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LARVAL BIOLOGY OF *ECTOMYELOIS MURISCIS*, (PYRALIDAE: PHYCITINAE), A COSTA RICAN FRUIT PARASITE OF *HYMENAEA COURBARIL* (LEGUMINOSAE: CAESALPINIOIDEAE)

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ABSTRACT

Ectomyelois muriscis (Pyralidae: Phycitinae) larvae mine in the pulp of mature and nearly mature fruits of *Hymenaea courbaril* (Leguminosae: Caesalpinioideae) in Costa Rica. The moth larvae are often associated with the attack of the seeds by *Rhinochenus stigma* (Curculionidae) weevil larvae, but do not themselves attack intact seeds. In Santa Rosa National Park (Guanacaste Province, northwestern Costa Rica), *E. muriscis* does not attack other species of plants and apparently has only one generation a year; it spends the other 10 months of the year as an adult waiting for the next fruit crop to ripen. The comparatively slow exit of *E. muriscis* adults from fallen *H. courbaril* fruits may be a relatively recent trait, allowed by the removal of the Pleistocene megafauna.

The fruits of many tropical trees are mined in by phycitine pyralid moth larvae. As part of a long-term study of the interaction of tropical trees with animals (e.g., Janzen 1970, 1976, 1980), I here document the natural history of the Costa Rican interaction between *Ectomyelois muriscis* Dyar (Pyralidae: Phycitinae) and the fruit of *Hymenaea courbaril* L., a large caesalpinaceous legume tree ("guapinol"). Detailed commentary on this particular interaction is offered here so as to be able to integrate it with the other ways that the fruit of *H. courbaril* interacts with animals (Janzen 1974, 1975, 1978, 1980, Janzen and Martin 1982, Whitehead 1976, Lewinsohn 1980). I first describe the interaction in Santa Rosa National Park (25 km south of La Cruz, northwestern Guanacaste Province, Costa Rica; 300 m elevation) and then include other parts of Costa Rica.

Ectomyelois muriscis in Santa Rosa National Park

Hymenaea courbaril flowers in the second half of the dry season (i. e., during March and April) and expands its green fruits to full-size within 1–2 months. About 8–9

months later (December–January) the fruit begins to ripen; this is indicated by solidification of the resins in the indehiscent thick fruit wall, change in color from green to brown, drying and sweetening of the pulp around the seeds, and hardening and darkening of the seed coats. At this time, an *E. muriscis* oviposits a clutch of as many as 20 eggs in the wall of the fruit. I suspect, but cannot demonstrate, that the eggs are placed in the hole cut in the fruit wall by the ovipositing female of a large weevil, *Rhinochenus stigma* (Linnaeus) (see below). The cream- to yellow-colored moth larvae enter the fruit and spend about a month mining in and eating the yellow semi-dry pulp in which the large hard seeds are imbedded (Figure 1). The larvae move freely about in the mass of silk and frass that they have deposited. There are generally 7 to 20 larvae in a fruit and they consume nearly all of the fruit pulp during their development. They do not mine into intact mature seeds.

About the time that fruit is fully mature and ready to fall from the tree as a form of presentation to earth-bound seed dispersers such as agoutis *(Dasyprocta punctata)* or Pleistocene megafauna, one or more of the larvae cuts an exit hole of 2 mm diameter through the very hard fruit wall, such that only a paper-thin layer of fruit epidermis still closes the exit. Then the larvae as a group form a mass of cocoons such that they are tightly packed side by side and with the head end of each pointed at the exit hole a few millimeters away (Figure 2). In several thousand fruits containing *E. muriscis,* I have never encountered other than one exit hole and one cluster of cocoons. Either non-sibs will pupate together, or only one moth oviposits in a particular fruit. About 2 weeks after spinning their cocoons, the moths emerge. The first one out pushes away the thin covering over the exit hole. They spread their wings outside of the fruit. Timing of emergence is such that the fruit is usually on the ground 1–3 weeks before the moths emerge.

The newly emerged adults disappear into the habitat and do not oviposit on *H. courbaril* fruits until the next fruit crop is of the appropriate age (10 months later, in December–January). I have opened samples of all the species of fruits at Santa Rosa which have fruits of a size and shape that could conceivably host *E. muriscis,* and never found the larvae of this moth. I therefore assume that just as do the other insects that feed on the fruits of *H. courbaril* at Santa Rosa, adult *E. muriscis* spend about 10 months of the year as active adults hiding in the vegetation while waiting for the next fruit crop to reach a susceptible stage.

