# Patterns of Host Utilization by Two Parasitoids (Hymenoptera: Braconidae) of the Eucalyptus Longhorned Borer (Coleoptera: Cerambycidae)

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**We studied the behavior and biology of the Australian parasitoids *Syngaster lepidus* Brullé and *Callibracon limbatus* (Brullé) (Hymenoptera: Braconidae), which are being introduced into California as biological control agents of the eucalyptus longhorned borer, *Phoracantha semipunctata* F. (Coleoptera: Cerambycidae). Studies conducted in Australia revealed that (1) female *S. lepidus* and *C. limbatus* actively searched the bark surface of eucalypt logs and apparently located their wood-boring hosts by substrate vibration or sound; (2) size of hosts selected for parasitism varied across parasitoid species and sexes—the largest hosts were parasitized by *C. limbatus* females, and the smaller hosts were parasitized by *C. limbatus* males, *S. lepidus* females, and *S. lepidus* males; (3) *C. limbatus* tended to dominate in logs that contained larger larvae, whereas *S. lepidus* were more abundant in logs with smaller larvae, suggesting that the two parasitoid species partition available host larvae; and (4) hosts of *S. lepidus* were under bark that was slightly thicker than that overlying hosts of *C. limbatus,* and this relationship was consistent with the relatively longer ovipositor of *S. lepidus.* Furthermore, (1) very thick bark (>17 mm) provided a refuge for borer larvae from both parasitoid species, (2) rates of parasitism averaged 27% across study sites and were inversely correlated with densities of host larvae in individual logs, and (3) rates of predation averaged only 6% and were positively correlated with abundance of host larvae in logs.** © 2001 Academic Press

***Key Words: Phoracantha semipunctata; Syngaster lepidus; Callibracon limbatus;* wood-boring; biological control; competition; niche partitioning.**

A common shortcoming of many biological control programs for insect pests is a lack of information on the biology of the control agents in their native habitat, in particular their role in regulation of prey populations (DeBach and Rosen, 1991; Stiling, 1993). This is especially problematic when multiple species of biological control agents are involved because they may interact in ways that reduce the efficacy of control of the target pest (Ehler and Hall, 1982). A poor understanding of the biology of natural enemies also hinders identification of qualities responsible for success or failure of control programs that otherwise could be used to improve methodologies (Ehler, 1990). Unfortunately, few biological control programs can afford the time and resources needed for extensive field studies of potential control agents; rather, most programs are limited to identification of natural enemies of the target pest, followed by importation and release (Ehler, 1990).

We examine the natural history, behavior, and ecology of two species of parasitic wasps, *Syngaster lepidus* Brullé and *Callibracon limbatus* (Brullé) (Hymenoptera: Braconidae), in their native Australia where they attack the eucalyptus longhorned borer, *Phoracantha semipunctata* F. (Coleoptera: Cerambycidae). *P. semipunctata* is a wood-boring beetle that is an economically important pest in many regions of the world where its eucalypt hosts have been introduced (Hanks *et al.,* 1995). Since its appearance in California in the early 1980s, it has killed innumerable eucalypts that serve as shade, ornamental, and windrow trees (Hanks *et al.,* 1995; Paine *et al.,* 1995). In Australia, however, *P. semipunctata* is rarely a pest (Chararas, 1969; Pook and Forrester, 1984), undoubtedly due, in part, to regulation by a guild of natural enemies, including generalist predators and more specialized hymenopterous parasitoids (Moore, 1963; Austin *et al.,* 1994). These parasitoids include species that attack only cerambycid larvae that feed subcortically in eucalypts, including the solitary *S. lepidus* and *C. limbatus,* four gregarious braconid species in the genus *Jarra,* and a few species

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of pteromalids, eurytomids, megalyrids, and ichneumonids, some of which may be hyperparasitoids (Austin *et al.,* 1994).

*S. lepidus* and *C. limbatus,* among the dominant parasitoids of *Phoracantha* species in southeastern Australia where we conducted our study, are both active throughout the year, with a summer peak in activity, and are similar in appearance and size, ranging from ~6–13 mm in length (Austin *et al.,* 1994). Little is known of the mechanisms by which these wasps locate their hosts, whether they compete for hosts, or the rates of parasitism that they inflict—information that is critical for assessing their potential value as biological control agents in multispecies introductions (reviewed by Van Driesche and Bellows, 1996).

To provide baseline data relevant to the use of *S. lepidus* and *C. limbatus* in biological control programs in California and elsewhere, we studied these wasps and their hosts in Australia with the following objectives: (1) to characterize behaviors involved in host location and oviposition by females of the two species, (2) to determine whether the two species partition the available host larvae by size or by the thickness of bark under which their hosts feed, and (3) to determine whether parasitism rates are correlated with density of host larvae.

