Behavior of Adult and Larval *Platysoma cylindrica* (Coleoptera: Histeridae) and Larval *Medetera bistriata* (Diptera: Dolichopodidae) During Subcortical Predation of *Ips pini* (Coleoptera: Scolytidae)

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The most abundant predators of the pine engraver, Ips pini *(Say), include* Platysoma cylindrica *(Paykull) and* Medetera bistriata *Parent. We amended "bark sandwiches" with pine engravers and adult* P. cylindrica *and larval* M. bistriata, *and report observations on these endophytic predators. Adult* P. cylindrica *preferred adult prey, and appeared to be facultative egg predators, which contrasts with other Histeridae. The larvae of* P. cylindrica *fed on pine engraver larvae. Protection from predators is generally assumed to be an advantage of an endophytic life history, but we found that this predator exploited the herbivore's gallery architecture to facilitate prey capture. Larval* M. bistriata *also fed on pine engraver larvae. Immediate paralysis or death of the prey followed a strike with their tentorial rods. Such rapid immobilization, in conjuction with the glandular histology of* Medetera spp., *suggests that they use a toxin to arrest prey.*

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INTRODUCTION

Ips pini (Say) (Coleoptera: Scolytidae) reproduces in weakened pine trees and logging slash throughout North America (Thomas, 1961; Schenk and Benjamin, 1969; Gara *et al.*, 1999). Males select suitable hosts, construct subcortical nuptial chambers, emit aggregation pheromones, and mate with two or three females under the bark (Wood, 1982). Each female constructs one 5- to 25-cm ovipositional gallery that radiates from the nuptial chamber in a collective X- or Y-shaped pattern, generally with the grain of the wood. Males remain in the nuptial chambers for up to 3 weeks after mating to aid in frass clearing from female tunnels (Schmitz, 1972; Reid and Roitberg, 1994; Lissemore, 1997). Females lay eggs in evenly spaced niches along their galleries and pack small amounts of frass against the eggs (Schmitz, 1972). The larvae mine the sapwood upon eclosion. The brood pupate in oval chambers and chew through the bark to disperse following maturation feeding (Thomas, 1961). At high beetle densities, live trees may be colonized, making these insects chronic pests in plantations in the Great Lakes region (Schenk and Benjamin, 1969).

A relatively diverse complex of insects is associated with trees colonized by *I. pini*. In the Great Lakes region, the most prevalent predators are *Thanasimus dubius* (F.) (Coleoptera: Cleridae), *Platysoma cylindrica* (Paykull) (Coleoptera: Histeridae), and *Medetera bistriata* Parent (Diptera: Dolichopodidae) (Herms *et al.*, 1991; Raffa and Dahlsten, 1995; Aukema *et al.*, 2000a,b, 2004b; Ayres *et al.*, 2001). The chemical ecology of these predators has been studied in some detail. *Thanasimus dubius* and *P. cylindrica* exploit *I. pini* aggregation pheromones as kairomones (Mizell *et al.*, 1984; Herms *et al.*, 1991; Aukema *et al.*, 2000a,b). *Medetera bistriata* also likely exploits *I. pini* pheromones, as they arrive simultaneously with *I. pini* to trees undergoing colonization (Aukema *et al.*, 2003b) and are attracted to aggregation pheromones of other bark beetles, such as *Dendroctonus frontalis* Zimmermann and *Ips grandicollis* Eichhoff (Williamson, 1971). Responses by these predators may be mediated by host tree compounds (Williamson, 1971; Erbilgin and Raffa, 2000, 2001; Aukema *et al.*, 2004b). Predator impacts on *I. pini*, particularly those of *T. dubius*, have been studied at multiple levels of scale, from laboratory assays examining colonization events on the bark surface (Aukema and Raffa, 2004b) to studies at the tree (Aukema and Raffa, 2002) and plantation levels (Erbilgin *et al.*, 2002). We lack information, however, on the basic life history and feeding behaviors of most of these insects due to the cryptic, endophytic environments in which they feed and reproduce.

