Biological Constraints on Host-Range Expansion by the
Wood-Boring Beetle *Phoracantha semipunctata* (Coleoptera: Cerambycidae)

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ABSTRACT The eucalyptus longhorned borer, *Phoracantha semipunctata* F., is a cosmopolitan pest of *Eucalyptus*. The developing larvae damage trees by boring through the outer bark and along the cambium layer. Although the borer has become established in many parts of the world where it has encountered novel host-plant species, it has restricted its attacks to *Eucalyptus* and a few closely related species. The goal of this study was to investigate the behavioral and ecological barriers to host-range expansion by *P. semipunctata*. In laboratory experiments, gravid female *P. semipunctata* showed a low propensity to oviposit on logs of nine novel host species even though they had been deprived of their natural oviposition hosts. Survivorship of neonate larvae artificially introduced into logs of some novel host species was similar to that of larvae in *Eucalyptus* logs. However, larval development time in these novel hosts was greatly prolonged and adult body size was reduced. These findings suggest that oviposition behaviors of the adult beetles could restrict the host range of *P. semipunctata* to *Eucalyptus* species, and that oviposition preferences correspond well with performance of the larvae.

KEY WORDS *Phoracantha semipunctata*, Cerambycidae, *Eucalyptus*

In its native Australia, the eucalyptus longhorned borer, *Phoracantha semipunctata* F., primarily infests wind-thrown *Eucalyptus* trees, fallen branches, and logging slash (Tooke 1935, Chararas 1969). However, in many other areas of the world where *Eucalyptus* has been extensively planted, such as South and Central Africa, the Mediterranean basin, and more recently, California, *P. semipunctata* is a severe pest, infesting and killing thousands of trees annually (e.g., Chararas 1969, Drinkwater 1975, Ivory 1977, González Tirado 1986, Hanks et al. 1995). The explosion of *P. semipunctata* population densities in these areas may be caused by the absence of significant natural enemies, coupled with large-scale planting of *Eucalyptus* on inappropriate sites where trees are stressed because of water deficits, poor soils, or extreme temperatures (Paine et al. 1993). Damage is caused by the developing larvae, which bore through the outer bark and rapidly consume the cambium layer. Extensive and irreparable damage to the vascular tissues usually ensures tree death.

*Phoracantha semipunctata* has a fairly restricted host range, as is generally true for cerambycids that attack stressed or dying trees (Duffy 1953, Linsley 1961). In Australia, *P. semipunctata* is confined to *Eucalyptus* and species in a few closely related genera (Duffy 1963), which together represent the majority of native trees (Heywood 1978). However, in other areas of the world where *P. semipunctata* has been accidentally introduced, the beetles are faced with a profusion of tree species in families only distantly related to *Eucalyptus*. In these areas, instead of being the dominant tree species, *Eucalyptus* may be much less common and patchily distributed. These ecological conditions would seem to encourage adaptation to utilize novel host species. Nevertheless, there are apparently no reports in the literature of such forced host shifts.

There may be several possible constraints to the successful colonization and utilization of a novel species by *P. semipunctata*. For example, the presence or absence of oviposition stimulants or deterrents may determine whether oviposition takes place (e.g., Nair & McEwen 1976). If eggs are indeed laid and they survive and hatch, the neonate larvae may then be faced with chemical and physical barriers preventing them from boring through the outer bark and into the nutrient-rich cambium layers. Once in the vascular tissues, the cambium layer may prove to be too thin, too tough, nutritionally deficient, lacking in appropriate feeding stimuli, or actually toxic to the larvae, and incapable of supporting the normal development of the larvae. Finally, because the mature larvae bore into the sapwood to pupate, the characteristics of the wood may determine whether the insects are able to pupate and complete development.

The potential for *P. semipunctata* to utilize non-*Eucalyptus* hosts encountered during colonization
of new regions of the world has only been cursorily investigated using four novel host species (Helal & El-Sebay 1980). Development and survival in those novel hosts were poor. Our goal in this study was to identify the behavioral and ecological barriers that may prevent the utilization of novel host species by *P. semipunctata*. We test the hypothesis that the host specificity of *P. semipunctata* is truly obligate. In particular, we determine whether utilization of novel hosts was inhibited by factors affecting oviposition by gravid *P. semipunctata* females, or establishment and development of *P. semipunctata* larvae.