## MATERIALS AND METHODS

### Study Sites

We studied the behavior and host relations of *S. lepidus* and *C. limbatus* in two independent studies that were conducted in consecutive years.

*Study I.* To study parasitoid behavior, we visited Wombat State Forest (near Daylesford, Victoria, Australia) on 27 March–27 April 1994. The site was dominated by *Eucalyptus obliqua* L'Héritier and had been logged 3–4 months previously. Logging debris in a ~300 × 400-m area was comprised primarily of small branches, limbs, and tree crowns and stumps (ranging in diameter from ~10 cm to 1 m), with debris scattered over the site. This host material was heavily infested with cerambycid larvae that varied from early instars (a few millimeters long) to fully developed larvae (~30 mm long), and parasitoids were abundant.

*Study II.* On 8 March–8 April 1995 we visited four sites in Victoria where large eucalypts had been felled and sectioned a few months earlier: Australian Paper Manufacturer Forest Property Limited (APM; 180 km east of Melbourne; 23 trees felled), Daylesford (DAYL; 100 km northwest of Melbourne; 6 trees), Mt. Disappointment (MT; near Broadford, 100 km north of Melbourne; 32 trees), and Wallace (WAL; 30 km east of Ballarat; 2 trees). Trunks of felled trees had been cut into large pieces that averaged 24.9 ± 7.7 (SD) cm in diameter and 3.4 ± 0.97 m long and were scattered on

the forest floor. All felled trees were of the species *E. obliqua,* except for the APM site, where they were *Eucalyptus globulus* LaBillardière.

### Behavior of Adult S. lepidus and C. limbatus

In Study I, we observed the behavior of adult *S. lepidus* and *C. limbatus* in the proximity of host logs from ~0900 to 1700 h. We recorded qualitative information on activity period, behaviors related to mate location and reproductive behavior, host location and oviposition, and intra- and interspecific interactions. After observing oviposition behaviors, we extracted the resulting parasitized host larvae from logs to measure their size and determined the percentage of hosts that were successfully parasitized, as indicated by a lack of movement; *S. lepidus* and *C. limbatus* females apparently inject a venom prior to oviposition that immobilizes the host and then deposit a single egg on the host (personal observations).

### Estimation of Body Size of Host Larvae by Gallery Width

To allow us to estimate body size of *P. semipunctata* larvae from the width of their feeding galleries at the time that they were parasitized, we characterized the linear relationship between gallery width and body size of larvae. We collected 44 larvae from three logs at the MT site in Study II, measured the widths of their gallery termini and the lengths of their bodies (from mandibles to apex of abdomen; with larvae straightened, but not compressed), and modeled the linear relationship between these two variables by regression analysis (Sokal and Rohlf, 1995).

### Host Size Preference

In both Studies I and II, we tested for differences between parasitoid species and sexes in the size of their host larvae by collecting parasitoid pupae from eucalypt logs and estimating the body size of host larvae at the time of parasitization (from gallery width, using the regression equation, above). Cocoons of *S. lepidus* and *C. limbatus* were similar in appearance, consisting of a paper-like material, elongate oval in form, and off-white to yellow-brown in color (due to staining by moisture). Cocoons adhere to the wood in host galleries, and they are easily collected by the peeling back of bark and the extraction of the cocoons with forceps. We placed cocoons in individually labeled plastic vials that were plugged with cotton and later shipped to the quarantine facility of the University of California, Riverside (UCR), where adults were reared under laboratory conditions (~20°C and ~50% RH). Emerging adult wasps were killed, pinned, and identified to sex and species. Voucher specimens of all species have been retained in the Entomology Research Mu-

seum of UCR. We used analysis of variance (ANOVA) to test differences between wasp species in host size; the assumption of homogeneity of variances was confirmed with the $F$-max test (Sokal and Rohlf, 1995).

To determine whether *S. lepidus* and *C. limbatus* partitioned the available host larvae, we tested for a linear relationship between densities of the two species in individual eucalypt logs; an inverse relationship would suggest that the two species compete for host larvae, whereas a positive correlation, or no correlation, would indicate a lack of competition (reviewed by Godfray, 1994). For this study, we used logs of Study II that contained at least 10 cocoons and regressed the number of *S. lepidus* cocoons on the number of *C. limbatus* cocoons (both $\log_{10}[n + 1]$ transformed).

### Influence of Bark Thickness on Parasitism and Predation Rates

To determine whether relative parasitism rates of *S. lepidus* and *C. limbatus* were influenced by bark thickness, we measured the thickness of bark overlying parasitized host larvae in Study II and collected the resulting parasitoid pupae to identify emerging adult wasps to species. Differences between parasitoid species in mean thickness of bark overlying cocoons were tested by ANOVA. In addition, we recorded the incidence of predation (indicated by empty larval galleries or presence of predaceous insect larvae or adults) while dissecting host logs in Study II to determine whether the predators were influenced by bark thickness.