The feeding behavior and reproduction of *T. dubius* have been well characterized (Thatcher and Pickard, 1966; Mignot and Anderson, 1969;

Frazier *et al.*, 1981; Reeve *et al.*, 1996; Reeve, 1997; Aukema and Raffa, 2002). However, few observations have been reported for *P. cylindrica* and *M. bistriata*. *Platysoma cylindrica* are heavily sclerotized, approximately the size of *Ips* (∼1.2 mm wide and 4.5 mm long), and described either generally, as predators of bark beetles (Thomas, 1955; Moser *et al.*, 1971), or more specifically, as predators of eggs and larvae of flies and subcortical woodborers (Savely, 1939; Howden and Vogt, 1951; Dillon and Dillon, 1961; Kovarik and Caterino, 2002). The feeding behavior of members of the Histerinae, such as *P. cylindrica*, has not been described, despite suggestions that they may be important biological control agents of scolytids (Taylor *et al.*, 1992; Mazur and Ôhara, 2000). There is one report of *Platysoma punctigerum* LeConte feeding on adult *Dendroctonus brevicomis* LeConte and *Ips* spp. after these bark beetles laid most of their eggs, thus leading to the supposition of eggs as their primary substrate (Furniss and Carolin, 1977).

There are no records of either the feeding behavior or the impact on bark beetle reproduction for *M. bistriata*. Observations of *Medetera aldrichii* Wheeler in western North America indicate that the adults are predators of insects generally smaller than bark beetles. Females make short, rapid flight or hopping movements, foreward, backward and laterally, along the bole of the tree and oviposit into bark crevices, close to bark beetle entrance or ventilation holes (De Leon, 1935; Hopping, 1947). The larvae enter bark beetle galleries and prey on developing subcortical borers. Studies on *Medetera* spp. have suggested that these flies may be important biological control agents of scolytids (De Leon, 1935; Hopping, 1947; Johnsey *et al.*, 1965; Beaver, 1966; Fitzgerald and Nagel, 1972; Nagel and Fitzgerald, 1975; Ounap, 2001).

The objective of the present study was to observe the feeding behavior and impact of *P. cylindrica* and larval *M. bistriata* within host trees colonized by *I. pini*.

METHODS

I. pini were sourced from a bulk laboratory culture reared on white pine. *Platysoma cylindrica* were captured in a red pine plantation near Wisconsin Dells, WI, in funnel traps (Lindgren, 1983) baited with an entantiomeric ratio of 3(+):97(−)-ipsdienol released from polyvinyl bubble cap pheromone lures (Pherotech Inc., Delta, BC). Larvae of *M. bistriata* were harvested from white pine logs that had been colonized in the laboratory with *I. pini*, transported to the same plantation, and left exposed for approximately 3 weeks.

We adapted the "bark sandwich" technique for studying the life history of bark beetles and predators (Bedard, 1933; Reid, 1958; Borden, 1969;

Schmitz, 1972; Kinn and Miller, 1981; Taylor *et al.*, 1992). Squares of fresh inner bark of white pine, *Pinus strobus* L., measuring 12.5×12.5 cm, were placed between 15×15-cm clear Plexiglas plates. The squares were surrounded with strips of foam pipe insulation to allow moderate airflow yet prevent desiccation. The plates were clamped with 5-cm binder clips on each corner.

One male beetle was placed at the middle of an edge that ran perpendicular to the grain of the wood. The foam insulation was cut away at the male entrance point so the insects could clear frass from the galleries to the edge of the glass. One day later, two females per male were added. Male pine engravers sometimes rejected females by pressing their elytral declivity against the female head and backing out of the gallery, especially if the male nuptial chamber was not fully constructed (Schmitz, 1972). When this occurred, we reintroduced another female on the following day, thus typically establishing two females per male. Beetles mated, tunneled through the phloem, and laid eggs against the glass. The bark sandwiches were kept upright in a dark box to simulate the subcortical environment.

