

Postattack deimatic display in the mountain katydid, *Acripeza reticulata*



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Prey use many strategies to avoid being detected by their predators. However, once detected and identified as potentially palatable, prey must employ a second line of defence such as performing a deimatic (startle) display. During the predation sequence, composed of the stages encounter, detection, identification, approach, subjugation and consumption, such defences should be deployed as the predator approaches, but before prey are brought under the predator's control (i.e. before subjugation). We tested this assumption in the mountain katydid (or bush cricket), which is cryptic at rest, but when disturbed flashes spectacular abdominal colours by lifting its wings, and is chemically defended. We experimentally determined which visual, auditory and tactile stimuli trigger their deimatic display via six treatments. Contrary to expectations of the predation sequence katydids required tactile cues before performing their deimatic display, that is, it was performed only after attempted subjugation. Field experiments also showed that katydids perform their deimatic display after experiencing tactile stimuli. Mountain katydid natural history may explain this counterintuitive behaviour. Being slow and cryptic, katydids cannot effect a fast escape after performing their deimatic display but their tough cuticle and chemical defences make survival of initial subjugation attempts likely. Holding their deimatic display until after initial subjugation may prevent continued attack and avoid the potentially large cost of revealing themselves to predators that have not yet noticed them. Performance of deimatic display after subjugation may be more common than currently recognized and we encourage further investigation.

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Animals avoid attack from predators in myriad ways and often have several lines of defence. Primary and secondary defences are varied and can occur early or late throughout the six stages of Endler's (1991) predation sequence: encounter, detection, identification, approach, subjugation and consumption (Bateman, Vos, & Anholt, 2014; Edmunds, 1974; Endler, 1991). Primary defences (which occur early in the sequence) prevent prey being encountered, detected and identified as viable dietary items (Endler, 2006). In many cases primary defences allow prey to remain visually concealed from predators via crypsis or masquerade (Ruxton, Sherratt, & Speed, 2004; Stevens, Rong, & Todd, 2013). Some prey animals have conspicuous warning signals as their primary defences that warn knowledgeable predators of the unprofitability of attack (Cott, 1940; Mappes, Kokko, Ojala, & Lindström, 2014). When

primary defences fail (either by chance or because a predator is not fooled) and approach is initiated, prey may attempt to actively dissuade predators by employing secondary defences (Edmunds, 1974).

The stage at which prey deploy their secondary defences varies between species but they are generally performed either early or late in a predation sequence (Bateman et al., 2014). Theory predicts that performing defences early reduces the likelihood of predator attack, but may also attract otherwise unlikely attention from predators. Alternatively, performing defences late in the attack may reduce the likelihood of initial detection and successful consumption but may increase the risk of injury (Bateman et al., 2014). Thus we expect that animals with tough bodies and/or toxins are more likely to deploy their defence late whereas those with soft bodies or with no other defence will deploy their defence early.

Secondary defences are broadly grouped into flight or fight reactions where flight is fleeing once detected and fight includes behaviours that intimidate, frighten and/or injure. To flee, prey

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animals may recoil into a shelter or utilize protean (erratic) escape (Edmunds, 1974). To ‘fight’ a predator, prey may feign death (thanatosis), deflect attack towards an expendable body part (e.g. autotomy; Cooper & Vitt, 1985), retaliate with weaponry or deploy deimatic behaviour (Maldonado, 1970). The latter is also known as responsive defence (Broom, Speed, & Ruxton, 2005; Higginson & Ruxton, 2009), startle display (Kang, Lee, & Jablonski, 2011; Olofsson, Eriksson, Jakobsson, & Wiklund, 2012; Ruxton et al., 2004) and frightening attitude (Roonwal, 1938; Varley, 1939). In deimatic behaviour, fight is tantamount to fright as prey suddenly produce sounds and inaudible vibrations (Dunning, 1968), froth and squirt chemicals (Carpenter, 1938), posture to increase apparent body size or mimic the shape of unprofitable prey e.g. phasmids imitating scorpions (Johnson & Brodie Jr, 1975; M. Robinson, 1973; M. H. Robinson, 1968a, 1968b), and/or flash conspicuous colour patterns (Kang et al., 2011; Lyytinen, Brakefield, Lindström, & Mappes, 2004; Lyytinen, Brakefield, & Mappes, 2003; Olofsson et al., 2012; Vallin, Jakobsson, & Wiklund, 2007). Deimatic behaviour is thought to protect prey by surprising a predator so that it is deterred from attempting subjugation or pauses in its pursuit long enough for the prey to escape (Ruxton et al., 2004; Stevens & Merilaita, 2011).

