



Fight or flight trade-offs and the defensive behaviour of the mountain katydid, *Acripeza reticulata*

Sebastiano De Bona ^{a,1}, Thomas E. White ^{b,*}, Kate D. L. Umbers ^{c,d}

^a Centre of Excellence in Biological Interactions, Department of Biological and Environmental Sciences, University of Jyväskylä, Jyväskylä, Finland

^b School of Life and Environmental Sciences, The University of Sydney, Sydney, NSW, Australia

^c School of Science & Health, Western Sydney University, Penrith, NSW, Australia

^d Hawkesbury Institute for the Environment, Western Sydney University, Penrith, NSW, Australia

ARTICLE INFO

Article history:

Received 7 May 2019

Initial acceptance 5 July 2019

Final acceptance 25 October 2019

MS. number: 19-00317R

Keywords:

antipredator
behaviour
defence
deimatism
evolution
startle

The defensive repertoires of prey are shaped by diverse ecological and evolutionary demands. This can generate trade-offs between the components of defences, as in the classic ‘fight or flight’ dichotomy, or dedicated investment in a singular end, allowing individuals in better condition to mount a more effective defence all round. Further, sexual dimorphism may drive sex differences in such responses, although our understanding of the interaction between sexual selection and defensive behaviour is in its infancy. Deimatic, or ‘startle’, defences typically combine multiple protective strategies, such as camouflage and aposematism, with a rapid transition between them, and thus offer unique opportunities for studying the dynamics of suites of defensive behaviours. Here we examined the display of the sexually dimorphic mountain katydid, with the goal of identifying the factors influencing individuals’ escape response and display intensity. In experimental assays designed to simulate encounters with predators, we found that sex and repeated exposure to predation attempts affected components of the defensive behaviour of individuals in diverse ways. Both short-distance (sprint) and longer-distance (endurance) speeds differed between the sexes, primarily via an interaction between the intensity of displays and exposure to repeated predation attempts. Display intensity was best explained by an interaction between experience and sex: males maintained their intensity across 3 days of repeated attacks, while females decreased it. These results reveal complex influences on the expression of antipredator behaviour, and identify potential trade-offs mediating individual responses which differ between the sexes. Our findings also highlight the need to consider sexual dimorphism and the effect of individual condition when studying complex behavioural defences.

© 2019 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Predation has driven the evolution of diverse adaptations for defence among prey. These span visual defences such as cryptic coloration (Barry, White, Rathnayake, Fabricant, & Herberstein, 2015; Stevens & Merilaita 2011), through physical adornments for protection (Swaffer & O'Brien 1996), to behaviours that enable rapid escape (Bateman & Fleming, 2014). Animal defences are typically composed of suites of such traits that have evolved in concert to a functional end, such as the coincidence of conspicuous colours, chemical defences and behaviours for effective warning signals (Arenas, Walter, & Stevens, 2015; Maan & Cummings, 2011; Rojas & Endler 2014). In more complex cases still, selection may favour a flexible repertoire of strategies from which one or more

defence may be independently deployed (Edmunds, 1974). The longfin squid, *Loligo pealeii*, presents a striking example, as it draws from a suite of defences depending on the nature of the threat faced (Staudinger, Hanlon, & Juanes, 2011). When approached by mobile predators, longfin squid display disruptive colour patterns, and only flee upon failure of this primary defence. In encounters with ambush predators, however, they immediately attempt escape while releasing a disorienting ink cloud (Staudinger et al., 2011).

Coevolution among defensive and broader life history traits inevitably forces trade-offs, as limited resources must be shared between often competing demands. In the case of aposematism (warning coloration), for example, individuals must balance the energetic costs of movement (e.g. foraging and mate location) with the sequestering and/or synthesizing of compounds de novo (e.g. for chemical defences and colourful conspicuous signals; Mappes, Marples, & Endler, 2005; Nokelainen, Hegna, Reudler, Lindstedt, & Mappes, 2012; Stevens & Ruxton, 2012). This can manifest as a

* Correspondence: T. E. White, School of Life and Environmental Sciences, The University of Sydney, Sydney, NSW, 2006, Australia.

E-mail address: thomas.white@sydney.edu.au (T. E. White).

¹ Authors contributed equally.

positive correlation between conspicuousness, toxicity and condition within species, since individuals in better condition are disproportionately able to invest in both defences and advertisement (Arenas et al., 2015; Blount et al., 2012; Maan & Cummings, 2011). This balancing act also plays out on the ecological stage, where species that have multiple defences must rely on decision rules to manage their use of particular strategies. Such rules need to be flexible, however, since the optimal response at any given time will vary and may depend on, among other things, individual condition, experience, sex, and the energetic and opportunity costs of escape (Forsman, 1999; Robinson, 1969; Ydenberg & Dill, 1986). Thus, individual responses to predation within a population may be context dependent and flexible.