One adult *P. cylindrica* was added to each of 12 plates where the males had entered and constructed nuptial chambers. It is not possible to determine the sex of *P. cylindrica* without dissection (Mazur, 1999). Histerids were added on the seventh day following the addition of the female *I. pini*, to coincide with the latter stages of their arrival in the field and allow time for *I. pini* establishment (Raffa and Dahlsten, 1995; Aukema *et al.*, 2000b). Periodic observations were made over a 24-day period. *Ips pini* galleries were scored for length, the number of egg niches, and larvae that successfully hatched. Observations were recorded under a light microscope.

One *M. bistriata* larva measuring approximately 6 mm in length was added to each of 28 plates close to the bark beetle entrance, 8 to 10 days after gallery initiation by *I. pini*. The larvae were inserted between the phloem and the glass after creating a small space for each insect by compressing the phloem with a needle. We used larvae 6 mm in length, as smaller larvae are typically killed during log dissections. *Medetera bistriata* larvae are soft-bodied, and only 13 of 28 larvae survived this implantation process. The fly larvae were observed over a 23-day period as they moved over the phloem and ate bark beetle larvae.

The effects of *P. cylindrica*, *M. bistriata*, and initial *I. pini* egg density on the mortality of *I. pini* immatures were examined using regression models in R, the open-source implementation of S-Plus (Ihaka and Gentleman, 1996). The initial egg density of *I. pini* was ln-transformed to normalize the data. Assumptions of each model, such as homogenous variances, were evaluated by visual inspection of residual plots. A comparison of mortality in plates with vs. without larval *P. cylindrica*, which appeared in some plates (see Results),

was performed on arcsin($\sqrt{y}$) transformed data with an independent two-sample *t* test, assuming equal variances, using $\alpha = 0.05$.

RESULTS

P. cylindrica

Male *I. pini* exhibited defensive behaviors against entering *P. cylindrica* adults and successfully blocked the entrance of 3 of 12 predators into their nuptial chambers. Defensive responses were similar to those noted for rejecting females (Schmitz, 1972). The male would back against the entrance and press its elytral declivity against the head of the *P. cylindrica*. If the histerid gained entrance to the gallery, a pushing match would ensue. *P. cylindrica* were often able to push past the male once inside the gallery, as the diameter of the nuptial chamber, ∼0.6 cm (Schmitz, 1972), is much wider than these predators.

Once inside the gallery, the histerids would open their mandibles and continue pushing past the male to enter a female ovipositional gallery. During gallery elongation, the female uses her elytral declivity as a scoop to push frass down the gallery to the nuptial chamber where the male clears it from the tree (Schmitz, 1972). As such, females were often oriented away from the nuptial chamber. When an adult histerid contacted a female pine engraver, the insects would push against each other or the female would move quickly to the terminal end of the gallery, followed closely by the histerid. The histerid, with mandibles open, would pin the *I. pini* against the gallery wall for up to 60 min. In such confined circumstances, the histerid would clamp its mandibles on any accessible *I. pini* parts. Sometimes the two locked insects would rotate in a spiral motion. *Platysoma cylindrica* would sometimes move under the ventral surface of the female and clip off her legs. We more often observed the histerid squeezing over the dorsal surface of the female and prying apart the elytra. The histerid would slide one or both heavily sclerotized mandibles under the elytra into the wings, and ultimately the abdominal and thoracic cavities, as the pine engraver was killed. Feeding behavior was difficult to observe directly, as these histerids often probed their heads into the body of the insect.

Male pine engravers also would be killed, sometimes after the female was eaten, but not always. Males were easiest to kill if they had constructed a short tunnel from the nuptial chamber, as they sometime do in advance of female introduction (Schmitz, 1972). In one instance, the histerid did not kill the male, but pushed it out of the nuptial chamber and plate after clipping its legs in a ventral attack.

