



# The effect of host size on the sex ratio of *Syngaster lepidus*, a parasitoid of Eucalyptus longhorned borers (*Phoracantha* spp.)

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## Abstract

The solitary larval ectoparasitoid, *Syngaster lepidus* Brullé, parasitizes the cryptic larvae of two wood-boring beetles, *Phoracantha recurva* Newman and *Phoracantha semipunctata* F. The objective of this study was to determine how the female parasitoids allocated the sex of progeny when presented with larval hosts of uniform size classes. Host size was directly correlated with age of the *Phoracantha* larval hosts. Groups of *Phoracantha* larvae of a single age class (2-, 3-, 4-, or 5-week-old) were exposed to parasitoids, and sex ratios of the resulting parasitoid progeny from each host age class were determined. A significant relationship was observed among the sizes of *P. recurva* and *P. semipunctata* hosts and the sex ratio of emerging parasitoids. Parasitized 2-week-old beetle larvae of both *Phoracantha* spp. produced only male *S. lepidus* progeny, whereas older larval hosts produced increasing proportions of female parasitoids (up to ~80% females from 5-week-old hosts). Two-week-old *Phoracantha* larvae of both species produced fewer parasitoids than host larvae 3–5-week-old. The size of parasitoid progeny consistently increased with host larval age (size), and female parasitoids were larger than males across all host size classes. Male *S. lepidus* developed in approximately 25 days from 2-week-old hosts, and 19–21 days in 3–5-week-old hosts. Female *S. lepidus* developed in 22–25 days, with developmental time increasing with host size. © 2002 Elsevier Science (USA). All rights reserved.

**Keywords:** Host size; *Phoracantha recurva*; *Phoracantha semipunctata*; Eucalyptus; *Syngaster lepidus*; Sex ratio; Biological control; Sex allocation

## 1. Introduction

A number of factors have been shown to influence the sex ratio of offspring of hymenopteran parasitoids. Distorted sex ratios have been associated with parental factors such as maternal age, size, number of matings, and with environmental effects including temperature, photoperiod, humidity, and seasonal influences (King, 1987). Hymenopteran sex ratios are also influenced by extrachromosomal genetic elements, which can result in either male biased, ‘paternal sex ratios,’ or female biased ‘maternal sex ratios’ (Godfray, 1994). Furthermore, the bacteria *Wolbachia* can cause thelytokous, all-female parasitoid strains such as those observed in *Trichogramma* (Stouthamer et al., 1999). It also has been hypothesized that the morphology of the spermatheca,

eggs, and oviducts may influence the percentage of eggs fertilized and thus the sex ratio (Flanders, 1956; King, 1961). Furthermore, a key environmental factor that has been demonstrated to affect the sex allocation of hymenopteran parasitoid progeny for solitary parasitoids, which oviposit one egg per host, is the size or quality of the host (Charnov et al., 1981).

Hymenoptera are haplodiploid, with fertilized eggs resulting in female offspring, and unfertilized eggs yielding males. Females may adjust progeny sex ratios in response to cues obtained during oviposition. Idiobiont parasitoids paralyze the host before ovipositing, and their offspring develop in a limited resource. These parasitoids typically allocate male progeny to smaller or lower quality hosts, while reserving female offspring for larger hosts, in accordance with the host size hypothesis proposed by Charnov et al. (1981). Charnov’s hypothesis specifically concerns solitary parasitoids, whereas gregarious parasitoids that oviposit more than one egg per host, adjusting clutch size and sex ratio to the

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available host resource, are often better addressed by Hamilton's (1967) local mate competition theory.

