

Seasonal Development of *Phoracantha recurva* and *P. semipunctata* (Coleoptera: Cerambycidae) in Southern California

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ABSTRACT A seasonal development study of the cerambycid beetles *Phoracantha recurva* Newman and *Phoracantha semipunctata* (Fabricius) (Coleoptera: Cerambycidae) was conducted under field conditions to look for differences in the developmental parameters of these congeneric species in southern California. Neonate larvae were introduced into eucalyptus logs in February, May, July, and October, and the infested logs were held in field cages at two locations: an inland desert site and a more temperate coastal site. Development times from neonate larva to emerged adult and percent emergence were recorded for beetles from all log cohorts at both sites. Under southern California climatic conditions, *P. semipunctata* seems to complete only one generation per year. Adult *P. semipunctata* emerged from infested logs from June to October. In contrast, *P. recurva* seems to be able to complete one generation and begin a second generation within the same year. Adult *P. recurva* emerged from infested logs from February to October. Across all treatments, a greater percentage of *P. recurva* ($70 \pm 2.5\%$) completed development in host logs than *P. semipunctata* ($64 \pm 1.5\%$). The majority of *P. recurva* (74.9%) and *P. semipunctata* (99.4%) emerged during June, July, and August. Host quality was correlated with beetle size. Overall, the differences in the developmental parameters of the two species may be contributing to the replacement of *P. semipunctata* by *P. recurva* in their shared habitat niche in southern California.

KEY WORDS *Phoracantha recurva*, *Phoracantha semipunctata*, seasonal development, competition, diapause

IN ITS NATIVE AUSTRALIA, the eucalyptus longhorned borer *Phoracantha semipunctata* (Fabricius) (Coleoptera: Cerambycidae) is a minor pest that primarily colonizes downed or stressed eucalyptus trees (Tooke 1935, Duffy 1963, Pook and Forrester 1984). In most areas of the world where eucalyptus have been introduced, *P. semipunctata* has also been accidentally introduced. In these regions, *P. semipunctata* is frequently a severe pest, causing significant tree mortality (Bytinski-Salz and Newmark 1952, Drinkwater 1975, Ivory 1977, Loytyniemi 1980, Mendel 1985, Gonzalez-Tirado 1986). California is no exception; since the introduction of the beetle into southern California in 1984 (Scriven et al. 1986), *P. semipunctata* has attacked and killed large numbers of trees (Paine et al. 1995).

In southern California, field surveys have shown that *P. semipunctata* is present from late April until October (Hanks et al. 1993). Adults of both sexes are attracted to volatile compounds emitted by stressed eucalyptus trees and logs, where they mate and oviposit (Drinkwater 1975, Ivory 1977, Scriven et al. 1986, Hanks et al. 1996). Adult females oviposit on the bark

surface beneath loose bark, in bark crevices, or on broken limbs (Ivory 1977, Hanks et al. 1993, Paine et al. 1995). Eggs hatch in 3–5 d, and the neonate larvae mine through the outer bark to feed in the cambium. Larval feeding results in the destruction of virtually the entire cambium layer and the rapid death of the tree (Chararas 1969, Drinkwater 1975, Scriven et al. 1986, Hanks et al. 1993). Mature larvae burrow into the sapwood, where they construct a chamber and pupate. After eclosion, adult beetles bore out of the pupal chamber by chewing through the plug of frass blocking the original entry tunnel to the chamber (Hanks et al. 1990). Anecdotal observations coupled with laboratory rearing and some experimental evidence suggested that *P. semipunctata* might have two or three overlapping generations per year in Tunisia, Zambia, Egypt, Israel, and California (Chararas 1969, Loytyniemi 1980, Helal and El-Sebay 1985, Mendel 1985, Ali et al. 1986, Hanks et al. 1990, Paine et al. 1995). In general, the life cycle seems to be as short as 2 mo in warm conditions and as long as 9 mo in cool conditions (Mendel 1985, Ali et al. 1986).

Development of adult *P. semipunctata* is linked closely with temperature. In trials under controlled temperature conditions, development from egg to

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adult took 246 d at 18.5°C and 98 d at 26.5°C (Bytinski-Salz and Newmark 1952). In Tunisia, *P. semipunctata* adults have been found from May to October at nocturnal temperatures as low as 18.5°C to as high as 27°C (Chararas 1969). In Israel, *P. semipunctata* individuals that began development between spring and mid-summer (March–July) took 100 d to emerge, whereas eggs laid in late summer (August–September) or fall (October–November) took 210 and 195 d, respectively, to complete development (Mendel 1985).