In two of four plates, *P. cylindrica* cleared frass plugs up to 2 cm in length in the ovipositional galleries, within 48 h, before killing the females. In these plates, the males had either left the galleries shortly after introduction of the females or died. The histerids would grasp the frass with their mandibles, back down the ovipositional gallery to the vacated male nuptial chamber, and deposit the frass. In the two plates where they did not remove the frass plugs, the histerids rested in the galleries in advance of the plugs. In addition to frass clearing, the histerids would clean the pine engraver galleries of sclerotized insect parts such as elytra and head capsules, which were not consumed. These parts would be grasped with the mandibles and dragged the length of the gallery to the male nuptial chamber or be pushed outside of the plate.

Adult *P. cylindrica* demonstrated facultative egg predation after adult *I. pini* were consumed. Overall, they consumed 64.7% of the eggs in an *I. pini* gallery system. There was no relationship between the number of eggs consumed (12.3 ± 5.9SD) and the number that were available (19.0 ± 4.4) ($F_{1,6} = 0.74$, $P = 0.42$). Larvae that had begun to mine away from the ovipositional gallery were safe from adult *P. cylindrica*. These larvae were typically at the proximal end of the gallery, as female *I. pini* commence oviposition there.

In five of the plates, larval *P. cylindrica* appeared within 17 days of the addition of the adults. Four plates contained one larva, and one contained three larvae. Larval *Platysoma* spp. are dorsoventrally flattened, which facilitates crawling in the subcortical habitat, and they develop rapidly through only two instars (Kovarik and Caterino, 2002). Larvae appeared to wander relatively indiscriminately through the subcortical environment, and had more room to search for prey as *I. pini* larvae mined the limited phloem within the plates. Larvae of *P. cylindrica* would prey on both *I. pini* larvae and pupae by closing their pincer-like mandibles on their much softer prey (Fig. 1A). Similar to adult feeding, the larvae would often enter the body cavity of their prey while feeding (Fig. 1B). Although we were able to rear many *I. pini* through pupation to adults in these plates, we were not able to rear any *P. cylindrica* to adult stages. This likely reflects *P. cylindrica*'s longer development time, which exceeds the period for which phloem sandwiches remain fresh. The average generation time of *P. cylindrica* is 59 days, although they may emerge in as little as 35 days (Aukema *et al.*, 2004a).

There was a 1.5 × increase in percentage mortality (number of initial *I. pini* eggs minus number of surviving pupae, divided by number of eggs) when at least one larval *P. cylindrica* was present in the plate, compared to the controls ($t_{10} = 2.48$, $P = 0.0328$). Plates with *P. cylindrica* larva(e) had mortality rates of $51.3 \pm 9.8\%$ (SE), while plates without predator offspring had mortality rates of $20.1 \pm 7.9\%$. Predation occurred
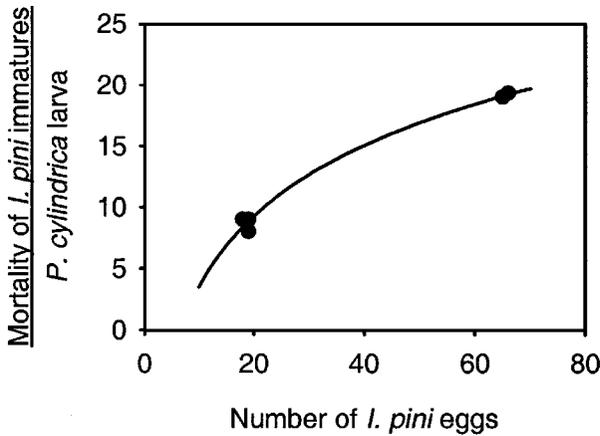
A

B

Fig. 1. Larva of *P. cylindrica* preying on pupa of *I. pini*. (A) *Platysoma cylindrica* larva pushing through frass to enter *I. pini* pupal chamber. (B) *Platysoma cylindrica* larva feeding inside dorsal region of head of *I. pini* pupa.