The host size theory has been tested with several hymenopteran parasitoids (Heinz and Parrella, 1990; King, 1990; Opp and Luck, 1986; Urano and Hiji, 1995), and the mechanisms involved in sex allocation have been investigated. In several systems, differential mortality between males and females has been eliminated as the factor responsible for the high proportion of males observed on smaller hosts (Heinz and Parrella, 1990; King, 1990; Opp and Luck, 1986). Physical cues, such as measurement of host length or curvature (Sandlan, 1979; Schmidt and Smith, 1987), and mechanical stimulation by host movement (Sugimoto et al., 1988, van den Assem, 1971) may be used by ovipositing females to assess host size and quality. Alternatively, chemical cues associated with hosts may be involved in the determination of host suitability (Chow and Mackauer, 1999; Field and Keller, 1999; van Baaren and Boivin, 1998).

The parasitoid wasp *Syngaster lepidus* Brullé (Hymenoptera: Braconidae = *Iphiaulax rubriceps* Froggatt), is a solitary ectoparasitoid, whose native distribution includes the eastern, southeastern, and southwestern portion of Australia and Tasmania (Austin et al., 1994). *Syngaster lepidus* was imported into California as a biological control agent for two adventive beetle species, *Phoracantha semipunctata* F. and more recently, *Phoracantha recurva* Newman (Coleoptera: Cerambycidae). These two species, also native to Australia, were first detected infesting Eucalyptus trees in California around 1984 (Scriven et al., 1986) and 1995 (Hanks et al., 1997), respectively. The larvae develop in a concealed environment under the bark, feeding on cambium and bark tissues (Froggatt, 1916). *Syngaster lepidus* uses its ovipositor to probe through the tree bark into the cambium containing host larvae. A host larva is injected with a paralyzing venom, and an egg is oviposited external to the immobilized host. The parasitoid larvae feed by consuming host fluids and tissue, and pupate within the larval gallery. Adult *S. lepidus*, which vary widely in size, are known to attack larvae of *Phoracantha* spp. (Moore, 1972), but there is no information about host size preference.

The theory proposed by Charnov et al. (1981) suggests that if a female parasitoid is presented with a range of host sizes, she will allocate female progeny to relatively large hosts and male progeny to relatively small hosts. The first objective of this study was to determine whether there was also a relationship between parasitoid sex ratio and larval host size for cohorts of female parasitoids presented with uniform sized hosts, using a system with concealed larval hosts. A second objective was to determine if there were differences between the suitability and acceptability of the two *Phoracantha* beetle species as hosts for the parasitoid. The results also have direct practical application; maintaining a female-

biased sex ratio of *S. lepidus* progeny is crucial for maximizing the production of adult female parasitoids for field releases (King, 1987). We measured the sizes of *Phoracantha* spp. larval hosts aged 2-, 3-, 4-, and 5-week-old at the time of parasitization, and determined the sex ratio of emerging parasitoid offspring from each *Phoracantha* larval age class. The effects of host size on male and female parasitoid progeny size and developmental times were also determined.

## 2. Materials and methods

### 2.1. Infesting logs with host larvae

Fresh cut log sections (~10 cm diameter × 40 cm long) of *Eucalyptus camaldulensis* were taken from a study site in Temecula, California in September, 1999. One hundred logs were stood on end on absorbent paper in the laboratory at  $27 \pm 2^\circ\text{C}$  and 50% RH (L14:D10) to drain excess water from the wood. The beetle larvae will not survive in logs with excessive moisture (Hanks et al., 1999). After drying for 10 days, the cut ends of the logs were dipped in melted Parowax paraffin wax, to seal the log and maintain residual log moisture.

Logs were infested with newly emerged *Phoracantha* larvae (< 48 h since hatch) the day following waxing at a density of one larva per 66 cm<sup>2</sup> of bark area, which had been previously determined to be optimal for larval survival (Hanks et al., 1993), resulting in approximately 25 larvae introduced per log. A utility knife was used to make an incision in the side of each log approximately 5 cm long × 0.5 cm deep into which neonate larvae were transferred with a fine paintbrush. Half the number of larvae assigned to each log were placed into one side of the log, and the following day the remaining larvae were deposited into another incision in the opposite side of the log. A piece of paper towel was stapled over each incision to prevent disturbance of the larvae. Fifty logs were infested with larvae of *Phoracantha semipunctata*, while another 50 were inoculated with *P. recurva*. All logs containing larvae were incubated in a greenhouse at  $27 \pm 2^\circ\text{C}$  and 50% RH for 2–5 week, depending on the treatment.

