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## The Effects of *Eucalyptus* Pollen on Longevity and Fecundity of *Eucalyptus* Longhorned Borers (Coleoptera: Cerambycidae)

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**ABSTRACT** The longevity and fecundity of adult *Phoracantha recurva* and *Phoracantha semipunctata* were strongly affected by diet. Female *P. recurva* fed a diet of *Eucalyptus* pollen and sucrose solution lived 34–56% longer than females fed diets containing other types of pollen, ground dog chow, or sucrose solution alone. Diet had no significant effect on longevity of *P. recurva* males. Similarly, longevities of *P. semipunctata* females were increased 48–71% on the *Eucalyptus* pollen diet compared with the other diets. Male *P. semipunctata* also lived longer on the *Eucalyptus* pollen diet than most of the other diets. Fecundity was dramatically affected by diet, with *P. recurva* females fed the *Eucalyptus* pollen diet laying  $\approx 4$ –8 times more eggs than females on the other diets. *Eucalyptus* pollen also increased the fecundity of *P. semipunctata* females  $\approx 3$ –5-fold. Diet resulted in only minor effects on egg size and percent egg hatch for both beetle species.

**KEY WORDS** insecta, *Phoracantha semipunctata*, *Phoracantha recurva*, pollen, nutrition, biological control, mass rearing

THE EUCALYPTUS LONGHORNED borers *Phoracantha semipunctata* F. and *Phoracantha recurva* Newman (Coleoptera: Cerambycidae) are native to Australia, where they develop in dead and dying *Eucalyptus* trees and slash (Wang et al. 1996, Wang 1998). Both species have been introduced accidentally into many other countries where *Eucalyptus* is grown, where in the absence of natural enemies both species have become moderate to severe pests, causing substantial mortality to *Eucalyptus* plantings (Chararas 1969a, 1969b; Drinkwater 1975; Scriven et al. 1986; Hanks et al. 1993b). Female beetles deposit eggs under exfoliating bark or in bark crevices, and the developing larvae feed in the cambium layers, rapidly girdling and killing infested trees. In contrast, the adult beetles feed on nectar and pollen, causing no apparent damage to their hosts (Scriven et al. 1986, Hanks et al. 1993a).

Attempts have been made to introduce and establish biological control agents for *Phoracantha* beetles in the countries in which the beetles have become significant pests, including South Africa, the countries around the Mediterranean sea, and the United States. For example, the egg parasitoid *Avetianella longoi* Siscaro (Hymenoptera: Encyrtidae) is now established in Italy and other Mediterranean countries (Longo et al. 1993), California (Hanks et al. 1995a, 1996), and South Africa (Hanks et al. 1996). Attempts have been made to introduce and establish parasitoids of *Phoracantha* larvae, including the wasp *Syngaster lepidus* Brullé

(Hymenoptera: Braconidae), in South Africa (Drinkwater 1975), Israel (Mendel 1987), and more recently, California (Hanks et al. 1996). Although evidence of breeding populations (empty cocoons, adult emergence holes) has been found in California (Hanks et al. 1996), it is uncertain whether the larval parasitoids have become permanently established in any of the countries in which they have been released.

Efforts to mass rear and establish natural enemies of *Phoracantha* beetles in exotic countries depend upon having a large and continuous source of beetle eggs and larvae as hosts for the parasitoids. Efficacious artificial diets for mass rearing the beetles have not yet been developed, and because of the beetles' long development times, artificial diets would probably be logistically impractical for large-scale rearing. Instead, methods of mass rearing both species of beetles on *Eucalyptus* logs have been developed (Hanks et al. 1993a). These methods consist of hand-infesting pre-conditioned logs with neonate larvae at a density that maximizes adult emergence and limits larval competition, storage of the infested logs under controlled temperature conditions for several months as the larvae develop, manipulation of temperatures to induce pupation and adult emergence, and collection of adults in emergence cages. The adults are then held with sucrose solution in mixed-sex cages for egg production.

The production of beetle eggs proved to be a limiting factor in efforts to mass rear the egg parasitoid *A. longoi*. Because of the substantial investment of time, labor, and facilities required to produce adult beetles, we reasoned that it might be more cost-effective to test methods of increasing egg production per female

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than to rear larger numbers of beetles. In the laboratory, female beetles lay as many as 30 eggs per day during their lifetimes of several weeks (Hanks et al. 1993a). We hypothesized that adult nutrition would be important in maximizing reproductive output, with ingested nutrients enhancing egg production. Adults of *Phoracantha* species, as with many species of the Cerambycinae, feed on nectar and pollen (Hanks 1999). Furthermore, frass from field-collected beetles consists primarily of exines of *Eucalyptus* pollen (Hanks et al. 1993a, 1998), indicating that pollen constitutes a significant proportion of the adult diet. We report here the results of a study designed to test the null hypotheses that dietary protein did not affect the longevity and fecundity of *P. semipunctata* and *P. recurva* under laboratory rearing conditions, and that all pollen sources, including host *Eucalyptus* pollen, were equivalent as sources of dietary protein for adult beetles.