Visually observable deimatic behaviour (deimatic displays) often involve sudden changes in colour or pattern as perceived by the predator (Umbers, Fabricant, Gawryszewski, Seago, & Herberstein, 2014). For example, when threatened, *Sepia officinalis* cuttlefish use fast physiological colour change to tailor the colour pattern of their deimatic display to different predator species (Langridge, 2009; Langridge, Broom, & Osorio, 2007). Several observations of fast mechanistic colour change in amphibians suggest prey attempt to deter predators by posturing to expose conspicuous venters (Brodie, 1977), groins (Williams, Brodie, Tyler, & Walker, 2000) and/or rumps (Lenzi-Mattos et al., 2005; Martins, 1989). Insects also often reveal conspicuous colours or patterns, for example on the hindwings of moths (Blest, 1957; Olofsson et al., 2012) and raptorial forelegs of praying mantises (Crane, 1952; Edmunds, 1972, 1976). Although

deimatic displays have been described for many species, their adaptive significance, survival value and releasers remain poorly understood. From the examples given above it is clear that deimatic displays can be honest or dishonest. For example, all known praying mantis species are palatable and yet they have among the most striking deimatic displays (Crane, 1952; Edmunds, 1972, 1976). This suggests that their display is a bluff, as they do not pose a real threat to their predator. At the same time, highly toxic amphibians perform deimatic displays such as suddenly revealing eye spots on their rumps or bright colours on their venters (Brodie, 1977; Martins, 1989). Honest deimatic displays may potentially be considered a type of aposematism but because of their dynamic nature are distinctly different to the static, conspicuous coloration classically associated with aposematic species.

Orthoptera (crickets, grasshoppers and katydids) are prey for a variety of predators and can be astonishingly cryptic at rest via disruptive coloration (Stevens & Merilaita, 2011) or general or special resemblance to foliage (Castner & Nickle, 1995). Once disturbed, Orthoptera may attempt to flee by employing protean tactics (Edmunds, 1972) and when captured most regurgitate crop fluid, adding a chemical component to their defence (Lymbery & Bailey, 1980; Sword, 2001). Katydid (Orthoptera: Tettigoniidae) provide great examples of crypsis, mimicry and masquerade as primary defence (Castner & Nickle, 1995) and for many it is their most important level of protection (Gwynne, 2001; Rentz, 1996).

Found in southeastern Australia, the mountain katydid is diurnal, large (<3 g), slow and clumsy. Mountain katydids are cryptic at rest (possibly masquerading as stones (females) or feathers (males)) but perform a remarkable defensive display when disturbed (Fig. 1). This species is chemically defended and thus their defensive display is likely to be honest; their abdominal secretions taste bitter and are toxic to birds and mammals (Cable & Nocke, 1975) and, intriguingly, are an insect aphrodisiac (Rothschild et al., 1979).

In the present study, we aimed to test the hypothesis that intensity of the mountain katydid’s deimatic display varies with the

