Resource Partitioning among Parasitoids (Hymenoptera: Braconidae) of Phoracantha semipunctata in Their Native Range


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The Eucalyptus longhorned borer, Phoracantha semipunctata (F.), is native to Australia, but it has been introduced without its natural enemies into many parts of the world in which its Eucalyptus spp. host has been planted. The beetle has developed large populations in these novel habitats and has been responsible for the mortality of large numbers of trees. Although there is a considerable catalogue of the parasitoids of the beetle in Australia, limited ecological information on the assemblage of parasitoids attacking P. semipunctata is available. We removed bark from 40 felled trees, recorded gallery width and bark thickness over parasitized larvae, and removed all parasitoids. Adult size, sex, and species were recorded when the parasitoid pupae eclosed. Syngaster lepidus Brullé, Jarra phoracantha Austin, Quicke, and Marsh, J. maculipennis Austin, Quicke, and Marsh, and J. painei Austin and Dangerfield were most commonly collected. The solitary parasitoid S. lepidus preferred smaller larvae than did the gregarious J. arra spp. The two species with shorter ovipositors, J. maculipennis and J. painei, parasitized larvae under thinner bark than did the other two species with longer ovipositors. There was a significant positive correlation between host larval size and number of parasitoid pupae of the gregarious species. Also, there was a significant positive correlation between host larval size and parasitoid adult size. The ecological relationships between this assemblage of parasitoids and their beetle host may be useful in establishing an effective biological control program.

Key Words: solitary parasitoid; gregarious parasitoid; Cerambycidae; Braconidae; resource partitioning; biological control; Phoracantha; Jarra; Syngaster; Eucalyptus.

INTRODUCTION

The Eucalyptus longhorned borer, Phoracantha semipunctata (F.), is distributed throughout the six biogeographical regions of Australia (Wang et al., 1996), where it colonizes Eucalyptus L'Héritier and Angophora Cav. spp. (Duffy, 1963). Females lay eggs on the bark surface, frequently under loose bark (Drinkwater, 1975). Newly eclosed larvae mine through the outer bark and feed extensively in the cambium, phloem, and outer xylem tissues (Hanks et al., 1993a). In its native range, beetles utilize broken branches and weakened or downed trees for larval development (Tooke, 1935; Chararas, 1969).

Eucalyptus spp. have been widely planted throughout the world as a commercial source of cellulose, fuel, and timber or as ornamental trees. P. semipunctata has been accidentally introduced into many of these regions and has become a significant mortality factor for the trees, particularly in regions with Mediterranean climates (Bytinski-Salz and Neumark, 1952; Chararas, 1969; Drinkwater, 1975; Ivory, 1977; Cavalcaselle, 1980; Cadahia, 1986; Gonzalez-Tirado, 1986; Hanks et al., 1993a, 1995a). It has been recognized previously that adult beetles are attracted to cut logs and to stressed trees in these novel environments (Drinkwater, 1975; Ivory, 1977; Gonzalez-Tirado, 1986). Trees that appear to be healthy and growing rapidly are colonized by the beetles at densities sufficient to destroy the cambium tissue, resulting in the death of the host, suggesting that trees are capable of vigorous growth even under stressful conditions that favor beetle attack. Consequently, the evaluation of tree stress and susceptibility to beetle-caused injury is very difficult. Trees are capable of surviving high levels of moisture stress in the absence of the beetle (T.D.P., pers. obs.), but introduction of the beetle combined with moisture stress has created a significant mortality risk to the trees. However, Hanks et al. (1991b) demonstrated that high bark moisture content is a
significant factor in the resistance of the tree to beetle infestation.

As with many other arthropods, many factors may function to regulate the density of P. semipunctata populations. Competition among larvae (Ivory, 1977; Mendel et al., 1984; Mendel, 1985; Haddan and Fraval, 1988), environmental conditions (Hanks et al., 1991a), host tree susceptibility (Hanks et al., 1991b, 1995a), and host tree suitability (Hanks et al., 1993b) have been examined as mortality factors in geographic locations where both the trees and the beetles are introduced species. However, because the insect has not been a significant problem in Australia (Duffy, 1963), there has been little work on population dynamics in its native range.