### 2.2. Host size determination

Beetle larval size at the time of parasitization could not be measured directly because larvae were concealed under the outer bark. Consequently, larval age was used as a proximate variable for larval size, and so it was necessary to establish the relationship between larval age and size, which was determined as follows. Larval gallery sizes and larval weight were measured from larvae in nonparasitized control logs that were prepared simultaneously with the logs used in the parasitization

trials. Thirty sets of measurements from each larval age category (2-, 3-, 4-, or 5-week) were obtained, by measuring widths of six randomly chosen galleries, and weighing the larvae removed from each gallery, on each of five logs containing each host size. Bark was chiseled off the logs to expose beetle larvae and galleries, and the larval galleries were measured at the widest point.

### 2.3. Parasitization of beetle larvae

One parasitoid oviposition cage (100 × 80 × 80 cm) was utilized for each host species. The top, sides, and backs of the cages were covered with nylon organdy. A Plexiglas door enclosed the front of the cage. Each week, five logs containing larvae of only one age (either 2-, 3-, 4-, or 5-week) were placed into each cage. For each trial, each cage housed 20 female and 10 male parasitoids of mixed ages randomly selected from a laboratory colony of *S. lepidus* reared on *P. semipunctata* and *P. recurva*. Based on preliminary data, the number of larvae available for parasitization was approximately twice what the number of females was capable of utilizing as hosts during the test intervals. Thus, the resulting sex ratio of progeny is an average of the decisions made by all females in the presence of an excess of uniformly sized hosts.

In the first week of the study, parasitoids were offered five logs that contained 2-week-old *Phoracantha* larvae. Parasitoids were allowed to oviposit for 4 days, then wasps were removed and frozen. Logs containing parasitized hosts were transferred to an emergence box (see below) for collection of parasitoid offspring, and larvae were only used for one trial. This procedure was repeated each week, but with logs containing 3-, 4-, or 5-week-old larvae, respectively. A new group of wasps was used for each trial.

### 2.4. Parasitoid emergence

To monitor parasitoid emergence, the logs from each trial were placed as a group in lidded cardboard emergence boxes (60 × 60 × 45 cm), and maintained in a greenhouse at 27 ± 2°C and 50% RH. The top side of each box had a 1 liter glass jar attached, which was monitored daily to collect the emerging, positively phototactic parasitoid adults. Wasp collection was terminated after no parasitoids had emerged from a particular set of logs for two consecutive weeks. The length of the right hind tibia of each collected parasitoid progeny was measured as an indicator of wasp size. Voucher specimens were deposited in the Entomology Museum, University of California, Riverside.

### 2.5. Data analyses

Analyses of variance (ANOVA) followed by Tukey's separation of means tests (SAS Institute, 1996) were

used to compare gallery widths across the four larval age classes within beetle species, as well as within an age class between the two species (*P. recurva* and *P. semipunctata*). Similarly, ANOVAs were used to compare larval weights across age classes within species, and between the two beetle species for each larval age class. Correlation and regression analyses were used to determine if there was a relationship between the more easily measured variable that remains etched into the log surface (larval gallery width) and the concealed biologically transient variable assessed by the wasp (larval size). Correlation coefficients were compared between the two *Phoracantha* spp. by testing for homogeneity of correlation coefficients using a Fischer's *z* transformation, which uses a  $\chi^2$  test statistic (Sokal and Rohlf, 1981).

Sex ratios are reported as the proportion of male parasitoids emerging from each host larval size. A chi-squared analysis was used to determine if the sex ratio (proportion male) differed from 50% in each age category within a species, and to examine differences in the proportion of males emerging from an age class (i.e. 2-week-old larvae) between the two *Phoracantha* species. The overall sex ratio for parasitoids emerging from each of the two hosts was also calculated.