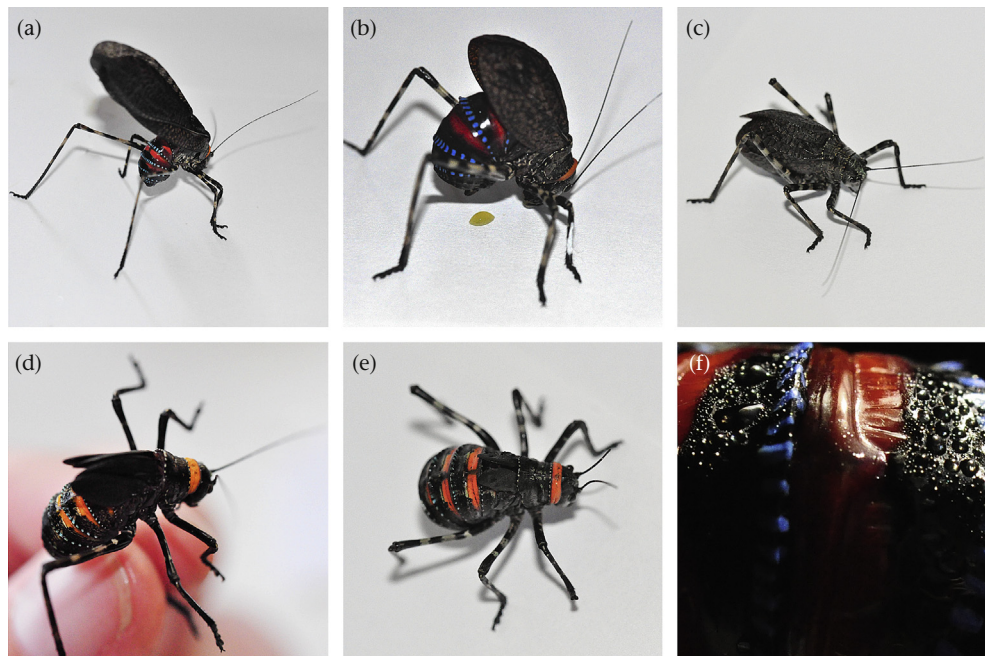


Figure 1. Deimatic display of *Acripeza reticulata* showing defensive posturing, coloration and exudate: (a) adult male in defensive posture, (b) adult female in defensive posture, (c) adult female in resting posture, (d) subadult male in defensive posture, (e) subadult female in defensive posture, (f) adult female dorsal abdominal surface showing distasteful exudate and blue, red and black coloration.

intensity of simulated attack stimuli. Based on the assumptions of Endler (1991)'s predation sequence we predicted that the mountain katydid's display would be triggered both by simulations of a predator's approach (noninvasive) and by simulations of predator attack (invasive), with low and high intensity, respectively. We further predicted that different modes of simulated attacks (visual, auditory, tactile) would result in different intensities of deimatic display.

METHODS

Forty mountain katydids (10 adult females, 10 adult males, 10 subadult females and 10 subadult males) were collected in Kosciuszko National Park in January 2013. Katydids were housed in mesh containers (40 cm cylinders, Pop-up Port-a-Bug, Insect Lore, Cornwall, U.K.) with ample food (*Senecio gunnii* and *Senecio pinnatifolius*) and water. Our laboratory was located at our field station in Guthega, Kosciuszko National Park (1650 m above sea level) in a room of similar temperature to outside (night: <8 °C; day: ca. 20 °C). Each adult was individually marked by gluing a unique bee tag to its right wing (Bostick Super Glue; Bee tag ĚslovanĚ, Czech Republic). Subadults were individually marked by applying a small drop of correction fluid on one of the six legs, and holding a maximum of six individuals, each marked on different legs, in any one enclosure.

To gain baseline behavioural observations on mountain katydids, we observed them in nature and in large, seminatural enclosures for several hours prior to our experiment and identified a suite of behaviours. When undisturbed, katydids walked, ate, stood, called (males), flew (males, rarely) and vibrated the foliage (males). After perceiving a threat, they attempted to escape (walk/run clumsily but hurriedly from disturbance) or performed a deimatic display. The intensity of the deimatic display varied but contained the following components (anterior to posterior): (1) antennae together, straight and vibrating, (2) orange membrane between head and pronotum revealed by tilting head forwards, (3) regurgitation of crop liquid, (4) wings opened perpendicular to body, (5) abdomen flexed ventrally to reveal red membranes and blue spots, and (6) abdomen glistened with exudate (Fig. 1a–f). The juvenile defensive display was the same in terms of posturing and movement as the adults but with wing buds and orange abdominal stripes (Fig. 1d, e).

As a result of our initial observations, we identified several factors to reliably score display intensity. The display intensity score was out of five and was scored immediately after the treatment was applied: (1) orange head–thorax membrane visible (1), not visible (0); (2) antennae together, straight and waspish (1), resting (0); (c) number of intersegmental stripes showing (how strongly an individual flexed its body; 0–3). How long katydids held their display (time display held) was scored via instantaneous scan sampling at 30 s intervals (time until antenna relaxed, head stripe was invisible, abdominal stripes were invisible). Walking speed was subjectively categorized as still, slow or fast.