The congeneric species *Phoracantha recurva* Newman is similar to *P. semipunctata* in size, appearance, and general biology, and in California, it shares the same habitat (Hanks et al. 1997). *P. recurva* is one of the most common *Phoracantha* species in its native Australia (Froggatt 1916, Lounsbury 1918), where it feeds on a wide range of dead or dying eucalyptus species (Froggatt 1916). More recently, both *P. recurva* and *P. semipunctata* have been described as two of the most widely distributed *Phoracantha* species in Australia (Wang 1995). Despite its wide biogeographic distribution in Australia, *P. recurva* has received little attention in its native habitat because populations seem to be held to low, nondamaging levels by a wide range of natural enemies (Froggatt 1916, Lounsbury 1918, Wang 1995). For example, it has been estimated that 70% of *P. recurva* are killed by parasites in the larval stage (Froggatt 1916). In Australia, as with *P. semipunctata*, *P. recurva* adults oviposit on fallen eucalyptus during the summer months, and larvae develop in the host cambium. *P. recurva* larvae have been reported to remain in eucalyptus wood for 6–7 mo, until adult emergence (Froggatt 1916). Little else is known about the life history of *P. recurva* except that, in South Africa, *P. semipunctata* was erroneously identified as *P. recurva* for many years (Lounsbury 1916), and it was easily controlled by good silvicultural management in plantations in Zambia (Loytyniemi 1980).

Phoracantha recurva was first detected in southern California in 1995 (Hanks et al. 1997), and in apparent contrast to many other areas of the world, it rapidly became a serious pest. In a period of ~4 yr, *P. recurva* populations dramatically increased while, apparently concurrently, populations of *P. semipunctata* in southern California have fallen to very low levels. Adult *P. semipunctata* are now rarely found in routine field surveys (Paine and Millar 2002).

Data from laboratory-rearing procedures conducted under standardized temperature conditions suggested that there could be several generations of these two species per year in California, but to date, developmental parameters of the beetles have not been evaluated under field conditions. Our first objective in the study described here was to determine and compare the seasonal development of *P. semipunctata* and *P. recurva* from neonate to adult under natural conditions in southern California. A second objective was to determine the possible effects of differences in climatic conditions on the beetles' development by comparing the patterns of emergence

from infested logs held at a temperate coastal site with logs held at an inland desert site.

Materials and Methods

The seasonal development of *P. semipunctata* and *P. recurva* was compared at two sites, a hot inland desert site at University of California, Riverside, CA, and a more temperate coastal site in Brea, CA. The experimental design was duplicated at each location.

Field cages (2.4 by 1.8 by 1.2 m) were built to house infested eucalyptus logs. Each cage was constructed from a 2.4 by 1.2 m by 1.9-cm plywood base, with the frame constructed from 5.1 by 10.2-cm wooden studs. Wooden braces (2.5 by 15.3 cm) were used as extra support to brace wall corners. The entire cage (walls and ceiling) was covered with 3 by 3-mm mesh fiberglass insect screen (Phifer Wire Products, Tuscaloosa, AL) with a fiberglass insect screen door (91.4 by 122 cm) for access. The Riverside cage was placed in a grove of eucalyptus trees, and 50% shade cloth was placed over the fiberglass screen ceiling. The Brea cage was located in full sun so 90% shade cloth was placed over the screen ceiling. Shade cloth was used to reduce direct sun exposure and subsequent overheating of the infested logs. Each cage was set on top of five concrete blocks to reduce problems associated with excess moisture and ants. Angle iron shelving was placed inside the cage, and infested logs were placed lengthwise on each shelf.

Infested logs were placed in individual screen bags to capture adults as they emerged. Bags were made from 82 by 90-cm squares of 3 by 3-mm mesh aluminum insect screening (Phifer Wire Products) rolled up and stapled closed on the bottom and side to create a bag for each log. The top was closed with two 5-cm binder clips (ACCO, Wheeling, IL).

Freshly cut *Eucalyptus camaldulensis* Dehnhardt logs from the Santa Margarita Ecological Preserve, ~5 km southwest of Temecula, CA, were used as host material. Logs ranged from 35 to 53 cm in length and from 25 to 46 cm in circumference. Forty logs were cut on 29 May 2000, 31 July 2000, 2 October 2000, and 19 February 2001. Logs were dried for 10 d at ~27°C, and the log ends were sealed by dipping them in paraffin wax to slow further desiccation. The surface area of each log was calculated to determine the number of *P. recurva* and *P. semipunctata* neonates necessary to infest each log at optimal larval density. This density, which limits competition and cannibalism among larvae, was previously determined to be ~83 larvae/m² of bark (Hanks et al. 1993). Laboratory-reared neonate larvae were manually introduced into logs by cutting a slit in the bark a few millimeters wide and deep. Larvae were transferred into the slit with a fine tipped paintbrush. To collect enough larvae to infest all logs on the same date, eggs were collected over a 12-d period from caged laboratory-reared adult beetles. Eggs collected on different days before the infestation date were held at different temperatures to synchronize hatching. Thus, eggs collected 10–12 d before infesting the logs were held at 15°C, 5–6 d

Table 1. Effect of infestation date on the length of the right elytron in millimeters (mean \pm SE) for *P. recurva* and *P. semipunctata* in Brea and Riverside

Infestation date	Brea (temperate)		Riverside (desert)	
	<i>P. recurva</i>	<i>P. semipunctata</i>	<i>P. recurva</i>	<i>P. semipunctata</i>
May 2000	12.83 \pm 0.37 a	14.92 \pm 0.41 a	13.36 \pm 0.37 a	14.40 \pm 0.49 a
July 2000	12.34 \pm 0.30 ab	12.79 \pm 0.41 b	11.57 \pm 0.44 b	13.10 \pm 0.43 a
October 2000	11.11 \pm 0.44 b	12.83 \pm 0.40 b	11.87 \pm 0.30 b	12.83 \pm 0.45 a

Significant differences ($P \leq 0.05$) among means within columns are indicated by different lowercase letters.

before infesting at 24°C, and 4–5 d before infesting at 27°C. This resulted in a sufficient number of neonate larvae to infest all logs in 1 d.