Deimatism (or 'startle' displaying) is a defensive strategy that is thought to afford protection through the exploitation of reflexive or fear responses in predators (Cott 1940, Edmunds, 1974, Skellhorn, Holmes, & Rowe, 2016; Umbers et al. 2015, 2017). Deimatic displays may include suddenly revealed conspicuous colour patterns and, by definition, are multicomponent (Umbers et al., 2017). They may combine multiple defensive strategies, such as camouflage and aposematism, with a quick transition between the two when 'performing' the display (Umbers et al., 2017). Because performing the display is optional for the prey, deimatic species can provide insight into the trade-offs between deploying a defence and escaping, when confronted with a threat.

The mountain katydid is a large orthopteran native to the montane regions of southeastern Australia and beyond (Rentz, 1996). Males and females appear camouflaged at rest and, upon attack, rapidly reveal a striking banded colour pattern on the dorsal surface of their abdomen, an orange intersegmental membrane between head and pronotum, and an antenna display reminiscent of a wasp's (Umbers & Mappes, 2015). The display can be performed while the katydid remains stationary, or while it attempts to escape by running. The simultaneous regurgitation of bitter fluids, along with the presence of alkaloid-rich secretions on the insect's abdominal integument, also suggests a degree of chemical protection (Cable & Nocke, 1975; Umbers et al., 2019). The sexes are dimorphic, with larger (ca. 3 g), flightless females and smaller (ca. 1 g), more mobile, winged males (Rentz, 1996). Here we examined the defensive dynamics of the mountain katydid's display via simulated predation events with a focus on three interrelated questions. (1) Is there a trade-off between display and escape behaviour? (2) How does display intensity, duration and escape behaviour vary with prey experience and condition? (3) Does the sexual dimorphism of katydids underlie differences in defensive responses between sexes?

METHODS

Katydid Collection and Husbandry

We collected mountain katydids ($N = 76$, 42 females and 34 males) from Kosciuszko National Park in April 2015 and housed them under natural outdoor temperature and diel cycles in a large mesh enclosure (1.5×0.4 m and 0.4 m high). We supplied trimmings of two of their preferred food plants (*Senecio gunnii* and *Senecio linarifolius*; Umbers, n.d.) and ample water, both on cotton wool and sprayed onto their plants to emulate morning dew. Within the first 48 h of capture and prior to trials, we obtained body mass (g) and femur length (mm) measurements from each live individual to calculate its body mass index (BMI; body mass/femur length³), before tagging each katydid using bee tags (Pender's Bee Supplies, Cardiff, NSW, Australia) for individual identification. Katydid collection was under NSW Government Permit Number SL101474.

Behavioural Assays

We used simulated predation attempts in artificial arenas to explore the nature of the relationship between katydids' display intensity and escape behaviours. Before the start of every trial we brought all individuals into a temperature-controlled room ($23\text{--}25^\circ\text{C}$) and allowed them to acclimate for at least 30 min. To simulate an attack, we rapidly plucked individual katydids from their large enclosure and placed them into the centre of an arena marked by three concentric circles with radii 25 mm, 150 mm and 300 mm. Following Umbers and Mappes (2015), the same researcher (K.U.) pinched and picked up katydids by the pronotum with finger and thumb, making sure to maintain approximately equal force in every trial. Our attack was meant to simulate the attacking behaviour of avian predators we had observed in the field (Umbers et al., 2019) and that is known to elicit natural defensive responses (Umbers & Mappes, 2015). The force of simulated attacks was standardized through practice (Blumstein and Yin 2018) and preliminary attempts to elicit responses from other individuals in the field that were not used in this experiment.

We tested each katydid in random order three times, once per day for 3 consecutive days. Owing to mortality, the sample size was reduced as the experiment proceeded (trial 1: 42 females, 34 males; trial 2: 40 females, 24 males; trial 3: 39 females, 22 males). The slight sex bias in mortality is curious and difficult to explain, although the relative fragility of significantly smaller males may be a contributing factor. Regardless, we have no reason to suspect it indirectly biased our results. We filmed all katydid behaviour from above using a Sony Camcorder (HXR-NX30P NXCAM), and from two opposing corners of the arena using GoPros (HD Hero4 Action Video Camera, GPCHDHY-401; GoPro Inc, www.gopro.com). All videos were subsequently analysed by people blind to the study's objectives.

In a given trial, when releasing a katydid at the conclusion of the simulated attack, we placed it at the centre of the arena and estimated the escape-speed as the time taken to completely cross the drawn lines that delineated the two larger concentric circles (150 mm and 300 mm radii). Individuals were given 60 and 180 s to exit the inner and outer concentric circles, respectively. We scored katydid display intensity immediately after release following the established protocol of Umbers and Mappes (2015) by summing the number of red abdominal stripes visible (0–3), whether or not the orange head-to-pronotum intersegmental membrane was exposed (0/1), and whether or not the katydid's antennae were vibrating (0/1). Thus, the highest possible intensity score, corresponding to a 'full display', was 5. We also ran each model considering only the number of stripes as our estimate of display intensity to explore any artefacts that might arise by combining binary and continuous measures across modalities, although our results were qualitatively unchanged (Appendix Tables A1–A4) and so are not discussed further here.

