

Scientific Note: Caterpillar mimicry across orders: Pine sawfly larvae as a possible model for an *Erythrina* Leafroller caterpillar, *Agathodes monstralis* (Lepidoptera, Crambidae)

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Abstract: While caterpillars are under huge selective pressure from predators and are frequently chemically protected, very few cases of caterpillar mimicry have been formally described in the scientific literature compared to the mimicry complexes found in adult Lepidoptera. Nevertheless, caterpillar mimicry may be common, so possible mimicry complexes should be described and, when possible, investigated. Here, it is proposed that caterpillars of the Redheaded Pine Sawfly, *Neodiprion lecontei* (Hymenoptera, Diprionidae), are chemically defended co-mimics with a crambid caterpillar, *Agathodes monstralis* (Lepidoptera, Crambidae), with which they are found in the same habitat in eastern United States. While both species are chemically defended, based on differences in behavior (open gregarious feeding for the sawfly larvae and concealed solitary feeding in the moth caterpillar), this mimicry complex is likely to be quasi-Batesian (both contribute to aposematic signal, albeit unequally). This mimicry hypothesis is supported by the strong phenotypic similarity between the larvae of the two insect taxa discussed here, and the obvious divergence in *Agathodes monstralis* in comparison with congeners outside the sawfly's range.

First described by Bates over a century ago (Bates, 1862), mimicry in Lepidoptera continues to contribute as a remarkable phenomenon for understanding mechanisms of evolution. For instance, characterization of microhabitat niches during field research (e.g., Willmott *et al.*, 2017) led to understanding of how distinct mimicry complexes and bird predators might partition habitats within a forest. Modern CRISPR work, such as gene silencing, allows researchers to dissect the formation of color patterns in mimetic butterflies, showing that congeneric co-mimics arrive at similar wing patterns using different developmental pathways (Concha *et al.*, 2019).

While there are numerous well documented mimicry complexes among adult Lepidoptera, there are less than two dozen caterpillar mimicry complexes that have been described in the scientific literature (Willmott *et al.*, 2011 and references therein). This is likely not as much due to the lack of mimicry complexes among caterpillars, but because they are rarely reported. For instance, Janzen *et al.* (2010) described eye-spot bearing caterpillars and pupae of tropical Lepidoptera as a “horde of counterfeit predator eyes.”

In their pursuit of understanding the mechanisms of convergent evolution, developmental biologists may want to turn their attention from well-known mimicry systems, such as those found among butterflies (e.g., Beccaloni, 1997), to immature stages, since the latter may provide amazing revelations. For instance, recent work has shown that the integument of a geometrid caterpillar can sense the color of its surrounding and change its color accordingly to fit the background (Eacock *et al.*, 2019).

When it comes to mimicry complexes involving caterpillars, they don't have to involve the same developmental

stages or even the same orders of insects. For instance, a larva of a species from one family, *Pryeria sinica* Moore, 1877 (Zygaenidae), may mimic a pupa of another species from a different family - *Ivela auripes* Butler, 1877 (Lymantriidae), as was recently described by Yazaki *et al.* (2019). An aposematic caterpillar can also be a co-mimic of the adult stage of the same species with which they co-share habitat, color pattern and defensive compounds, as had been proposed by Scott (2016) and Sourakov (2016) for the geometrids (Geometridae) *Meris alticola* Hulst, 1896 and *Abraxas grossulariata* (Linnaeus, 1758), and for the tiger moths (Erebidae) in the genus *Utetheisa* Hübner, [1819].

Pine Sawfly/Erythrina Leafroller mimicry

Humans frequently confuse Lepidoptera caterpillars with larval sawflies (Hymenoptera, Symphyta), and because sawflies are frequently gregarious and chemically defended, it is quite possible that they serve as models for some Lepidoptera caterpillars, as suggested by Willmott *et al.* (2011) for ithomiine butterflies. Here, I propose that the Redheaded Pine Sawfly, *Neodiprion lecontei* (Fitch, 1859) (Hymenoptera, Diprionidae) (Fig. 1B), a species of commercial importance that defends itself by regurgitating substances sequestered from pine needles and feeds gregariously, is a model for caterpillars of *Agathodes monstralis* Guenée, 1854 (Crambidae). The sawfly can become quite prominent, especially during outbreaks (DeBerry, 2014), and has been described as a pest of many pine species, especially while they are less than 5 m tall, including Longleaf Pine, *Pinus palustris* (Pinaceae).

In the understory of these pine trees grows Coral Bean



Figure 1. (A) Caterpillar of Erythrina Leaf-roller (*Agathodes monstralis*), a proposed mimic of the chemically-defended model, Redheaded Pine Sawfly (*Neodiprion lecontei*) larvae (B), which feed openly and frequently gregariously on Longleaf Pine and other pine species in south-eastern United States. Photos from Gainesville, Florida, USA.

Erythrina herbacea L. (Fabaceae), a plant defended from herbivores by a variety of alkaloids, but on which several Lepidoptera species, including *A. monstralis*, are specialists (Sourakov, 2012). The larvae of *A. monstralis* are very similar to those of the sawfly (Fig. 1A). It is very likely that this putative moth mimic of Redheaded Pine Sawfly is also distasteful due to traces of alkaloids, as has been demonstrated by liquid chromatography (Sourakov *et al.*, unpublished), and hence this system may be a case of quasi-Batesian mimicry, in which both species contribute to the aposematic signal, though unequally.