Arenas (20 × 20 cm and 10 cm deep) were furnished with a 15 cm sprig of *S. pinnatifolius* (host plant) and katydids were given 2 min to acclimate after introduction. Behaviours were recorded every 30 s for 5 min before and after treatments. Three treatments were nontactile: (1) 'fly over' (visual only, mimicking bird flying over): 20 cm × 30 cm book was passed over katydid at 30 cm distance and at 1 per m; (2) 'tap near head' (visual + auditory): Sharpie pen sharply tapped once next to the head without touching it; (3) 'blow on' (tactile, gentle): from 20 cm distance for 2 s. Two treatments were tactile: (4) 'poke' (to simulate bird peck): Sharpie sharply tapped once on pronotum; (5) 'pinch & lift' (simulate bird attack): squeezed laterally with forceps, lifted 5 cm and dropped, whole treatment duration: 2 s. The sixth treatment was a control in which katydids were observed only. Each individual received each treatment once, the order of the treatments was assigned

systematically to include as many different treatment orders as possible (40/720 possibilities), and katydids were rested for more than 4 h after poke and pinch & lift treatments. Treatments were administered by a single investigator (J.M.) to maximize consistency.

We compared katydid display intensity score and walking speed among the six treatments before and after the stimulus using Friedman tests and post hoc pairwise Wilcoxon tests. We chose nonparametric tests as the data were ordinal. We compared time display held between treatments, ages and sexes with Cox's proportional hazard reduction regression using the SURVIVAL package in R. We included time display held as the response variable (as a SURV object) and age (binomial) and sex (binomial) as predictor variables. All analyses were conducted in R (R Development Core Team, 2008).

We also recorded the responses of 32 adult katydids (16 males and 16 females) to the pinch & lift stimulus in the field. We described katydid behaviour in three states: (1) at rest (observed from >2 m), (2) when disturbed by approaching to within 10 cm and shaking foliage, (3) after being attacked with the pinch & lift stimulus. We scored and tallied the following behaviours: still, walking, calling, flying, jumping and deimatic display.

Ethical Note

The animals in this study were collected in Kosciuszko National Park and the work was carried out under the NSW National Parks and Wildlife Scientific Licence S12256. The katydids were housed in pop-up mesh containers and provided with adequate food, water, airflow, heat and light. They were handled gently and not manipulated except for the administration of our treatments. No katydids showed any signs of ongoing distress after our experiment and all continued their natural behaviours (calling, eating, walking). Katydids were held in captivity for a further study and maintained until they died, at which time they were preserved in 70% ethanol.

RESULTS

A clear majority of katydids performed their defensive display in the poke (95%) and pinch & lift (95%) treatments whereas a majority of katydids showed no defensive reaction in the fly over, tap near head and blow on treatments (95%; 90%; 8%) which did not differ from the control (98%) (Friedman tests with post hoc Wilcoxon paired tests: $\chi^2_5 = 153.12$, $P < 0.01$; pairwise comparisons of all nontactile treatments and controls: all $V < 1$, all $P > 0.07$; pairwise comparison of tactile treatments: $V = 0$, $P = 1$; all comparisons of tactile and nontactile or control: $V > 38$, $P < 0.01$). Only the treatments involving tactile stimuli (poke and pinch & lift) resulted in high display intensity scores (Fig. 2, see video in the Supplementary Material). This pattern was the same for both the sex and the age groups (Friedman tests with post hoc Wilcoxon paired tests: adult females before: no difference between treatments because every response was 0; adult females after: $\chi^2_5 = 44.03$, $P < 0.01$; adult males before: $\chi^2_5 = 5.00$, $P = 0.42$; adult males after: $\chi^2_5 = 43.13$, $P < 0.01$; subadult females before: $\chi^2_5 = 3.46$, $P = 0.63$; subadult females after: $\chi^2_5 = 43.84$, $P < 0.01$; subadult males before: $\chi^2_5 = 4.68$, $P = 0.46$; subadult males after: $\chi^2_5 = 40.77$, $P < 0.01$; Fig. 2). There was no difference in intensity of display between the pinch & lift and the poke treatments (Wilcoxon paired test: $V = 235$, $P = 0.24$).