Thickness of bark might influence relative parasitism rates, especially if *S. lepidus* and *C. limbatus* differed in ovipositor length. To test this hypothesis, we dissected ovipositors from 15 females of each species that represented a broad range of body sizes (to allow for allometric relationships); *S. lepidus* females were from our laboratory colony, whereas *C. limbatus* females were collected at the DAYL site on 3–10 April 1994. We tested for differences between slopes of regression lines for ovipositor length versus length of the right hind tibia for *S. lepidus* and *C. limbatus* using analysis of covariance (GLM Procedure; SAS Institute, 1988). Tibial length was used as a measure of body size because distortion of the abdomen in dried specimens rendered measure of total body length inaccurate. In this analysis, if the interaction between the parasitoid species effect and the covariate (tibia length) is not significant (slopes not significantly different), the probability value for the species effect can be used to determine whether the heights of the regression lines differed, confirming differences in ovipositor length for a given tibial length (Sokal and Rohlf, 1995). To assess variation in length of the tibia and ovipositor in natural populations, we measured lengths of the body, tibiae, and ovipositors of 30 randomly selected *S. lepidus* and *C. limbatus* females collected during Study I.

### Relationship between Density of Host Larvae and Parasitism and Predation Rates

To determine whether parasitism and predation rates were influenced by host density, we used regression analysis to identify linear relationships between the percentage of host larvae killed and their density in individual logs. These data were collected in Study II by complete dissection of all of the logs at the four sites (only 11 MT logs and 2 DAYL logs were used to estimate predation rate). We measured parasitism rate as the proportion of larvae parasitized (by both *S. lepidus* and *C. limbatus* combined) divided by total number of larvae (parasitized and unparasitized). Predation rate was calculated by division of the number of killed larvae (those missing and presumably eaten plus those being attacked at the time of dissection) by the total number of larvae (including parasitized larvae).

## RESULTS

### Behavior of Adult S. lepidus and C. limbatus

At the time that we visited Site I, a few large *P. semipunctata* larvae had begun constructing prepupal chambers in the sapwood, but we found no completed chambers. Few adult beetles were observed, probably owing to their crepuscular habits and the lateness of the season. However, adult *S. lepidus* and *C. limbatus* were abundant, either searching for hosts, ovipositing, or resting on logs; both species were so numerous that several hundred adults could be collected with an insect net in a few hours.

*Female oviposition behavior.* Adult *S. lepidus* and *C. limbatus* flew to eucalypt logs as morning temperatures warmed, with short hovering flights. By midday, six or more adults were often present on or around each host log. Adults were active until mid to late afternoon, when light levels began to decrease; they were not active on cool or rainy days (temperature <15°C). We were not able to locate adult wasps during inclement weather or at night. If disturbed, female parasitoids flew swiftly upward and away from the site; female *S. lepidus* were more easily disturbed than *C. limbatus* and so were more difficult to observe and capture. Female *C. limbatus* subjected to rough handling (as when netted) curled up and feigned death for 1 min or longer, but *S. lepidus* did not show this behavior.

Females appeared to alight on logs arbitrarily, rather than in proximity to a potential host. Four wasps searched for only a brief period (1–18 min) on one log that contained no host larvae (determined by dissection). While searching for hosts on eucalyptus logs, female *S. lepidus* and *C. limbatus* adopted a characteristic pose with legs straight and antennae spread to ~120° and still. Bouts of this pose of several minutes were interspersed with short bouts of walking as the wasp oriented to a host. The female curved her ovipos-

itor sheath back under the abdomen, cocking the abdomen high to drill through the bark (also described by Moore, 1963). As the wasp probed, hosts produced a clearly audible scratching sound that suddenly ceased, presumably as the venom took effect. The wasp then moved the ovipositor backward and forward while depositing an egg on the surface of the paralyzed host. Once oviposition was completed, the wasp rested briefly, withdrew the ovipositor, and groomed it with the hind legs for several minutes, retracting it into its sheath.

In each of 17 oviposition attempts by *C. limbatus* that we observed from initiation of drilling to oviposition, females were positioned over the host larvae, but only 12 were successful (host found in dissection to be immobilized and parasitoid egg present). Probing and oviposition required a considerable investment of time and energy, lasting an average of $101.3 \pm 28.1$ min (SD; $N = 12$). In the 5 cases of unsuccessful oviposition, females attempted to insert their ovipositors two to four times before giving up after 40–110 min and flying away.