### Methods and Materials

Adult beetles were collected daily as they emerged from logs held in large cages, with collected adults being segregated by species and sex. Newly emerged adults were held in groups of five females and three males in cylindrical hardware cloth cages (15 cm diameter  $\times$  15 cm high) with plastic Petri dish tops and bottoms (Hanks et al. 1993a). This sex ratio had been found to produce a vigorous, fertile colony (Hanks et al. 1993a). Because beetles hide under loose bark during daylight hours, a refuge consisting of a square of cardboard (6.5 cm  $\times$  6.5 cm) was clipped on the inside wall of each cage. The cage floor was lined with a 12.5-cm diameter circle of filter paper. Each cage contained a 9-cm diameter plastic Petri dish with a filter paper wrapped under the bottom and around the sides of the dish. The tight space between the paper-covered Petri dish and the filter paper floor provided the thigmotactic stimulus that females prefer for oviposition, and eggs were laid in batches sandwiched between the two papers. Cages were maintained in the laboratory under ambient light and temperature conditions ( $\approx 25^{\circ}\text{C}$  and 44%RH). To distinguish males within a cage, the three males were marked with different colors of Liquid Paper correction fluid. Males that died were replaced with fresh males as necessary to maintain the 5:3 ratio. Females that died were not replaced. The experiments were continued until all females had died.

Diet treatments consisted of: (1) sucrose solution (0.4 M in distilled water); (2) sucrose solution and granules of dog chow; (3) sucrose solution and mixed-composition bee pollen from the desert areas of the southwestern United States which could contain some *Eucalyptus* pollen; (4) sucrose solution and mixed composition bee pollen from British Columbia, Canada, which would not contain any *Eucalyptus* pollen; (5) sucrose solution and *Eucalyptus* pollen. Sucrose solution was dispensed from 10-ml glass vials, 1.5 cm diameter by 5 cm long, which were plugged with nonsterile cotton dental rolls, size #2, 3.5 cm long by

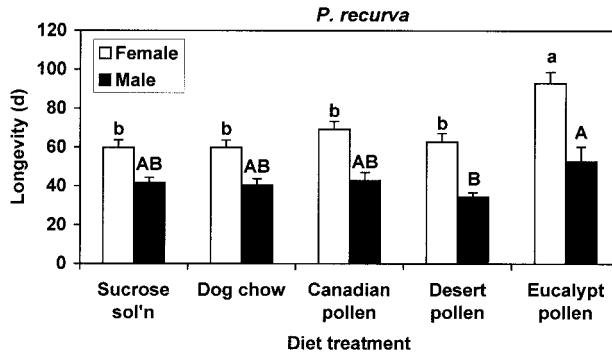
1 cm diameter (Patterson Dental Supply Co., St. Paul MN). Two vials of the solution were used in each cage of the sucrose solution only treatment. The Pedigree dog chow diet (Kal Can Foods Inc., Vernon CA; 21% protein) was ground briefly in a blender, then sieved through a Tyler Standard Screen Scale size seven into screen size eight to produce pellets averaging 3 mm in diameter, similar in size to the pollen granules (see below). The pollen diets consisted of granules of honey bee-collected pollen  $\approx 3$  mm in diameter, including a mixed-composition pollen from the southwestern deserts of the United States (High Desert Bee Pollen Granules, C.C. Pollen Co., Phoenix AZ; 17% protein), a mixed composition pollen from Canada (Chilliwack River Valley Raw Bee Pollen, Agnes Coutts, Sardis, B.C., Canada; protein content not listed), and Australian jarrah tree pollen (*Eucalyptus marginata* Sm.; Jarrah Tree Pollen, Great Health, Brea CA; 28.6% protein). Dog chow or pollen (0.13 g;  $\approx 16$ –20 granules) and one vial of sucrose solution were placed into the small Petri dish in each cage. All diets were replenished every second day for the duration of the study. All five diets were fed to both *P. semipunctata* and *P. recurva*, with 15 replicates of each diet per species. Diets were randomly assigned to cages. It was not possible to measure the amount of each diet consumed because the pollen and dog chow granules rapidly disintegrated as the beetles crushed them with their mandibles and the residue was mixed with beetle frass and dampened by fluid from the vials of sucrose solution.

Cages were checked every second day to assess beetle survival. Eggs were collected from the cages and counted every second day, and the mean numbers of eggs laid per 2-d period were calculated for females of both *P. semipunctata* and *P. recurva*. At the end of the experiments, average lifetime fecundities were determined for females of each species.