Fig. 2. Mortality of *I. pini* immatures that survived predation by adult *P. cylindrica* per larval *P. cylindrica* at different *I. pini* egg densities. Morality was calculated as the number of eggs minus the number of pupae.

in a density-dependent manner (Fig. 2; $y = 8.35\ln(x) - 15.746$; $R^2 = 0.99$, $F_{1,3} = 351.74$, $P = 0.0003$).

M. bistriata

Medetera bistriata behaved in a manner similar to *M. aldrichii* in these bark sandwiches (Nagel and Fitzgerald, 1975). The predators compressed dorsoventrally and crawled over the phloem as they squeezed against the Plexiglas covering. They seemed to orient toward mining prey and did not necessarily travel through the larval frass.

Medetera bistriata larvae would cautiously approach the pine engraver larvae but not always attack, perhaps to avoid the mandibles of their prey (Nuorteva, 1959). Although scolytid larvae have sharp mandibles for tearing phloem, we did not observe any *M. bistriata* larvae injured by their prey, perhaps due to their greater motility. Similar to *M. aldrichii*, attacks were made by forcefully thrusting their tentorial rods forward, forcing the anterior tip of the median piece forward and upward against the mandibular hooks working down and outward (De Leon, 1935). This quick strike ruptured the cuticle and rendered the prey immobile. The predators tended to sometimes kill two or three pine engraver larvae in an immediate area before returning to feed. Feeding occurred by inserting the tentorial rods and head through the integument of the prey and sucking its fluids. Only the head capsule and outer integument of the prey larvae remained after feeding.
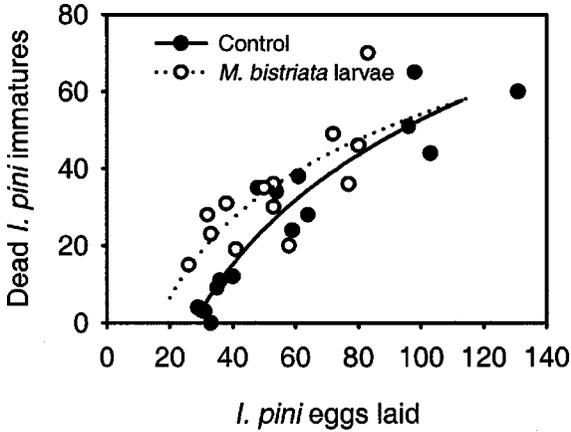
Fig. 3. Effect of the presence of *M. bistriata* larvae on the number of *I. pini* that die between egg and pupation life stages at different *I. pini* egg densities. Line of best fit for control (dashed line) is $y = 40.98 - 136.05\ln(x)$; $R^2 = 0.89$, $F_{1,13} = 108.07$, $P < 0.0001$. Line of best fit (solid line) for *M. bistriata* is $y = 29.61 - 82.24\ln(x)$; $R^2 = 0.58$, $F_{1,11} = 15.09$, $P = 0.0025$.

The mortality to *I. pini* immatures (i.e., the number of teneral adults minus the number of eggs) with and without *M. bistriata* larvae present is shown in Fig. 3. The greatest impact of *M. bistriata* larvae (the difference between the curves) occurred at the lowest *I. pini* egg densities. The eventual convergence of the relationships in Figure 3 suggests that at high *I. pini* densities, *M. bistriata* may have been eating *I. pini* immatures that would have otherwise been lost to intraspecific competition anyway.

DISCUSSION

Preference for adult prey by *P. cylindrica* represents an unusual behavior among histerids. Feeding on larvae is more typical, and Carlton *et al.* (1996) state that the only records of adult predation are of *Psiloscelis opacus* (LeConte) feeding on adult ants and the Chilean saprinine *Euspilotus bisignatus* (Erichson) feeding on the head contents of adult blow flies. An endophytic life history strategy is generally thought to provide herbivores some measure of protection from predators relative to an exophytic life history (Hawkins *et al.*, 1997). In this system, the restricted opening of the nuptial chamber facilitates defense by male pine engravers against *P. cylindrica* access. Female pine engravers may construct ventilation holes, which could provide alternate access. However, such holes are generally not