Analyses

All statistical analyses were performed in R (v3.5.2; R Core Team, 2018) using the packages lme4 (v1.1-21; Bates, Maechler, Bolker, & Walker, 2015) and coxme (v2.2-10; Therneau, 2018). We visually confirmed the assumptions of normality among residuals and homogeneous variance structures for all models.

Is there a trade-off between display intensity and escape behaviour? Escape response. Since some individuals never left the centre of the arena when attacked, we analysed the 'decision' to escape separately from the escape speed. The decision to escape was modelled with a generalized linear mixed model (GLMM) with binomial error distribution and logit link function. Individual ID was included as a random effect to account for repeated measures. We included sex,

trial (1–3) and display intensity (0–5) as explanatory variables to examine sex-specific behaviours, trends through time and the presence of a trade-off between escape decision and display, respectively. We also included two- and three-way interactions among these variables to test whether trade-offs were sex specific and changed with time. Finally, we accounted for body condition of katydids by including the proportional deviation from mean BMI. Given the documented intersexual differences in body weight, we calculated this as the difference between individual BMI and sex-specific average BMI (females: 4.11 g/mm³; males: 0.74 g/mm³), divided by the sex-specific average BMI. Here, and in all subsequent analyses that include BMI as a fixed effect, the intercept refers to females of average body condition in trial 1, displaying at the lowest intensity (0). We simplified the model by removing interactions that were not significant at the 0.10 level, in a hierarchical fashion (first three- then two-way interactions), and in order of significance (see Appendix Tables A5–A7 for full model selection details).

Escape speed: short and long distance. We analysed the time to exit each sector as a proxy for escape speed. We considered short-term (sprint) speed as the time to exit the inner sector of the arena (ca. 150 mm diameter) and long-distance (endurance) speed as the time to fully exit the arena (ca. 300 mm). We modelled the time to exit the respective sectors as time-to-event data, analysed with a Cox mixed-effect regression with individual ID as a random effect to account for the repeated measures design structure and avoid pseudoreplication. We included display intensity as a fixed factor, which tested whether the strength of display affects escape speed, thereby modelling a possible trade-off between display intensity and escape effort. Moreover, we included sex and trial and all two- and three-way interactions between display intensity, sex and trial number. This allowed us to test for intersexual differences in defensive responses and for (sex-specific) changes in any trade-off through time. As above, we accounted for individual condition by including the deviation from the mean BMI as a main effect. The model was simplified following the same procedure as described above.

Do display dynamics vary with experience, condition and sex?

We analysed the proportional display intensity score (actual score divided by the maximum value of 5) immediately following the simulated attack using a GLMM with a binomial error distribution and a logit link function. We included individual ID as a random effect. We accounted for individual condition by including the deviation from the mean BMI and included main effects and the interaction between sex and trial (as experience) as fixed factors to test for sex-specific changes in display intensity after consecutive simulated attacks.

RESULTS

Is There a Trade-off Between Display Intensity and Escape Behaviour?

Escape response

The propensity for individuals to escape varied by trial and sex (Table 1). Females were more likely to escape than males during the first trial: a female of average condition, displaying at low intensity, is predicted to escape 88% of the time (confidence interval, CI: 58–98%), against the 53% predicted for males (CI: 27–77%). During consecutive trials, the females' propensity to escape decreased (65%; CI: 37–85% in the third trial), while males' increased (99%, CI: 75–100%; Fig. 1).

Table 1
The escape response of katydids

Fixed effect	Estimate	SE	z	P
Intercept	2.007	0.861	2.331	0.020
Score	0.296	0.204	1.452	0.147
Sex	−1.904	0.841	−2.265	0.024
BMI deviation	−0.086	1.072	−0.080	0.936
Trial	−0.697	0.406	−1.716	0.086
Sex*Trial	3.238	1.176	2.753	0.006

Model estimates for the effects of condition (via proportional deviation from mean BMI, BMI deviation, calculated separately for the sexes), experience (via trial number), display intensity score and sex on the escape response of katydids. Katydid ID was a random effect with a variance of 0.224. Bold estimates are significant at $P < 0.05$. $N = 170$, conditional $R^2 = 0.426$.

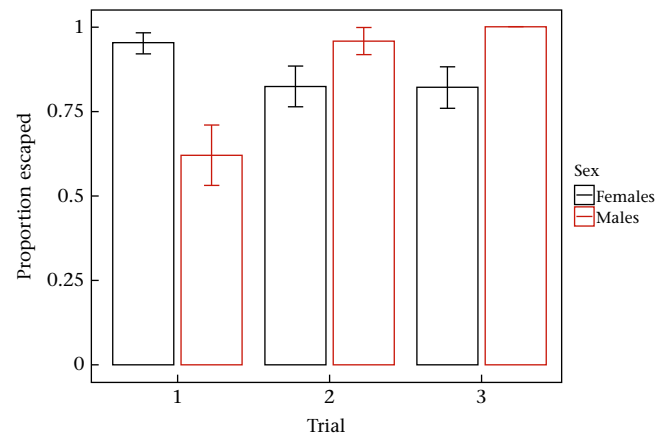


Figure 1. The average (\pm SD) observed proportions of female and male katydids that fled following a simulated predation attempt, repeated across three consecutive trials.