Time display held ranged from 30 s to longer than 300 s (Fig. 3). There was a clear difference between the treatments (Fig. 3): the tactile treatments elicited the longest display time compared to the other three treatments (nontactile treatments) and the control (Cox's proportional hazard reduction regression: $\chi^2_5 = 158$,

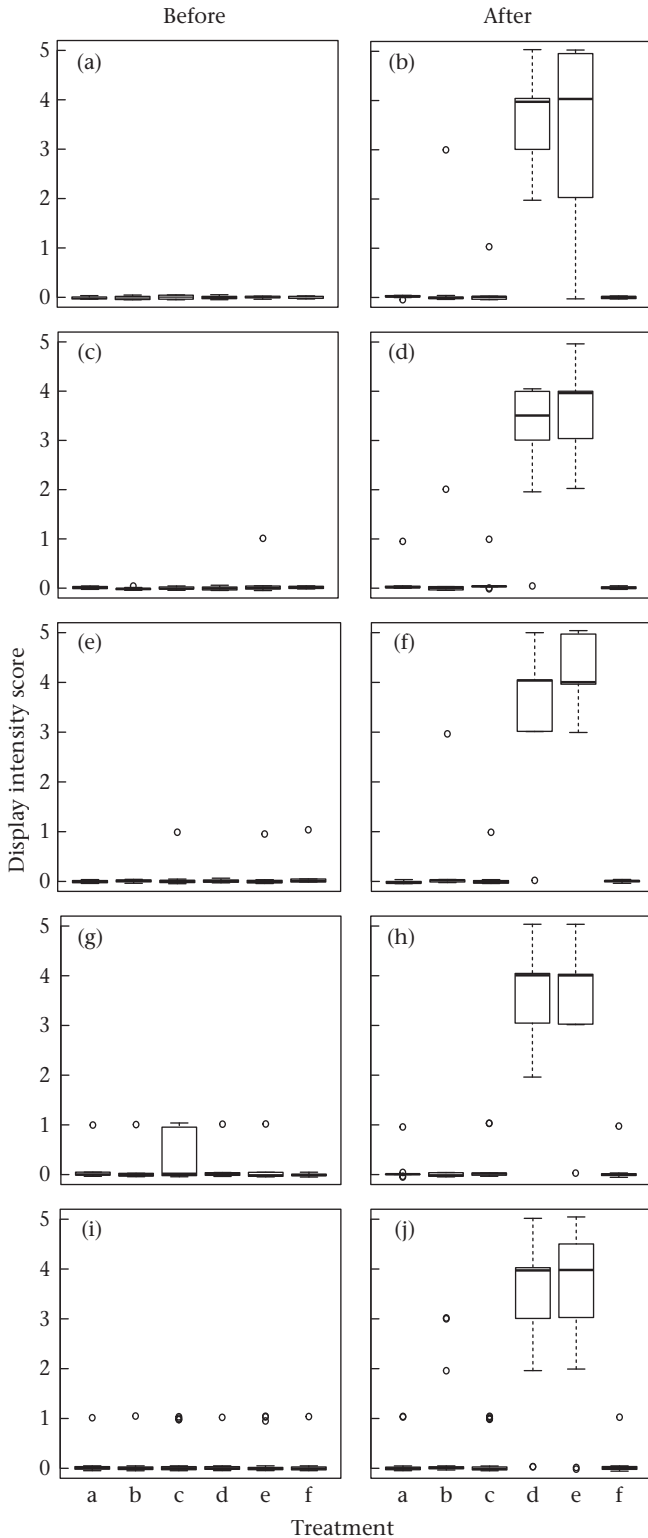


Figure 2. Box plots showing *Acripeza reticulata*'s display intensity score before and after simulated attack treatments: (a) adult females before, (b) adult females after, (c) adult males before, (d) adult males after, (e) subadult females before, (f) subadult females after, (g) subadult males before, (h) subadult males after, (i) all katydid before, (j) all katydids after. Treatments: a: fly over; b: tap near head; c: blow on; d: poke; e: pinch & lift; f: control. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.

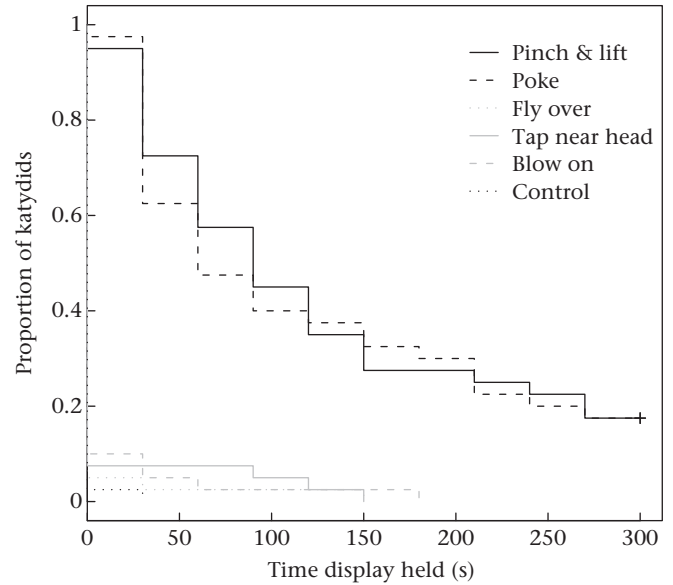


Figure 3. Survival curve of time *Acripeza reticulata* spent displaying for all treatments for all katydids ($N = 40$).

