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Endless forms most hidden: katydids that masquerade as moss

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In the cloud forests of the central range of the Colombian Andes, we discovered a species of katydid (Orthoptera: Tettigoniidae) that imitates mosses to an uncanny degree and is exceedingly difficult to detect (Fig. 1). The photographs were taken in the Santuario de Fauna y Flora Otún Quimbaya, at an elevation of 1900 m. With a mean annual precipitation of 2600 mm, the forest is humid and a variety of mosses cover its rocks, tree trunks and palm leaves. The katydid has a dorsally green head and pronotum, and bands on the abdomen that closely match the color of the moss where it hides. The legs, pronotum and abdomen have green-colored triangular projections that imitate moss leaves, completing the disguise. The insect remains motionless for prolonged periods of time.

The insect in the picture belongs to the genus *Adeclus* (Orthoptera: Tettigoniidae: Pseudophyllinae: Pleminiini). It is an adult, brachypterous male, and wing coloration pattern, pronotal and cerci shape suggest this species is *A. trispinosus* (Cadena-Castañeda 2011). Resemblance to moss has evolved independently across several taxa of orthopteroid insects (Mugleston et al 2013, Song et al 2015). It is very common in the Pleminiini, a tribe with some 200 species described, and also in other groups of Tettigoniidae (e.g., in nymphs of *Panacanthus varius* and *P. intensus*) (Montealegre-Z and Morris 2004). Such camouflage has also been observed in stick insects of the genus *Acanthoclonia* (Phasmatodea) and in the moss mantids genera *Pogonogaster* and *Majangella* (Mantodea) (Gutiérrez and Bacca 2014, Svenson et al. 2015).

In the 1890s, British evolutionary biologist Edward B. Poulton recognized the mastery of orthopterans over what he termed protective resemblance (Bidau 2014). Katydids are masters of disguise, a strategy that presumably helps them to avoid attack by visually-oriented predators. To a human observer, many katydids exhibit an exceptional resemblance to a dead leaf, complete with midrib, holes and mildew patches. Leaf-like wings have evolved independently in at least six lineages of Tettigoniidae (Mugleston et al. 2013). Some species also resemble green leaves or lichens (Braun 2011, Bidau 2014). Katydids are particularly diverse in humid tropical forests, where they include an astounding range of disguises. Of the 378 species of katydids collected by Nickle and Castner (1995) at three sites in Loreto Province, Peru, 273 species had green or brown colors that helped conceal the animals in vegetation. Another 53 exhibited more refined forms of camouflage, resembling bark, twigs, leaves and lichens. Mapping these diverse forms of camouflage (including moss resemblance) in Mugleston's et al. (2013) phylogeny suggests multiple origins.

How do animals disguise themselves so thoroughly as this katydid does? Currently, the concept of camouflage recognizes a variety of strategies that make detection and recognition difficult (Ruxton et al. 2004, Stevens and Merilaita 2009, 2011). Crypsis refers to strategies that prevent detection. In a type of crypsis known as background matching, an animal presents an appearance (color, pattern) that helps it blend into the background. In contrast to background matching, disruptive coloration reduces the probability of detection by breaking up an animal's outline so that its shape cannot be perceived (Cuthill et al. 2005, Webster et al. 2013). Another form of camouflage known as masquerade works not to prevent detection, but rather recognition (Skelhorn and Ruxton 2010). Masquerading animals resemble irrelevant objects in the environment such as sticks or bird droppings so that as not to attract attention.

The katydid we found uses these different strategies to conceal itself: background matching, disruptive coloration, and masquerade. Each of these strategies may come into play depending on the distance at which the insect is viewed; from afar, it may appear to simply be part of the mossy bark on which it rests, and escape detection through background matching. The greenish knobs and brown sections on its limbs occur at a spatial frequency similar to the distribution of those elements on the bark (Fig. 1). Closer inspection may fail to detect the katydid because the different parts of its disguise disrupt its outline: the various chunks of color make it difficult to resolve its legs or body segments. Finally, recognition may elude even the most assiduous assailants because its very body parts masquerade as elements of a mossy tree: the legs resemble moss leaves; the long antennae pass for thin twigs. The fine details of these components may increase the probability that they are perceived as distinct objects, making the whole insect harder to notice through an effect that might operate similarly to disruptive coloration, yet exploit object recognition rather than edge detection.