The mean sizes of male and female parasitoid progeny emerging from different larval ages were compared with ANOVA, with means separated by Tukey's tests, within a beetle species across age classes, and among beetle species for each age class. Similarly, mean developmental times were determined for wasps, and calculated as the number of days from first oviposition to the day that adult parasitoids emerged. ANOVA was used to detect significant differences in developmental times of individuals emerging from the four larval age classes. All statistical comparisons in this study are made at a significance level of 0.05.

## 3. Results

### 3.1. Host size determination

Larval gallery widths increased significantly with each larval age class within both beetle species (*P. recurva*,  $F = 78.59$ ,  $df = 3, 115$ ,  $P < 0.0001$ ; *P. semipunctata*,  $F = 101.82$ ,  $df = 3, 116$ ,  $P < 0.0001$ ) (Table 1). Comparisons of the gallery widths in a single age class (e.g., 2-week-old larvae) between the two *Phoracantha* spp. demonstrated that *P. semipunctata* had larger larval gallery widths than *P. recurva* in the 2 and 5 week age classes (2 weeks,  $F = 6.24$ ,  $df = 1, 57$ ,  $P = 0.02$ ; 5 weeks,  $F = 6.88$ ,  $df = 1, 58$ ,  $P = 0.01$ ), whereas gallery widths of 3- and 4-week-old larvae were not significantly different (3 weeks,  $F = 0.09$ ,  $df = 1, 58$ ,  $P = 0.76$ ; 4 weeks,  $F = 1.70$ ,  $df = 1, 58$ ,  $P = 0.20$ ).

Table 1  
Host gallery width and larval weight (mean  $\pm$  SE) of four larval age classes for *P. recurva* and *P. semipunctata*<sup>a</sup>

N	Larval age (week)	Gallery width (cm)		Larval weight (g)	
		<i>P. recurva</i>	<i>P. semipunctata</i>	<i>P. recurva</i>	<i>P. semipunctata</i>
29	2	0.27 $\pm$ 0.01a	0.31 $\pm$ 0.01a	0.007 $\pm$ 0.001a	0.019 $\pm$ 0.004a
30	3	0.67 $\pm$ 0.03b	0.66 $\pm$ 0.03b	0.075 $\pm$ 0.006b	0.060 $\pm$ 0.003a
30	4	0.84 $\pm$ 0.03c	0.92 $\pm$ 0.06c	0.142 $\pm$ 0.010c	0.201 $\pm$ 0.021b
30	5	1.03 $\pm$ 0.05d	1.20 $\pm$ 0.04d	0.208 $\pm$ 0.025d	0.264 $\pm$ 0.026c

<sup>a</sup> A one-way ANOVA was performed within each column, with means separated using Tukey's test. Lowercase letters indicate means are significantly different within a column at  $\alpha = 0.05$ .

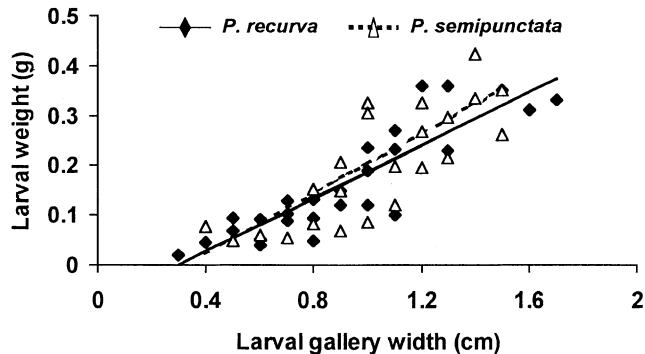


Fig. 1. Regression analysis of larval weight and gallery width for *P. recurva* ( $Y = -0.079 + 0.266x$ ,  $F = 303.09$ ,  $df = 1, 117$ ,  $P < 0.0001$ ,  $r^2 = 0.72$ ) and *P. semipunctata* ( $Y = -0.096 + 0.300x$ ,  $F = 325.21$ ,  $df = 1, 118$ ,  $P < 0.0001$ ,  $r^2 = 0.73$ ).

