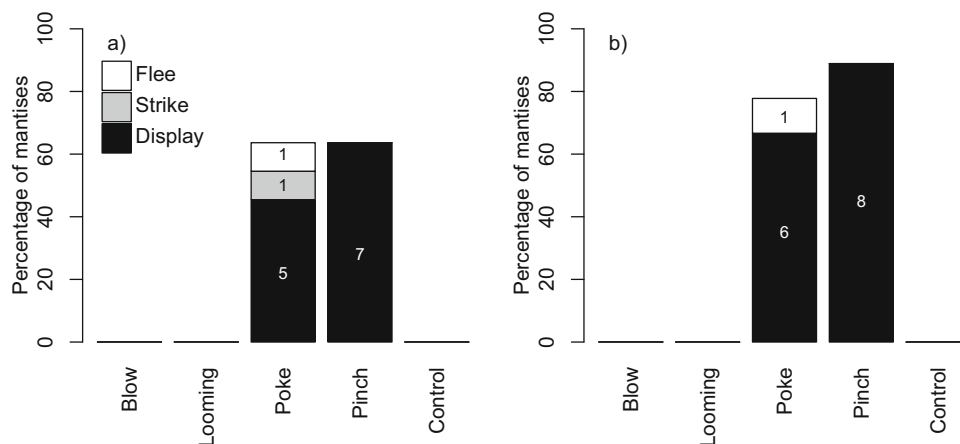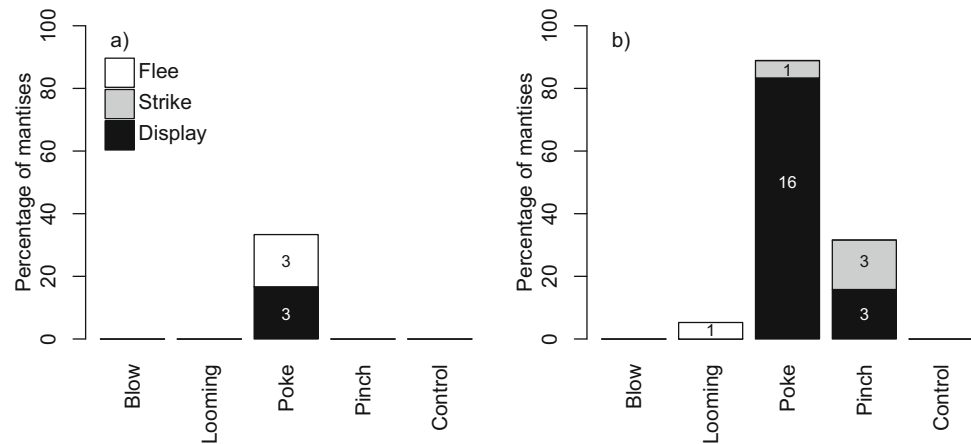
Fig. 3 Frequency of behavioural responses of *Pseudomantis albofimbriata* males (**a**; $n = 6$) and females (**b**; $n = 19$) to different stimuli simulating a predatory approach. Numbers on bars indicate the tally of individual mantises exhibiting this behaviour. The frequency of mantises that exhibited 'no response' are not plotted here

likely to respond to the 'poke' stimulus ($\chi^2_6 = 30.17$, $p < 0.001$). There was a significant effect of sex ($\chi^2 = 9.210$, $p = 0.002$) and only a small number of males (2 out of 6) responded in any way.

Each species' display was distinct and consisted of several components. *Archimantis latistyla* lifted their pronotum, raised their forelimbs and wings and tilted their abdomen upwards slightly. *Hierodula majuscula* also lifted their pronotum, wings and forelimbs. When their forelimbs were lifted outwards, contrasting dark patches on the inner surfaces of their femur were visible. When *Pseudomantis albofimbriata* did display, they did not raise their wings but lifted their pronotum and stretched their forelimbs outwards. None of the species studied here have 'eye-spots' on their hindwings.