Escape speed: short distance (sprint)

We found a significant effect of sex on sprint speed, with males being almost three times faster than females over short distances if they were not involved in a full display (Table 2). The interaction between score and sex was weak and statistically nonsignificant, albeit only marginally so, which suggests that males tended to be slower as the intensity of their display increased (in contrast to females). The interaction between trial and score was moderate, suggesting a temporal change in the correlation between escape speed and display, with score affecting escape speed more positively as trials passed.

Escape speed: long distance (endurance)

Over the longest distance at which we measured escape speed, males were more than three times faster than females if their display was weak, but the negative interaction between sex and display intensity suggests that this reverses, as males that

Table 2
The short-distance (sprint) escape speed of katydids

Fixed effects	Estimate	Exponentiated estimate	SE	z	P
BMI deviation	0.659	1.933	0.602	1.09	0.270
Trial	−0.199	0.819	0.259	−0.77	0.440
Score	0.151	1.163	0.151	1.00	0.320
Sex	1.088	2.968	0.542	2.01	0.045
Score*Trial	0.196	1.217	0.088	2.24	0.025
Score*Sex	−0.373	0.689	0.192	−1.95	0.051

Model estimates for the effects of condition (via proportional deviation from mean BMI, BMI deviation, calculated separately for the two sexes), experience (via trial number), display intensity score and sex on the short-distance (sprint) escape speed of katydids. Katydid ID was a random effect with a variance of 0.709. Bold estimates are significant at $P < 0.05$. $N = 149$, pseudo- $R^2 = 0.800$.

Table 3
The long-distance (endurance) escape speed of katydids

Fixed effects	Estimate	Exponentiated estimate	SE	z	P
BMI deviation	0.905	2.471	0.626	1.45	0.150
Trial	−0.131	0.877	0.267	−0.49	0.620
Score	0.223	1.250	0.162	−1.38	0.170
Sex	1.554	4.731	0.571	2.72	0.007
Score*Trial	0.196	1.216	0.091	2.15	0.032
Score*Sex	−0.729	0.482	0.211	−3.45	< 0.001

Model estimates for the effects of condition (proportional deviation from mean BMI, BMI deviation, calculated separately for the two sexes), experience (trial number), intensity score and sex on the long-distance (endurance) escape speed of katydids. Katydid ID was a random effect with a variance of 0.696. Bold estimates are significant at $P < 0.05$. $N = 139$, pseudo- $R^2 = 0.799$.

performed intense displays were slower to escape (Table 3). The interaction between score and sex was relatively strong, again suggesting that males tended to be slower along longer distances as the intensity of their display increased.

Do Display Dynamics Vary with Experience and Condition?

We identified an effect of both trial and the interaction between trial and sex on display intensity (Fig. 2). During the first trial females displayed at a higher intensity than males: the predicted display of a female of average body condition was 3.67 (CI: 2.92–4.22), while that of a male of average condition was 1.42 (CI: 0.71–2.44). Male display intensity increased slightly throughout the 3 consecutive days of the experiment, while female display intensity decreased with time, approaching values similar to males by the third trial (Table 4). Regardless of sex, individuals in better body condition displayed more intensely.

DISCUSSION

The defensive repertoires of prey are shaped by competing demands, although such processes are poorly characterized in the context of defences under behavioural control. In simulated attacks on mountain katydids, we found that display intensity, sex and