Natural enemies have been long recognized as critical factors in the regulation of insect populations within ecological communities (e.g., Hairston et al., 1960). Whereas the limitations on beetle population growth imposed by the relations between the insect and their host trees may be similar in the introduced and native ranges of the insect, the mortality caused by natural enemies in Australia also may be critical in regulating the population and limiting its pest status. Several important taxonomic studies have described the parasitoid species that utilize P. semipunctata as a host (Austin et al., 1994; Austin and Dangerfield, 1997); however, the ecological interactions among the assemblage of parasites exploiting the beetle as a resource are not well understood. For the purposes of introducing natural enemies for biological control, it may be useful to understand the relationships among parasitoids and their hosts in the native range so that the efficacy of introductions into new environments can be optimized for maximum regulation of target host populations. The objectives of the research presented here were to determine (1) parasitism levels by an assemblage of species in one region of Australia and (2) partitioning of resources among parasitoid species and sex allocation within species, as a function of larval host size and tree bark thickness. These data also provide a benchmark of information that will be necessary for evaluation of the success of the introductions in the new geographic range.

MATERIALS AND METHODS

Four E. globulus Labill. and E. nitens (Deane and Maiden) Maiden plantations (Amcor Plantations Proprietary Limited) growing within a 40-km radius of Morwell, Victoria, Australia were used as study sites. All trees within a plantation were planted in a single year, and all the plantations were established between 1971 and 1973 as part of provenance trials for future selection of genetic material based on pulping quality of the wood fiber. Ten trees at each site were felled at the end of November 1995 to obtain small wood samples to test cellulose and pulping characteristics. The remainder of each trunk was left on the ground at the site.

The felled trees were sampled between 20 and 31 May 1996. All of the felled trees had been infested by P. semipunctata, and if the borer larvae had been parasitized, development of the parasitoid had reached the late larval or pupal stages. Bark was removed from the entire infested portion of the trunk of each tree to expose the parasitized beetle larvae. Parasitoid larvae or pupal cocoons were collected and placed into separate vials for each individual host larva. The width of the host larval gallery, the bark thickness covering the gallery, the date, and the collection site were recorded on each vial.

The braconid wasps that use P. semipunctata as hosts are idiobiont parasitoids. Ovipositing female wasps inject a paralyzing venom into the host larvae prior to oviposition, halting further growth or feeding by the larva. Thus, the larval gallery at the time of parasitization provides a permanent record of host larval size, even though the larva may have been totally consumed by the developing wasp. A previous study conducted in Victoria had established that there was a strong correlation between the P. semipunctata larval length and the width of the larval gallery (Hanks et al., 2000). Consequently, terminal gallery width was used as an indication of host larval size to examine the preference of ovipositing parasitoid females.

The vials containing the parasitoids were sent by air to the quarantine facility at the Department of Entomology, University of California, Riverside. The vials were examined daily for emergence of adult wasps. Each emerged adult was briefly anesthetized with CO₂, the species and sex were determined, and the length of one hind tibia was measured. The wasps were subsequently placed into rearing colonies as part of a larger biological control program for P. semipunctata in California.

The differences among species in host size preference and in bark thickness were determined using analysis of variance (General Linear Models Procedure) and Tukey’s Studentized range test (Sokal and Rohlf, 1981) for means separation on SAS (SAS Institute, 1988). Regression analysis (SAS Institute, 1988) was used to determine the relationship between number of parasitoid pupae or emerged wasp size and host larval size.

RESULTS

A total of 185 parasitized P. semipunctata larvae were discovered when the bark was removed from felled trees. These larvae produced a total of 431 individual parasitoids of five different braconid species (Table 1). Each of the three gregarious J arra species
had moderately female-biased sex ratios, whereas the most prevalent solitary parasitoid, Syngaster lepidus Brullé, had a moderately male-biased sex ratio that was almost the inverse of the most female-biased gregarious species, Jarra phoracantha Austin, Quicke, and Marsh. Because Callibracon limbatus Brullé was relatively uncommon in the samples collected from this area, it was excluded from all subsequent analyses.

The preferred sizes of host larvae were significantly different among the four commonly recovered parasitoid species ($F = 10.05; \text{df} = 3, 405; P = 0.0001)$. It appeared that S. lepidus preferred the smallest size of larvae (Fig. 1). There were no significant differences in larval size preferences among the three Jarra species.

A significantly different pattern was revealed when bark thickness was used as a factor to explain potential host preference ($F = 109.07; \text{df} = 3, 340; P = 0.0001$). Both Jarra maculipennis Austin, Quicke, and Marsh and Jarra painei Austin and Dangerfield females have relatively short ovipositors [Jarra maculipennis female body length 5.0–6.0 mm with ovipositor 4.0–5.0 mm (Austin et al., 1994) and Jarra painei female body length 4.5–7.0 mm with ovipositor 3.0–5.0 mm (Austin and Dangerfield, 1997)] and utilize larvae under significantly thinner bark (Fig. 2). In contrast, both Jarra phoracantha and Syngaster lepidus females have ovipositors that approach or exceed their body length [Jarra phoracantha female body length 4.5–8.0 mm with ovipositor

