BRENESIA 16:213—219. 1979

#135

NATURAL HISTORY OF *PHELYPERA DISTIGMA* (BOHEMAN), CURCULIONIDAE, A COSTA RICAN DEFOLIATOR OF *GUAZUMA ULMIFOLIA* LAM. (STERCULIACEAE)

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Key Word Index: Coleoptera. Curculionidae. *Phelypera.* Ecology. Costa Rica.

ABSTRACT

The aposematic larvae of the medium-sized brown weevil *Phelypera distigma* feed exclusively on the new foliage of the sterculiaceous tree *Guazuma ulmifolia* in the deciduous forest Pacific coastal lowlands of Costa Rica. It has only one generation per year and appears to ignore new foliage that appears after the new adults appear after a developmental cycle of about a month. Three hypotheses are proposed as to why this apparent food source is ignored.

The primary leaf-eaters of the tree *Guazuma ulmifolia* Lam. (Sterculiaceae) in Costa Rica are the larvae of the hyperine curculionid beetle, *Phelypera distigma* (Boheman). Here I briefly describe the interaction between the beetle and its larval host as part of a habitat-wide study of the herbivores of lowland deciduous forest plants in Santa Rosa National Park in north-western Costa Rica (e.g., Janzen 1975). *P. distigma* is the only weevil larva among several hundred species of large larvae that do prominent damage to the foliage of deciduous forest trees in the Park. The natural history reported here applies specifically to the beetle populations in the Park but is generally representative of all the lowland deciduous forest on the Pacific side of Costa Rica.

In early May, shortly before the rains begin, adult *G. ulmifolia* put out new branches which continue to elongate, and thereby add leaves, for about three months. When the branch is only a few decimeters in length, female *P. distigma* glue a double row of about 20-25 tightly appressed shiny black eggs to the branch (mid-May). These hatch within about two weeks and the first instar larvae move as several small groups to nearby branch ends with new and nearly fully expanded leaves. They eat large holes out of the leaf blade and eventually consume nearly the entire leaf blade. A group stays together and moves on to other newly expanded leaves on the end of its branch and consumes a half to all of these leaves. Larvae do not feed on more than the terminal 3—5 newest leaves of a branch, but a group

usually finds enough food within these leaves on one branch for full development. There is usually only one group per branch end.

The larvae require between 1 and 2 weeks to reach full-size (for example, in 1977 most larvae were about half size by 11 June and the first cocoons had appeared; by 15 June, most of these larvae had spun cocoons).

They then spin loose silken cocoons in a mass on the underside of an intact leaf adjacent to the ones on which they have been feeding. They pupate on the day following the spinning of the cocoon, and emerge from the pupa 3–5 days later. The reddish-brown and slightly mottled adults (about 1 cm long and 6 mm wide) emerge from the cocoon about a day after eclosion. For the following 2 weeks, adults can be found eating small holes in the leaf blades of new foliage or hiding among overlapping leaves on the plant. They gradually change in color from rusty-red to mottled beige-brown with a few very dark spots. About this time they disappear from the *G. ulmifolia* plants. I have not encountered them in the habitat until the next May, 10–11 months later, despite having collected insects with sweep nets, Malaise traps, blacklights and observation in the site for the past 12 years. I can state with certainty that they do not go through further generations on the leaves of *G. ulmifolia* or any other plant in the habitat. They have never been observed to mate and I presume they do so later in the year.

Adult *P. distigma* have been collected from lowland subtropical México to Colombia (D. R. Whitehead, personal communication) and *G. ulmifolia* occurs over this range (Janzen 1975).

Abundance

P. distigma is one of the very common insects in the habitat at the time of its larval and pupal development. *G. ulmifolia* is one of the commonest trees in pastures, forest edge and all stages of woody plant succession. It is moderately common in hillside deciduous undisturbed forest. Every *G. ulmifolia* tree shows damage by *P. distigma* and a large crown of *G. ulmifolia* commonly contains 100 to 1000 small groups of *P. distigma* larvae or cocoons. Consequently, it is commonplace for a view through the edge of a *G. ulmifolia* crown to look like that in Figure 1. In addition to being numerically abundant, *P. distigma* larvae are also conspicuous. Wherever the leaves are damaged, the larvae or cocoons can be found on the underside of the nearest relatively intact leaf. The larvae are black with white flecks and various amounts of white and black frass stuck to them, and have black heads and sparse long black hairs. The clusters of cocoons are silvery white, looking like balls of fluffy cotton. A diligent collector can easily obtain 500 clusters of cocoons in an afternoon.