Because oviposition was such a lengthy process, it was not uncommon for wandering females to encounter ovipositing conspecifics. After brief antennation, the second female usually rested nearby or moved away. Although we observed no aggressive interactions among individuals of the same or different species, we have observed wing-fanning displays between conspecific females of both species in laboratory colonies (unpublished information); similar displays in other hymenopteran parasitoids have been interpreted as aggressive (Mills, 1991). Occasionally, two female wasps drilled within a few millimeters of one another, apparently targeting the same host larva. This behavior also was common in our laboratory colonies, undoubtedly due to artificially high densities of wasps. Superparasitism that might result from this competition occurred in only one host larva in Study I, which had two wasp eggs, and a single host of hundreds collected in Study II, which produced two *S. lepidus* cocoons.

*Behavior of males.* Adult male *S. lepidus* and *C. limbatus* spent most of their time resting on logs, with occasional short flights or walking bouts. Contacts with conspecifics or heterospecifics were brief and not aggressive. We observed only a single incidence of mating by *S. lepidus* in the field. In that case, several males aggregated for hours around a point on a eucalypt log where a female later emerged, and one mated with her very briefly (a few seconds) as soon as she emerged. We saw no other instances of sexual attraction or aggregation during hundreds of hours of observation on host logs, suggesting that mating occurs only upon emergence or elsewhere, such as at feeding sites of adults, which remain unknown. We did not observe *C. limbatus* mating in the field.
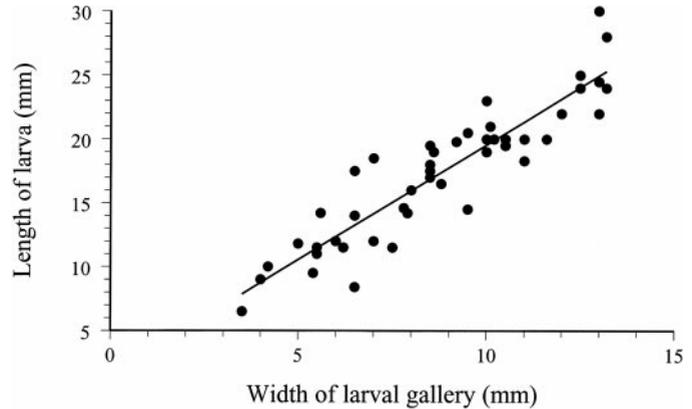


**FIG. 1.** Relationship between the maximum width of feeding galleries and the body length of wood-boring beetle larvae. Best fit regression line: $Y = 1.8X + 1.56$; $r^2 = 0.84$; $F = 224$; $df = 1, 44$; $P < 0.0001$.

### Estimation of Body Size of Host Larvae by Gallery Width

Body length of wood-boring larvae was positively correlated with the maximum width of their feeding galleries (Fig. 1). We subsequently used the resulting least squares regression equation to estimate the size of larvae from the width of their feeding galleries at the time that they were parasitized.

### Host Size Preference

Relative abundances of parasitoid species varied considerably across study sites and sampling dates. Study I cocoons yielded 118 *S. lepidus* and 24 *C. limbatus,* whereas Study II cocoons yielded 244 *S. lepidus,* 374 *C. limbatus,* and 52 groups of the gregarious parasitoid *Jarra phoracantha* Marsh and Austin (Hymenoptera: Braconidae). Relative proportions of these three primary parasitoids varied across Study II sites, with *J. phoracantha* dominating at APM, *S. lepidus* at DAYL and WAL, and *C. limbatus* at MT. In Study II, we also collected seven cocoons of possible hyperparasitoid species; suspected hyperparasitoids of the parasitoids of *Phoracantha* include eurytomid, pteromalid, and ichneumonid species (Austin *et al.,* 1994).

*C. limbatus* females developed on the largest hosts (average $18.0 \pm 0.34$ mm in length estimated from gallery width; Fig. 2), with progressively smaller hosts yielding *C. limbatus* males ($12.7 \pm 0.26$ mm), *S. lepidus* females ($12.0 \pm 0.25$ mm), and *S. lepidus* males ($8.7 \pm 0.13$ mm); means significantly different; overall ANOVA $F = 137$; $df = 7, 690$; $P < 0.0001$; significant terms were Year ($F = 19.1$, $P < 0.0001$), Location ($F = 5.24$, $P = 0.0014$), Species ($F = 219$, $P < 0.0001$), and Sex ($F = 280$, $P < 0.0001$). For 26 logs containing at least 10 parasitoid cocoons, the density of *S. lepidus* cocoons ($\log_{10}$) was inversely correlated with density of *C. limbatus* (Fig. 3).
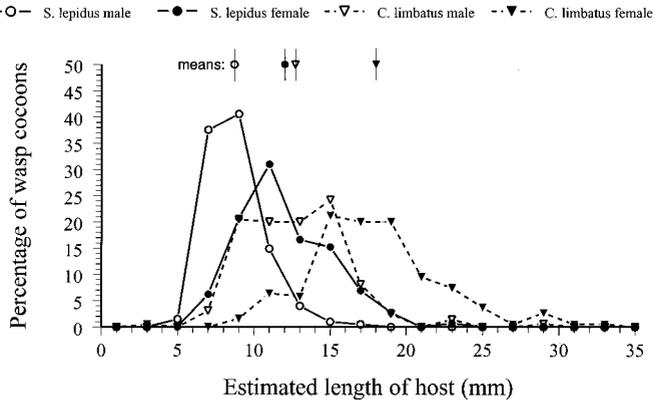
FIG. 2. Relationship between the body length of host larvae (estimated from gallery width with the equation in Fig. 1) and the percentage of *S. lepidus* and *C. limbatus* collected from host larvae (2 years data combined). Means are indicated by markers at top (standard errors are listed in the text). Sample sizes for 1994 were: *S. lepidus* females ($N = 39$) and males ($N = 79$); *C. limbatus* females ($N = 12$) and males ($N = 12$). Sample sizes for 1995 were: *S. lepidus* females ($N = 106$) and males ($N = 123$); *C. limbatus* females ($N = 177$) and males ($N = 149$).