### Materials and Methods

#### Novel and Natural Host Logs

Novel host logs presented to adult *P. semipunctata* included logs from nine species of trees in four plant families, most of the superorder Rosidae (Table 1; choice of host species depended on availability of logs). Host logs were cut from trees at Kearney Agricultural Center in Parlier, CA, on 5 March 1992. Logs were taken from the trunks of freshly killed trees (plum, nectarine, apricot) or were cut from the large branches of standing trees (cherry, peach, almond, persimmon, pistachio, walnut). *Eucalyptus* logs were taken from an *E. tereticornis* Small tree that was felled on 3 March 1992 at the Moreno Valley field station of the University of California in Riverside County. The ends of all logs were waxed with hot paraffin to slow desiccation (see Hanks et al. 1993a).

#### Oviposition Response of Adult *P. semipunctata* to Logs of Novel Host Species

To determine whether *P. semipunctata* would oviposit on logs of novel host species in the absence of their natural *Eucalyptus* hosts, adult beetles were caged with three logs each of the nine novel tree species. Adult females readily oviposited on *Eucalyptus* logs in cages and will even oviposit on such inappropriate materials as filter paper and plywood in the absence of host logs (L.M.H., unpublished data). A large cage was prepared by covering a greenhouse bench (310 cm long, 110 cm wide, and with 14-cm-high sides) with aluminum window screen. The 27 logs were arrayed randomly in the cage with equal spacing between logs (=10 cm), and the logs parallel to the long axis of the bench. Logs were chosen to minimize differences in length, because length would strongly influence the chances that a log would be encountered by walking beetles. Study logs, therefore, did not differ significantly in length (Table 2; *F* = 0.96; df = 8, 18; *P* > 0.05), but logs of some species had greater circumferences than others (*F* = 5.12; df = 8, 18; *P* = 0.002) which resulted in significant differences between species in surface area (*F* = 4.70; df = 8, 18; *P* = 0.003).

On 10 March 1992, 10 female and five male *P. semipunctata* were released into the cage, and another 10 females and five males were added on 20 March 1992 to further ensure that gravid females were present. All beetles were from a laboratory colony reared from *Eucalyptus* logs and were ≥10 d old. Fecundity of all female beetles was verified before the study by their ovipositing on filter paper in laboratory cages. Beetles in the study cage were provided with 5% sugar water as food. On this diet, adult beetles live for ≈2 mo, continuously ovipositing batches of eggs (Hanks et al. 1993a). Logs were exposed to beetles until 25 March 1992, at which time they were bagged individually in nylon mesh to capture emerging adult beetles. Bagged logs were stored in a temperature-controlled rear-

### Table 1. Taxonomic relationships between *Eucalyptus* and the nine novel tree species that were used as host logs for *P. semipunctata* (Heywood 1978)

<table>
<thead>
<tr>
<th>Superorder Dilleniidae</th>
<th>Order Rosales</th>
</tr>
</thead>
<tbody>
<tr>
<td>Family Rosaceae: almond (P. amygdalus Batsch), apricot (P. armeniaca L.), cherry (P. serotina Ehrh.), nectarine (P. persica 1atsch), peach (P. persica Batsch), plum (P. domestica L.)</td>
<td></td>
</tr>
<tr>
<td>Order Juglandales</td>
<td></td>
</tr>
<tr>
<td>Family Juglandaceae: walnut (Juglans regia L.)</td>
<td></td>
</tr>
<tr>
<td>Order Sapindales</td>
<td></td>
</tr>
<tr>
<td>Family Anacardiaceae: pistachio (<em>Pistacia vera</em> L.)</td>
<td></td>
</tr>
<tr>
<td>Order Myrtales</td>
<td></td>
</tr>
<tr>
<td>Family Myrtaceae: <em>Eucalyptus</em></td>
<td></td>
</tr>
<tr>
<td>Family Ebenaceae: persimmon (<em>D. sapios virginiana</em> L.)</td>
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</tr>
</tbody>
</table>

### Table 2. Dimensions in centimeters (mean ± 1 SD) of logs used as hosts for larvae of *P. semipunctata* in two experiments (see Materials and Methods)