Larval weights increased significantly with age for the four larval age classes of *P. recurva* and *P. semipunctata* (Table 1). Between species comparisons of larval weights showed no clear trend, with 2- and 4-week-old *P. semipunctata* being heavier than the *P. recurva* counterparts, whereas 3-week-old *P. recurva* larvae weighed significantly more than those of *P. semipunctata*. Larval weights were highly correlated with larval gallery widths for both *P. recurva* ( $r = 0.85$ ) and *P. semipunctata* ( $r = 0.86$ ), and the test for homogeneity of correlation coefficients found no difference between the two species ( $X^2 = 0.06$ ,  $df = 1$ ,  $P = 0.81$ ). Regressions of larval weight and gallery widths were significant for *P. recurva* and for *P. semipunctata* (Fig. 1).

### 3.2. Parasitoid sex ratios and total emergence

Two-week-old larvae of both *Phoracantha* spp. produced only male parasitoids (Fig. 2). The proportions of male *S. lepidus* emerging from the various larval ages of *P. recurva* differed significantly as larval host age and size increased ( $X^2 = 26.03$ ,  $df = 3$ ,  $P = 0.001$ ). A significantly larger proportion of males than females emerged from 2 week than 3-week-old *P. recurva* larvae ( $X^2 = 5.54$ ,  $df = 1$ ,  $P = 0.019$ ), whereas the sex ratios of *S. lepidus* from 3- and 4-week-old *P. recurva* were not significantly different ( $X^2 = 3.00$ ,  $df = 1$ ,  $P = 0.084$ ). Both 3- and 4-week-old *P. recurva* produced a signifi-

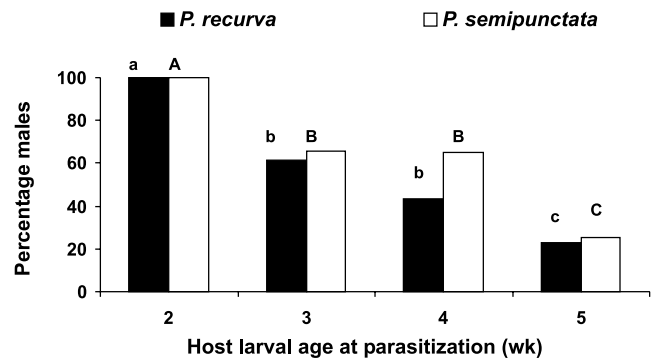


Fig. 2. The proportions of male *S. lepidus* progeny obtained from each host age class of *P. recurva* and *P. semipunctata*. Within a species, the proportions of males emerging from each host age class were compared using  $\chi^2$  analysis. Bars surmounted with different letters (lowercase letters for *P. recurva*, uppercase letters for *P. semipunctata*) are significantly different ( $\alpha = 0.05$ ).

cantly larger proportion of male *S. lepidus* than 5-week-old larvae ( $X^2 = 22.31$ ,  $df = 1$ ,  $P = 0.001$ ;  $X^2 = 38.60$ ,  $df = 1$ ,  $P = 0.001$ ) (Fig. 2). A similar pattern was observed for the sex ratio of parasitoids emerging from *P. semipunctata* larvae (Fig. 2). Sex ratio comparisons between *P. recurva* and *P. semipunctata* from each host age class revealed no significant differences in the proportions of male parasitoids emerging from 3-, 4-, or 5-week-old larvae.