$P < 0.01$; Fig. 3). There was no difference between pinch & lift and poke treatments (Cox's proportional hazard reduction regression: $\chi^2_5 = 0$, $P = 0.84$).

The full model including time display held as the response variable (as a SURV object) and age (binomial) and sex (binomial) as predictor variables was significant and explained 20% of the variation in time display held (Wald test: 8.44, $df = 2$, $R^2 = 0.19$, $P < 0.01$). Age had the largest effect size and was the only significant predictor variable (estimate = -1.09 , $P < 0.01$). When we dropped sex from the analysis the resulting simplified model remained essentially unchanged (Wald test: 8.42, $df = 1$, $R^2 = 0.19$, $P < 0.01$; estimate = -1.09 , $P < 0.01$). Age was negatively correlated with time display held indicating that juveniles held their displays longer than adults.

In all treatments, there was an increase in walking speed after stimuli were applied (before versus after all treatments: $V = 1154$, $P < 0.01$). The same result was seen when considering only the three nontactile treatments (before versus after nontactile treatments: $V = 620$, $P < 0.01$). A greater proportion of katydids increased their walking speed after stimuli were applied in poke near head and blow on but not fly over compared to the control treatment (fly over: 0.23; poke near head: 0.38; blow on: 0.43; control: 0.08; Friedman test: $\chi^2_3 = 15$, $P < 0.01$; Wilcoxon paired tests: all $P > 0.05$ except poke near head versus control: $V = 97.5$, $P < 0.01$; blow on versus control: $V = 105$, $P < 0.01$).

In the field, adult katydids ($N = 32$) were found sitting still (81%) or walking (19%). When approached, and the foliage they were upon disturbed, katydids became still (6%), walked (69%), jumped (19%) or flew (3%) and a single katydid performed its deimatic display (3%). When subjected to the pinch & lift treatment, all katydids performed their deimatic display (100%).

DISCUSSION

Somewhat congruent with our predictions, our results show that mountain katydids were more likely to perform their deimatic display, do so more intensely, and for longer, when encountering tactile than nontactile stimuli and that only tactile stimuli reliably and repeatedly triggered the display. Results from our field

observations supported our results from laboratory experiments indicating that katydids always performed their display when subjected to the pinch & lift stimulus but almost never performed it when they were merely approached and the foliage they were sitting on was disturbed. The combined findings of the present study provide an interesting exception to the assumptions of Endler's predation sequence hypothesis which predicts that defensive displays should be stimulated by a predator's approach (early) rather than by a predator's subjugation attempt (late) (Endler, 1991). The mountain katydid's antipredator strategy seems more akin to a co-specialization defence in which we see the coupling of early and late defences (Bateman et al., 2014).

It is commonly expected that organisms with deimatic displays should perform them upon predator approach to either deter or disrupt the predation sequence (Edmunds, 1974; Ruxton et al., 2004). In some species, such as praying mantises, frogs and lepidopterans, predator approach elicits deimatic displays before the predator makes contact (Crane, 1952; Edmunds, 1972, 1976; Maldonado, 1970; Yamawaki, 2011). Praying mantises are palatable and as such they may pay a large penalty if their display is too late because once they are subjugated they are likely to be consumed (Crane, 1952). However, unpalatable, toxic amphibians such as *Physalaemus nattereri*, *Physalaemus deimaticus* and *Pleurodema brachyops* (Martins, 1989; Lenzi-Mattos et al., 2005) perform deimatic displays before subjugation indicating that they are unlikely to avoid injury from a preliminary, investigative attack. That is, an organism's toxicity does not preclude the evolution of deimatic behaviour if that behaviour reduces the risk of attack in the first instance.