Table 1 Regression coefficients and 95% confidence intervals for Firth's Bias-Reduced Logistic Regression examining the likelihood of mantises exhibiting a defensive display following experimental treatments

	B	CI		χ^2	p
A. latistyla					
Blow	1.672	− 0.888	6.610	1.509	0.219
Looming	2.328	− 0.020	7.220	3.916	0.048
Poke	4.392	2.246	9.212	28.15	< 0.001
Pinch	5.567	3.347	10.38	52.02	< 0.001
H. majuscula					
Blow	< 0.001	− 5.236	5.236	< 0.001	0.999
Looming	< 0.001	− 5.236	5.236	< 0.001	0.999
Poke	3.986	1.671	8.777	16.42	< 0.001
Pinch	4.863	2.460	9.636	26.55	< 0.001
P. albofimbriata					
Blow	< 0.001	− 5.223	5.223	0.000	1.000
Looming	< 0.001	− 5.223	5.223	0.000	1.000
Poke	5.192	2.759	9.936	31.52	< 0.001
Pinch	2.086	− 0.334	6.984	2.728	0.099

Discussion

Defensive displays were performed most often after tactile stimuli that simulated predator attacks. This was most apparent in females, and in the two largest species *A. latistylus* and *H. majuscula*. This contrasts with our prediction that mantises should display early in the predation sequence. Recent research has demonstrated how post-attack defensive displays can be effective in species with distasteful chemical defences that presumably render them unprofitable (Umbers and Mappes 2015; Kang et al. 2016b). With repeated encounters, predators can learn to associate the display with the cryptic form (Kang et al. 2016a). However, our data suggest that post-attack displays are not unique to chemically defended prey.

Our findings add to previous observations of post-attack displays in mantises, suggesting that this may be a common strategy within the order. The lack of response to non-tactile stimuli by praying mantises may be interpreted as resulting from the inherent risk in revealing conspicuous cues. Camouflaged animals should avoid displaying, and compromising their camouflage, until they have reliable cues that a predator presents a threat (Lima and Dill 1990). An attack from a predator is likely to be a reliable cue that the predator is aware of the prey's location and suitability as a profitable dietary item. Once this occurs, potential costs associated with performing the display drop drastically. It is perhaps therefore not surprising that pre-attack displays should be rare.

Post-attack displays in mantises could be deimatic, that is, sufficient to startle the predator enough to stop attacking, or drop the prey before it is significantly damaged, ceasing or delaying further attack. We note that this is not necessarily inconsistent with displays performed late in the sequence provided preys are robust enough to withstand the initial attack (e.g. Umbers and Mappes 2015). Whether displaying mantises are further pursued is likely to be context-dependent and potentially influenced by factors such as predator experience and satiation.

Additionally praying mantis defensive displays may function to highlight their weaponry (Edmunds 1974; Speed and Ruxton 2005). A full view of mantis' formidable raptorial forelimbs could provide an indication of unprofitability in place of a chemical defence. There are many anecdotal observations of praying mantises using their forelimbs to capture prey larger than themselves including small vertebrates such as birds, lizards and frogs (Prete et al. 1999; Nyffeler et al. 2017). Further experiments are required to understand if praying mantis weaponry functions this way. If so, this may raise the possibility that mantis displays could function as 'facultative aposematism' or in 'facilitation of predator learning'.

Alternatively artificial stimuli may not sufficiently simulate approaching predators, thus reducing the likelihood of pre-attack displays. When presented with looming stimuli simulating a predator the mantis *Tenodera aridifolia* rarely exhibits a defensive display and is more likely to exhibit 'crypsis-enhancing' behaviours such as lowering its body close to the substrate and remaining motionless (Yamawaki 2011; Sato and Yamawaki 2014). Novel and artificial stimuli such as those used in this study are commonly used for investigating anti-predator responses (Sato and Yamawaki 2014; Umbers and Mappes 2015; Kang et al. 2016a, b). There is little known about the ability of praying mantises to recognise predators and we may be underestimating their ability to accurately identify threats. Conducting experiments using real predators (e.g. Crane 1952; Maldonado 1970) or stimuli that more accurately represent predators (i.e. body outline and behaviour) may reveal whether mantises can identify cues associated with approaching predators that could inform the decision to display pre-attack.