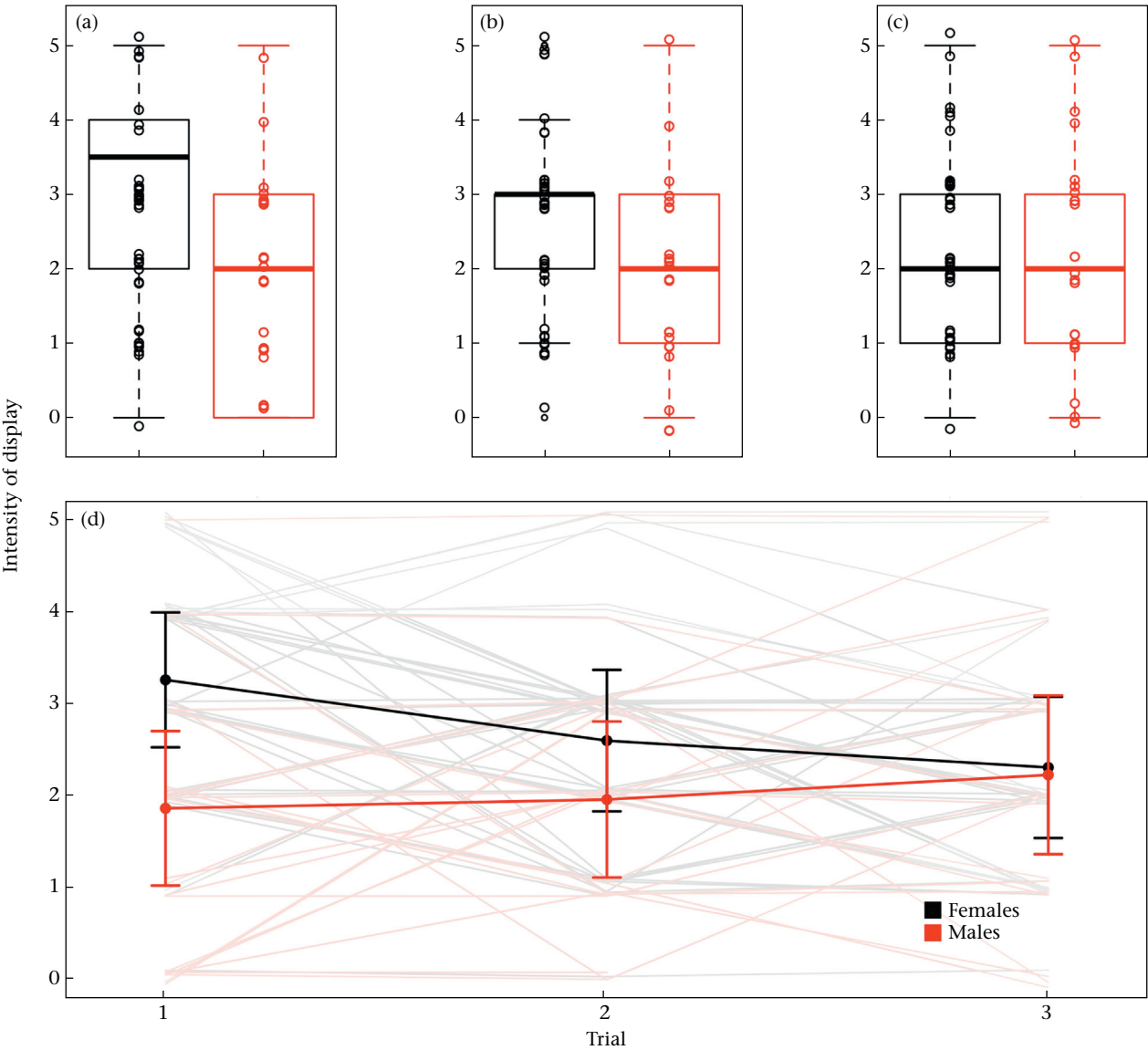


Figure 2. The intensity of male and female defensive displays across three simulated predation attempts on consecutive days. (a) Trial 1, (b) trial 2 and (c) trial 3. Box plots show medians, lower and upper quartiles and maximum and minimum scores along with raw data (circles). (d) The mean plot denotes mean scores $\pm 95\%$ confidence intervals (solid foreground lines) overlying the individual scores of male and female katydids (pale background lines).

Table 4
The intensity of katydid's deimatic displays

	Estimate	SE	z	P
Intercept	1.009	0.345	2.924	0.004
Trial	−0.670	0.260	−2.577	0.010
Sex	−1.936	0.573	−3.382	< 0.001
BMI deviation	1.815	0.752	2.415	0.016
Trial*Sex	1.075	0.436	2.468	0.014

Model estimates for the effects of condition (proportional deviation from mean BMI, BMI deviation, calculated separately for the two sexes), experience (trial number) and sex on the intensity of deimatic displays. Katydid ID was a random effect with a variance of 0.063. Bold estimates are significant at $P < 0.05$. $N = 170$, conditional $R^2 = 0.171$.

repeated exposure to predation have diverse effects on the defensive responses of individuals. Our results, discussed below, support the existence of a trade-off between display intensity and escape responses, albeit with unequal effects between the sexes. They also suggest prey experience and condition may moderate the overall intensity of displays, although this too differed between the sexes.

Our results revealed complex effects on escape behaviours. We found a weak, statistically nonsignificant effect of display intensity on individuals' initial decision to flee, as well as an interaction of sex and trial, with females becoming less likely to escape and males becoming more likely over repeated trials (Fig. 1, Table 1). These imply an absence of discrete, fight-or-flight defensive responses among mountain katydids, like those commonly found among prey that possess a defensive 'repertoire' (Langridge, Broom, & Osorio, 2007; Staudinger et al., 2011). The selective use of defences is often associated with diversity in predator communities and, more precisely, diversity in the sensory capacity of predators. This is well demonstrated among cuttlefish, which respond differentially depending on the category, but not the intensity, of the threat (e.g. Langridge, 2009; Langridge et al., 2007). The homogeneity of the katydids' predators in the wild, which are almost exclusively visually oriented birds (Umbers et al., 2019), may thus favour the singular 'display-then-flee' response our results imply (Table 1), although the ultimate drivers of variation in defensive behavioural flexibility remain an open question.