Currently, the use of multiple camouflage strategies by the same individual is a burgeoning topic of research. Background matching and disruptive coloration operate via distinct mechanisms, but are challenging to separate mechanistically (Webster et al. 2013). Sophisticated image analysis can tease them apart, however. Recent studies have shown that bird eggs rely on both background matching and disruptive coloration for concealment (Stoddard et al. 2016), and that individuals can lay eggs on substrates where one strategy or the other is enhanced (Lovell et al. 2013). Moths can also enhance the effects of background matching and disruptive coloration by repositioning their bodies after landing (Kang et al. 2015). An interesting aspect of these studies is their emphasis on the importance of habitat selection in determining which camouflage strategy predominates.

There remain many interesting questions about the function of multiple camouflage strategies. They may interact to protect animals when they are perceived both from afar and close up, to improve camouflage on specific microhabitats, or increase the versatility of camouflage to work in different microhabitats. To study these possibilities, we must take into account the perceptual systems of the relevant predators: what is the spatial acuity of their vision, how do the retinas of their eyes detect edges, and how do their brains recognize shapes and place them in categories (Stoddard 2012)? At the same time, there is an urgent need to pair such organismal research with more detailed knowledge of how camouflage is perceived in the wild. For example, to understand how prey will be perceived, we need to know the distance at which predators search for their prey to know which perceptual processes are most likely to function when camouflaged prey enter their field of vision. Birds such as woodcreepers (Dendrocolaptinae) that move along branches searching for prey may have a very different perceptual experience from birds that search for prey from perches, like some flycatchers (Tyrannidae). Approaches used in studying the relationship between warning coloration (aposematism) and camouflage may be helpful, as these two antipredator strategies can also co-exist within a single organism to protect it from predators that see it at different distances (Tullberg et al. 2005, Barnett and Cuthill 2014). Observing the behavior of either human or wild predators upon encountering camouflaged prey would be helpful in better understanding the function of multiple camouflage strategies in nature.

The camouflage exhibited by our particular katydid seems quite specific. What are the evolutionary consequences of this sort of specialization? Can camouflage specialization increase speciation rates? Selection to maintain effective disguises can result in reproductive isolation between populations specialized for different microhabitats (Nosil et al. 2002), which makes it reasonable to speculate that camouflage may increasing diversification rates. Does camouflage also come at the price of elevated extinction risk? This possibility must be considered because although antipredator defenses are often thought of as leading to “escape-and-radiate” dynamics where diversification follows innovation that allows expansion into new niches (Schluter 2000), recent work has shown unexpected extinction risk associated with some antipredator adaptations (Arbuckle and Speed 2015). Highly specialized camouflage would seem an ambiguous case because of its obvious benefits, but also potential costs such as inhabiting habitats with low carrying capacities (Arbuckle and Speed 2015), vulnerability to predators at high densities if predators form search images (Endler 1988), or metabolic trade-offs with thermoregulation (Carrascal et al. 2001). Groups such as the Tettigoniidae provide a tantalizing opportunity for their exceptional diversity, wide geographic distribution, and striking array of disguises suggest that many independent evolutionary experiments have already taken place.

Future evolutionary experimentation may be just around the corner as local microclimates shift in response to anthropogenic activities, which can be challenging for invertebrate camouflage specialists (Gröning et al. 2007). Although the Santuario de Fauna y Flora Otún Quimbaya will benefit from government efforts to restore the local watershed and forest, the impact of global climate change on habitat suitability for species that rely on camouflage remains an unknown. For better or worse, different climate projections produce conflicting estimates for whether precipitation in the region will increase or decrease. They agree, however, that relative humidity will decrease (Collins et al. 2013), which may present a test of adaptability for taxa that hide amidst the moss.

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Captions: Now you see it, now you don´t. (a) Picture of a moss katydid in its overall context. Tip: the animal is located in the center bottom of the picture, facing left. (b) Close up of the same individual that shows coloring and anatomical features that resemble the moss on which it is sitting. The long antennae are reddish brown with specs of green and are almost twice as long as the animal (see Fig 1a again).