constructed until the gallery has been elongated, during which time the primary kairomonal attraction of *P. cylindrica* has ceased (Raffa and Dahlsten, 1995). Although paternal care is not the norm among insects (Zeh and Smith, 1985), pine engravers have been previously noted to defend their gallery systems against intrusion by egg and larval predators and parasites such as *Corticeus* spp., *Lasconotus* spp., and *Roptrocerus xylophagorum* (Ratzeburg) (Bushing, 1967; Reid and Roitberg, 1994). However, the gallery architecture of *I. pini* also facilitates predation by *P. cylindrica*. These predators use the walls of *I. pini*'s tunnels to trap and pin their prey. In contrast, adult *P. cylindrica* do not attack adult *I. pini* when placed in an open arena, such as a petri dish, or even a more narrow container such as a collecting vial.

The killing action of *M. bistriata* strongly suggests the use of a toxin. After being struck, prey ceased moving immediately. This behavior was also noted when they attacked late-instar larvae of another subcortical borer, *Monochamus* spp. (Coleoptera: Cerambycidae), in holding containers while initiating these experiments. *Monochamus* spp. larvae are much larger than *M. bistriata* larvae but, like pine engravers, ceased all movements after being attacked. It seems unlikely that such rapid paralysis could be due to mere mechanical injury. Moreover, morphological studies on *M. aldrichii* indicate two distinct enlargements of the salivary glands in segments 4 and 8, four times the diameter of the rest of the glands. The contents of these segments stain blue and red, respectively, with Delafield's hematoxylin (De Leon, 1935). The anterior segment appears to have a fibrous texture, while the posterior enlargement has large hexagonal epithelial cells with large nuclei (De Leon, 1935). These morphological observations, combined with the rapid immobilization of the prey, suggest the use of a neurotoxin, perhaps a peptide, during predation.

Both *P. cylindrica* and *M. bistriata* appear to be good candidates for the biological control of *I. pini*. Field experiments have shown that *P. cylindrica* are attracted to *I. pini* pheromones, which would be useful in predator augmentation (Raffa and Dahlsten, 1995; Aukema *et al.*, 2000b). Moreover, this insect feeds on all life stages of *I. pini*. They have also been observed arriving at trees colonized solely by *Dendroctonus frontalis* Zimmermann (Moore, 1972) and may be useful predators of these scolytids as well. Although they can clear small amounts of frass from *I. pini* galleries, we lack data on their effectiveness in egg galleries of *Dendroctonus* spp., which leave copious resinous frass perhaps to impede predators (Reid and Roitberg, 1994).

Additional information is needed to extrapolate these results to the field. For example, mortality by *M. bistriata* may be overestimated by our use of later-instar larvae. Conversely, it may be underestimated by our deployment of lower numbers of flies (0.64 larva/dm^2) than occur in nature

(1.1 larvae/dm^2 within trees; 0.7 adult female/dm^2 bark surface) (De Leon, 1935; Hopping, 1947), the lower prey availability in our assays (0.64 male, 0.64–1.28 females/dm^2) than in the field (1 male, 2 females/dm^2) (Robins and Reid, 1997), and the loosening of bark in infested trees rather than bound Plexiglas, which facilitates predator movement (Savely, 1939). In natural settings, a diverse assemblage of other fauna is also present within hosts colonized by *I. pini* (Aukema *et al.*, 2004b), rather than single predators. Predation by *M. bistriata*, for example, may be enhanced by adult *P. cylindrica* removing frass plugs, or conversely, these predators may eat each other and thereby reduce their impact on subcortical herbivores. Multiple predator studies with *P. cylindrica* and *T. dubius*, however, have indicated an absence of complex density-dependent interactions in this predator species pair when examining effects on prey, with their combined effects being predominantly additive (Aukema and Raffa, 2004a; Aukema *et al.*, 2004a).

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