Every 2 wk, percent egg hatch was assessed by taking a subset of 10 eggs from each cage, still attached to slips of filter paper, and placing each slip into a plastic Petri dish sealed with Parafilm. The dishes were held under ambient laboratory light and temperature conditions for 10 d, by which time all viable eggs had hatched. The numbers of hatched and nonviable eggs were counted. To determine egg size, subsets of eggs (10 per cage) from randomly selected egg masses were gently separated, and the length and width of each egg was measured with a dissecting microscope fitted with a micrometer.

**Data Analysis.** Two-way analysis of variance (ANOVA) was used to test the effects of diet treatments and cage on adult longevity (SAS Institute 1996). Because it was not possible to determine which female in a cage laid a specific egg mass, differences in total fecundity among diet treatments were determined using one-way ANOVA using the cage as the replicate. Eggs were randomly selected from all cages and pooled for analysis using one-way ANOVA to test for differences in egg size and percent hatch. Differences between means were assessed with Tukey's tests (Sokal and Rohlf 1995). For each species, male and

A



B

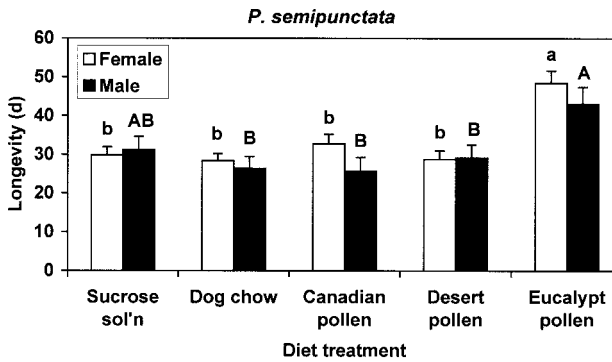


Fig. 1. Effects of diet on longevity of *Phoracantha recurva* (A) and *P. semipunctata* beetles (B). Data (mean  $\pm$  SE) for each species and sex were analyzed separately by two-way ANOVA, and differences between means were determined with Tukey's tests ( $\alpha = 0.05$ ). Bars surmounted by different letters are significantly different.

female survival on individual diets were compared by one-way ANOVA. Interspecific comparisons of longevity of male or female beetles on a particular diet, and fecundity of females on a particular diet, also were determined by one-way ANOVA.

Results

Diet had a significant effect on longevity of both beetle species (Fig. 1). *Phoracantha recurva* females lived longer (mean  $\pm$  SE, 93.0  $\pm$  5.8 d) on the *Eucalyptus* pollen diet than on any of the other four diets

(Fig. 1A and  $F = 11.30$ ,  $df = 4, 282$ ,  $P < 0.0001$ ). Mean longevities of females fed the other proteinaceous diets were not significantly different than the mean longevity of females fed only sucrose solution, suggesting that the other two types of pollen and the dog chow did not contribute significantly to the nutrition of females. In contrast, southwestern desert pollen was the only diet that resulted in reduced male *P. recurva* longevity compared with the *Eucalyptus* pollen diet ( $F = 2.51$ ,  $df = 4, 146$ ,  $P = 0.044$ ). The effect of cage was significant for both female ( $F = 4.03$ ,  $df = 12, 282$ ,  $P < 0.0001$ ) and male ( $F = 2.08$ ,  $df = 12, 146$ ,  $P = 0.02$ )

Table 1. Comparisons of adult beetle longevity on different diets, between *Phoracantha* species (ANOVA)

Diet additive <sup>a</sup>	Females	F	df	P	Males	F	df	P
<i>Eucalyptus</i> pollen	recurva > semipunc	46.28	1, 109	<0.0001	recurva = semipunc	1.29	1, 53	0.26
Desert pollen	recurva > semipunc	48.95	1, 117	<0.0001	recurva = semipunc	2.07	1, 58	0.15
Canadian pollen	recurva > semipunc	60.08	1, 117	<0.0001	recurva > semipunc	8.80	1, 56	0.004
Dog chow	recurva > semipunc	56.87	1, 133	<0.0001	recurva > semipunc	8.55	1, 63	0.005
Sucrose solution only	recurva > semipunc	46.06	1, 123	<0.0001	recurva > semipunc	5.70	1, 55	0.02

<sup>a</sup> All diets contained a vial of sucrose solution.