Once in place, larvae were protected by a paper cover stapled over the slit in each log, which prevented larvae from being dislodged before they initially tunneled into the cambium. The neonate larvae were allowed 24 h to bore into logs before the logs were placed in individual screen bags, transported to the appropriate field cage, and placed lengthwise on angle iron racks. Additional information regarding egg handling and mass rearing of *Phoracantha* beetles can be found in Hanks et al. (1993).

Of the 40 logs cut on each date, 20 were infested with *P. recurva* and 20 with *P. semipunctata* neonates. Ten *P. recurva* and 10 *P. semipunctata* logs were placed as above at each of the two field sites. Logs were monitored for beetle emergence by examining each log for new exit holes and adult beetles every second day from February to October, the time when beetles were actively emerging. From November to January, logs were checked once per week for adult emergence. When the first beetle emerged in late winter, the monitoring schedule returned to every second day. After emergence, the date of emergence, log number, species, and length of the right elytron (an index of beetle size) of each emerging beetle were recorded. The number of days from infestation until emergence was calculated. Loose bark was periodically removed throughout the experiment to prevent adult beetles from hiding and escaping detection. Temperature was recorded continuously at each site using Hobo Pro/Series Temp/RH monitors (Environmental Sensors, Victoria, Canada).

The percentage of beetles to emerge (the number of adults to emerge divided by the number of neonates introduced) was calculated for each log. The time for the first beetle to emerge and the total duration of adult emergence (the difference in the number of days between first and last beetle emergence) were also calculated for each log.

Statistical analyses were conducted to determine differences among date of infestation (May, July, or October), site (hot desert and temperate coastal), and species (*P. recurva* and *P. semipunctata*), with logs as replicates in all cases. Analysis of variance (ANOVA) was used to test for differences among treatment means. Data sets were tested to ensure that they satisfied the assumptions of statistical tests used. The Tukey-Kramer method was used to identify significant differences among multiple means (Sigma Stat 1997).

Percentage data were normalized using arcsine square root transformations. The influence of different treatments on elytron length and number of days until adult emergence was tested using the general linear models procedure for nested data, with infested log as the replicate and emerged beetles as the sample (SAS Institute 1996).

When data failed to meet three-way ANOVA assumptions, the nonparametric Kruskal-Wallis method was used to test differences among means (Sigma Stat 1997). To account for running multiple Kruskal-Wallis tests, a Bonferroni adjustment was made to the type I probability level. In the results presented here, these adjusted values are $\alpha = 0.0125$ for four Kruskal-Wallis analyses and $\alpha = 0.0083$ for six analyses.

One July *P. semipunctata* replicate was discovered to have been infested with both species and was subsequently removed from the analysis.

Results

The logs infested in February 2001 were excluded from data analyses because only 17 of the 40 logs had beetles emerge, whereas all logs from other treatments had beetles emerge. Of the 7 February logs that produced adult *P. recurva*, only 46% of the larvae matured to adults, and of the 10 February logs that produced adult *P. semipunctata*, only 20% of the larvae completed development.

Percentage of Beetles to Emerge. All of the logs infested in May, July, and October had adults emerge. A greater percentage of *P. recurva* (70 \pm 2.5%) completed development than *P. semipunctata* (64 \pm 1.5%; $F = 6.60$; $df = 1,108$; $P = 0.012$). There was no difference between the percentages of beetles that emerged at the two locations (temperate 65.3 \pm 2.0% and desert 68.5 \pm 2.0%; $F = 1.38$; $df = 1,108$; $P = 0.24$). There were also no significant differences in the percentages of beetles to emerge among the different infestation times (May, 67.4 \pm 2.0%; July, 68.3 \pm 3.0%; October, 65.1 \pm 3.0%; $F = 0.52$; $df = 2,108$; $P = 0.60$).

Beetle Size. Beetle size, as assessed by the length of the right elytron, was significantly different depending on the infestation date. Adult *P. recurva* that emerged from logs infested in May from the temperate site had the longest elytra, whereas elytra of beetles emerging from October logs were the shortest, and those of adults from July logs were not significantly different from beetles from May or October logs ($F = 4.64$; $df = 2,27$; $P = 0.019$; Table 1). There were also significant differences among *P. semipunctata* adults

Table 2. Effect of infestation date on the number of days until emergence for *P. recurva* and *P. semipunctata* in Brea and Riverside (mean ± SE)

Infestation date	Brea (temperate)		Riverside (desert)	
	<i>P. recurva</i>	<i>P. semipunctata</i>	<i>P. recurva</i>	<i>P. semipunctata</i>
May 2000	353.9 ± 18.2 a	392.1 ± 8.0 a	336.7 ± 14.2 a	386.7 ± 14.8 a
July 2000	353.6 ± 15.3 a	340.9 ± 8.3 b	334.9 ± 26.8 a	329.6 ± 14.9 b
October 2000	343.4 ± 22.1 a	323.5 ± 8.2 b	316.2 ± 22.1 a	320.4 ± 16.2 b

