

## Evasive mimicry: too beetle, or not too beetle?

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Mimics are the protagonists of evolutionary plays occurring in ecological theaters. In these Darwinian tragicomedies, predators, prey, or even partners act as the mimics' dupe. The ability to mimic other species is a striking example of evolution by natural selection, which has long attracted the attention of naturalists (e.g., Bates 1862, Müller 1879). By copying signals from a model organism, some mimics are able to fool predators that usually avoid poisonous or disgusting species (Ruxton et al. 2018). A particular form of protective mimicry involves the resemblance to species that quickly flee away from the presence of predators, turning any predation attempt highly costly in energetic terms (van Someren and Jackson 1959, Lindroth 1971). This kind of mimicry is called "evasive mimicry" or "locomotor mimicry" (Ruxton et al. 2018). Ruxton et al. (2004) developed a mathematical model showing that evolution of evasive Batesian mimicry could be likely if pursuing evasive prey is costly for predators, if mimics are less frequently encountered than models, and if there are abundant alternative prey. Although plausible, unequivocal demonstrations of evasive mimicry in nature are still lacking.

The eminent naturalist Alfred Russel Wallace was the first to recognize that co-occurrence of mimics and models is the first requisite to support any mimicry hypothesis (Wallace 1867). In 2007, I recorded a mimic beetle and its model side by side (Fig. 1) in Brazilian mountaintop grasslands (43°33' W, 19°15' S, 1,300 above sea level). This beetle has an external coloration extremely

similar to flesh flies (Sarcophagidae), including species within the genera *Ravinia*, *Peckia* (*Euboettcheria*), and *Oxysarcodexia* (Vanin and Guerra 2012). The illusion made by colored scales forming two large reddish spots on each side of weevils' pronotum, resembling flesh flies' red eyes, is remarkable. There are also alternating light and dark stripes in the weevils' pronotum and elytra, whereas the latter half of weevils' elytra changes in color to resemble the transparent wings of a fly. Moreover, weevils mimic the stereotyped behavior of flesh flies while walking on the plant, even performing a typical fly display by scrubbing its legs (Video S1).

I sent some specimens to Sergio Vanin, a Brazilian taxonomist who found it to be an undescribed weevil species (Curculionidae, Conoderinae), later named *Timorus sarcophagoides* (Vanin and Guerra 2012). In the process, I learned that some Neotropical beetles have a striking coloration pattern and external morphology resembling flies that makes them some of the finest candidates for evasive mimics in nature (Hespenheide 1973). Mostler (1935) offered flies, including flesh flies (*Sarcophaga* sp.), to captive birds and found that they do not seem to be protected by unpalatability. Therefore, flies would comprise palatable albeit hard to catch prey, acting as the evasive models in this mimicry complex, which involves convergent/parallel evolution of color pattern among nearly 70 beetle species in six families (Hespenheide 1973, 1995). Allegedly, the adaptive significance of fly mimicry by beetles relates to deception of visually oriented predators, such as birds, which could recognize and avoid the high costs of capturing evasive flies (Hespenheide 1973). Hespenheide suggested this mimicry as Müllerian, assuming that beetles would be as quick and elusive as flies. Nevertheless, the natural history of fly-mimic species is virtually unexplored and hypotheses concerning the evolution of fly mimicry by beetles remain largely untested.

*Timorus sarcophagoides* is a highly specialized phytophagous weevil living exclusively on the mistletoe *Psittacanthus robustus* (Loranthaceae; Vanin and Guerra 2012). From May 2008 to April 2009, I monitored 78 adult mistletoe plants on a monthly basis to examine the occurrence of flesh fly mimics and its relationship with plant phenology. The weevil has an annual life cycle with the mimic adult stage synchronic with mistletoes' flowering peak, mostly from November to January (Fig. 2A). Because the adult stage is so brief, a weevil's ability to mimic an evasive prey could be crucial for its survival and reproduction. This must be especially true since mimic weevils occur during the wet and hot season, when selective pressures could be intensified during the breeding period of their potential predators (Poulin et al. 1992). Moreover, this period could also correspond to the period



FIG. 1. The weevil *Timorus sarcophagoidea* (bottom right) and its flesh fly model (top left) sharing microhabitat, a clear example of mimic and model co-occurrence in nature. In detail, the remarkable resemblance between the mimic weevil and a flesh fly model. Photos: Tadeu J. Guerra.

of increased abundance of alternative prey, favoring the evolution of evasive mimicry (Ruxton et al. 2004). Whereas weevil occurrence seems highly restricted in space and time, the short-lived flesh flies seem to be widespread in the vegetation, being commonly observed throughout the year in the study site. Consequently, predators' encounters with flesh fly models could be much more frequent than with mimic weevils, another circumstance expected for evolution of evasive mimics (Ruxton et al. 2004). This would allow predators to learn that pursuing prey items with color pattern exhibited by flesh flies might involve high costs for them (Gibson 1974).