In a pooled sample of several thousand fruits of *H. courbaril* from various trees and years from Santa Rosa (Janzen, unpublished) about 20 percent of those fruits which did not contain *Rinochenus transversalis* Chevrolat contained *E. muriscis; R. transversalis* is a large weevil whose larva mines through the fruit and eats a portion of each seed as well as nearly all the fruit pulp. The moth and this weevil were only very rarely found in the same fruit. I suspect that the weevil larva consumes or outcompetes the *E. muriscis* larvae, or more rarely, they do the same to it. *R. transversalis* occupies 10–50 percent of a fruit crop. In the same sample of fruits, about 80 percent of the fruits containing *E. muriscis* larvae also contained larvae or adults of *Rinochenus stigma.* In strong contrast to *R. transversalis, R.*

stigma larvae (as many as 12–15 per fruit) develop inside the seeds and emerge from them as adults. The adults then live in the indehiscent fruit, eating pulp. and seed remains there until the fruit is opened by a potential seed dispersal agent (Janzen 1974). By the time that the adult *R. stigma* emerge from the seeds, the *E. muriscis* have ususally already left the fruit. However, if the moths are still in the pupal (or even larval) stage, there is no indication that they are molested by the weevils. If there are *E. muriscis* larvae present in the fruit containing adult *R. stigma,* the moth larvae also feed on the remaining contents of the damaged seeds.

As a pre-dispersal seed predator, the effect of *E. muriscis* on *H. courbaril* is trivial. The larvae feed in the fruit pulp late enough in the ripening cycle such that the seeds are hard and independent of the parent plant, so their pulp-eating does not directly harm the seeds. If the *R. stigma* larvae have killed (mined into) only about half of the seeds (as is usually the case, in contrast with a *R. transversalis* larva, which usually kills all seeds), the remainder are not damaged by either the moth larvae or the *R. stigma* adults. However, once a fruit has fallen (been presented to dispersal agents), the presence of damage by *E. muriscis* may influence the fate of the surviving seeds. If no dispersal agent appears for several months, the moth exit hole is an easy access point for ants, termites and other insects which may either attack the seeds (not likely) or convert the fruit into a nest site. I suspect, but cannot yet demonstrate, that such conversion to nest sites renders the fruit uninteresting to the potential seed dispersal agents because both the bait (fruit pulp) is gone and the fruit smells (I suspect) like something other than a ripe fruit. However, if there is a high visitation rate by vertebrates, then I suspect that the fruit is taken before this can occur. When the fruit is newly abandoned by the adult moths, it still has the odor (to my nose) of a normal fruit; there may be substantial amounts of fruit pulp remaining in such fruits. These fruits are probably opened by agoutis in search of seeds to prey upon as well as to bury (in addition to fruit pulp), and it is these animals that release the *R. stigma* adults from the fruit. They also consume the weevils when they catch them. Their response to moth larvae is unknown. Fruits that have had *R. transversalis* larvae in them are marked by the large exit hole cut by the larva, have severely damaged fruit pulp, and generally offer no seed rewards; they are usually ignored by the agoutis.

Within the Park, where agoutis are common, there is a well-developed population of *E. muriscis* and the two weevils. Outside of the Park, where the habitat has been variously disturbed, this is not the case.

Outside of Santa Rosa National Park

Lowland Guanacaste Province (below about 400–500 m elevation), was once largely deciduous forest with patches and strips of evergreen forest along watercourses, and semi-deciduous forest in locally more moist sites. *Hymenaea courbaril* occurred throughout this vegetation type at elevations of about 100–400 m, with a few trees

higher and lower (in Puntarenas Province, to the south, and along the sides of the large valley from the city of Puntarenas nearly to San Jose, *H. courbaril* reached elevations of as much as 1200 m before most of the forest was removed by agriculture). At present, most of the Guanacaste portion of the *H. courbaril* range has been cleared for pastures and agriculture (or timber harvest); the few *H. courbaril* survivors in fencerows, riparian strips and open pastures still produce fruit crops. These fruit crops have *E. muriscis* in about 1 percent of the fruits; *R. transversalis* is commonplace (up to 30–90% of the fruits) and *R. stigma* is essentially extinct (about 1 out of 5000 fruits is attacked by this beetle, and I assume that such attacks are the work of females that wander out of the few forested areas where agoutis still open fruits). The low frequency of attack could be due to the fruits having few access points (oviposition holes cut by *R. transversalis?*) or be due to the moth population being low owing to habitat destruction.

H. courbaril is (was) a common tree in the coastal lowlands of Central America north to the lowlands of Mexico (e. g., Pennington and Sarukhan 1968). Samples of fruits collected from southern Chiapas to Costa Rica in 1976 had highly variable amounts of fruits that contained *E. muriscus* larvae and cocoons. The population of *H. courbaril* extends south from the vicinity of Puntarenas along the Costa Rican coastal plain. It is a common tree in the foothills along the Pan-American highway 2–15 km inland from Palmar Norte in southeastern Costa Rica; at this site *E. muriscus,* occupies a variable but small number of the fruits (field collections, 1976).

In the rainforests of Corcovado National Park (Osa Peninsula, southwestern Costa Rica), *H. courbaril* occurs in the foothills of the southern portion (Los Chiles, 200–400 m elevation) and *E. muriscus* occurs in a small percent of the fruits. Here it shares the fruit crops with *Rhinochenus janzeni* Whitehead as well as *R. stigma* and *R. transversalis* (see Whitehead 1976). The individuals of *E. muriscus* from Corcovado have a wingspread about 2 mm greater than do those of Santa Rosa, and appear to be heavier in body weight as well. The fruits of the *H. courbaril* from Corcovado are commonly, but not always, about 20–30 percent heavier than those at Santa Rosa.