Watanabe and Yano (2010) found that praying mantises presented pre-attack displays to an approaching predator (Japanese skink, *Tachydromus tachydromoides*). Interestingly, this was only common in adult praying mantises, whereas juveniles relied heavily on crypsis and rarely signalled their presence. Furthermore, smaller mantis species (e.g. *Statilia maculata*) did not display at all (Watanabe and Yano 2010). This suggests that the size of an animal is an important factor in the utilisation and evolution of such displays. Remaining inconspicuous may be more difficult for larger animals than smaller animals, and thus switching to an alternative strategy may offer greater protective value (Remmel and Tammaru 2009; Hossie et al. 2015; Kang et al. 2017). Similarly, we noted that the smallest mantis species in our study *P. albofimbriata* was least likely to exhibit a display, and post-attack displays were particularly rare. We also noted that females, which in praying mantises are generally larger than males, were more likely to perform defensive displays. In addition, many female mantises are poor fliers compared with males, so it is possible that with reduced capacity to flee, females stand and put up a fight.

Further work is needed to tease apart effects of size, sex, escape capacity and tendency to display.

As is becoming commonly noted in research surrounding animal defence mechanisms, the function of defensive behaviours and adaptations is often based on intuitive assumptions whilst empirical research demonstrating their effectiveness is relatively uncommon (Skelhorn et al. 2010; Stevens 2016). This is certainly true of defensive displays where few species have received empirical research testing their protective value (for summary, see Umbers et al. 2017). Fundamental questions remain regarding the effect these displays have on predator psychology and whether they function to simply delay attacks or are sufficient to deter attacks altogether. Furthermore do factors such as camouflage, body toughness and escape capacity influence the trade-off between revealing their presence to predators too early and risking injury by displaying too late.

Whilst praying mantises exhibit some of the most spectacular defensive behaviours, we still do not fully understand the degree to which they are utilised in the wild, or the specific advantages the displays can confer. There is great diversity in defensive displays across the order Mantodea (Crane 1952; Edmunds 1976; Edmunds and Brunner 1999). Whilst some species behavioural responses are combined with conspicuous colour stimuli, others are not, and there are many species in which displays are not known to occur at all (e.g. O'Hanlon 2011). As such, this group offers an ideal system in which to study the evolution of defensive displays to understand the sources of variation in defensive behaviours and address questions as to when it is beneficial to use such a risky predator avoidance strategy.

References

Barry KL, White TE, Rathnayake DN, Fabricant SA, Herberstein ME (2015) Sexual signals for the colour blind: cryptic female mantids signal quality through brightness. Funct Ecol 29:531–539

Bateman AW, Vos M, Arnholt BR (2014) When to defend: antipredator defenses and the predation sequence. Am Nat 183:847–855

Cable J, Nocke H (1975) Isolation of s-Butyl β-D-glucopyranoside from *Acripeza reticulata*. Aust J Chem 28:2737–2739

Cott HB (1940) Adaptive coloration in animals. Methuen & Co. Ltd., London

Crane J (1952) A comparative study of innate defensive behavior in Trinidad mantids (Orthoptera, Mantoidea). Zoologica 37:259–293

Edmunds M (1972) Defensive behaviour in Ghanian praying mantids. Zool J Linnean Soc 51:1–32

Edmunds M (1974) Defence in animals: a survey of antipredator defences. Longman, California

Edmunds M (1976) The defensive behaviour of Ghanian praying mantids with a discussion of territoriality. Zool J Linnean Soc 58:1–37

Edmunds M, Brunner D (1999) Ethology of defenses against predators. In: Prete FR, Wells H, Wells PH, Hurd LE (eds) The praying mantids. John Hopkins University Press, Baltimore, pp 276–299

Endler JA (1991) Interactions between predators and prey. In: Krebs JR, Davies NB (eds) Behavioural ecology. Blackwell, Oxford, pp 169–196

Heinze G, Ploner M (2016) logistf: Firth's Bias-Reduced Logistic Regression. R package version 1.22

Hossie TJ, Skelhorn J, Breinholt JW, Kawahara AY, Sherratt TN (2015) Body size affects the evolution of eyespots in caterpillars. Proc Natl Acad Sci 112:6664–6669