## Influence of Bark Thickness on Parasitism and Predation Rates

Host trees varied slightly in the thickness of their bark across study sites in Studies II, with trees at WAL having bark about 21% thicker than trees at the APM site (means for sites APM, DAYL, MT, and WAL: 8.6 ± 0.7, 11.3 ± 0.5, 10.3 ± 0.3, and 10.4 ± 1.2 mm; means significantly different, ANOVA $F = 3.3$; $df = 3, 53$; $P = 0.028$).

Bark thickness had a significant, though subtle association with both species and sex of parasitoids (Fig. 4). Hosts of *S. lepidus* were under bark that was on average 6.7% thicker than that overlying hosts of *C. limbatus* (bark thickness 10.4 ± 0.15 and 9.7 ± 0.11
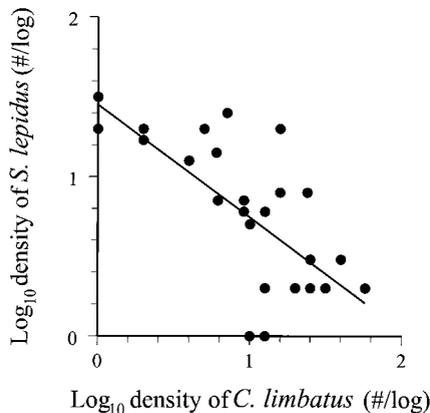


FIG. 3. Relationship between the number of *S. lepidus* and *C. limbatus* cocoons ($\log_{10} [n + 1]$) in 26 eucalypt logs. Best fit regression line: $Y = -0.71X + 1.45$; $r^2 = 0.46$; $F = 20.7$; $df = 1, 24$; $P < 0.0001$.
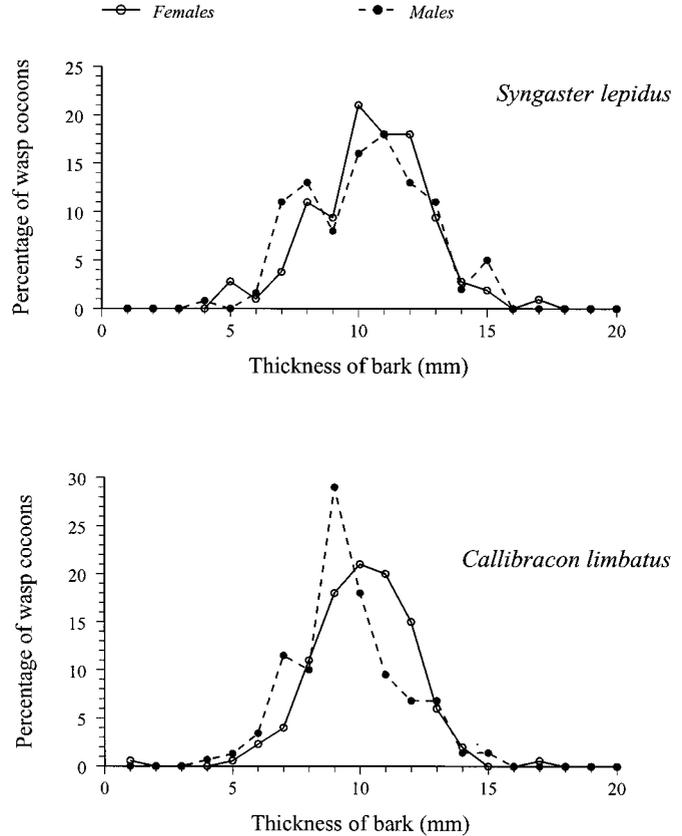




FIG. 4. Relationship between the thickness of bark overlaying host larvae and the relative percentages of wasp species parasitizing them ($N = 106$ female and 123 male *S. lepidus,* 171 female and 148 male *C. limbatus*).

mm, respectively). Furthermore, female *C. limbatus* were under bark 6% thicker than males (10.0 ± 0.15 and 9.4 ± 0.16 mm), whereas sexes of *S. lepidus* showed no such difference (means 10.4 ± 0.2 and 10.3 ± 0.2 mm; overall ANOVA $F = 8.24$; $df = 2, 545$; $P = 0.0003$; species effect $F = 11.4$, $P = 0.0008$; sex effect $F = 5.1$, $P = 0.024$; interaction term not significant, $P > 0.05$).