Significant differences ($P \leq 0.05$) among means within columns are indicated by different lowercase letters.

emerging from the temperate site; logs infested in May produced beetles with elytra that were longer than those from logs infested in July or October ($F = 8.31$; $df = 2,27$; $P = 0.002$; Table 1). Elytron lengths were also significantly different for *P. recurva* emerging from logs held at the desert site. Elytra of beetles from logs infested in May were longer than those of adults from logs infested in either July or October ($F = 7.34$; $df = 2,27$; $P = 0.003$). There were no differences in elytron lengths for *P. semipunctata* adults emerging from any of the sets of logs held at the desert site ($F = 2.67$; $df = 2,26$; $P = 0.09$).

When comparing elytron lengths between the two sites, there were no significant differences for *P. recurva* from logs infested in May ($F = 1.94$; $df = 1,18$; $P = 0.27$), July ($F = 1.47$; $df = 1,18$; $P = 0.24$), or October ($F = 1.94$; $df = 1,18$; $P = 0.18$). There were also no significant differences between the two sites in *P. semipunctata* elytron lengths for beetles emerging from logs infested in May ($F = 0.46$; $df = 1,18$; $P = 0.51$), July ($F = 0.26$; $df = 1,17$; $P = 0.62$), or October ($F = 0.00$; $df = 1,18$; $P = 1.00$).

In comparing the two species, *P. semipunctata* adults were larger than *P. recurva* adults emerging from the logs at the temperate site for logs infested in May ($F = 12.72$; $df = 1,18$; $P = 0.002$) or October ($F = 8.60$; $df = 1,18$; $P = 0.009$), but not for logs infested in July ($F = 0.77$; $df = 1,18$; $P = 0.39$). There were no differences between species in the length of the right elytron among adults that emerged from logs infested in May ($F = 2.62$; $df = 1,18$; $P = 0.12$), July ($F = 4.29$; $df = 1,17$; $P = 0.06$), or October ($F = 3.43$; $df = 1,18$; $P = 0.08$) at the desert site.

Beetle Emergence. There were no differences among infestation dates in the mean number of days between infestation and emergence for *P. recurva* emerging from logs held at the temperate site ($F = 0.08$; $df = 2,27$; $P = 0.92$) or the desert site ($F = 0.31$; $df = 2,27$; $P = 0.73$; Table 2). In contrast, *P. semipunctata* from logs infested in May took longer to emerge than beetles from logs infested in July or October at both sites (temperate: $F = 18.20$; $df = 2,27$; $P < 0.0001$; desert: $F = 6.02$; $df = 2,26$; $P = 0.007$; Table 2).

In comparing the two sites, there were no differences in the mean developmental times of *P. recurva* beetles from logs infested in May ($F = 0.25$; $df = 1,18$; $P = 0.63$), July ($F = 1.74$; $df = 1,18$; $P = 0.20$), or October ($F = 1.17$; $df = 1,18$; $P = 0.29$). There were also no significant differences in developmental times between locations for *P. semipunctata* emerging from logs infested in May ($F = 1.25$; $df = 1,18$; $P = 0.28$) or

October ($F = 0.01$; $df = 1,18$; $P = 0.92$), but *P. semipunctata* from logs infested in July emerged more quickly at the Riverside site than at the temperate Brea site ($F = 71.58$; $df = 1,17$; $P < 0.0001$).

There were no differences between *P. recurva* and *P. semipunctata* in the mean developmental times for beetles emerging from logs held at the Riverside site for logs infested in May ($F = 3.44$; $df = 1,18$; $P = 0.08$), July ($F = 0.30$; $df = 1,17$; $P = 0.59$), or October ($F = 0.02$; $df = 1,18$; $P = 0.89$). There were also no differences between developmental times of the two species at the temperate Brea site for logs infested in May ($F = 2.72$; $df = 1,18$; $P = 0.12$), July ($F = 2.00$; $df = 1,18$; $P = 0.17$), or October ($F = 0.54$; $df = 1,18$; $P = 0.47$).

First Emergence and Duration of Emergence.

There were few differences among the infestation dates in the average time to emerge, but the patterns of emergence were different for the two species (Figs. 1 and 2). Consequently, two new parameters, the time between infestation and the emergence of the first beetle, and the total duration of emergence, were used to examine the differences among the treatments in more detail. The first *P. recurva* began emerging in a shorter amount of time at the temperate site from logs infested in May or October than from logs infested in July ($H = 15.96$; $P < 0.001$; Table 3). At the temperate Brea site, the first *P. semipunctata* from logs infested in October emerged in the shortest number of days, whereas adults from the logs infested in May were slowest to begin emerging. The time to first emergence of beetles from logs infested in July was intermediate between those of May or October logs ($H = 25.97$; $P < 0.001$).