Kang C, Lee S-I, Jablonski PG (2011) Effect of sex and bright coloration on survival and predator-induced wing damage in an aposematic lantern fly with startle display. Ecol Entomol 36:709–716

Kang C, Cho H-J, Lee S-I, Jablonski PG (2016a) Post-attack aposematic display in prey facilitates predator avoidance learning. Front Ecol Evol 4:35

Kang C, Moon H, Sherratt TN, et al (2016b) Multiple lines of anti-predator defence in the spotted lanternfly, *Lycorma delicula* (Hemiptera: Fulgoridae). Biol J Linn Soc. https://doi.org/10.1111/bij.12847

Kang C, Zahiri R, Sherratt TN (2017) Body size affects the evolution of hidden colour signals in moths. Proc R Soc B 284:20171287

Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool 68:619–640

Liske E, Köchy K, Wolff HG (1999) Ontogeny of defensive behaviors. In: Prete FR, Wells H, Wells PH, Hurd LE (eds) The praying mantids. John Hopkins University Press, Baltimore, pp 3–18

Maldonado H (1970) The deimatic reaction in the praying mantis Stagmatoptera biocellata. J Comp Physiol A Neuroethol Sens Neural Behav Physiol 68:60–71

Mappes J, Marples N, Endler JA (2005) The complex business of survival by aposematism. Trends Ecol Evol 20:598–603

Nyffeler M, Maxwell MR, Remsen JV Jr (2017) Bird predation by praying mantises: a global perspective. Wilson J Ornithol 129: 331–334

O'Hanlon JC (2011) Intraspecific interactions and their influence on habitat utilisation in the praying mantid *Ciulfina biseriata*. J Ethol 29: 47–54

Prete FR, Wells H, Wells PH (1999) The predatory behavior of mantids: historical attitudes and contemporary questions. In: Prete FR, Wells H, Wells PH, Hurd LE (eds) The praying mantids. John Hopkins University Press, Baltimore, pp 3–18

R Development Core Team (2011) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Remmel T, Tammaru T (2009) Size-dependent predation risk in tree-feeding insects with different colouration strategies: a field experiment. J Anim Ecol 78:973–980

Ruxton GD, Sherratt TN, Speed MP (2004) Avoiding attack: the evolutionary ecology of crypsis, warning signals and mimicry. Oxford University Press, New York

Sato K, Yamawaki Y (2014) Role of a looming-sensitive neuron in triggering the defense behavior of the praying mantis *Tenodera aridifolia*. J Neurophysiol 112:671–682

Sivinski J (1981) The nature and possible functions of luminescence in Coleoptera larvae. Coleopt Bull 35:167–179

Skelhorn J, Rowland HM, Speed MP, Ruxton GD (2010) Masquerade: camouflage without crypsis. Science 327:51

Skelhorn J, Holmes GG, Rowe C (2016) Deimatic or aposematic? Anim Behav 113:e1–e3

Speed MP, Ruxton GD (2005) Warning displays in spiny animals: one (more) evolutionary route to aposematism. Evolution 59:2499–2508

Stevens M (2016) Cheats and deceits: how animals and plants exploit and mislead. Oxford, Oxford University Press

Umbers KDL, Mappes J (2015) Postattack diematic display in the mountain katydid, *Acripeza reticulata*. Anim Behav 100:68–73

Umbers KDL, Mappes J (2016) Towards a tractable working hypothesis for deimatic displays. Anim Behav 113:e5–e7

Umbers KDL, De Bona S, White TE et al (2017) Deimatism: a neglected component of antipredator defence. Biol Lett 13:20160936

Watanabe H, Yano E (2010) Stage-specific defensive strategies of three mantid species *Tenodera aridifolia*, *Heirodula patellifera*, and *Statilia maculata*, against a natural enemy, *Takydromus tachydromoides*. Ann Entomol Soc Am 103:293–299

Yamawaki Y (2011) Defence behaviours of the praying mantis *Tenodera aridifolia* in response to looming objects. J Insect Physiol 57:1510–1517