Of the individual katydids that attempted escape, males were faster than females over shorter distances when the display was weak, although this sex difference narrowed across repeated trials. Irrespective of sex, however, we found a strengthening of the positive correlation between display intensity and sprint speed with repeated exposure to predation attempts. Katydid's enhanced their escape behaviour with short-term experience by combining faster escapes with more intense displays, which is a common response among prey in answer to a perceived increase in predation intensity (Gyssels & Stoks, 2005; Martin & López, 2003). Across longer distances, the results were qualitatively similar. Males continued to escape faster than females, although here the effect chiefly arose via a negative interaction with display intensity. That is, there was an apparent trade-off between display intensity and longer-distance escape speed that disproportionately affected males (Table 3). Mechanical constraints on locomotion offer a likely proximate explanation, as might be expected from the more extreme postural changes required for displays in the smaller, longer-winged males (Rentz, 1996; Umbers et al., 2015). The strengthening of the positive correlation between display intensity and sprint speed also held at longer distances.

When considering predictors of the intensity of the displays themselves, we found that individuals in better condition displayed more intensely, irrespective of sex (Table 4). This may simply reflect the ability of individuals in better condition to more readily bear the energetic cost of sustained displays. Although not fully testable with the data at hand, it is also consistent with theoretical

predictions that defensive responses should vary as a function of initial condition (as broadly estimated by BMI), as well as the energetic and opportunity costs of escape and the expected fitness loss due to predation risk (Cooper & Frederick, 2009; Ydenberg & Dill, 1986). Where costs are borne unequally between the sexes, such as through differential predation, we may expect sex differences in defensive responses to predation (Lagos & Herberstein, 2017; Wing, 1988). Consistent with this view, we identified an interacting effect of sex and trial number (Table 4). Females initially presented more intense displays, although the intensity ultimately declined to match that of males over the 3 trial days.

Since the defensive signals of mountain katydids are not known to be used in sexual contexts (unlike, for example, the aposematic and sexually dimorphic poison frogs; Maan & Cummings, 2009), intersexual differences in defensive behaviours are most likely to be the indirect result of differential selection on key life history traits, such as adult body size and locomotory capacity for dispersal (Blanckenhorn, 2005) and, as discussed above, unequal predation pressure (Lagos & Herberstein, 2017; Wing, 1988). Leading explanations for the ubiquity of sexual size dimorphism in Orthoptera include the existence of sex-specific fitness optima, or intersexual resource competition leading to character displacement (reviewed in Hochkirch & Gröning, 2008; Whitman, 2008). Either way, such processes may also indirectly drive intersexual differences in defence. As noted above, theory predicts optimal defensive responses will, in part, depend on the energetic costs of escape, which is almost certainly greater for female mountain katydids than for males (consistent with our results, Table 4; Cooper & Frederick, 2009; Lagos & Herberstein, 2017). This presents a tentative explanation for the apparently greater investment in initial escape response and display intensity by females (Figs. 1 and 2) which, when considered alongside their slower escape speed (Tables 2, 3), hint at the existence of subtly different defensive strategies between the sexes. These findings also stress the importance of studying defensive strategy at an intraspecific level, especially in the case of dimorphic species, since differences in morphology between the sexes can result in different defensive strategies and trade-offs. At the same time, heterogeneity in individual condition can cause high interspecific variation in the defences deployed. Fully testing such possibilities will demand both experimental and comparative work, and the complexities of deimatism offer fertile ground for unravelling the proximate and ultimate drivers of defensive adaptations.

Acknowledgments

We thank Brendan Baker for assistance in data handling and processing, and the Hermon Slade Foundation (HSF 14/3) and the Linnean Society of NSW for financial support. We thank two anonymous referees and the Editor for thoughtful and constructive feedback.

References

- Arenas, L. M., Walter, D., & Stevens, M. (2015). Signal honesty and predation risk among a closely related group of aposematic species. *Scientific Reports*, 5, 5.
- Barry, K. L., White, T. E., Rathnayake, D. N., Fabricant, S. A., & Herberstein, M. E. (2015). Sexual signals for the colour-blind: Cryptic female mantids signal quality through brightness. *Functional Ecology*, 29(4), 531–539.
- Bateman, P. W., & Fleming, P. A. (2014). Switching to plan B: Changes in the escape tactics of two grasshopper species (acrididae: Orthoptera) in response to repeated predatory approaches. *Behavioral Ecology and Sociobiology*, 68(3), 457–465.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48.
- Blanckenhorn, W. U. (2005). Behavioral causes and consequences of sexual size dimorphism. *Ethology*, 111(11), 977–1016.
- Blount, J. D., Rowland, H. M., Drijfhout, F. P., Endler, J. A., Inger, R., Sloggett, J. J., et al. (2012). How the ladybird got its spots: Effects of resource limitation on the honesty of aposematic signals. *Functional Ecology*, 26(2), 334–342.