### TABLE 1

<table>
<thead>
<tr>
<th>Parasitoid species</th>
<th>No. of parasitized larvae</th>
<th>Total No. of parasitoids recovered</th>
<th>Sex ratio (male:female)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Syngaster lepidus</td>
<td>77</td>
<td>77</td>
<td>1:0.65</td>
</tr>
<tr>
<td>Callibracon limbatus</td>
<td>4</td>
<td>4</td>
<td>1:3.00</td>
</tr>
<tr>
<td>Jarra phoracantha</td>
<td>58</td>
<td>247</td>
<td>1:1.57</td>
</tr>
<tr>
<td>Jarra maculipennis</td>
<td>7</td>
<td>41</td>
<td>1:1.06</td>
</tr>
<tr>
<td>Jarra painei</td>
<td>34</td>
<td>61</td>
<td>1:1.18</td>
</tr>
</tbody>
</table>

* Five host larvae were parasitized by one or more unidentified species.

![Graph](image.png)

**FIG. 1.** Gallery width (mean, SE) associated with P. semipunctata larvae parasitized by one of four species of braconid wasps. Significant differences ($P = 0.05; \text{df} = 405$) are indicated by different lowercase letters above the bars.
4.0–10.0 mm and S. lepidus female body length 8.0–12.5 mm with mean ovipositor 4.5–13.5 mm (Austin et al., 1994); females of these species were able to utilize larvae found under thicker bark.

Whereas there appeared to be little difference in preference for host larvae of different sizes, two of the three gregarious Jarra species evinced a significant positive relationship between number of pupae and beetle gallery width (J. maculipennis, $F = 0.58; P = 0.4760$; J. phoracantha, $F = 18.75; r^2 = 0.2577; P = 0.0001$; Fig. 3; J. painei, $F = 4.94; r^2 = 0.1374; P = 0.0337$; Fig. 4). Similarly, the significant positive slopes of the regressions on the size of the emerging adult parasitoids and host gallery width for two of the three Jarra species (J. maculipennis, $F = 1.42; P = 0.2408$; J. phoracantha, $F = 82.11; r^2 = 0.2614; P = 0.0001$; Fig. 5; J. painei, $F = 9.48; r^2 = 0.1345; P = 0.0031$; Fig. 6) indicate that females ovipositing on large larvae may confer a fitness advantage to their progeny. Although the relationships with host larval size are significant in both analyses for two of the species, the low $r^2$ values suggest that other factors also may be important. The number of Phoracantha larvae found to be parasitized by J. maculipennis was very low and the lack of significance in the relationships between beetle size and parasite progeny number and size may be a reflection of the small number of samples.

**DISCUSSION**

The members of the assemblage of parasitoids utilizing P. semipunctata larvae must locate trees that have been infested by the beetle at some earlier date. There is limited information regarding parasitoid location of wood-boring host larvae, but certain assumptions can be made. Parasitoids of wood-boring insects orient to potential host habitat using long-range odor or visual cues. Once on an infested tree or branch, short-range orientation to potential hosts is likely to involve some combination of odor, vibration, or acoustic cues. The proper cues will result in arrest, probing, and oviposition by female wasps.

There are analogous systems of parasitoid host location that have been well studied and may provide an insight to understanding host location by parasitoids of P. semipunctata. Parasitoids of scolytid bark beetles arrive at host trees well after the initial colonization when the larval hosts are at a suitable stage of development (Camors and Payne, 1973; Salom et al., 1991). The parasitoid response is mediated by semiochemicals associated with the infested trees (Borden, 1982; Payne, 1989).

In our study, the trees had been felled 6 months prior to sampling. The beetles had colonized the cut logs at some point after felling, and the larvae had developed to a stage suitable for parasitization. However, for the...
parasitoid to arrive when the host insect is in the stage suitable for parasitoid development, the parasitoids must use cues characteristic of an aged host. These cues may be different from those used by the beetles searching for mating and oviposition sites several months previously when the logs were relatively fresh (Hanks et al., 1996a, b).

*Stenonema* may use cues slightly different from those that the *Jarra* species use to locate host habitat because they preferentially use smaller, younger larvae and, therefore, must arrive earlier than the gregarious species. Alternatively, all species may use the same cues, but the solitary species may simply select smaller larvae among those available for oviposition. Once on the host tree, however, there is some assortment among the members of the assemblage according to bark thickness. How the wasps assess bark thickness is not clear, but it could be a combination of a direct measure with the ovipositor or an indirect measure, possibly through vibrational cues.

