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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.

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, Lindstrtr, & 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). Katydids (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

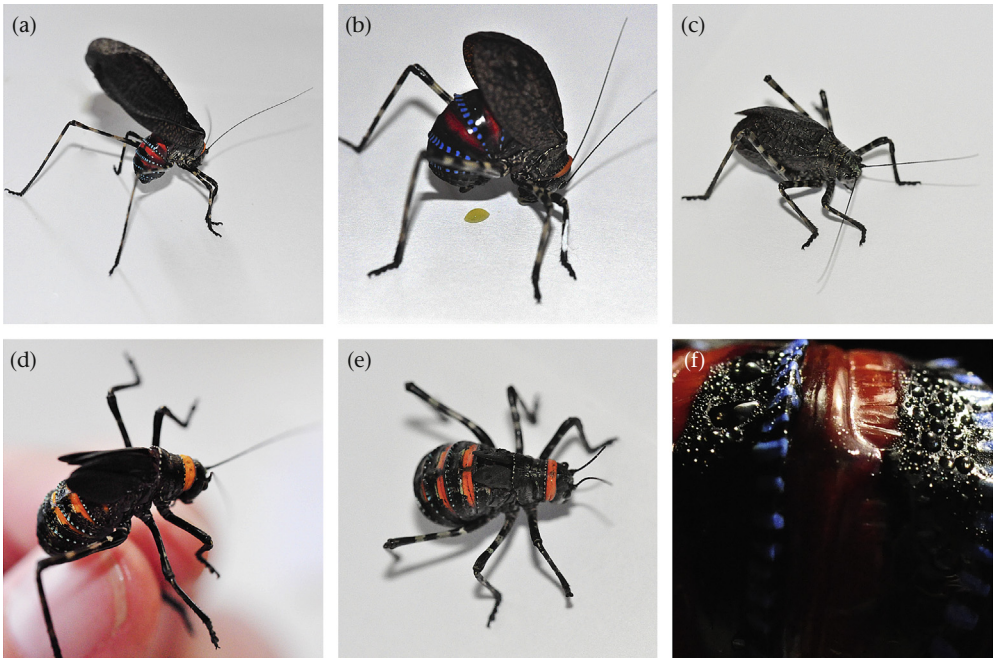

Figure 1. Deimatic display of *Acripeza reticulata* showing defensive posturing, coloration and exudate: (a) adult male in defensive posture, (b) adult female in defensive posture, (c) adult female in resting posture, (d) subadult male in defensive posture, (e) subadult female in defensive posture, (f)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