I can confirm the Pacific coastal of Central America as part of the known range of *E. muriscis* (Haiti, Puerto Rico, British West Indies, Guatemala to Panama, Colombia, Bolivia, British Guiana, Frech Guiana, and Brazil, Heinrich 1956) but I suspect that this moth will disappear as the last *H. courbaril* are cut. Heinrich (1956) lists the large fruits of *Mammea americana* (Sapotaceae) and *Theobroma cacao* (Sterculiaceae) as hosts of *E. muriscis,* and there may be other large fruits suitable as hosts in Central American rainforests. While the fruit of *T. cacao* is superficially similar enough to that of *H. courbaril* (indehiscent, tough husk around a juicy pulp in a cavity filled with large seeds), I find it hard to believe that *E. muriscis* would develop in the solid single-seeded fruit of *M. americana.*

About 10,000 years ago, when much of the Central American Pleistocene herbivorous megafauna disappeared (Janzen and Martin 1982), I suspect that the

environment of *E. muriscis* changed dramatically. Once the large mammals whose mouths would have crunched up *H. courbaril* fruits were eliminated, the agouti would have been left as the usual animal to open the fruits. While the large mammals would have killed or severely disturbed the cocoon mass of *E. muriscis* by crushing the fruits, the agouti gnaws through the fruit wall and would often miss the mass (unless it sought the moth pupae as food). Second, with a full compliment of large mammals, I suspect that many of the *H. courbaril* fruits were picked up shortly after they fell, while in a forest where the agouti is the primary disperser, it usually takes months for the agoutis to get to all of the fallen fruits. At present *E. muriscis* therefore has much longer after fruit fall to feed and be a pupa. It would not be surprising to find that the moth has responded to this relaxation of selective pressure by taking longer to develop in the fruit than would have been the case in the Pleistocene and earlier.

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Resumen

Las larvas de la mariposa nocturna *Ectomyelois* (Pyralidae: Phycitinae) minan en la pulpa de los frutos maduros y casi maduros de *Hymenaea courbaril* (Leguminosae: Caesalpinioideae) o guapinol en Costa Rica. Las larvas están muchas veces asociadas con ataque de las semillas por las larvas del gorgojo *Rhinochemus sitgma* (Curculionidae) pero las larvas de la mariposa no atacan las semillas directamente. En el Parque Nacional Santa Rosa (Provincia de Guanacaste, noroeste de Costa Rica), *E. muriscis* no ataca otras especies de plantas y parece que pasan 10 meses del año como adultos, esperando que maduren los siguientes frutos. El comportamiento de salir despacio de los frutos después de caer del árbol es tal vez una característica más o menos reciente, es permitida por la falta de agentes de dispersión de las semillas del Pleistoceno.

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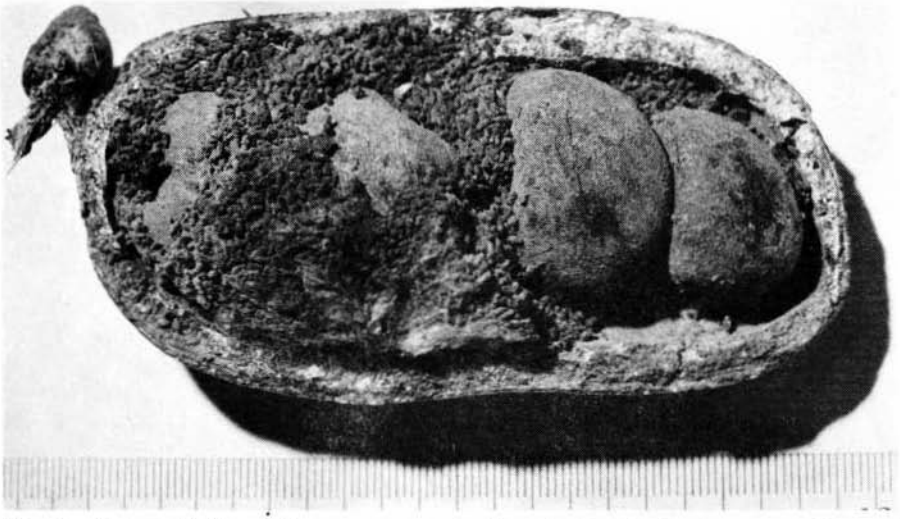

Fig. 1. Mature fruit of *Hymenaea courbaril* split lengthwise to expose frass of *Ectomyelois muriscis* (grainy material) and large seeds almost completely cleaned of fruit pulp by the feeding larvae (Santa Rosa National Park, Costa Rica).

Fig. 2. Mass of cocoons of *Ectomyelois muriscis* broken out of a mature fruit of *Hymenaea courbaril*. The moth exit hole through the fruit wall is visible as a hole cut through the fruit wall at the point of convergence of the cocoons (Santa Rosa National Park, Costa Rica).