Dispersal of the Eucalyptus Longhorned Borer (Coleoptera: Cerambycidae) in Urban Landscapes

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ABSTRACT
We conducted 2 mark–recapture experiments in urban landscapes to examine the dispersal behavior of the eucalyptus longhorned borer, *Phoracantha semipunctata* (F.), a crepuscular beetle whose larvae bore into woody tissues of stressed or weakened eucalypts and fallen branches. Temporal changes in attractiveness of trees to beetles resulted in a correlation between beetle abundance and sample date. A mark–recapture study revealed that rates of beetle recapture declined with increasing air temperature, suggesting that beetles were less likely to disperse long distances on cool evenings. Dispersal behavior was not influenced by body size of either sex; however, larger males were more likely to gain mates than were smaller males. Estimated population size averaged ~328 beetles per night. In another mark–recapture experiment, *P. semipunctata* were captured on 6 piles of eucalypt logs, 3 positioned inside a eucalypt grove and 3 outside. Males captured on the outside log piles were larger than those captured inside, suggesting that larger males were more likely to disperse longer distances than smaller males. Low 24-h recapture rates (<35%) of adult *P. semipunctata* in both experiments suggested that *P. semipunctata* dispersed actively in urban landscapes. These beetles may show little site fidelity because they must alternately search for vigorous eucalypts in flower on which they feed and for stressed larval hosts that are unpredictably distributed in time and space.

KEY WORDS
*Phoracantha semipunctata*, Cerambycidae, eucalyptus, wood boring, dispersal

Dispersal plays an essential role in the structure, dynamics, and evolution of insect populations (e.g., Denno and Peterson 1995, Thomas and Hanski 1997, Hanks and Denno 1998). Among cerambycid beetles, dispersal behavior of the adults appears to be related to the nature of the larval hosts (Hanks 1999). For example, larvae of *Semanotus japonicus* Lacordaire develop in living trees and adults may feed and oviposit on the same host plant individuals, and the predictability of this resource has apparently selected for a sedentary nature in adults (Shibata 1986a). In contrast, cerambycid species whose larval hosts are weakened or dying trees must seek different host individuals for feeding and ovipositing, and this dispersal requirement is reflected in their greater vagility (Hanks 1999). Examples of these latter species are *Callidium rufipenne* Motschulsky (Shibata 1994), *Hoplocherambyx spinicornis* Newman (Singh and Misra 1981), and *Monochamus alternatus* Hope (Shibata 1981, 1986b; Togashi 1990).

Larvae of eucalyptus longhorned borer, *Phoracantha semipunctata* (F.), mine the cambium of stressed or weakened eucalypts, fallen branches, or freshly cut eucalypt logs (see Hanks et al. 1993a, 1995). This beetle is one of the more destructive pests of eucalypts in the many regions of the world where eucalypts have been introduced (see Hanks et al. 1995). Eucalypt hosts from which adult *P. semipunctata* emerge are entirely unsuitable for further development of larvae because of degraded nutritional quality (Hanks et al. 1993b); adults must therefore disperse in search of new larval hosts. Larval hosts are an unpredictable and ephemeral resource because their availability depends on such fortuitous events as branch fall or environmental stresses that weaken eucalypts, and quality of the cambial tissues on which the larvae feed declines rapidly after death (see Hanks 1999). Thus, the earliest larvae to colonize a host plant will have a competitive advantage over later colonists in nutrition, as well as a size advantage in aggressive competition with conspecifics and other wood-boring species.

We hypothesize that spatial unpredictability and the ephemeral quality of larval hosts would select for strong dispersal abilities in adult *P. semipunctata*. In this article, we test this hypothesis by investigating the dispersal behavior of *P. semipunctata* in urban landscapes in which eucalypts are among the dominant tree species and the beetle is an economically important pest (Paine et al. 1995). We describe mark–recapture experiments that evaluate site fidelity and host consistency, adult feeding behavior, the influence of air temperature on dispersal behavior, the influence of body size on dispersal and mating success, and local population size. To further assess the influence of body size on reproduction, we examine the relationship between body size and mating success.