Parasites and predators

In 1973 I brought about 300 second-instar larvae of *P. distigma* into captivity and reared them through to adults in screen cages. Aside from apparent developmental failures, the only deaths were associated with three adult tachinid flies that emerged from three separate cocoons. In 1974 several hundred cocoon masses were roughly thrown in plastic bags and the beetles allowed to emerge; again, no parasites emerged. In 1977, 105 cocoon masses (3 to 10 cocoons each) at the pre-pupa stage and 154 cocoon masses at the pupal stage were hung in large plastic bags (easily done by stapling the cocoon-bearing leaves to a string and hanging the string in an inflated bag). One tachinid adult emerged from these cocoons and all the remainder produced adult beetles except about 1 percent that shriveled up and died. I have examined hundreds of cocoon masses in the field and have never seen pupae with apparent parasite exit holes in them (the pupae are visible through the loosely spun walls of the cocoon). I conclude from these observations that unless there are egg parasites or parasites that emerge from the adults several weeks after adult eclosion, the *P. distigma* population does not usually lose individuals to insect parasitoids.

The larvae of *P. distigma* rest in a tight cluster with their heads pointing outward (Figure 1), and this behavior seems to be an anti-predator stance among siblings. I have observed a large worker ant (*Pseudomyrmex gracilis*) attempt to extract a single worker from this mass, and eventually give up and wander off. I have also observed a worker ant of the same species grab and sting a single 8 mm long larva of *P. distigma* and carry it away. On three occasions I have observed a pentatomid bug with a large larva of *P. distigma* hanging from its probiscis while it sucked out the body fluids. I have seen no evidence of predation on *P. distigma* larvae or cocoons by birds, and have watched these animals enough so that I am confident that if such predation occurs, it is rare. The newly emerged adult beetles seem to be cryptically colored, though against the green leaves they are fairly conspicuous. I presume the brownish color has been selected with respect to the habitat in which they spend the 11 months between generations.

I fed newly emerged adults to six naive humans (June 1977) and all described them as tasteless or with a slight flavor of raw sweet-corn; the larvae had not been offered to vertebrates.

Based on the above observations, I suspect that the primary mortality of *P. distigma* is as young larvae from insect predators, and as adults at large in the habitat taken by arthropod and vertebrate predators.

Host plant interactions

G. ulmifolia produces further new leaves on the branch on beyond those attacked by *P. distigma.* I am struck by the absence of oviposition on these new leaves, since they appear to be at exactly the same developmental stage as those eaten by the

larvae only a few weeks earlier. There are at least three possible evolutionary explanations for this behavior, a behavior which I have also observed among the larvae of many moths and butterflies that feed on other deciduous woody plants in the same habitat.

By the time the first generation of *P. distigma* has emerged, the population of parasitoids and predators may have built up to a level whereby a female would produce more new adults by waiting until the beginning of the next rainy season than by ovipositing at this time. Owing to the apparent lack of parasitoids or severe predation on the *P. distigma* larvae, I find this a fairly unconvincing hypothesis.

Second, the new leaves produced on a branch on past the damaged leaves may have an elevated content of secondary defensive compounds (just as tomato leaves may elevate their content of protease inhibitors following feeding by a phytophagous beetle (e.g., Green and Ryan 1972, 1973 and Walker-Simmons and Ryan 1977). Therefore, while the leaves appear the same as those on which the larvae have just developed, they may be chemically quite different. However, even if *G. ulmifolia* does respond in this manner to defoliation, there are many branches on the trees whose leaves have not been attacked by *P. distigma* larvae; why don't the female beetles oviposit on the ends of these branches? For this reason I am again not convinced by this hypothesis, even if the tree does respond facultatively to damage.

Third, most of the crowns of *P. ulmifolia* observed in contemporary habitats are fully exposed to the sun and by the nature of the problems of visibility, it is the competition-free margins of these crowns that the biologist tends to notice. I suspect that the crowns of *P. ulmifolia* in closed-canopy forest produce a flush of new leaves and then no more, even around the margins. In this circumstance, most newly emerging adults would not be able to produce a second generation because the leaves are generally too old and no longer contain the low concentrations of certain secondary defensive compounds found in young leaves (in a manner analogous to the system described for oak leaves by Feeny 1970). This hypothesis can be tested and will be.

Acknowledgments

This study was supported by NSF grant DEB 77–04889, and in part by EARTHWATCH and The Center for Field Research of Belmont, Massachusetts. D. Janzen and G. Vega aided in collecting larvae of *P. distigma*. The cooperation and support of Santa Rosa National Park and the Servicio de Parques Nacionales de Costa Rica is very gratefully acknowledged. D. R. Whitehead identified the weevil. The study is dedicated to the baby birds that are going to die by being fed *P. distigma* larvae.

Resumen

Las larvas aposomáticas del gorgojo *Phelypera distigma*, de tamaño intermedio y de color café, comen exclusivamente las hojas nuevas del árbol *Guazuma ulmifolia* (Sterculiaceae) de los bosques caducifolios del Pacífico de Costa Rica. *Phelypera* tiene sólo una generación por año y parece que no da importancia a las hojas nuevas que emergen después de la llegada de adultos nuevos al final del ciclo de desarrollo de más o menos un mes. Tres hipótesis se proponen para explicar el rechazo del nuevo follaje como alimento.

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Figure 1. View through the crowns of two trees of *Guazuma ulmifolia* several weeks after attack by the larvae of *Phelypera distigma;* note production of new foliage distal to damaged leaves and lack of damage to oldest leaves on the branch.