Few wasps of either species parasitized larvae under bark thicker than 17 mm (Fig. 4). This threshold in bark thickness accounts for some of the variation in parasitism rates within logs: for 13 logs at the DAYL and MT sites, areas of bark overlying 373 parasitized beetle larvae averaged 11.5 ± 1.9 (SD) mm thick, whereas the bark overlying 3308 larvae that had escaped parasitism averaged 19.9 ± 5.5 mm thick.

The ability of *S. lepidus* females to reach hosts under thicker bark is consistent with their longer ovipositors relative to *C. limbatus* of a given body size (Fig. 5). For both species, ovipositor length was strongly correlated with length of the hind tibia (Fig. 5); slopes of the regression lines were similar for the two species (species × tibia length interaction term not significant; $P > 0.05$), but the *S. lepidus* line was significantly higher
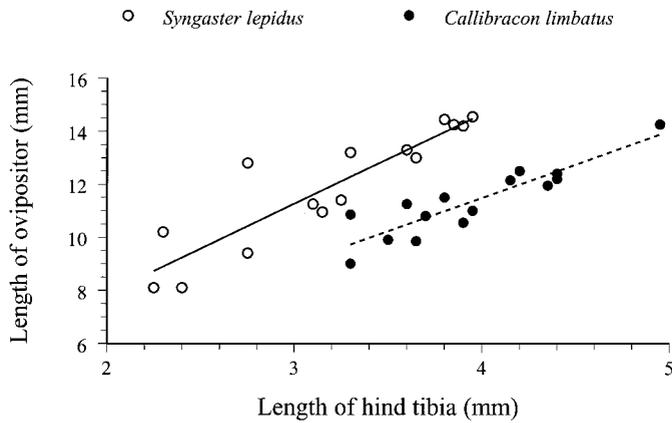
FIG. 5. Relationship between ovipositor length of 15 *S. lepidus* and *C. limbatus* females and body size (measured as length of the right hind tibia). Best fit regression lines: *S. lepidus*, $Y = 3.38X + 1.13$; $r^2 = 0.80$; $F = 58.1$; $df = 1, 13$; $P < 0.0001$; *C. limbatus*, $Y = 2.52X + 1.42$; $r^2 = 0.79$; $F = 53.0$; $df = 1, 13$; $P < 0.0001$.

than that for *C. limbatus* (species term; $F = 58.5$, $df = 1, 26$; $P < 0.0001$). Though *S. lepidus* females can be considerably smaller than *C. limbatus* females, the largest *S. lepidus* females have longer ovipositors than most *C. limbatus,* allowing them to reach hosts under slightly thicker bark.

Our sampling of wasps collected in the field shows that, at least during Study I, *S. lepidus* females were 23% smaller than *C. limbatus* (tibia length $2.9 \pm 0.097$ mm versus $3.8 \pm 0.04$ mm; ANOVA $F = 81.1$; $df = 1, 60$; $P < 0.0001$), but ovipositors of *S. lepidus* females were 17% longer than those of *C. limbatus* ($10.1 \pm 0.41$ mm versus $8.6 \pm 0.11$ mm; ANOVA $F = 9.9$; $df = 1, 60$; $P = 0.0027$). Tibial length was strongly correlated with total body size among sample specimens of both species (regression equations: *S. lepidus* tibial length $= 0.30 \times$ body length $- 0.25$, $r^2 = 0.92$, $df = 30$, $P < 0.0001$; *C. limbatus* tibial length $= 0.18$ body length $- 1.85$, $r^2 = 0.28$, $df = 30$, $P = 0.0022$). The lower correlation coefficient in *C. limbatus* was probably due to distortion of the abdomen in dried specimens.

The complete dissection of 13 study logs in Study II yielded 158 predators (clerid beetles) feeding on beetle larvae or parasitoid pupae. Of these predators, 51% were present in 1 log that had very thick bark (averaging 28 mm) and no areas of thin bark (which explains an absence of parasitized larvae); however, the abundance of the remaining predators in other logs was not consistently associated with thick bark (regression analysis of number of predators and average bark thickness; $P > 0.05$).