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Materials and Methods

First Mark–Recapture Experiment. We investigated dispersal patterns of adult *P. semipunctata* by marking and releasing individuals that were captured on 3 large *Eucalyptus viminalis* Labill. trees (>3 m in basal circumference) that stood within 12 m of one another on the campus of the University of California, Riverside. Eucalypts are abundantly planted on campus and many trees are large and mature. The 3 study trees had experienced a period of water deficit caused by failure of an irrigation system during early July 1990 and promptly became highly attractive to adult *P. semipunctata*. No other trees near our study trees were under attack by the beetle. Within a few weeks, all 3 trees were dead and larval densities were such that the crackling sound of their feeding could be heard from a distance of 4 m.

We collected *P. semipunctata* adults by hand from the lower 2.5 m of the tree trunks on 20 nights between 22 July and 28 August 1990. Capture of beetles was facilitated by their tendency to wander downward from upper branches, eventually reaching the lower trunk. On 18 nights, we collected beetles for 1 h after sunset; however, on the nights of 4 and 12 August 1990, we attempted to better measure total beetle abundance by collecting until no more beetles were present (confirmed by visual inspection of upper branches with binoculars and a powerful flashlight). Captured beetles were weighed and measured (total body length from the tip of the mandibles to the end of the elytra), uniquely marked with a paint-color and dot-pattern scheme (using model enamel; Testor’s, Rockford IL), and released on their original tree at ≈2300 hours of the same night they were captured. We tested for temporal patterns in the activity of adult *P. semipunctata* by regressing the number of beetles captured per night (using only the dates when we conducted 1-h samples) on sample day. We also tested for relationships between capture rate and ambient temperature using weather data from a weather station of the California Irrigation Management Information System (CIMIS) located ≈1 km from the study site. During sampling, wind speeds were moderate, averaging 1.45 ± 0.39 m/s.

We evaluated dispersal rates of adult *P. semipunctata* using recapture data. Because these beetles may live longer than 2 mo (Chararas 1969a, Hanks et al. 1993a), we assumed that beetles seen only once during the study had dispersed rather than died. We have not observed predation of the adults except when we have forced them to fly during the day and they were captured by birds. Presumably, adults would also be subject to predation by bats during aerial dispersal and large spiders on larval hosts.

We tested for linear relationships between the proportion of beetles recaptured each night and air temperature at dusk. Proportional recapture was calculated by dividing the number of individuals recaptured on a particular night (of those released the previous night) by the total number of beetles captured. This proportion would decline with emigration of previously captured beetles or immigration of new beetles into the area, both a result of dispersal behavior. We tested for body size effects on dispersal behavior by comparing average lengths of beetles seen only once with those of individuals captured 2 or more times.

Using the mark–recapture data, we were also able to study the following 4 other behaviors of *P. semipunctata* related to dispersal: (1) Some researchers claim that these beetles do not feed in the adult stage (Helal and El-Sebay 1980), whereas others report their feeding on eucalypt pollen and nectar (Chararas 1969a, Scriven et al. 1986). We have seen flower feeding in the field only once in 6 yr, but feeding may be difficult to observe if beetles feed high in the canopy after dusk. Adults do readily feed on nectar and eat anthers of eucalypt flowers in the laboratory (J.G.M. and L.M.H., unpublished data). Moreover, the brief longevity and low fecundity of starved *P. semipunctata* (Hanks et al. 1993a) suggests that feeding must be critical for reproduction. To confirm that wild beetles were feeding, we tested for changes in body mass of individual beetles captured at different times, using time intervals between captures of <4, 4–6, 7–9, 10–12, and >12 d and calculating proportional change in mass = (initial mass - final mass)/initial mass. Starved *P. semipunctata* gradually lose mass with age (unpublished data). (2) To determine whether beetles developed preferences for particular host trees (which would tend to restrict movement), we compared the proportion of times that beetles were captured twice on the same tree with that expected if they selected among the 3 host trees at random (resulting in 1/3 of recaptures being on the original host). (3) We evaluated the influence of body size on mating success by comparing body lengths of females and males that were never observed with a mate with those paired with at least 1 mate. (4) We estimated the size of the local *P. semipunctata* population (the number of beetles active within the ambit of the 3 host trees) using the Jolly–Seber method (Krebs 1989).