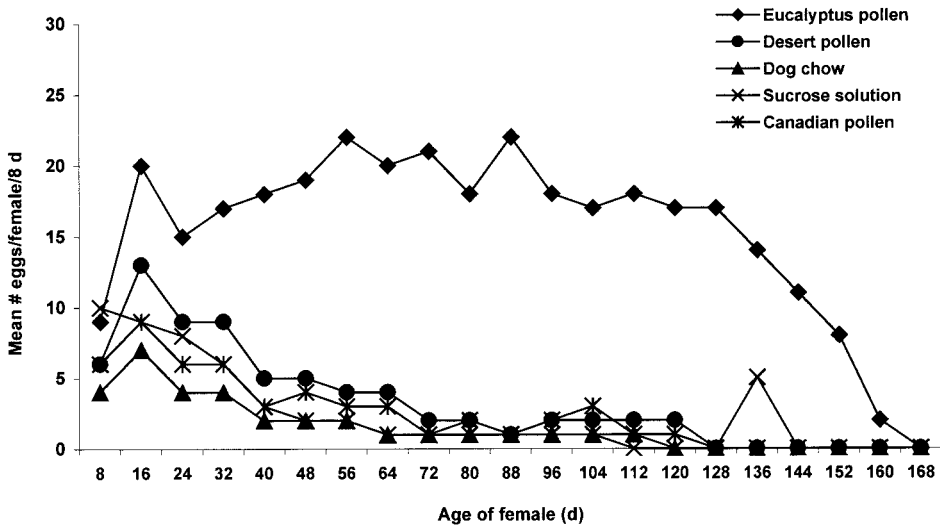


Fig. 2. Mean numbers of eggs produced every 8 d by *P. recurva* females fed on different diets. Eggs were collected every 2 d, but are shown in the figure as mean values calculated over 8 d to simplify the graphical presentation.

longevity. Overall, *P. recurva* females lived significantly longer ( $68.2 \pm 2.1$  d) than males ( $41.9 \pm 1.9$  d,  $F = 71.9$ ,  $df = 1, 460$ ,  $P < 0.0001$ ).

*Phoracantha semipunctata* females also survived longer when fed the *Eucalyptus* pollen diet than any of the other diets (Fig. 1B;  $F = 11.9$ ,  $df = 4, 305$ ,  $P < 0.0001$ ). Unlike *P. recurva* males, the longevity of *P. semipunctata* males was affected by diet, with males fed the *Eucalyptus* pollen diet living significantly longer than males fed diets containing Canadian pollen or dog chow ( $F = 4.05$ ,  $df = 4, 127$ ,  $P = 0.004$ ). The effect of cage was significant for both female ( $F = 3.41$ ,  $df = 12, 293$ ,  $P < 0.0001$ ) and male ( $F = 2.97$ ,  $df = 12, 115$ ,  $P = 0.0012$ ) longevity. For both species, some cages contained individuals that had relatively short

lives, while others had individuals which were very long-lived, resulting in a significant cage effect. The overall longevities of male ( $31.4 \pm 1.7$  d) and female *P. semipunctata* ( $33.2 \pm 1.1$  d) were not significantly different ( $F = 0.84$ ,  $df = 1, 440$ ,  $P = 0.36$ ).

Comparisons of the longevities of female beetles between *Phoracantha* species fed a particular diet revealed that *P. recurva* females lived significantly longer than *P. semipunctata* females on all of the five diets (Table 1). Male *P. recurva* lived significantly longer than *P. semipunctata* males on three of the five diets (sucrose solution alone, and sucrose solution plus either dog chow or Canadian pollen; Table 1).

Diet had a major effect on oviposition for both *P. recurva* (Fig. 2) and *P. semipunctata* (Fig. 3), and on

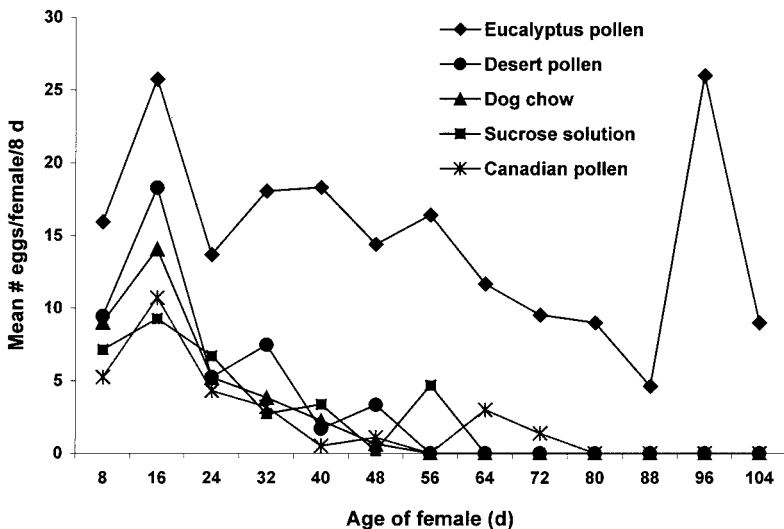


Fig. 3. Mean numbers of eggs produced every 8 d by *P. semipunctata* females fed on different diets. Eggs were collected every 2 d, but are shown in the figure as mean values calculated over 8 d to simplify the graphical presentation.