The total number of *S. lepidus* emerging from all four age classes of *P. recurva* varied significantly ( $X^2 = 19.21$ ,  $df = 3$ ,  $P = 0.001$ ). However, there were no significant differences in emergence among 3–5-week-old larvae ( $X^2 = 0.785$ ,  $df = 1$ ,  $P = 0.675$ ), indicating that the 2-week-old larvae produced fewer parasitoids (Fig. 3). Similarly, the numbers of *P. semipunctata* progeny emerging from 3 to 5-week-old larvae were not significantly different ( $X^2 = 0.909$ ,  $df = 2$ ,  $P = 0.635$ ). Wasps emerging from *P. recurva* hosts had an overall sex ratio of 45% males, whereas those produced from *P. semipunctata* were 60% males.

### 3.3. Parasitoid size and developmental time

Male and female parasitoid sizes increased with increasing host size, and females were consistently larger

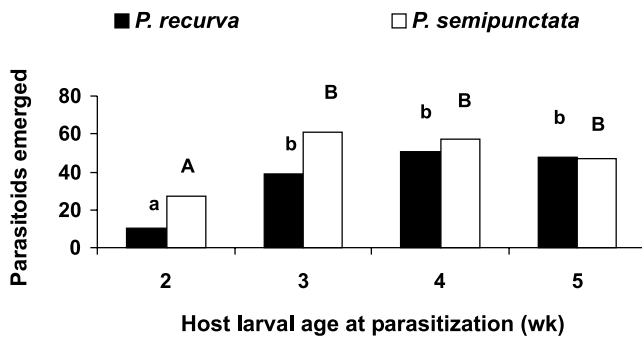


Fig. 3. The total number of adult *S. lepidus* emerging from each host age class of *P. recurva* and *P. semipunctata*. Within a species, the numbers of wasps emerging from each host age class were compared using  $\chi^2$  analysis. Bars surmounted with different letters (lowercase letters for *P. recurva*, uppercase letters for *P. semipunctata*) are significantly different ( $\alpha = 0.05$ ).

than males in all age classes for both host species (Table 2). The influence of host species on parasitoid size and developmental time was examined for each larval age class. Male wasps developing in *P. recurva* had a significant increase in hind tibia length as host size increased ( $F = 32.9$ ,  $df = 3, 63$ ,  $P < 0.0001$ ). No females were obtained from 2-week-old larvae of either *Phoracantha* spp., but female *S. lepidus* emerging from 3–5 weeks *P. recurva* hosts increased significantly in size with increasing host size class ( $F = 78.4$ ,  $df = 2, 78$ ,  $P < 0.0001$ ). Hind tibia lengths of females were consistently larger when reared on *P. recurva* than on *P. semipunctata* (Table 2). The size of adult male and female *S. lepidus* emerging from *P. semipunctata* exhibited a similar pattern.

Developmental times of male *S. lepidus* were consistently more rapid than those of females emerging from the same size hosts (Table 2). Furthermore, males emerging from 2-week-old hosts of *P. recurva* and *P. semipunctata* took significantly longer to develop than males from older hosts (*P. recurva*,  $F = 41.67$ ,  $df = 3, 63$ ,  $P < 0.0001$ ; *P. semipunctata*,  $F = 130.19$ ,  $df = 3, 112$ ,  $P < 0.0001$ ). Male parasitoids from the

3- and 4-week-old hosts took longer to develop in *P. recurva* than *P. semipunctata* (3 weeks,  $F = 4.59$ ,  $df = 1, 62$ ,  $P = 0.036$ ; 4 weeks,  $F = 6.3$ ,  $df = 1, 57$ ,  $P = 0.015$ ) (Table 2).