Once on the host tree, parasitoid females must locate the larvae under the bark. Richerson and Borden (1972) proposed that *Coeloides brunneri Viereck* were able to detect infrared emissions from bark beetle larvae under the bark. A subsequent evaluation of the detection of heat by this parasitoid discounted that conclusion and proposed, alternatively, that parasitoid females use chemical cues for short-range host location (Mills et al., 1991). In scolytid bark beetles, these volatile cues used by parasitoids may be associated with frass and excrement (Berisford and Franklin, 1971) or may originate directly from the larvae (Camors and Payne, 1973). However, in some bark beetle systems that have been investigated, volatile cues appear to be derived from fungi and yeasts characteristically associated with the beetle larvae (Leufvén and Birgersson, 1987; Birgersson and Leufvén, 1988). There is no indication that specific fungal microorganisms are associated with *P. semipunctata*, although production of other chemical cues that can be perceived by the adult wasps cannot be ruled out.

Ryan and Rudinsky (1962) suggested that female parasitoids used vibrations from the larvae to locate bark beetle larvae under the bark. It is possible that female *S. lepidus* and *Jarra* spp. use a combination of chemical and physical cues (sonic or surface vibration) to detect and evaluate the size of beetle larvae beneath the bark. *P. semipunctata* larvae feed on both the hard outer xylem tissue and the softer inner bark. The cutting or rasping actions of the mandibles create a sound that is audible to the human ear over a distance of several meters (T.D.P., pers. obs.), as well as surface

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**FIG. 3.** Regression of number of *J. phoracantha* pupae with the width of the host *P. semipunctata* larval gallery ($y = 0.9843x - 1.4111$). $R^2 = 0.2577$
vibrations. The intensity or frequency of the sound or vibration may be a direct function of larval size. Adult wasps may perceive these vibrations through either tarsal or antennal contact with the substrate (Hanks et al., 2000). It is also possible that females drum the bark surface with either their antennae or their legs as

**FIG. 4.** Regression of number of *J. painei* pupae with the width of the host *P. semipunctata* larval gallery (*y* = 0.16x + 1.07).

**FIG. 5.** Regression of length of hind tibia of emerged *J. phoracantha* adults with the width of the host *P. semipunctata* larval gallery (*y* = 0.11x + 0.82).
they search for larval hosts. The size of the feeding cavity below the surface would produce a different resonance to this surface vibration.

Our study reveals several distinct biological characteristics of the parasitoid assemblage that could be important to incorporate into an optimal biological control program for *P. semipunctata*. *S. lepidus* utilized significantly smaller larvae as hosts than the other members of the assemblage. Larval size is a function of both individual age and host plant quality; larvae are smaller and development time is prolonged in poorer quality hosts (Hanks et al., 1995c). Thus, introduction of *S. lepidus* could facilitate parasitism of both young larvae and larvae colonizing drier or aged host tissue, whereas introduction of one or more of the *Jarra* species could facilitate parasitism of both older larvae and larvae colonizing moist or fresh host tissue.

Bark thickness was also a factor that separated members of the assemblage into distinct groups. Both *S. lepidus* and *J. phoracantha* utilize larvae under thicker bark than *J. maculipennis* or *J. painei*. Establishment of at least one member from each of these pairs would facilitate parasitism of larvae in thin- and thick-barked Eucalyptus species or in trees of different ages or on different parts of the same trees (e.g., lower stems and upper canopy branches).

The final distinguishing characteristic among members of the assemblage that could influence an optimal introduction strategy is their reproductive biology. However, there is not enough information yet available on the ecology of the parasitoids in the assemblage to determine whether there is an advantage for the introduction of solitary and gregarious species. Greathead (1986) presented a series of characteristics comprising an ideal monophagous parasitoid for use in classical biological control and suggested that high fecundity and short generation time were important. He drew no conclusions regarding the relative merits of solitary or gregarious reproductive strategies for natural enemies introduced as part of a biological control program (Greathead, 1986).

Eucalyptus have been widely established throughout much of California and the tress have become significant components of urban forests (Paine et al., 1997). The trees show rapid growth and tolerance for a wide range of environmental conditions in their new environment. Introduction of the beetle has resulted in significant tree mortality and beetle activity now indicates where the trees are growing under stressful conditions. The establishment of an egg parasitoid *Avetianella longoi* Siscaro has had a significant impact on the population dynamics of the beetle (Hanks et al., 1995b, 1996c). Establishment of an optimal assemblage of larval parasitoids should further enhance this impact. However, it will be important to integrate the biological control strategy with other elements of a tree
management program that includes species selection, host resistance, sanitation, and cultural practices (Hanks et al., 1991b, 1993b, 1995a; Paine et al., 1993, 1995, 1997) to reduce the potential for outbreaks in beetle populations and maintain the risk of tree mortality at consistently low levels.

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