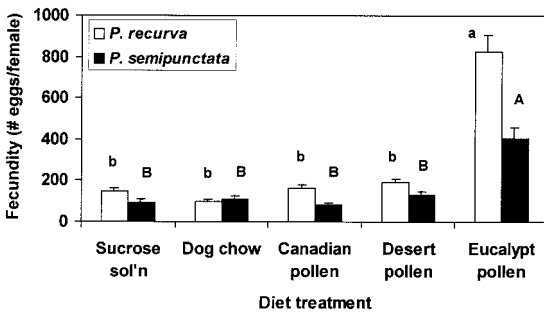


Fig. 4. Mean ( $\pm$ SE) lifetime fecundities of *P. recurva* and *P. semipunctata* fed on different diets. Data for each species were analyzed separately by ANOVA, and differences between means were determined with Tukey's tests ( $\alpha = 0.05$ ). Bars surmounted by different letters are significantly different.

the total lifetime fecundities per female (Fig. 4). Female *P. recurva* laid more than four times as many eggs when fed the *Eucalyptus* pollen diet throughout their lives than when fed any of the other diets ( $F = 67.00$ ,  $df = 4, 54$ ,  $P < 0.0001$ ). The total fecundities of females maintained on any of the other four diets were not significantly different. Analogous results were obtained with *P. semipunctata*; females fed the *Eucalyptus* pollen diet produced three to five times more eggs than females fed any of the other diets ( $F = 25.48$ ,  $df = 4, 58$ ,  $P < 0.0001$ ). There were no significant differences in total fecundities of females maintained on any of the other four diets. In comparisons between species fed a specific diet, *P. recurva* females laid significantly more eggs than *P. semipunctata* females when fed on the *Eucalyptus* pollen ( $F = 19.53$ ,  $df = 1, 21$ ,  $P = 0.0002$ ), the southwestern desert pollen ( $F = 7.61$ ,  $df = 1, 22$ ,  $P = 0.011$ ), the Canadian pollen ( $F = 14.97$ ,  $df = 1, 22$ ,  $P = 0.0008$ ), and the sucrose solution diet ( $F = 6.86$ ,  $df = 1, 23$ ,  $P = 0.015$ ).

For both species, egg size was relatively insensitive to diet (Table 2). The mean lengths and widths of eggs laid by female *P. recurva* on the different diets varied from 2.42 to 2.57 mm long and from 0.58 to 0.61 mm

wide, respectively. Although the eggs from females on the *Eucalyptus* pollen diet were significantly longer ( $F = 81.81$ ,  $df = 4, 2730$ ,  $P < 0.0001$ ) and wider ( $F = 41.44$ ,  $df = 4, 2730$ ,  $P < 0.0001$ ) than the other eggs, the relatively small variations in egg size with diet indicates that egg size was affected only slightly by diet. Similar results were obtained with *P. semipunctata* eggs (Table 2), which varied in mean length from 2.34 to 2.49 mm, and in width from 0.67 to 0.71 mm. The three pollen diets resulted in eggs that were significantly larger than those produced by females on the dog chow or sugar water diets (length,  $F = 25.24$ ,  $df = 4, 1,710$ ,  $P < 0.0001$ ; width  $F = 14.77$ ,  $df = 4, 1,710$ ,  $P < 0.0001$ ), but within the three pollen diets, eggs produced by females on the *Eucalyptus* pollen diet were similar in width to those produced by females fed southwestern desert pollen and similar in length to those produced by females fed Canadian pollen.

The percentages of egg hatch were uniformly high on all diets for both species (Table 3), and were minimally affected by diet. For *P. recurva*, mean egg hatch rates ranged from 87 to 93% on the five diets ( $F = 2.57$ ,  $df = 2, 287$ ,  $P = 0.038$ ). The mean hatch rate (93%) for *P. recurva* eggs from females fed on the *Eucalyptus* pollen diet was significantly higher than the hatch rate of eggs from the southwestern desert pollen and the other three treatments. For *P. semipunctata*, mean egg hatch rates ranged from 86 to 91% on the five diets (Table 3), with no significant differences between any of the treatments ( $F = 0.78$ ,  $df = 4, 150$ ,  $P = 0.54$ ).

## Discussion

There is abundant evidence that nectar and pollen constitute a major portion of the diet of adult *Phoracantha* (Chararas 1969b, Scriven et al. 1986, Hanks et al. 1993a). Adult *Phoracantha* have been observed feeding at *Eucalyptus* flower clusters without causing damage to the inflorescences, indicating that they were feeding on nectar and/or pollen rather than the flower tissues. Examination of the frass of field-col-

Table 2. Mean egg sizes for eggs laid by *Phoracantha recurva* and *P. semipunctata* females fed on different diets. Within each species, egg size data were analyzed by ANOVA, and means were separated with Tukey's test. Values followed by different letters are significantly different from each other ( $P = 0.05$ ).