In support of the mimicry hypothesis, the caterpillars of other *Agathodes* Guenée, 1854, as well as the closely related crambid genera *Liopasia* Möschler, 1882, and *Terastia* Guenée, 1854, diverge, sometimes sharply, from the pattern displayed by *A. monstralis*, while maintaining their ecological association with *Erythrina*. For instance, the caterpillars of *Agathodes ostentalis* (Geyer, 1837) found in South-East Asia, India and Australia are dark-striped on a pale cream background with a black head, sometimes turning bright red as prepupae (Herbison-Evans & Crossley, 2021) resembling other sawfly larvae, such as, for example, the European Pine Sawfly, *Neodiprion sertifer* (Geoffroy, 1785). The Redheaded Pine Sawfly (*Neodiprion lecontei*) is found in the eastern United States from the Great Lakes to Texas and Florida and, while the *Agathodes monstralis/A. designalis* species complex is distributed from southeastern United States to Argentina, *A. monstralis* is its northern member, and the caterpillar morphology in Central and South America begins to diverge, with caterpillar colored cryptically green rather than aposematically (Sourakov *et al.*, 2015; Pereira & Da Silva, 2013). Other closely related

Erythrina-feeding crambids that would not benefit from aposematism as they feed concealed inside pods or stems, such as *Terastia meticulosalis* (Guenée, 1854) (co-occurring with *A. monstralis*) or the South American *Liopasia ochracealis* (Walker 1865), are drab-colored (Pereira & Da Silva, 2013). These observations, together with the similarity and co-habitation between *A. monstralis* and Redheaded Pine Sawfly, are consistent with the idea that the color pattern of the former has been subject to selection to resemble the latter.

LITERATURE CITED

- Bates, H. W. 1862. Contributions to an insect fauna of the Amazon valley. Lepidoptera: Heliconiidae. *Transactions of the Linnean Society of London* 23: 495-566.
- Beccaloni, G. W. 1997. Ecology, natural history and behaviour of ithomiine butterflies and their mimics in Ecuador (Lepidoptera: Nymphalidae: Ithomiinae). *Tropical Lepidoptera Research* 8(2): 103-124.
- Concha, C., Wallbank, R. W., Hanly, J. J., Fenner, J., Livraghi, L., Rivera, E. S., Paulo, D. F., Arias, C., Vargas, M., Sanjeev, M., Morrison, C. 2019. Interplay between developmental flexibility and determinism in the evolution of mimetic *Heliconius* wing patterns. *Current Biology* 29(23): 3996-4009.
- DeBerry, S. 2014. Redheaded pine sawfly, *Neodiprion lecontei* (Fitch) (Insecta: Hymenoptera: Diprionidae). *Featured Creatures*, Publication Number: EENY-488. http://entnemdept.ufl.edu/creatures/trees/sawfly/redheaded_pine_sawfly.htm. Accessed 7 February 2021.
- Eacock, A., Rowland, H. M., van't Hof, A. E., Yung, C. J., Edmonds, N., Saccheri, I. J. 2019. Adaptive colour change and background choice behaviour in peppered moth caterpillars is mediated by extraocular photoreception. *Communications Biology* 2(1): 1-8.
- Herbison-Evans, D., Crossley, S. 2021. *Australian Caterpillars and their Butterflies and Moths* <http://lepidoptera.butterflyhouse.com.au/spil/ostentalis.html>. Accessed 7 February 2021.
- Janzen, D. H., Hallwachs, W., Burns, J. M. 2010. A tropical horde of counterfeit predator eyes. *Proceedings of the National Academy of Sciences of the USA* 107: 11659-11665.
- Pereira, C. M., Da Silva, P. R. 2013. Capacidade de predação de sementes de *Erythrina falcata* Benth. (Fabaceae, Faboideae) por larvas de três espécies de Lepidoptera-Crambidae e o efeito de parasitoides sobre a interação. *Biotemas* 26(4): 69-74.
- Scott, J. A. 2016. *Meris alticola* (Geometridae), a poisonous Müllerian mimic moth, and its co-mimic moths and *Euphydryas* and *Poladyras* butterflies (Nymphalidae). *News of the Lepidopterists' Society* 58(2): 100-101.
- Sourakov, A. 2012. On the biology of moths that feed on *Erythrina* in Florida. *Tropical Lepidoptera Research* 22(2): 110-118.
- Sourakov, A. 2016. On adult caterpillar mimicry: cases from the moth world. *News of the Lepidopterists' Society* 58(2): 97-99.
- Sourakov, A., Plotkin, D., Kawahara, A. Y., Xiao, L., Hallwachs, W., Janzen, D. 2015. On the taxonomy of the erythrina moths *Agathodes* and *Terastia* (Crambidae: Spilomelinae): Two different patterns of haplotype divergence and a new species of *Terastia*. *Tropical Lepidoptera Research* 25(2): 80-97.
- Willmott, K. R., Elias, M., Sourakov, A. 2011. Two possible caterpillar mimicry complexes in Neotropical danaïne butterflies (Lepidoptera: Nymphalidae). *Annals of the Entomological Society of America* 104(6): 1108-1118.
- Willmott, K. R., Robinson Willmott, J. C., Elias, M., Jiggins, C. D. 2017. Maintaining mimicry diversity: optimal warning colour patterns differ among microhabitats in Amazonian clearwing butterflies. *Proceedings of the Royal Society B: Biological Sciences* 284(1855): 20170744.
- Yazaki, H., Kishimura, M., Tsubuki, M., Hayashi, F. 2019. Müllerian mimicry between cohabiting final-instar larval *Pryeria sinica* Moore, 1877 (Lepidoptera: Zygaenidae) and pupal *Ivela auripes* (Butler, 1877) (Lepidoptera: Lymantriidae). *The Pan-Pacific Entomologist* 95(2): 83-91.