There were also significant differences among infestation times for first adult emergence of *P. recurva* at the desert site. It took fewer days for the first adults to emerge from logs infested in May or October than from logs infested in July ($H = 21.20$; $P < 0.001$). Adults emerged earlier from logs infested with *P. semipunctata* in October in the desert site than from logs infested in May, whereas the time to first emergence of beetles from logs infested in July was intermediate between those of logs infested in May or October ($H = 18.67$; $P < 0.001$).

When comparing the two sites, there were no differences in the number of days until first beetle emergence for *P. recurva* emerging from logs infested in May ($H = 0.0059$; $P = 0.94$), July ($H = 4.56$; $P = 0.033$), or October ($H = 0.023$; $P = 0.88$; Table 3). There were also no differences between sites for *P. semipunctata* emerging from logs infested in May ($H = 0.37$; $P =$

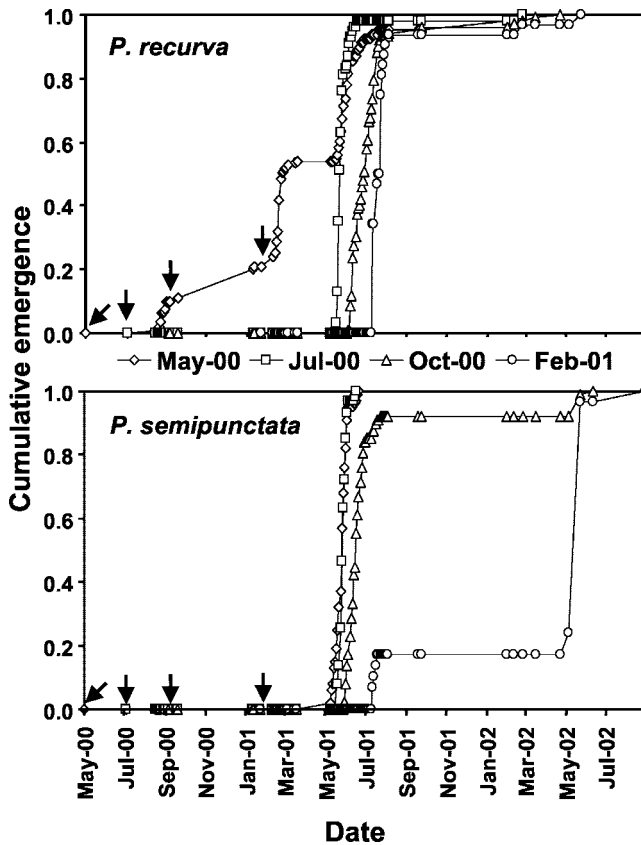


Fig. 1. The cumulative emergence of *P. recurva* and *P. semipunctata* from infested logs in Brea (temperate) for each infestation date. Arrows indicate infestation dates.

0.54) or October ($H = 0.59$; $P = 0.45$), but the first adults emerged significantly earlier from logs infested in July at the desert site than at the temperate Brea site ($H = 14.60$; $P < 0.001$).

The first *P. recurva* emerged earlier than the first *P. semipunctata* from the logs infested in May in both the desert site ($H = 11.11$; $P < 0.001$) and the temperate Brea site ($H = 9.22$; $P = 0.002$; Table 3). However, there were no differences between species in the time to first emergence from logs infested in July at either the desert site ($H = 0.08$; $P = 0.78$) or the temperate Brea site ($H = 3.65$; $P = 0.06$). There were also no differences between species for logs infested in October and held at the desert site ($H = 3.57$; $P = 0.06$) or the temperate Brea site ($H = 1.49$; $P = 0.22$).

There were no significant differences among infestation dates in the duration of *P. recurva* emergence at the temperate site ($H = 6.81$; $P = 0.03$), but logs infested in May had a significantly shorter duration of emergence for *P. semipunctata* than logs infested in October. Logs infested with *P. semipunctata* in July were not different from logs infested in either May or October ($H = 10.80$; $P = 0.005$; Table 4). At the desert site, the duration of emergence of *P. recurva* from logs infested in May was significantly longer than from logs infested in July, with logs infested in October being no different from logs infested in either May or July ($H =$

13.98; $P < 0.001$). The duration of emergence was not different among infestation dates for *P. semipunctata* emerging from logs held at the desert site ($H = 5.03$; $P = 0.08$).

When comparing the duration of beetle emergence between the two sites, there were no differences for *P. recurva* emerging from logs infested in May ($H = 0.07$; $P = 0.79$), July ($H = 4.37$; $P = 0.036$), or October ($H = 0.07$; $P = 0.79$; Table 4). There were also no differences between sites for *P. semipunctata* emerging from logs infested in May ($H = 1.68$; $P = 0.20$), July ($H = 2.17$; $P = 0.15$), or October ($H = 2.68$; $P = 0.10$).

The duration of emergence of *P. recurva* was longer than that of *P. semipunctata* for logs infested in May at both the desert site ($H = 11.59$; $P < 0.001$) and the temperate site ($H = 9.16$; $P = 0.002$; Table 4). There were no differences between species for logs infested in July at the desert site ($H = 0.15$; $P = 0.70$) and the temperate site ($H = 4.19$; $P = 0.041$) or logs infested in October at the desert site ($H = 0.00$; $P = 1.00$) and temperate site ($H = 1.49$; $P = 0.22$).