Second Mark–Recapture Experiment. We conducted another mark–recapture study to examine patterns of dispersal of *P. semipunctata* near a ≈3-ha grove of *Eucalyptus cladocalyx* F. Muller adjacent to the UC Riverside campus (Fig. 1). Eucalypts of a variety of species and sizes occurred within 1 km of this grove and were common in the surrounding urban landscape. *P. semipunctata* were active within the grove, with fallen branches and cut eucalypt logs quickly becoming infested with larvae (see Hanks et al. 1993b). We examined dispersal behavior by attracting beetles to piles of freshly cut logs of *Eucalyptus tereticornis* Small (6 logs, ≈2.5 m long, 30–40 cm circumference); 3 log piles were located inside the grove and another 3 piles were located 50–125 m outside the grove (Fig. 1). We positioned the outside log piles downwind (Fig. 1) so as not to lure beetles out of the grove but rather to intercept those that were either dispersing from the grove or originating from elsewhere (beetles undergoing longer range dispersal).

Our initial approach was to release laboratory-reared male *P. semipunctata* (uniquely marked with...
larval hosts within the grove or disperse out of the grove. To confirm that adult *P. semipunctata* were feeding on eucalypt pollen, we microscopically examined the frass deposited in petri dishes overnight, crushing it in water on a glass slide and identifying eucalypt pollen by exine shape (see Pryor 1976). We collected frass from 24 beetles, 12 captured inside and outside the grove.

Statistics. We used analysis of variance (ANOVA) to test differences between treatment means. The *F*<sub>max</sub>-test (Sokal and Rohlf 1995) was used to confirm that data satisfied the assumptions of ANOVA (sample variances not significantly different). Where data failed to meet ANOVA assumptions, we used the non-parametric Kruskal–Wallis method to test differences between means (PROC NPAR1WAY, SAS Institute 1988). The Tukey–Kramer method was used to identify significant differences among multiple means (SAS Institute 1988). Frequency data were tested using the G-test of independence (Sokal and Rohlf 1995). Linear relationships between variables were examined by regression analysis and curvilinear trends were tested by sequentially adding quadratic and cubic terms to the regression equation and independently testing their significance (PROC REG, SAS Institute 1988) to obtain the best fit equation (Sokal and Rohlf 1995). Only significant terms were included in the regression model.

We present means ± 1 SD except when means are being statistically compared, in which case we present means ± 1 SEM.

**Results**

First Mark–Recapture Experiment. On 37 nights, we collected 550 adult *P. semipunctata* from the 3 eucalypts, 174 females and 376 males (sex ratio 32% female). There were no temporal patterns in sex ratio other than somewhat higher values (44 and 46% female) during the first 2 sample dates (22 and 23 July). Females were ≈4% larger than males with body lengths averaging 2.33 ± 0.022 cm compared with 2.24 ± 0.019 cm for males (means significantly different, ANOVA *F* = 7.95, df = 1, 548; *P* = 0.005).

Insect abundance per night (1-h samples) varied from 2 to 47 beetles and when plotted against date described a nearly normal curve with a truncated leading edge (Fig. 2). This truncation was not natural, but occurred because the trees were already stressed and attracting beetles on the date we started capturing them. Capture rate was not correlated with ambient temperature at dusk (linear regression: *r* = 0.07; df = 20; *P* > 0.05). On the 2 nights that we conducted more complete collections (4 and 12 August 1990), we captured 68 and 107 beetles (respectively), ≈2–4 times the number collected during 1-h periods on adjacent nights. After ≈2330 hours, no more beetles were present on the trees. On all sampling nights, marked beetles released on host trees soon dispersed and few if any beetles were present after 2400 hours.