<table>
<thead>
<tr>
<th>Species</th>
<th>Oviposition response experiment</th>
<th>Larval development experiment</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Length</td>
<td>Circumference</td>
</tr>
<tr>
<td>Almond</td>
<td>24 ± 1.7</td>
<td>36 ± 4.04</td>
</tr>
<tr>
<td>Apricot</td>
<td>26 ± 6.9</td>
<td>26 ± 8.7</td>
</tr>
<tr>
<td>Cherry</td>
<td>23 ± 2.5</td>
<td>28 ± 3.1</td>
</tr>
<tr>
<td>Eucalyptus</td>
<td>27 ± 3.4</td>
<td>31 ± 2.5</td>
</tr>
<tr>
<td>Nectarine</td>
<td>21 ± 1.5</td>
<td>32 ± 3.2</td>
</tr>
<tr>
<td>Peach</td>
<td>24 ± 2.9</td>
<td>33 ± 2.4</td>
</tr>
<tr>
<td>Persimmon</td>
<td>22 ± 1.5</td>
<td>22 ± 5.8</td>
</tr>
<tr>
<td>Pistachio</td>
<td>22 ± 2.1</td>
<td>30 ± 2.3</td>
</tr>
<tr>
<td>Plum</td>
<td>22 ± 1.6</td>
<td>37 ± 2.7</td>
</tr>
<tr>
<td>Walnut</td>
<td>21 ± 0.58</td>
<td>34 ± 0.05</td>
</tr>
</tbody>
</table>
ing facility (\(\approx 30 \pm 5^\circ C, \approx 40\%\) RH, natural daylight). After beetle emergence from logs had ended, logs were stripped of bark and examined for the characteristic shallow furrows in the cambium made by newly hatched larvae trying to colonize the log, and the larger and deeper feeding galleries left by older larvae.

**Development of *P. semipunctata* Larvae in Logs of Novel Host Species.** To document whether larvae could develop in logs of novel host species, first instars were transferred into three logs of each species (including three *Eucalyptus* logs). Because our choice of logs was limited, these study logs varied greatly in size (Table 2); logs did not differ significantly in circumference (\(F = 1.31; df = 9, 20; P > 0.05\)), but logs of some species were longer than other species (\(F = 4.65; df = 9, 20; P = 0.002\)), to the extent that surface area of walnut logs averaged \(\approx 2.5\) fold that of cherry logs (\(F = 3.09; df = 9, 20; P = 0.017\)). Density of larvae was standardized by adjusting the number of first instars transferred to logs to yield an initial density of one larva per 100 cm\(^2\) of surface area. Thus, an average of 5 to 13 larvae were introduced into individual logs of the 10 species (see surface area means, Table 2).

Larvae were introduced into logs by cutting a slit in the bark a few millimeters wide and deep enough to reach the cambium and transferring the larvae into this slit with a damp paintbrush (Hanks et al. 1993a). Logs were infested on 17–25 March 1992, bagged individually in nylon mesh to capture adult beetle progeny, and stored in the rearing facility (environmental conditions described above). Survival of larvae to maturity was indicated by frass-plugged holes leading to the pupal chamber in the sapwood, and open holes indicated that an adult beetle had completed development and emerged. From these data we calculated larval survivorship (from neonate to mature larva) and total survivorship (from neonate to adult) for each log.

**Phenology, Body Size, and Fertility of Adult *P. semipunctata* Reared from Logs.** The dates that adult beetles emerged from study logs were recorded, and body size (tip of mandible to tip of right elytron) was measured. Beetles were then caged under standard rearing conditions to test fertility (see Hanks et al. 1993a for caging details); individual male and female beetles that emerged from study logs were paired with a mate from the laboratory colony to document that they were fertile. Eggs laid by all female beetles were counted and then isolated on filter paper in petri dishes to determine hatching success.

**Statistical Analysis.** Analysis of variance (ANOVA; Sokal & Rohlf 1981, SAS Institute 1988) was used to test for differences between treatment means. Where data did not meet the assumptions of ANOVA (variances were not homogeneous), we tested overall differences between means with the Kruskal–Wallis test (SAS Institute 1988). Because of the presence of zeros for some survivorship means, statistical differences between pairs of means were tested by determining whether each mean fell outside of the 99% CI of the other. We used the Tukey–Kramer method to test for differences between means for measures of body size (SAS Institute 1988). Means ± 1 SD are presented throughout.

**Results**

**Oviposition Response of Adult *P. semipunctata* to Logs of Novel Host Species.** Adult *P. semipunctata* that were caged with logs of the nine species of novel hosts trees laid very few eggs; logs of peach and walnut showed no signs of penetration by neonate larvae, and very low numbers of neonates occurred in almond (2.7 ± 1.5 larvae per log), apricot (2.0 ± 1.7 larvae), cherry (0.67 ± 1.2 larvae), nectarine (1.3 ± 2.3 larvae), persimmon (1.7 ± 1.2 larvae), pistachio (1.0 ± 1.7 larvae), and plum (2.0 ± 2.6 larvae) (means for all nine host species not significantly different; Kruskal–Wallis statistic = 10.4, \(P > 0.05\)). Because of the very low numbers of larvae obtained, it was not possible to test host species effects on larval survivorship in this experiment.