The majority of beetles of both species emerged during the summer (June, July, and August) when both the average daily low and high temperatures increased (Fig. 3). However, a substantial fraction of *P. recurva* (temperate, 25.1%; desert 27.6%) emerged during the spring and fall, whereas virtually

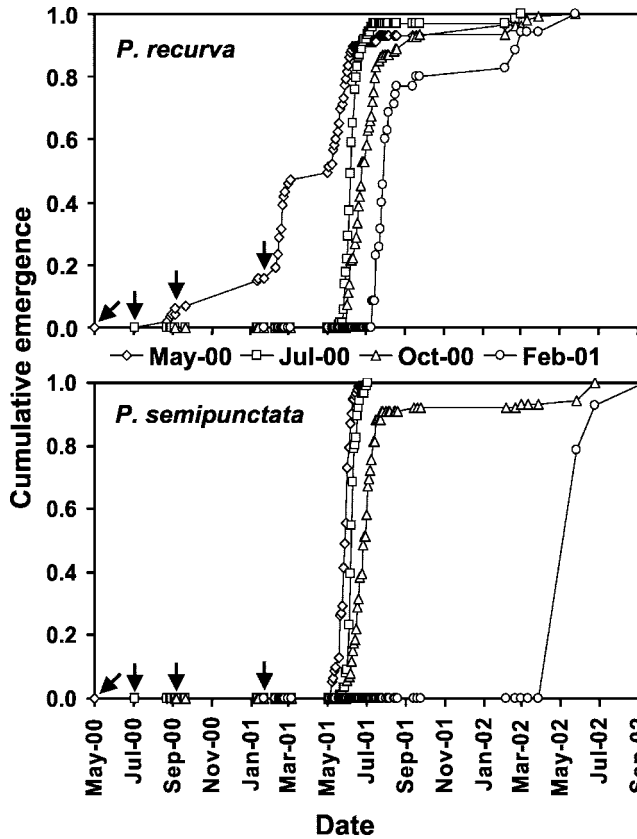


Fig. 2. The cumulative emergence of *P. recurva* and *P. semipunctata* from infested logs in Riverside (desert) for each infestation date. Arrows indicate infestation dates.

no *P. semipunctata* emerged during spring and fall (temperate, 0.7%; desert, 0.6%; Fig. 3).

Discussion

As assessed by the length of the right elytron, the largest *P. recurva* and *P. semipunctata* beetles emerged from logs infested in May, with three of the four sets of May logs producing larger beetles than logs infested at other times. The May logs were infested just before the peak time of year for *P. recurva* and *P. semipunctata* to emerge from naturally infested logs. Larvae introduced into logs in May had all summer to develop, and a few individuals completed development and emerged that fall, but the majority delayed emergence

until the following summer. Because these larvae were able to complete the majority of their development before cold winter temperatures slowed or stopped development, they fed on host material when it was freshest and of highest quality, providing a possible explanation for the large beetles produced from these logs. Although the ends of the experimental logs were waxed to slow desiccation, over time the logs still continued to dry and deteriorate in quality. Thus, the infestation times in July and October did not allow the larvae as much time to develop before winter, and larvae had to complete a larger fraction of their development in the poorer quality hosts the following spring. As temperatures increased in the spring and

Table 3. The median number of days until first beetle emergence from each log for each treatment

Infestation date	Brea (temperate)		Riverside (desert)	
	<i>P. recurva</i>	<i>P. semipunctata</i>	<i>P. recurva</i>	<i>P. semipunctata</i>
May 2000	199 A	383 B	254 a	385 b
July 2000	329 A	335 A	320 a	321 a
October 2000	287 A	280 A	288 a	276 a

Significant differences ($P \leq 0.05$) between means in a given row and site are indicated by different letters.

Table 4. The median duration of beetle emergence in days for each log for each treatment

Infestation date	Brea (temperate)		Riverside (desert)	
	<i>P. recurva</i>	<i>P. semipunctata</i>	<i>P. recurva</i>	<i>P. semipunctata</i>
May 2000	214 a	21 a	241 a	16 a
July 2000	44 a	40 ab	17 b	14 a
October 2000	40 a	69 b	34 ab	32 a

Significant differences between means in a given row and site are indicated by different letters (P values in the text). Differences between sites are discussed in the text.