Diet <sup>a</sup>	N	Width (mm)		Length (mm)	
		Mean $\pm$ SE	Range	Mean $\pm$ SE	Range
<i>P. recurva</i>					
Eucalypt pollen	1067	0.61 $\pm$ 0.001a	0.47-0.73	2.57 $\pm$ 0.006a	1.83-3.23
Desert pollen	501	0.58 $\pm$ 0.002b	0.47-0.70	2.42 $\pm$ 0.008b,c	2.00-3.00
Canadian pollen	518	0.58 $\pm$ 0.002b	0.50-0.70	2.45 $\pm$ 0.008b,c	1.97-3.00
Dog chow	287	0.58 $\pm$ 0.003b	0.47-0.70	2.46 $\pm$ 0.011b	2.00-2.97
Sucrose solution only	362	0.58 $\pm$ 0.003b	0.47-0.70	2.42 $\pm$ 0.011c	2.00-3.17
<i>P. semipunctata</i>					
Eucalypt pollen	673	0.69 $\pm$ 0.002b	0.50-0.83	2.49 $\pm$ 0.006a	2.00-2.90
Desert pollen	366	0.69 $\pm$ 0.002b	0.57-0.87	2.39 $\pm$ 0.008b,c	2.00-2.87
Canadian pollen	161	0.71 $\pm$ 0.004a	0.57-0.87	2.42 $\pm$ 0.016a,b	2.00-3.00
Dog chow	249	0.68 $\pm$ 0.003c	0.57-0.83	2.36 $\pm$ 0.012c,d	2.00-2.83
Sucrose solution only	266	0.67 $\pm$ 0.003c	0.50-0.83	2.34 $\pm$ 0.011d	1.83-2.73

<sup>a</sup> All diets contained sucrose solution.



Table 3. Effect of diet on percent egg hatch for eggs laid by *Phoracantha recurva* and *P. semipunctata* females. Within each species, egg hatch data were analyzed by ANOVA, and means were separated with Tukey's tests. Values followed by different letters are significantly different from each other ( $P = 0.05$ )

Diet <sup>a</sup>	<i>P. recurva</i>			<i>P. semipunctata</i>		
	N <sup>b</sup>	Percent hatch	Range	N <sup>b</sup>	Percent hatch	Range
Eucalypt pollen	108	93 ± 1a	60–100	61	91 ± 2	43–100
Desert pollen	51	87 ± 3b	9–100	26	91 ± 2	64–100
Canadian pollen	50	93 ± 1a,b	63–100	11	91 ± 4	64–100
Dog chow	43	91 ± 2a,b	57–100	24	86 ± 4	25–100
Sucrose solution only	40	93 ± 1a,b	60–100	33	90 ± 2	70–100

<sup>a</sup> All diets also contained sucrose solution.

<sup>b</sup> The total number of egg masses that were sampled for each species and diet.

lected beetles determined that it was largely composed of the exines of *Eucalyptus* pollen, clearly indicating that it constitutes a major portion of the diet of adult beetles (Hanks et al. 1993a, 1998). Furthermore, although *P. semipunctata* adults in a laboratory colony were observed to feed on pollen collected by honey bees (mostly from plants of the Asteraceae), they apparently were unable to assimilate the nutrients efficiently because a diet of honey bee pollen and sucrose solution did not improve survivorship over sucrose solution alone (Hanks et al. 1993a).

In the study described here, the *Eucalyptus* pollen diet clearly increased longevity and fecundity of *P. recurva* and *P. semipunctata* in comparison to the other diets. It is unlikely that the effects were a result of differences in the ability of the beetles to locate the various pollens or the dog chow granules using olfactory cues because the beetles were confined in small cages, so that they inevitably contacted the food sources while moving around the cages. Consequently, the effects of diet were most likely a result of differences in feeding stimulation or nutritional quality, or both. Either factor would be predicted to increase fecundity, the first by increasing the intake of nutrients for assimilation (assuming that each of the five diets would have some nutritional value), and the second by providing nutrients that were assimilated most efficiently into eggs. What was not expected was that the differences between the different pollen types would be so dramatic.