**Survivorship of *P. semipunctata* Larvae in Logs of Novel Host Species.** For neonate larvae artificially introduced into logs, larval survivorship (from neonate to mature larva) differed significantly among the 10 tree species (nine novel hosts plus *Eucalyptus*). The numbers of larvae surviving to maturity in logs were 3 ± 1.2 for almond, 0 for apricot, 0.33 ± 0.3 for cherry, 5.0 ± 0.6 for *Eucalyptus*, 2.3 ± 0.3 for nectarine, 0 for peach, 6.7 ± 1.4 for persimmon, 0.33 ± 0.3 for pistachio, 3.3 ± 2.4 for plum, and 0.33 ± 0.3 for walnut. Mean survivorship was significantly higher in logs of *Eucalyptus* and persimmon than in nectarine, but survivorship in all three of these species was higher than in pistachio, cherry, walnut, peach, and apricot (Fig. 1; Kruskal–Wallis statistic = 23.2, \(P = 0.006\)). In logs of almond and plum, larval performance was more variable with the result that mean survivorship was not significantly different from that of all other species except for peach and apricot (Fig. 1).

Host species also differed in total survivorship (neonate to emerging adult), with 1.7 ± 1.2 adults emerging from logs of almond, 0 from apricot, 0 from cherry, 2.7 ± 0.3 from *Eucalyptus*, 1.7 ± 0.7 from nectarine, 0 from peach, 5.3 ± 2.3 from persimmon, 0.33 ± 0.3 from pistachio, 3.3 ± 2.4 from plum and 0.33 ± 0.3 from walnut. Mean survivorship was significantly higher in *Eucalyptus*, persimmon, nectarine, and plum than in cherry, peach or apricot (Fig. 1; Kruskal–Wallis statistic = 20.2, \(P = 0.017\)).

**Phenology, Body Size, and Fertility of Adult *P. semipunctata* Reared from Logs.** Host species had a dramatic effect on the phenology of *P. semipunctata* adult emergence. Larvae developing in
their natural *Eucalyptus* hosts emerged as adults after 71.8 ± 5.0 d (n = 8 beetles from logs of both experiments), whereas those colonizing logs of novel host species required >1.0 y to complete development, averaging 454 ± 4.5 d for almond (n = 10 beetles), 451 ± 6.4 d for cherry (n = 3), 445 ± 5.8 d for nectarine (n = 5), 448 ± 6.1 d for persimmon (n = 17), and 447 ± 7.5 d for plum (n = 10).

Body sizes of adult *P. semipunctata* emerging from host logs differed significantly among host species (including only measurements for host species that yielded more than two beetles from both experiments). Beetles emerging from *Eucalyptus* were significantly larger (2.65 ± 0.05 cm) than those from all of the novel host species, including almond (2.43 ± 0.19 cm), nectarine (2.57 ± 0.26 cm), persimmon (2.34 ± 0.31 cm), and plum (2.32 ± 0.22 cm) (F = 3.22; df = 4, 43; P = 0.021; differences between means indicated by Tukey–Kramer P < 0.05). However, these four novel host species did not differ significantly in adult beetle size (Tukey–Kramer P > 0.05). This influence of host species on body size of adult beetles was slight: the largest beetles emerging from *Eucalyptus* logs were only 14% longer than the smallest from plum logs.

When paired with a mate from the laboratory colony, female beetles reared from novel host logs laid eggs, and male beetles from these logs were successful in fertilizing the eggs of virgin female beetles. More than 90% of all of the eggs hatched, confirming that all adult beetles were fertile.

**Discussion**

Gravid *P. semipunctata* showed only a minimal inclination to oviposit on logs of nine species of novel hosts, despite there being no alternative oviposition sites. There was no evidence of attempted larval colonization of peach and walnut logs (no evidence of larval galleries in the cambium), even though logs had been exposed to 200 beetle-days of oviposition activity for a >15-d period. Logs of the other seven species averaged one to three larval galleries per log, indicating low levels of utilization of the novel hosts by ovipositing females. This contrasts with oviposition on *Eucalyptus* logs, where multiple egg masses are laid per log, with typical egg masses being 20–30 eggs, and at least 35% of the resulting neonate larvae penetrating to the cambium layers (e.g., Way et al. 1992; L.M.H., unpublished data).