### Relationship between Density of Host Larvae and Parasitism and Predation Rates

Wood-boring larvae in eucalypt logs of Study II numbered from 4 to 690, averaging $121 \pm 157$ larvae/log, for
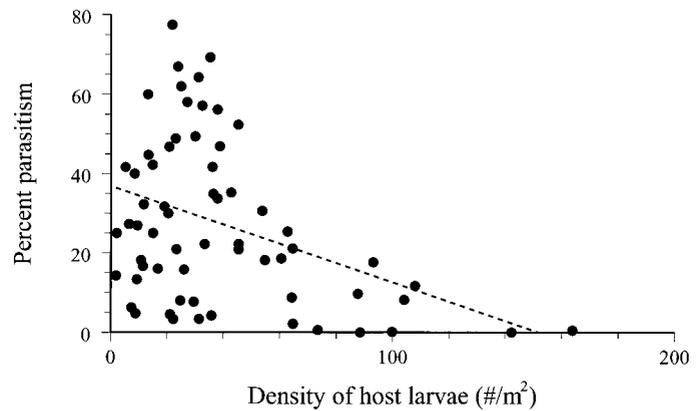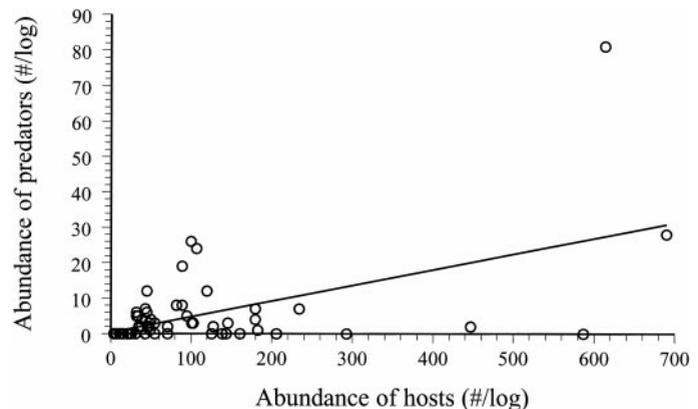


FIG. 6. Relationship between the density of host larvae (No./m² of bark) and parasitism rate. Best fit regression line: $Y = -0.23X + 36$; $r^2 = 0.13$; $F = 8.4$; $df = 1, 57$; $P = 0.0054$.

a density per unit bark area of $39.3 \pm 34$ larvae/m². Parasitism and predation rates in individual eucalypt logs averaged $27.4 \pm 21$ and $6.1 \pm 9.5\%$, respectively. Parasitism rate was inversely correlated with the density of hosts per unit of bark area (Fig. 6), but was only weakly correlated with the number of larvae per log ($r^2 = 0.1$; $F = 6.2$; $df = 1, 57$; $P = 0.016$). Predation rate was not significantly correlated with host density (regression $P > 0.05$); however, the number of predators in logs was significantly correlated with the number of host larvae (Fig. 7).

### DISCUSSION

Rates of parasitism averaged 27% across our study sites and were inversely correlated with densities of host larvae in individual logs; inverse density dependence has been taken as evidence that natural enemies do not regulate populations of their prey at low equilibrium densities (but see review by Van Driesche and



FIG. 7. Relationship between the density of host larvae (No./log) and the abundance of predators in individual eucalypt logs. Best fit regression line: $Y = 0.04X + 0.43$; $r^2 = 0.29$; $F = 23.1$; $df = 1, 57$; $P < 0.0001$.

Bellows, 1996). Thickness of bark overlying borer larvae also subtly influenced the species composition of immature parasitoids under the bark. *S. lepidus* pupae occurred under slightly thicker bark than did *C. limbatus* pupae, and this relationship was consistent with the relatively longer ovipositor of *S. lepidus*. Very thick bark, however, apparently provided a refuge for borer larvae from both parasitoid species and may account for unsuccessful oviposition that we observed. Thick bark did not protect larvae from predators; rates of predation averaged only 6% and were positively correlated with abundance of host larvae in logs.

The fact that female *S. lepidus* and *C. limbatus* did not appear to discriminate among logs that contained few or many host larvae suggests that they do not use host-produced chemicals to locate their prey. Once on a log, wasps appeared to locate hosts by sound or vibrational cues associated with feeding, a behavior similar to that of other parasitoids whose hosts feed in concealed locations (see Godfray, 1994), including bark beetles (Ryan and Rudinsky, 1962) and leafminers (Sugimoto *et al.*, 1988). *P. semipunctata* larvae emit a crunching sound as mandibles snip woody tissues; in heavily infested logs these sounds are clearly audible to humans from several meters away (Hanks *et al.*, 1998). Later instars also produce a loud scratching sound by rubbing the mandibles against the rough ceiling of their galleries (observed by partially removing bark near the gallery terminus; L.M.H.). The importance of sound or vibration in location of hosts was illustrated by the brief period that wasps search for hosts in a log that contained no larvae.