- Blumstein, D. T., Diaz, A., & Yin, L. (2018). Marmots do not consistently use their left eye to respond to an approaching threat but those that did fled sooner. *Current Zoology*, 64(6), 727–731.
- Cable, J., & Nocke, H. (1975). Isolation of s-Butyl β D-glucopyranoside from *Acricpeza reticulata*. *Australian Journal of Chemistry*, 28, 2737–2739.
- Cooper, W. E., Jr., & Frederick, W. G. (2009). Predator lethality, optimal escape behavior, and autotomy. *Behavioral Ecology*, 21(1), 91–96.
- Edmunds, M. (1974). *Defence in animals: a survey of anti-predator defences*. London, U.K.: Longman.
- Forsman, A. (1999). Temperature influence on escape behaviour in two species of pygmy grasshoppers. *Ecoscience*, 35–40.
- Gyssels, F. G., & Stoks, R. (2005). Threat-sensitive responses to predator attacks in a damselfly. *Ethology*, 111(4), 411–423.
- Hochkirch, A., & Gröning, J. (2008). Sexual size dimorphism in Orthoptera (sens. str.)—a review. *Journal of Orthoptera Research*, 17(2), 189–196.
- Lagos, P. A., & Herberstein, M. E. (2017). Are males more scared of predators? Differential change in metabolic rate between males and females under predation risk. *Physiology & Behavior*, 173, 110–115.
- Langridge, K. V. (2009). Cuttlefish use startle displays, but not against large predators. *Animal Behaviour*, 77(4), 847–856.
- Langridge, K. V., Broom, M., & Osorio, D. (2007). Selective signalling by cuttlefish to predators. *Current Biology*, 17(24), R1044–R1045.
- Maan, M. E., & Cummings, M. E. (2009). Sexual dimorphism and directional sexual selection on aposematic signals in a poison frog. *Proceedings of the National Academy of Sciences*, 106(45), 19072–19077.
- Maan, M. E., & Cummings, M. E. (2011). Poison frog colors are honest signals of toxicity, particularly for bird predators. *The American Naturalist*, 179(1), E1–E4.
- Mappes, J., Marples, N., & Endler, J. A. (2005). The complex business of survival by aposematism. *Trends in Ecology & Evolution*, 20(11), 598–603.
- Martin, J., & López, P. (2003). Changes in the escape responses of the lizard *Acanthodactylus erythrurus* under persistent predatory attacks. *Copeia*, (2), 408–413, 2003.
- Nokelainen, O., Hegna, R. H., Reudler, J. H., Lindstedt, C., & Mappes, J. (2012). Trade-off between warning signal efficacy and mating success in the wood tiger moth. *Proceedings of the Royal Society B*, 279, 257–265.
- R Core Team. (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Rentz, D. R. (1996). *Grasshopper country*. Randwick, Australia: University of New South Wales Press.
- Robinson, M. H. (1969). The defensive behaviour of some orthopteroid insects from Panama. *Transactions of the Royal Entomological Society of London*, 121(7), 281–303.
- Rojas, B., Devillechabrolle, J., & Endler, J. A. (2014). Paradox lost: Variable colour-pattern geometry is associated with differences in movement in aposematic frogs. *Biology Letters*, 10(6), 20140193.
- Skelhorn, J., Holmes, G. G., & Rowe, C. (2016). Deimatic or aposematic? *Animal Behaviour*, 113, e1–e3.
- Staudinger, M. D., Hanlon, R. T., & Juanes, F. (2011). Primary and secondary defences of squid to cruising and ambush fish predators: Variable tactics and their survival value. *Animal Behaviour*, 81(3), 585–594.
- Stevens, M., & Merilaita, S. (Eds.). (2011). *Animal camouflage: mechanisms and function*. Cambridge, U.K.: Cambridge University Press.
- Stevens, M., & Ruxton, G. D. (2012). Linking the evolution and form of warning coloration in nature. In *Proceedings of the Royal Society of London B* (vol. 279, pp. 417–426).
- Swaffer, S. M., & O'Brien, W. J. (1996). Spines of *Daphnia lumholtzi* create feeding difficulties for juvenile bluegill sunfish (*Lepomis macrochirus*). *Journal of Plankton Research*, 18, 1055–1061.
- Therneau, T. M. (2018). *Coxme: Mixed effects Cox models*. R package version 2.2-10. <https://cran.r-project.org/package=coxme>.
- Umbers, K.D.L., (n.d.) [Natural history data] Unpublished raw data.
- Umbers, K. D. L., De Bona, S., White, T. E., Lehtonen, J., Mappes, J., & Endler, J. A. (2017). Deimatism: A neglected dimension of anti-predator defense. *Biology Letters*, 13(4), 20160936.
- Umbers, K. D. L., Lehtonen, J., & Mappes, J. (2015). Deimatic displays. *Current Biology*, 25(2), R58–R59.
- Umbers, K. D., & Mappes, J. (2015). Postattack deimatic display in the mountain katydid, *Acricpeza reticulata*. *Animal Behaviour*, 100, 68–73.
- Umbers, K. D. L., White, T. E., De Bona, S., Haff, T., Ryeland, J., Drinkwater, E., et al. (2019). The protective value of a defensive display varies with the experience of wild predators. *Scientific Reports*, 9(1), 463.
- Whitman, D. W. (2008). The significance of body size in the Orthoptera: A review. *Journal of Orthoptera Research*, 17(2), 117–134.
- Wing, S. R. (1988). Cost of mating for female insects: Risk of predation in photinus collustrans (Coleoptera: Lampyridae). *The American Naturalist*, 131(1), 139–142.
- Ydenberg, R. C., & Dill, L. M. (1986). The economics of fleeing from predators. *Advances in the Study of Behavior*, 16, 229–249.