The distinct differences in oviposition and host utilization between *Eucalyptus* and novel host logs are unlikely to be caused by physical characteristics of the bark because *P. semipunctata* females oviposit readily on *Eucalyptus* species with widely varying bark characteristics, from rough, or fibrous to very smooth, and the neonate larvae have little difficulty in establishing (Powell 1978). Additionally, female *P. semipunctata* lay eggs under clean filter paper if they are confined to rearing cages in laboratory colonies (Hanks et al. 1993a). This lack of discrimination in selecting oviposition sites suggests that the elicitation of oviposition behavior in this beetle requires few specific stimuli. For this reason, our study results showing very low levels of colonization of novel hosts are somewhat surprising and suggest that logs of these tree species may contain oviposition deterrents.

Development of *P. semipunctata* larvae in artificially infested logs of some of the novel host species supports the hypothesis that the minimal levels of host utilization observed in the oviposition response study were the result of low rates of oviposition. Several novel host species seemed to be adequate hosts for neonate *P. semipunctata*. However, the ability of larvae to utilize host tissues did not appear to correlate with taxonomic relatedness of hosts. For example, survivorship was similar in *Eucalyptus* and the distantly related persimmon (Fig. 1; Table 1), but within the genus *Prunus*, beetles completed development in some species (nectarine and plum) but not in others (cherry, peach, apricot).

Total survivorship in four of the nine novel host species was not significantly different from that in logs of *Eucalyptus tereticornis*, a natural host of *P. semipunctata*. Successful development of larvae in wood of these novel host species is probably related to the production in the larval midgut of a cellulase enzyme which aids in the digestion of generic wood constituents (see Chararas & Chipoulet 1983). Poorer development seen in logs of the remaining novel host species may have several possible causes, such as cambial toughness, poor nutritional quality, or presence of deterrent or toxic secondary metabolites. A combination of these factors rather than the lack of essential nutrients specific to *Eucalyptus* is indicated, because *P. semipunctata* have been successfully reared on artificial diets that do not include *Eucalyptus* material (De
Viedma et al. 1985). Furthermore, the inability of *P. semipunctata* to complete development on some of the novel species can not be explained by resistance of these species to wood borers in general because all of these species are attacked by other species of wood-boring insects (e.g., Duffy 1953, Johnson & Lyon 1988).

The most significant difference in developmental parameters between beetles reared on *Eucalyptus* versus novel host logs was a >6-fold increase in the developmental times on novel host logs compared with natural host (*Eucalyptus*) logs. Prolonged development in cerambycid larvae is typically caused by low-quality host material (Duffy 1953, 1963). The slow development of *P. semipunctata* larvae in logs of the novel species may reflect a lack of physiological adaptation and poorer host utilization abilities rather than lower nutrient content of the freshly cut logs. Slow development of early instars in novel hosts would result in still greater prolongation of the life cycle because the nutritional quality of cambium tissues declines rapidly after death of woody tissues (Haack & Slansky 1987). Delayed development of early instars, and declining nutritional quality of host tissues, could be responsible for the smaller body size of beetles emerging from logs of the novel host species. Nevertheless, all beetles emerging from study logs were reproducibly viable.

Although the study logs were held in a greenhouse under relatively constant temperatures, seasonal weather patterns may have contributed to the prolonged development times of *P. semipunctata* in novel host species. Larvae of this species will remain in a quiescent stage throughout the winter months even when kept under constant warm temperatures and a long daylight cycle (L.M.H., unpublished data). The life cycle, therefore, may have been extended by several months because larvae had not pupated before summer’s end. The high degree of synchronicity in the emergence of adult beetles from novel host logs (SD < 8 d) was probably caused in part by the influence of seasonal weather conditions; the first larvae to complete development would have become quiescent the earliest, allowing slower developing larvae to reach the same stage before weather conditions prompted all of the larvae to pupate in the spring.

In summary, although *P. semipunctata* is a voracious pest of living and freshly killed trees of a large number of species in the genus *Eucalyptus*, gravid females showed a low propensity to oviposit on tree species of other plant families. Even when beetles were artificially introduced into the cambium, larvae either failed to establish or development times were prolonged enormously and adult body size was reduced. Thus, rejection of novel hosts as oviposition substrates by the adult beetles coincides with the poor performance of their larvae in these hosts. These findings correspond well with an earlier study that showed that adult *P. semipunctata* maximize larval fitness by discriminating among potential larval hosts (Hanks et al. 1993b). The current study supports the hypothesis that the host specificity of *P. semipunctata* is obligated and provides indications as to why this important insect pest has not extended its host range to include novel host species as it has colonized new regions.

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