Male *P. semipunctata* were more likely than females to be captured more than once: 90% of females (156/
174) were captured only 1 time, 9% were captured twice and 1% were captured 3 times; however, 67% males (253/376) were seen once, 24% twice, 6% were seen 3 times, and 3% were seen 4–7 times (differences between sexes were significant, Kruskal–Wallis statistic = 31.2, \( P < 0.0001 \)). Beetles seen only once did not differ significantly in size from those that were recaptured more often (means 2.28 ± 0.026 and 2.26 ± 0.35 cm, respectively; ANOVA \( F = 0.16; \text{df} = 1, 228; P > 0.05 \)). This finding suggests that dispersal behavior was not influenced by body size. The maximum number of days between capture dates for individual females ranged from 1 to 19 d and averaged 6.42 ± 1.3 d, and from males ranged from 1 to 30 d and averaged 5.58 ± 0.44 d for males (means not significantly different, ANOVA \( F = 0.46; \text{df} = 1, 139; P > 0.05 \)). Beetle body mass varied by no more than 3.0% between capture dates separated by \(< 4 (N = 84), 4–6 (N = 36), 7–9 (N = 22), 10–12 (N = 17), \) and \( > 12 d (N = 17) \); mean proportional changes in mass not significantly different, ANOVA \( F = 0.86; \text{df} = 4, 191; P > 0.05 \)). Stability of body mass over time suggests that beetles had fed between capture dates.

Proportion of recaptured beetles declined with air temperature at dusk (Fig. 3; \( r^2 = 0.8; P < 0.001 \)), suggesting that warmer temperatures encouraged longer range dispersal, resulting in emigration or immigration of new beetles into the area. Both sexes showed a tendency to return consistently to a particular host tree, with 47.6% of multiply captured females (10/21) and 50.3% of males (90/179) recaptured on their original host rather than on one of the other 2 trees. For males, this proportion was significantly different from the value of \( \frac{1}{2} \) that would be expected if beetles chose randomly among the 3 host trees (G test; \( G = 22.9; P < 0.001 \)). Lack of statistical significance for females (G test; \( G = 1.91; P > 0.05 \)) may be due to smaller sample size.

Female P. semipunctata apparently had greater mating success than males: 44% of females (77/174) were paired with mates when captured compared with only 20% of males (74/376); number of paired individuals differ between the sexes because some individuals were paired with >1 mate). Females paired with different mates (on different nights) were \( \approx 10 \) larger on average than those seen with a mate only once or never (mean body lengths: 2.56 ± 0.062, 2.32 ± 0.032, and 2.31 ± 0.03 cm, respectively); however, size differences were not statistically significant (ANOVA \( F = 2.2; \text{df} = 2, 171; P > 0.05 \)). Males did show significant body size effects related to mating success (ANOVA \( F = 10.7; \text{df} = 2, 375; P < 0.0001 \)): individuals that were never observed with a mate (mean body length 2.20 ± 0.021 cm) were 8% smaller on average than those captured with 1 mate (2.37 ± 0.041 cm), and 16% smaller than males that had been paired with 2 mates (2.63 ± 0.12 cm). None of the 6 females and 8 males captured with >1 mate were observed with the same mate twice. Perhaps as a result of aggressive competition for mates, males were much more likely than females to be missing appendages (antennae, tarsi, legs), with 11.7% of males (44/376) showing such injuries compared with only 2.9% of females (5/174); differences significant, G test for independence, \( G = 14.0; P < 0.001 \).

Population size estimates (calculated by the Jolly–Seber method from capture data for 20 nights) ranged from 70 to 665, with an average of 328 ± 162 beetles.

Second Mark–Recapture Experiment. Of the 171 laboratory-reared male P. semipunctata released inside the eucalypt grove, only 12 (7%) were captured on sticky cards on the log piles. Seven beetles were captured on the night they were released, and the others were captured 2–4 d after release. Low recapture rates suggest that marked males dispersed from the grove soon after release and did not return.

Between 11 and 27 August 1992, we captured 42 female and 56 male P. semipunctata (45% female) on the log piles with sticky cards and by hand. As in the 1st mark–recapture experiment, females were slightly larger (\( \approx 9.6\% \)) than males, averaging 2.41 ± 0.049 cm long compared with 2.20 ± 0.048 cm (means significantly different, \( F = 8.45; \text{df} = 1, 96; P = 0.0045 \)). The 31 females captured inside the grove did not differ significantly in size from the 20 captured outside the grove (Fig. 4, top; averaging 2.40 ± 0.063 and 2.43 ± 0.06 cm, respectively; means not significantly differ-
linators such as honey bees, which commonly visit eucalypt flowers by more polyphagous pollinators, with eucalypt pollen in frass probably had been deposited in eucalypt flowers. Frass not containing pollen consisted of amorphous material. We conclude that this material was residue of the larval diet or wood fragments from the frass plug of the pupal chamber (ingested during emergence) because there have been no reports of adult P. semipunctata feeding on plant tissues other than eucalypt flowers and because freshly emerged adults caged without food produce similar frass for several days (L.M.H., unpublished data).