Appendix

Alternative models of display intensity

The models in Tables A1–A4 represent the equivalent of the models illustrated in Tables 1–4, when the number of stripes alone (0–3) is used as a descriptor of display intensity.

Model selection

Tables A5–A7 summarize the model selection procedure used to reduce model complexity. The likelihood ratio tests and associated χ^2 and P values correspond to the comparison between a model and the model above, containing one more interaction term.

Table A1
GLMM for escape decision

Fixed effect	Estimate	SE	z	P
Intercept	−2.192	0.880	−2.491	0.013
Score	−0.296	0.258	−1.147	0.252
Sex	1.890	0.863	2.188	0.029
BMI deviation	−0.083	1.059	−0.078	0.938
Sex*Trials	−3.252	1.169	−2.782	0.005

Katydid ID was a random effect with a variance of 0.245. Bold estimates are significant at $P < 0.05$. $N = 170$, conditional $R^2 = 0.412$.

Table A2
Cox mixed-effect regression for short-distance escape speed

Fixed effect	Estimate	Exponentiated estimate	SE	z	P
BMI deviation	0.620	2.860	0.597	1.04	0.300
Trial	−0.178	0.837	0.263	−0.68	0.500
Score	0.333	1.395	0.229	1.46	0.150
Sex	1.305	3.687	0.586	2.23	0.026
Trial*Score	0.227	1.255	0.114	2.00	0.046
Score*Sex	−0.476	0.621	0.262	−1.82	0.069

Katydid ID was a random effect with a variance of 0.694. Bold estimates are significant at $P < 0.05$. $N = 149$, pseudo- $R^2 = 0.801$.

Table A3
Cox mixed-effect regression for long-distance escape speed

Fixed effect	Estimate	Exponentiated estimate	SE	z	P
BMI deviation	0.873	2.394	0.597	1.46	0.140
Trial	−0.170	0.844	0.269	−0.63	0.530
Score	0.247	1.281	0.230	1.07	0.280
Sex	1.320	3.742	0.586	2.25	0.028
Trial*Score	0.241	1.273	0.117	2.06	0.039
Score*Sex	−0.779	0.459	0.270	−2.88	0.004

Katydid ID was a random effect with a variance of 0.609. Bold estimates are significant at $P < 0.05$. $N = 139$, pseudo- $R^2 = 0.787$.

Table A4
GLMM for the display intensity (number of stripes)

Fixed effect	Estimate	SE	z	P
Intercept	1.911	0.453	4.224	< 0.001
Trial	−0.611	0.298	−2.050	0.040
Sex	−2.673	0.652	−4.103	< 0.001
BMI deviation	0.608	0.818	0.743	0.457
Trial*sex	1.312	0.468	2.800	0.005

Katydid ID was a random effect with a variance of 0.245. Bold estimates are significant at $P < 0.05$. $N = 170$, conditional $R^2 = 0.232$.

Table A5
GLMM for the decision to escape based on display intensity, sex, trial and individual body condition

DI	Sex	Trial	DI	DI*Sex	DI*Sex	BMI	df	logLik	AIC	χ^2	P
			*Sex	*Sex	*Sex						
+	+	+	+	+	+	+	10	−58.138	136.28		
+	+	+	+	+	+	+	9	−58.143	134.29	0.011	0.918
+	+	+	+	+	+	+	8	−58.194	132.39	0.102	0.749
+	+	+	+	+	+	+	7	−58.848	131.70	1.308	0.253

Plus signs indicate which traits are included in the model. DI = display intensity score, BMI = body mass index, logLik = log likelihood, AIC = Akaike information criterion.

Table A6

Cox mixed-effect regression for short-distance escape speed, based on display intensity, sex, trial and individual body condition

DI	Sex	Trial	DI *Sex	DI *Trial	Sex *Trial	DI*Sex *Trial	BMI	df	logLik	AIC	χ^2	P
+	+	+	+	+	+	+	+	9	−585.11	11.78		
+	+	+	+	+	+		+	8	−585.62	12.77	1.021	0.312
+	+	+	+	+			+	7	−585.73	14.55	0.220	0.639

Plus signs indicate which traits are included in the model. DI = display intensity score, BMI = body mass index, logLik = log likelihood, AIC = Akaike information criterion.

Table A7

Cox mixed-effect regression for long-distance escape speed, based on display intensity, sex, trial and individual body condition

DI	Sex	Trial	DI *Sex	DI *Trial	Sex *Trial	DI*Sex *Trial	BMI	df	logLik	AIC	χ^2	P
+	+	+	+	+	+	+	+	9	−534.51	14.25		
+	+	+	+	+	+		+	8	−534.17	16.21	0.036	0.845
+	+	+	+	+			+	7	−534.18	18.21	0.007	0.935

Plus signs indicate which traits are included in the model. DI = display intensity score, BMI = body mass index, logLik = log likelihood, AIC = Akaike information criterion.