Developing female *S. lepidus* emerging from both 5-week-old *P. recurva* and *P. semipunctata* hosts took significantly longer to emerge than females from 3- and 4-week-old hosts (*P. recurva*,  $F = 4.24$ ,  $df = 2, 78$ ,  $P = 0.018$ ; *P. semipunctata*,  $F = 17.53$ ,  $df = 2, 74$ ,  $P < 0.0001$ ). Comparisons of the mean developmental times for females between the two host species found that females emerging from *P. recurva* took significantly longer to develop than those emerging from *P. semipunctata* for all age classes (3 weeks,  $F = 15.34$ ,  $df = 1, 34$ ,  $P = 0.0004$ ; 4 weeks,  $F = 20.85$ ,  $df = 1, 48$ ,  $P = 0.0001$ ; 5 weeks,  $F = 8.87$ ,  $df = 1, 70$ ,  $P = 0.004$ ) (Table 2).

#### 4. Discussion

##### 4.1. Parasitoid sex ratios and total emergence

The sex ratio of emerged *S. lepidus* shifted from 100% male to strongly female biased as host size increased, for both *Phoracantha* spp. Although 2-week-old *P. semipunctata* produced larger galleries than similar aged *P. recurva* larvae, 2-week-old hosts of both species produced only male parasitoids. In contrast, 5-week-old *Phoracantha* larvae produced approximately 20% males, a significantly lower proportion than that emerging from younger and smaller hosts.

Our study was not a direct test of the host quality model proposed by Charnov et al. (1981), which predicts the sex allocation behavior of individual females presented with a range of host sizes simultaneously. However, parallel outcomes might be expected, because Charnov's model further predicts that a female should preferentially lay sons in hosts that she perceives to be small, and daughters in hosts that she perceives to be

Table 2  
Hind tibia lengths and developmental times (mean  $\pm$  SE) of *S. lepidus* developing on *P. recurva* or *P. semipunctata*

Larval age (week)	<i>Phoracantha</i> spp.	Hind tibia length (cm) <sup>a</sup>				Developmental time (d) <sup>b</sup>			
		Male	N	Female	N	Male	N	Female	N
2	<i>P. recurva</i>	1.56 $\pm$ 0.10	10	N/A		25.70 $\pm$ 0.45	10	N/A	
	<i>P. semipunctata</i>	1.44 $\pm$ 0.04	27	N/A		25.50 $\pm$ 0.33	27	N/A	
3	<i>P. recurva</i>	2.29 $\pm$ 0.09	24	2.97 $\pm$ 0.07*	15	20.88 $\pm$ 0.21**	24	23.87 $\pm$ 0.22**	15
	<i>P. semipunctata</i>	2.19 $\pm$ 0.05	40	2.72 $\pm$ 0.07	21	20.30 $\pm$ 0.16	40	22.52 $\pm$ 0.25	21
4	<i>P. recurva</i>	2.42 $\pm$ 0.12	22	3.37 $\pm$ 0.10*	29	20.41 $\pm$ 0.32**	22	24.00 $\pm$ 0.38**	29
	<i>P. semipunctata</i>	2.31 $\pm$ 0.06	37	2.87 $\pm$ 0.13	20	19.57 $\pm$ 0.18	37	21.67 $\pm$ 0.30	20
5	<i>P. recurva</i>	3.45 $\pm$ 0.09*	11	4.30 $\pm$ 0.04*	37	21.45 $\pm$ 0.39	11	25.19 $\pm$ 0.34**	37
	<i>P. semipunctata</i>	2.92 $\pm$ 0.19	12	3.95 $\pm$ 0.06	35	21.08 $\pm$ 0.38	12	23.89 $\pm$ 0.26	35

<sup>a</sup> ANOVA within larval age class, analyzing males and females independently (by column). An \* indicates a significant difference ( $\alpha = 0.05$ ).

<sup>b</sup> ANOVA within larval age class, analyzing males and females separately (by column). Two \*\* indicates a significant difference ( $\alpha = 0.05$ ).

large. However, the Charnov model assumes that the perception of host sizes is relative and not absolute, and that females presented with a mixture of small and medium hosts will allocate sons to small hosts and daughters to medium hosts, whereas females presented with medium and large hosts will lay sons and daughters in medium and large hosts, respectively. Uniform quality hosts are predicted to result in a slightly male-biased sex ratio.