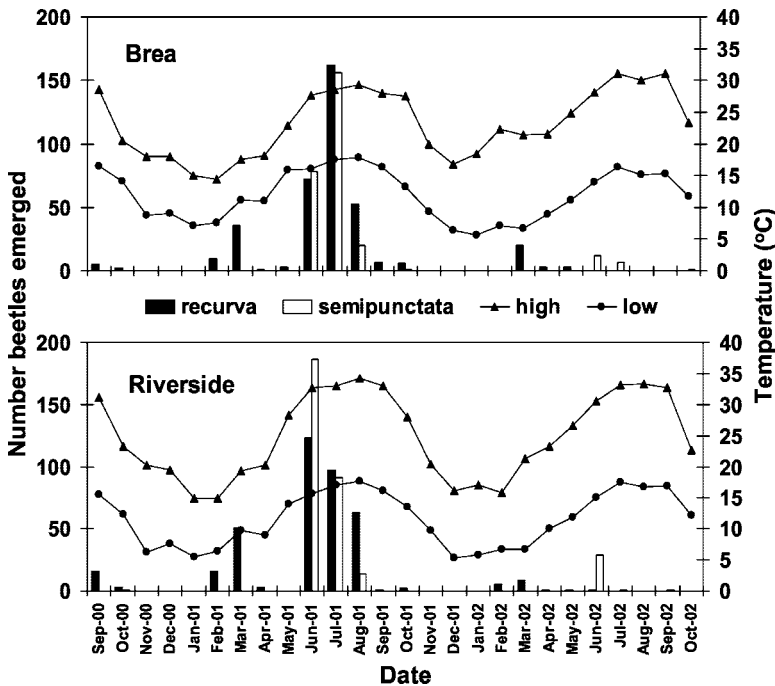


Fig. 3. Mean monthly low and high temperatures in Brea (temperate) and Riverside (desert) and monthly emergence of *P. recurva* and *P. semipunctata*.

development resumed, the reduced quality of the host logs (specifically, reduced moisture content) provided a possible explanation for the smaller beetles. The only set of May logs that did not produce large beetles was the set of *P. semipunctata* logs at the temperate site. This was also the only May treatment in which none of the beetles emerged until the following summer.

The size of the adult provides an important selective advantage for male reproductive success. Although the lengths of male beetle antennae were not recorded in this study, larger males have longer antennae (Hanks et al. 1996b). In *P. semipunctata*, longer antennae increase the rate at which males discover their mates, resulting in greater mating success (Hanks et al. 1996b). However, there does not seem to be any advantage of size in the probability of mating for female *P. semipunctata* (Hanks et al. 1996a).

There were no differences between the temperate and the desert sites for the time of first emergence or duration of emergence, suggesting that the climatic differences between sites were not biologically relevant to the beetles. The majority of both *P. recurva* and *P. semipunctata* adults emerged in the summer (June, July, and August). However, *P. recurva* emergence from May logs at both sites was spread over two seasons. Beetle emergence began in September of the same year and halted for the winter, before resuming sporadically from February onward until the majority of beetles emerged in the summer. Remarkably, small numbers of *P. recurva* continued to emerge sporadically until March of the following year (Figs. 1 and 2).

In contrast, by the end of the year only a single *P. semipunctata* had emerged from logs infested in May 2000; the remainder waited until the following summer to emerge (Figs. 1 and 2).

Despite the 3-mo difference in the infestation dates of the July and October logs, all *P. recurva* and *P. semipunctata* adults from these logs began emerging in June of the following year. These insects are cryptic and following their development is difficult. However, if larvae have to reach a specific developmental stage before becoming quiescent during cold conditions, a possible explanation for our results may be that the beetles introduced into logs in July developed to this specific stage and subsequently slowed or stopped further development during the winter months. The beetles infested in October may have continued to develop until they also reached this same stage before winter. Thus, as temperatures increased in the spring, beetles from both treatments were synchronized at the same developmental stage, and adults from both treatments began emerging at the same time.

Although the duration of emergence was not always significantly different among different infestation times, there did seem to be general trends that each species followed depending on the infestation time. Logs infested with *P. recurva* in May had the longest duration of emergence, beginning in September 2000 and extending until March 2002, with about one-half of the emergence clustered in the summer of 2001 (Figs. 1 and 2). In contrast, at both sites, *P. semipunctata* emergence from logs infested in May 2000 was much more tightly synchronized, with almost all

adults emerging during June and July 2001 (Figs. 1 and 2). Emergence of all *P. recurva* and *P. semipunctata* from July logs was also tightly synchronized, extending over ~1 mo beginning in mid-June (Figs. 1 and 2). Adults from the logs infested in October began emerging 1–2 wk after adults from the July logs, but the pattern of emergence was less synchronized than that of the beetles that emerged from July logs; small numbers of beetles from October 2000 logs continued to emerge through the spring and summer of 2002.

The February logs, although excluded from analysis, offer some interesting insights into the development of *P. recurva*. In southern California, *P. semipunctata* has only been observed from late April or early May until October (Hanks et al. 1993), so infesting logs with neonate *P. semipunctata* in February does not really reflect natural conditions. However, the February treatment was added to the experiment in an effort to have one set of logs that corresponded to the earliest beetle emergence in a calendar year. *P. recurva* beetles had been observed in the field as early as February in 2000. In addition, after a period of mild winter days in the first week of February 2001, adult *P. recurva* began to emerge from the logs infested in May 2000, thus confirming that *P. recurva* could indeed emerge during the winter months. During this same week in 2001, adult *P. recurva* were also collected from field populations.

Periods of increased temperature extending for several days to a week or more at this time of year are not uncommon and could be long enough for *P. recurva* to emerge, mate, and lay eggs. If this period of warm temperatures is long enough, *P. recurva* larvae may develop sufficiently to survive. Unfortunately, because of the time required to cut, dry, and infest the logs, there was an unavoidable 13-d period between the first recorded spring emergence (7 February 2001) and the day the logs were placed in the field (20 February 2001), by which time temperatures had dropped.