Differences between these parasitoid species, and between sexes, in body size of hosts on which they developed suggest that adult females are able to estimate the size of the host by some unknown mechanism and adjust the sex of the egg deposited accordingly. Females of other species of parasitic Hymenoptera adjust the sex ratio of their eggs in response to the size of the host (e.g., Sandlan, 1979); however, parasitoids of wood-boring insects, and of other types of concealed prey, cannot assess host size directly and must use other cues that are correlated with host size when making oviposition decisions (e.g., King, 1994). This ability also has been documented in braconid parasitoids of other subcortically feeding beetles (Urano and Hijii, 1991). Consistent with host location using sound or substrate vibration was the rarity of superparasitism and multiple parasitism; hosts immobilized by envenomation and parasitism would be undetectable by adult parasitoids arriving later.

*S. lepidus* and *C. limbatus* were the most abundant parasitoid species in beetle-infested eucalypt logs at all of the study sites except APM (where *J. phoracantha* dominated), in agreement with previous reports from southeastern Australia where our study sites were located (Austin *et al.*, 1994). Differences between study sites in the densities of *S. lepidus* and *C. limbatus* cocoons could reflect geographical patterns in relative abundance, but other explanations are also possible. For example, because the species differ in preferred host size (Fig. 2), dominance could also be an artifact of the phenology of host beetle colonization in relation to the times that our studies were conducted. The largest host larvae utilized by *C. limbatus* were ~30 mm long (Fig. 2), about the size of mature *P. semipunctata* larvae (personal observations). Because few wood-boring beetles of eucalypts are much larger than *P. semipunctata* (Wang, 1995), we assume that all larvae of this size were approaching maturity. At the other extreme, some *S. lepidus* males completed development on early instar hosts only ~7 mm long. Thus, *S. lepidus* would dominate in logs that were felled in late spring because larval hosts would be small at the time adult wasps became active. *C. limbatus*, which require larger hosts, would be more likely to dominate at sites were trees had been felled earlier and host larvae were larger. Such phenological effects could explain why *S. lepidus* cocoons were more abundant in Study II logs at the DAYL and WAL sites, despite the fact that *C. limbatus* adults outnumbered *S. lepidus* adults at the time that we collected the cocoons (J.G.M., personal observations).

This phenological effect may also explain the inverse correlation between densities of *S. lepidus* and those of *C. limbatus* in a given log (Fig. 3): depending on when a log was colonized by beetle larvae, one or the other parasitoid species would predominate. Therefore, this inverse relationship is not necessarily indicative of competition between parasitoid species, but rather suggests that they complement one another by killing host larvae of a broad range of sizes and over sequential, but overlapping time periods.

*S. lepidus* and *C. limbatus* also partitioned host larvae by subtle differences in thickness of the bark that females must penetrate to oviposit; other braconid and ichneumonid parasitoids of wood borers also show variation in parasitism rates that are related to differences in ovipositor length (Heatwole and Davis, 1965; Urano and Hijii, 1991). Female *S. lepidus* and *C. limbatus* were apparently incapable of parasitizing host larvae under bark thicker than ~17 mm, suggesting that bark of greater thickness could serve as a refuge from these two parasitoid species. Moore (1963) found that parasitism of eucalypt borers was greatest if bark was less than ~17 mm thick and lowest under bark ~25 mm thick. Thus, the thick bark of many of the logs and branches used in our studies could account for the generally low parasitism rates that we observed. Predators, on the other hand, reached beetle larvae under very thick bark and showed a numerical response to host density. Because predators are more generalized in their diets, their use as biological control agents could pose a threat to nontarget native species outside

of Australia (see Follett and Duan, 1999), unless they are specialized to attack only prey under the bark of eucalypts.

We conclude that *S. lepidus* and *C. limbatus* meet several of the criteria of effective biological control agents (see Murdoch, 1990; DeBach and Rosen, 1991): (1) the two species are the dominant species in the parasitoid guild attacking wood-boring larvae of eucalypts in their native region (Austin *et al.,* 1994); (2) they are host specific on wood borers of eucalypts (Austin *et al.,* 1994), eliminating nontarget concerns; (3) their broad distribution in Australia (Austin *et al.,* 1994) indicates that they are adapted to a wide range of environmental conditions; (4) adult females efficiently locate hosts in their habitat and can discriminate between eucalypt logs that contain host larvae and those that do not, resulting in aggregation of adults on infested logs (present study); (5) the two species complement one another by attacking different sizes of host larvae and, to a lesser extent, larvae under bark of different thickness (present study); and (6) together, the two species kill larvae of a broad range of sizes (present study). Nevertheless, low parasitism rates, particularly under thick bark, and inverse density dependence suggest that these parasitoids may not regulate population densities of *P. semipunctata* at low densities.

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