In contrast, in our experiments, sex allocation by female *S. lepidus* presented with groups of uniform quality hosts resulted in strongly biased sex ratios at either end of the host quality spectrum. Furthermore, the wasps used in our experiments were randomly selected from the breeding colony, and consequently were a mix of naïve and experienced females. The fact that no females at all were obtained from the poorest quality hosts, even from the fraction of parasitoids that were naïve and which might be predicted to lay a mixture of sons and daughters, suggests that sex allocation by *S. lepidus* is determined primarily by host quality. Furthermore, adult *S. lepidus* are naturally highly variable in size (Hanks et al., 2001), suggesting that female wasp larvae can indeed use small hosts for development. Although the possibility of differential mortality of male and female progeny in the poorest quality hosts cannot be excluded, results from other host-parasitoid systems suggest that differential mortality is probably not a crucial factor. For example, the eulophid wasp *Diglyphus begini*, which parasitizes the leafminer *Liriomyza trifolii* (Diptera: Agromyzidae), allocated male progeny to smaller hosts and females to larger hosts (Heinz and Parrella, 1990). Furthermore, by moving female eggs that had been oviposited on large hosts, and allowing these to develop on small hosts, Heinz and Parrella (1990) found no differential mortality of females on small hosts. The sex ratio in the emerging progeny was determined at oviposition, and was not a consequence of differential mortality between sexes. Differential mortality has been eliminated as a factor influencing the sex ratio in other systems as well (reviewed in King, 1987).

#### 4.2. Parasitoid size and developmental time

Male and female *S. lepidus* increased in size with host size, and females were significantly larger than males for each age class. Hurlbutt (1987) found several hundred examples of this size disparity in over 21 families of hymenopteran parasitoids, indicating that sexual dimorphism is widespread in the parasitic Hymenoptera. Larger female progeny may result in higher fitness for the parent wasp if female offspring have a larger fitness return with increasing size than males (Charnov et al., 1981). For example, large females have been shown to have a higher reproductive rate than smaller females (Lawrence, 1971) and can search for hosts over longer

distances (Bolt, 1974), whereas the size of males had no influence on the number of matings (Napoleon and King, 1999).

Although there were significant differences in the developmental times of parasitoids emerging from *P. semipunctata* and *P. recurva* host larvae of each age class, the differences generally were small, suggesting that the two beetle species were similar in their suitability as hosts. For example, male wasps developed more slowly in 3 and 4 weeks old hosts of *P. recurva* than *P. semipunctata*, but the difference was less than one day. Female wasps also took slightly longer to develop in *P. recurva* than in *P. semipunctata* but progeny which emerged from *P. recurva* hosts were larger than those from *P. semipunctata* hosts. Overall, males developed more rapidly than females in both host species, a pattern that has been observed in other parasitoids (Kawaguchi and Tanaka, 1999; Otto and Mackauer, 1998).

The influence of host size on parasitoid sex ratio can be exploited in the mass rearing of parasitoids used as biological control agents (Heinz, 1998). In our study system, more *S. lepidus* parasitoids can be produced for release with a female-biased sex ratio in the parental population. Thus, determination of the host size that produces a female-biased sex ratio is a critical factor in minimizing rearing costs per parasitoid. For *S. lepidus* ovipositing on a single age class of *P. recurva* and *P. semipunctata* larva, 5-week-old hosts produced approximately 80% females, whereas 3-week-old hosts produced only about 40% females. Thus, allowing potential hosts to mature two additional weeks before being exposed to parasitoid oviposition doubled the number of female progeny. In parasitoid production systems such as this, which require intensive labor inputs to cut and process trees as breeding material for host larvae, to hand infest logs with host larvae, and to box logs for parasitoid emergence, the resulting cost per parasitoid produced is decreased by offering older, larger hosts to ovipositing parasitoid females, resulting in a strongly female-biased sex ratio in the progeny.

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