In the early winter of 2002, after 21 mo of little to no emergence from the February logs, the bark was removed from the logs infested with both *P. recurva* and *P. semipunctata* to determine the fate of the beetles. The site of infestation was easily found, with many small galleries tunneling away from the site in different directions, only to end after 2–3 cm, suggesting that the neonate and early-instar larvae were not able to survive the February conditions. These neonates came from laboratory colonies, and there was no concomitant mortality of larvae collected at the same time and used to infest logs for laboratory cultures of beetles. This suggested that the mortality in the logs held outdoors was not caused by poor-quality larvae, but rather, that the neonates were not able to survive the climatic conditions at that time of year.

The faster development time of *P. recurva*, its ability to emerge over a greater portion of the year, and the greater percentage of individuals that successfully complete development may all contribute to the increase of its populations in the habitat shared with *P. semipunctata* in southern California. For example,

logs infested with *P. recurva* in May 2000 and February 2001 had many beetles emerge the same year the logs were infested. In contrast, only one *P. semipunctata* beetle emerged the same year from the analogous sets of logs infested in May, and a few beetles emerged from the February 2001 logs at the end of the summer. This suggests that *P. semipunctata* may have an obligatory diapause. Once the larvae have excavated their pupation chambers, there is no evidence that they continue to feed or develop. Thus, mature larvae may remain quiescent in their pupation chambers for many months before resuming development to the relatively short pupal stage (several weeks; Hanks et al. 1991). It had been previously estimated that *P. semipunctata* might complete two or three generations per year in southern California (Hanks et al. 1990), based on laboratory rearing procedures in which temperatures were manipulated to force completion of development (Hanks et al. 1991, 1993). However, the data collected in this study suggest that this estimate was erroneous and that, in southern California, *P. semipunctata* may have only one generation per year, whereas *P. recurva* may complete one generation and begin a second generation. These relatively low numbers of generations, in contrast to data reported from other areas of the world where *Phoracantha* spp. have become established (Tunisia, Chararas 1969; Zambia, Loytyniemi 1980; Egypt, Helal and El-Sebay 1985; Israel, Mendel 1985) may be caused in part by the relatively low nighttime temperatures in southern California during a good part of the year (Fig. 3).

Although *P. semipunctata* emergence has been detected in southern California as early as late April (Hanks et al. 1993), in this study, *P. semipunctata* did not begin emerging until June. In contrast, *P. recurva* began emerging in February, and emergence of both species continued until October. In Israel, *P. semipunctata* was found to complete its development in as little as 100 d, with an estimated two or three overlapping generations per year. Adults were also detected laying eggs as early as March and as late as November (Mendel 1985). In the late summer and fall in both Israel and California, *P. semipunctata* delayed emergence until the following spring. However, in Israel, eggs laid in the spring through midsummer (March–June) completed development in ≈100 d so that adult beetles emerged in late summer of the same year. Our data suggest that this does not occur in California. Mendel (1985) suggested that temperature and bark moisture content were two major factors influencing the length of a generation, with three other factors (number of larvae per host, bark thickness, and eucalypt species) also probably contributing.

In Egypt, a 2-yr seasonal development study indicated that *P. semipunctata* had two or three overlapping generations per year (Helal and El-Sebay 1980). *P. semipunctata* was also reported to have a longer seasonal activity period in Egypt than in California. In Egypt, there were two main generations, the first from March until June and the second from August until December, and *P. semipunctata* was reported to esti-

vate during the hottest weather from June until August.

The biology of *P. semipunctata* in many parts of the world is relatively well studied compared with what is known about the biology of *P. recurva*. The earliest confirmed reports of *P. recurva* outside Australia were from Zambia in 1977 (Ivory 1977), but this and other studies (Loytyniemi 1980) were focused on pest management. There have not been reports from other locations of rapid population growth of *P. recurva* and simultaneous dramatic decline in the population levels of *P. semipunctata*, as we have documented in California. The differences in the biology of the two species under southern California environmental conditions may allow *P. recurva* to colonize and exploit available host resources during periods of the year when *P. semipunctata* is inactive. Early colonization of hosts confers a distinct advantage in interspecific competition for the eucalyptus cambium and inner bark tissues (Paine et al. 2001). Heavy infestations of *Phoracantha* larvae cause the destruction of virtually the entire cambium layer, indicating that it is a limited resource (Chararas 1969, Drinkwater 1975, Scriven et al. 1986). High densities of developing larvae result in larval cannibalism and reduced survival of smaller, less fit larvae (Powell 1982).

The community of herbivores that attack eucalyptus in California and their associated natural enemies is greatly simplified relative to what has been documented in Australia, and the biology of the species that are present in California seems to be different from what has been documented elsewhere. Consequently, it is possible that the balance of ecological factors regulating the populations may also be different in different parts of the world. In southern California, that balance of factors has resulted in rapid decline in populations of an initial colonizing species, *P. semipunctata*, and the rapid expansion of populations of a subsequent congeneric colonizer, *P. recurva*. Although competition or introduced natural enemies may be among the many possible factors contributing to the turnover in populations, the different responses of the two species to the novel environment may also be important.

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