Pollen feeding is common in invertebrates, with pollen providing amino acids and proteins, lipids, carbohydrates, sterols, vitamins, and minerals (Dobson and Peng 1997, Roulston and Cane 2000). Indeed, many insects require pollen feeding for survival and maturation of eggs. For example, pollen feeding has been shown to influence both the longevity and lifetime fecundity of insects as diverse as *Heliconius* butterflies (Boggs 1987), weevils (Dobson 1994), and thrips (Kirk 1985, Leskey et al. 1997). However, pollens may vary widely in their suitability and acceptability as sources of nutrients. In particular, some insects and mites that specialize on only a few host plant species undergo optimal development and reproduction on pollen from their specific hosts (Kirk 1985, Grout and Richards 1992, James and Whitney 1993, Yue et al. 1994, Bruce-Oliver et al. 1996, Leskey et al. 1997, Grafton-Cardwell et al. 1999, Broufas and

Koveos 2000), whereas generalists tend to be more catholic in their acceptance and utilization of pollen from a variety of sources (Kirk 1985). However, the exact mechanisms that are involved in assessing and choosing pollens as nutritional sources are not well understood. There is evidence to suggest that insects use pollen odors to locate pollen (Dobson 1994, Dobson and Bergstrom 2000), and specific pollens also have been shown to contain feeding stimulants (Lin and Mullin 1999, Hollister and Mullin 1999, Dobson and Bergstrom 2000). However, the relative importance of olfactory versus gustatory cues for pollen feeding insects, and the interplay between the two types of cues, remains largely unknown (Lin and Mullin 1999).

The improved performances of the *Phoracantha* beetles when fed *Eucalyptus* pollen are most easily understandable when placed in the context of their native habitat, Australia, where eucalypts dominate the temperate and subtropical forest. In California and other areas into which both *Eucalyptus* and *Phoracantha* beetles have been introduced, the close association between the beetles and their host trees has persisted. The beetles apparently have not expanded their range of acceptable hosts in areas where they have been introduced (Hanks et al. 1995b), despite the fact that *Eucalyptus* trees represent a scarcer resource in these novel countries.

Our discovery that *Eucalyptus* pollen greatly increases the fecundity and longevity of *Phoracantha* beetles has increased the efficiency of our mass rearing of both egg and larval parasitoids of the beetles. The approximate quadrupling of the number of eggs obtained from each female beetle has enabled us to rear and release >200,000 egg parasitoids and 10,000 larval parasitoids annually, with minimal increase in the labor or materials required.