Discussion

Abundance of adult P. semipunctata on stressed eucalypts (in the 1st experiment) was strongly influenced by host condition, gradually declining with tree death and increasing larval density. Eucalypt logs also decline in attractiveness to P. semipunctata with time, becoming minimally attractive ~1 mo after cutting (Hanks et al. 1993b). Responses of adult beetles to eucalypts trees and logs is correlated with their quality as larval hosts: P. semipunctata larvae develop faster and reach a larger adult body size in freshly killed hosts compared with hosts that have been dead and allowed to desiccate for a longer period (Chararas 1969b; L.M.H., unpublished data).

Male P. semipunctata on eucalypt hosts outnumbered females in both experiments, and male-biased sex ratios on larval hosts have also been observed in other field studies of P. semipunctata (Hanks et al. 1993b, 1996a), as well as other cerambycid species (Hughes and Hughes 1982, Shibata 1994). Nevertheless, primary sex ratios of P. semipunctata usually approximate 1:1 (Helal and El-Sebay 1980, Hanks et al. 1993b). Biased sex ratios may be the result of females spending less time on larval hosts than males because greater nutritional requirements (related to oogenesis) necessitate their dispersing more often in search of flowering eucalypts for feeding. Moreover, males may be more abundant because their probability of encountering females, and hence reproductive success, is maximized by remaining on larval hosts.

On eucalypt trees (in the 1st experiment), larger males were more successful in gaining mates than were smaller males. Body size effects on male mating success is attributable to dominance relationships in aggressive competition for mates (Hanks et al. 1996b), resulting from the relative scarcity of females (see Lawrence 1986). Body size may also impart an advantage in long-range dispersal of males, as indicated by the larger size of males captured on log piles outside the eucalypt grove than inside in the 2nd experiment. Body size may not have influenced mating success of females (Fig. 4) because they were much less numerous than males and in demand.

Low recapture rates of P. semipunctata (<35%) on eucalypt trees (in the 1st experiment) and logs (in the 2nd experiment) suggest that these beetles are mobile and readily disperse through urban landscapes. Indeed, P. semipunctata are known to fly >5 km in search of suitable hosts for their larvae (Drinkwater 1975, Martinez-Egea 1982). The decline in recapture rates with increasing air temperature (in the 1st experi-
ment) suggests that beetles tended to undergo longer-range dispersal on warmer evenings. Although other researchers have reported temperature thresholds for flight by *P. semipunctata* of \(\approx 10 - 15^\circ\text{C}\) (Bytinski-Salz and Neumark 1952, Chararas 1969b, Løyttynieni 1983, González-Tirado 1990), nightly average temperatures were used in at least some of these studies, which may not accurately reflect conditions at dusk when beetles are active. The curvilinear relationship between recapture rate and air temperature in the current study (Fig. 3) suggests that aerial dispersal declines sharply as air temperature falls below \(\approx 22^\circ\text{C}\).

Recapture of 17 *P. semipunctata* \(>12\) d after their release (in the 1st experiment) can be taken as evidence that they were indeed feeding because starved *P. semipunctata* live \(<12\) d in the laboratory (Hanks et al. 1993a), and longevity would be still shorter in starved wild beetles that must expend energy in flight. Feeding was further shown by stability of body mass (in the 1st experiment) and verified by exines of eucalypt pollen in the frass of field captured beetles (in the 2nd experiment). Lower incidence of pollen in the frass of beetles captured outside compared with inside the eucalypt grove suggests that most beetles undergoing longer-range dispersal (travelling between eucalypt stands) have recently emerged and are in search of food. Energy derived from eucalypt flowers may power dispersal of *P. semipunctata* in their search for plants that are suitable hosts for their larvae.

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