Although a visual defensive display that is revealed only after attack seems unlikely and counterintuitive, our evidence suggests that this is the case for the mountain katydid. It is possible that any other cue (visual, wind-driven movement of bushes, vibrations; Endler, 1992) is not a reliable trigger and thus revealing their display inappropriately may make them conspicuous to predators that had previously not identified them. Alternatively, in the field katydids are likely to receive multiple cues about the presence of predators (Hettley et al., 2011); for example, the combination of sighting a bird and the simultaneous (or near simultaneous) tactile sensation of wind generated by wing beats may trigger their defensive display. This potential for the effects of multimodal attack cues should be the subject of future studies.

Several species, although chemically defended, have been reported to rely on crypsis as a primary strategy (Endler & Mappes, 2004). For example, *Papilio machaon* larvae appear cryptic from a distance but aposematic close up (Tullberg, Merilaita, & Wiklund, 2005). Remaining cryptic as long as possible is a good strategy for species with poor potential to flee (Ozel & Stynoski, 2011; Rojas, Devillechabrolle, & Endler, 2014; Willink, Brenes-Mora, Bolaños, & Pröhl, 2013). Mountain katydids have poor fleeing ability. Both sexes have extremely reduced jumping legs, and while males can fly, females have lost flight completely with their single pair of tegmina more akin to elytra than wings (Fig. 1). After initial subjugation, if the predator drops a katydid after tasting the alkaloids, its deimatic display must provide a reinforcing signal that prevents the predator from attacking again (Aplin, Benn, & Rothschild, 1968; Guilford, Nicol, Rothschild, & Moore, 1987). However, predators have no opportunity to transfer this knowledge to future encounters because the deimatic display is not performed upon approach, but after subjugation has already been attempted. This suggests that the katydid's strategy is selfish with no protection afforded to other subsequently encountered katydids but might be advantageous if they commonly encounter naïve predators.

The combination of mountain katydid's mechanical and chemical defences may allow it to successfully risk injury and hold its

defensive display until late in the interaction (Bateman et al., 2014). Adult mountain katydids have a seemingly tough exterior (tegmina) which, coupled with their chemical defence, probably enhances their chances of surviving initial attack. Juveniles held their display longer than adults, which may be because they lack tough wings and thus are more vulnerable to predation, but this suggestion requires further investigation.

The mountain katydid may be an example of defence co-specialization where large costs of late defences can drive the evolution of early defences coupled with late defences (Bateman et al., 2014). Mountain katydids are equipped with both an early and a late defence, their crypsis and deimatic display, respectively. Evidence from the present study indicates that mountain katydids do not reveal their hidden aposematic display but maintain crypsis until they have encountered tactile stimuli. While this strategy helps katydids avoid early detection and consumption, they risk injury by using their defence late in the predation sequence (Bateman et al., 2014). Theory predicts that such increasing costs of late displays lead to co-specialization (an early defence coupled with a late defence). The mountain katydids' cryptic appearance and tough tegmina (wings) may have reduced the costs of their late defence and allow them to withstand initial stages of an attack facilitating the evolution of both crypsis and a deimatic display (Bateman et al., 2014).

There is no information about predators of katydids and during our fieldwork we did not observe any direct attacks. We did, however, observe large populations of little ravens, *Corvus mellori*, and Australian magpies, *Cracticus tibicen*, in the area. Both species' large size and powerful bill would make them potentially dangerous predators for katydids. Interestingly, these birds tend to investigate prey with their bill before consumption and this may give them a chance to see the deimatic display of katydids after initial contact. We are also aware of candidate reptiles and crepuscular and nocturnal insectivorous mammals that are somewhat common in the alps. We are currently aiming to identify katydids' predators and determine whether the katydids' display can help it survive an attack.

Dynamic defensive displays such as deimatic behaviour are complex multimodal, multicomponent cues. Despite being a remarkable natural history phenomenon, deimatic behaviour has received relatively little research attention. Our results provide an exception to the assumption that prey should perform their deimatic displays during the approach phase of a predation event. Mountain katydids performed their display not during approach, but after subjugation had been attempted. Our results support the hypothesis that conspicuousness, even in toxic animals, is often costly (Endler & Mappes, 2004). This may explain why the mountain katydid hides its aposematic signal and reveals it as a sudden flash of conspicuous colour. Definitions of deimatic behaviour should be extended to include late defenders such as the mountain katydid and more theory is needed to explore how such traits evolve.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2014.11.009>.

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