#### Acknowledgments

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## References Cited

- Boggs, C. L. 1987. Ecology of nectar and pollen feeding in lepidopteran species, pp. 369–391. In F. Slansky Jr. and J. G. Rodriguez [eds.], *Nutritional ecology of insects mites, spiders, and related invertebrates*, Wiley, NY.
- Broufas, G. D., and D. S. Koveos. 2000. Effect of different pollens on development, survivorship, and reproduction of *Euseius finlandicus* (Acari: Phytoseiidae). *Environ. Entomol.* 29: 743–749.
- Bruce-Oliver, S. J., M. A. Hoy, and J. S. Yaninek. 1996. Effect of some food sources associated with cassava in Africa on the development, fecundity, and longevity of *Euseius fustis* (Acari: Phytoseiidae). *Exp. Appl. Acarol.* 20: 73–85.
- Chararas, C. 1969a. Étude biologique de *Phoracantha semipunctata* F. (Coléoptère Cerambycidae xylophage) spécifique des Eucalyptus en Tunisie et recherches sur la vitalité et l'adaptation de ces essences. *Comptes Rendus Acad. Agric. France* 55: 47–57.
- Chararas, C. 1969b. Biologie et écologie de *Phoracantha semipunctata* F. (Coléoptère Cerambycidae xylophage) ravageur des *Eucalyptus* en Tunisie, et méthodes de protection des peuplements. *Annales de l'Institut National de Recherches Forestières de Tunisie* 2: 1–37.
- Dobson, H.E.M. 1994. Floral volatiles in insect biology, pp. 47–81. In E. A. Bernays (ed.), *Insect-Plant Interactions*, vol. V. CRC, Boca Raton, FL.
- Dobson, H.E.M., and G. Bergstrom. 2000. The ecology and evolution of pollen odors. *Plant Syst. Evol.* 222: 63–87.
- Dobson, H.E.M., and Y.-S. Peng. 1997. Digestion of pollen components by larvae of the flower-specialist bee *Cheilosoma florissomne* (Hymenoptera: Megachilidae). *J. Insect Physiol.* 43: 89–100.
- Drinkwater, T. W. 1975. The present pest status of eucalyptus borers *Phoracantha* spp. in South Africa, pp. 119–129. In *Proceedings of the 1st Congress of the Entomology Society of South Africa*. Entomology Society of South Africa, Pretoria, South Africa.
- Grafton-Cardwell, E. E., Y. Ouyang, and R. L. Bugg. 1999. Leguminous cover crops to enhance population development in *Euseius tularensis* (Acari: Phytoseiidae). *Biol. Control* 16: 73–80.
- Grout, T. G., and R. I. Richards. 1992. The dietary effect of windbreak pollens on longevity and fecundity of a predacious mite *Euseius addoensis addoensis* (Acari: Phytoseiidae) found in citrus orchards in South Africa. *Bull. Entomol. Res.* 82: 317–320.
- Hanks, L. M. 1999. Influence of the larval host plant on reproductive strategies of cerambycid beetles. *Annu. Rev. Entomol.* 44: 483–503.
- Hanks, L. M., J. S. McElfresh, J. G. Millar, and T. D. Paine. 1993a. *Phoracantha semipunctata* (Coleoptera: Cerambycidae), a serious pest of Eucalyptus in California: biology and laboratory-rearing procedures. *Ann. Entomol. Soc. Am.* 86: 96–102.
- Hanks, L. M., T. D. Paine, and J. G. Millar. 1993b. Host species preference and larval performance in the wood-boring beetle *Phoracantha semipunctata* F. *Oecologia (Berl.)* 95: 22–29.
- Hanks, L. M., J. R. Gould, T. D. Paine, J. G. Millar, and Q. Wang. 1995a. Biology and host relations of *Avetianella longoi* (Hymenoptera: Encyrtidae), an egg parasitoid of the Eucalyptus longhorned borer (Coleoptera: Cerambycidae). *Ann. Entomol. Soc. Am.* 88: 666–671.
- Hanks, L. M., J. G. Millar, and T. D. Paine. 1995b. Biological constraints on host-range expansion by the wood-boring beetle *Phoracantha semipunctata* (Coleoptera: Cerambycidae). *Ann. Entomol. Soc. Am.* 88: 183–188.
- Hanks, L. M., T. D. Paine, and J. G. Millar. 1996. Tiny wasp helps protect eucalypts from eucalyptus longhorned borer. *Calif. Agric.* 50 (May–June): 14–16.
- Hanks, L. M., J. G. Millar, and T. D. Paine. 1998. Dispersal of the *Eucalyptus* longhorned borer (Coleoptera: Cerambycidae) in urban landscapes. *Environ. Entomol.* 27: 1418–1424.
- Hollister, B., and C. A. Mullin. 1999. Isolation and identification of primary metabolite feeding stimulants for adult western corn rootworm, *Diabrotica virgifera virgifera* Lecont, from host pollens. *J. Chem. Ecol.* 25: 1263–1280.
- James, D. G., and J. Whitney. 1993. Cumbungi pollen as a laboratory diet for *Amblyseius victoriensis* (Womersley) and *Typhlodromus doreanae* Schicha (Acari: Phytoseiidae). *J. Austral. Entomol. Soc.* 32: 5–6.
- Kirk, W.D.J. 1985. Pollen feeding and the host specificity and fecundity of flower thrips (Thysanoptera). *Ecol. Entomol.* 10: 281–290.
- Leskey, T. C., D. A. Teulon, and E. A. Cameron. 1997. Effects of temperature and sugar maple pollen on oviposition and longevity of pear thrips (Thysanoptera: Thripidae). *Environ. Entomol.* 26: 566–571.
- Lin, S., and C. A. Mullin. 1999. Lipid, polyamide, and flavonol phagostimulants for adult western corn rootworm from sunflower (*Helianthus annuus* L.) pollen. *J. Agric. Food Chem.* 47: 1223–1229.
- Longo, S., V. Palmeri, and D. Sommariva. 1993. Sull'attività di *Avetianella longoi* ooparasitoide di *Phoracantha semipunctata* nell'Italia meridionale. *Redia* 76: 223–239.
- Mendel, Z. 1987. Major pests of man-made forests on Israel: origin, biology, damage, and control. *Phytoparasitica* 15: 131–137.
- Roulston, T. H., and J. H. Cane. 2000. Pollen nutritional content and digestibility in animals. *Plant Syst. Evol.* 222: 187–209.
- SAS Institute. 1996. SAS user's guide for statistics, release 6.13 edition. SAS Institute, Cary, NC.
- Scriven, G. T., E. L. Reeves, and R. F. Luck. 1986. Beetle from Australia threatens *Eucalyptus*. *Calif. Agric.* 40 (July–August): 4–6.
- Sokal, R. R. and F. J. Rohlf. 1995. *Biometry*, 3rd ed. W. H. Freeman and Co., New York.
- Wang, Q. 1998. The phoracanthine beetles (Coleoptera: Cerambycidae: Cerambycinae): taxonomic overview and generic relationships. *Invert. Taxon.* 12: 667–684.
- Wang, Q., I.W.B. Thornton, and T. R. New. 1996. Biogeography of the Phoracanthine beetles (Coleoptera: Cerambycidae). *J. Biogeog.* 23: 75–94.
- Yue, B., C. C. Childers, and A. H. Fouly. 1994. A comparison of selected plant pollens for rearing *Euseius mesembrinus* (Acari: Phytoseiidae). *Int. J. Acarol.* 20: 103–108.

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