I also examined microhabitat use and adult weevil behavior, by tagging and monitoring six individuals in January 2009. I recorded each individual's behavior and the location on host plants during 10-s scan observation in 5-min intervals, totaling 13 h of observation (156 recordings) during daylight and 6 h (72 recordings) during the night. During nocturnal observations, all weevils were motionless underneath the mistletoes' leaves. During the day, they were active most of the time (Fig. 2B), although they spent considerable time motionless on the mistletoe's roots, shoots, and leaves (~44%). Active weevils often walked along the entire plants (25%) or fed on flower buds (~21%), less frequently ovipositing on roots (~7%) and eventually performing fly displays (~3%). Weevils spend 14 min on average feeding on single flower buds (range 11–20,  $N = 6$ ). Feeding behavior consisted of inserting the long rostrum into mistletoe tissues, remaining virtually still on the spot, chewing contents using gentle up and down movements of the head. The same occurs when females

oviposit, as they insert the entire rostrum to pierce holes in the mistletoe's root before placing egg masses. Females may spend up to 25 min piercing the mistletoe root before ovipositing.

These observations on the natural history of *T. sarcophagoidea* have important implications for understanding the adaptive significance of flesh fly mimicry. First, mimics are diurnal and their resemblance involves conspicuous coloration, therefore their dupes are probably diurnal visually oriented predators, such as birds. In fact, most bird species occurring in the study site are foliage-dwelling insectivores (Costa and Rodrigues 2012) and could comprise the selective force driving evolution of evasive mimics. Second, weevils spent considerable time feeding on mistletoe's inflorescences, a markedly contrasting background. Likewise, weevils become an easy target for visual hunters since they cannot quickly disengage the rostrum from the mistletoe's buds or roots. While mimic walking is relatively quick for a beetle, it is not a hard task for predators to grab them, especially while feeding or ovipositing. I collected by hand all the weevil specimens directly from host plants. On the other hand, I found the flesh flies virtually uncatchable, and I tried many times. Therefore, it is likely that this putative case of evasive mimicry is Batesian rather than Müllerian as suggested by Hespenheide (1973), with the nonevasive weevils enhancing their survivorship by mimicking a true evasive model.

Central to demonstrating evasive mimicry in nature is confirming that predators avoid flesh flies because they are too difficult to capture, not for another reason, such as distastefulness or noxious effects. However, what flesh fly species match the size and coloration pattern exhibited

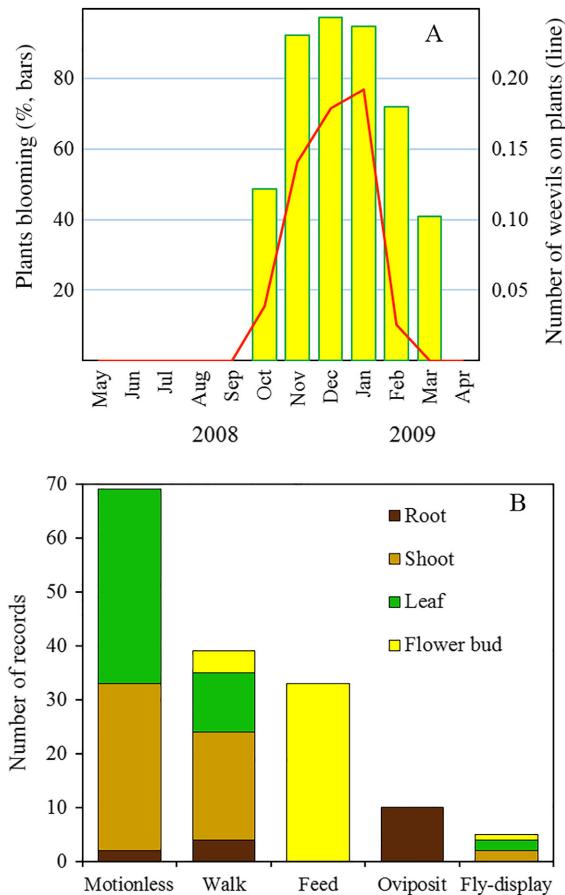


FIG 2. (A) Abundance of adult weevils matching mistletoes' blooming period along the year (values are means). (B) Frequency of behaviors and microhabitats used by six mimic weevils observed during the daylight.

by mimic weevils? Are they true evasive models? Do birds exert the selective pressure favoring evasive mimicry evolution? Could they recognize flesh flies as hard to catch prey and avoid attacking them? Do fly traits copied by *T. sarcophagoides* actually enhance weevil survival by fooling avian predators? To demonstrate if this is a genuine evasive mimicry play or not, it will be necessary to perform field experiments manipulating weevils' coloration pattern to assess their survival, as well as experiments offering both red-eyed flesh flies and mimic weevils to potential predators. Moreover, field experiments using plasticine replicas of weevils placed on their microhabitat (e.g., Pfennig et al. 2001) could be used to test the idea that adaptive significance of flesh fly mimicry relates to selective pressure exerted by avian predators.

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