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Effect of variation in host size on sex ratio, size, and survival of *Syngaster lepidus*, a parasitoid of *Eucalyptus* longhorned beetles (*Phoracantha* spp.): II

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Abstract

Larvae of the cerambycid beetle *Phoracantha recurva* Newman colonize the inner bark of stressed or dying *Eucalyptus* trees. These cryptic larvae are parasitized by the solitary ectoparasitoid *Syngaster lepidus* Brullé. When denied a choice of host sizes in a previous study, parasitoid females produced only male progeny in 2 week old larvae, but when given access to only large larvae, the sex ratio of the progeny was significantly female biased. When female wasps were simultaneously presented with a range of host sizes in the study presented here, the sex ratio was significantly male biased for wasps produced from the smallest host class (2 weeks old), but was not different among the 3, 4, or 5 week old hosts. The sex ratio of progeny remained constant throughout the life of the ovipositing females. Fertility peaked during the second week of adult life, then declined to zero by the fourth week, with females producing about 22 progeny during their lifetimes. Longevity of females was significantly greater than that of males. Significantly more progeny were produced from 3 week old hosts than from any other age class. There was no difference in the number of progeny emerging from 2 or 4 week old hosts, but significantly fewer progeny were produced from 5 week old hosts. The size of emerging wasps increased with host size for both males and females. In Australia, a complex of parasitoids, uses *Phoracantha* larvae as hosts. *S. lepidus* prefers to use younger, smaller larvae, while other members of the parasitoid guild exploit larger larval hosts. The results from this study suggest tradeoffs between sex allocation and percent survival in different host size classes, and reflect the observations from previous field studies of this host–parasitoid complex in Australia.
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1. Introduction

The pattern of female parasitoids being produced from larger hosts and males from smaller hosts has been observed for many years (Clausen, 1939; West and Sheldon, 2002). Charnov et al. (1981) formulated a significant contribution to sex ratio theory by proposing that females would maximize their reproductive fitness in a variable resource environment by differential allocation of sexes based on resource availability. The fundamental assumptions of this theory were that: (1) immature individuals with more resources available to them would grow into larger adults, (2) larger females produce more eggs than smaller females, and (3) there is a greater reproductive advantage in producing large females than large males. Solitary idiobiont hymenopteran parasitoids paralyze hosts prior to oviposition, halting further feeding and development of the host. As a result, the paralyzed host represents a finite pool of resources available to the developing parasitoid, and there should be a selective advantage to allocation of female progeny to larger hosts and male progeny to smaller hosts.

Allocation of females to larger hosts has been demonstrated in a number of host–parasitoid systems (e.g., Urano and Hijii, 1995) and the concept is now widely

accepted (Charnov, 1982; Godfray, 1994; King, 1993; Ode and Hunter, 2002; West and Sheldon, 2002). Parasitoid females locate potential hosts, and assess the size or quality of the host using physical (Schmidt and Smith, 1987), acoustic (Sugimoto et al., 1988), or chemical (Chow and Mackauer, 1999) cues prior to oviposition. Once host size has been assessed, the female can lay an unfertilized haploid male egg or a fertilized diploid female egg. Although it may not be possible to determine whether the realized sex ratio at emergence from cryptic hosts is due to differential mortality between the sexes rather than differential sex allocation at the time of oviposition, several studies have eliminated differential mortality as a critical factor (Heinz and Parrella, 1990; King, 1990; Opp and Luck, 1986).

Phoracantha recurva Newman and *Phoracantha semipunctata* F. (Coleoptera: Cerambycidae) are native to Australia and have been introduced from there into many *Eucalyptus*-growing regions of the world, including California (Hanks et al., 1993a,b, 1997). The beetles have been responsible for widespread *Eucalyptus* mortality in California and in many other geographic regions with Mediterranean climates (Hanks et al., 1993a,b; Paine and Millar, 2002). Females of both species lay their eggs on the bark of stressed or recently killed *Eucalyptus* L'Heritier, *Corymbia* Hill and Johnson, and *Angophora* Cav. trees. The neonate larvae penetrate through the outer bark. Larvae develop in the inner bark, phloem, cambium, and outer layers of xylem and pupate in chambers excavated deep in the xylem tissues (Paine and Millar, 2002). Thus, once the neonate larvae bore into the bark of the host tree, all development occurs in a concealed environment.

Syngaster lepidus Brullé (Hymenoptera: Braconidae) is a solitary parasitoid of both species of *Phoracantha* (Austin et al., 1994; Millar et al., 2002). Females walk along the bark surface searching for suitable host beetle larvae that are feeding at the cambium/xylem interface. The female parasitoids appear to use vibration or sound as cues for detecting the presence of the larvae concealed under the bark (Hanks et al., 2001). Once a larva has been detected, the parasitoid probes through the bark with her ovipositor, injects the host with venom that induces paralysis, and lays an egg on the external surface of the paralyzed host. It appears likely that female parasitoids use cues obtained during the process of searching on the bark surface and probing with the ovipositor to determine whether to lay a male or a female egg on the host larva. The parasitoid consumes the host during larval development, and pupates in a distinctive papery cocoon at the end of the host's gallery (Millar et al., 2002).

In a previous study, Joyce et al. (2002) demonstrated that *S. lepidus* females exposed to log sections containing only young larvae produced only male progeny, whereas the sex ratio of progeny produced when females were given access to only large larvae was significantly female biased. However, sex allocation by females when simultaneously presented with a range of host sizes (i.e., a variable range of resources in the sense of Charnov et al. (1981)) was not tested. The objectives of the present study were to determine: (1) the sex ratio of progeny produced when *S. lepidus* females were provided hosts of different sizes, (2) whether the ages of female parasitoids influenced the sex ratio of progeny, (3) the lifetime fecundities of females given a range of host sizes, and (4) whether the size of preferred hosts varied over the lifetime of the female wasps. The results are important to understand resource allocation behavior of a parasitoid using concealed hosts and to potentially improve the procedures used to rear parasitoids for release in a biological control program.

2. Materials and methods

2.1. Host beetle inoculation and parasite culture

Phoracantha recurva host larvae were reared in *Eucalyptus camaldulensis* Dehnhardt logs for the experiment. Log sections (approximately 12 cm diameter × 40 cm length) were cut from freshly fallen trees from the Santa Margarita Ecological Reserve (Riverside, CA). Logs were stood vertically on one end on absorbent paper for approximately 10 days to remove excess moisture prior to infestation with larvae. Once log moisture was reduced to a level that could support larval development (Hanks et al., 1999), the log ends were sealed with melted paraffin wax to slow further dessication.

Newly eclosed beetle larvae were introduced into logs at a density ($1/66 \text{ cm}^2$ of bark surface area) previously determined to ensure optimal survival (Hanks et al., 1993a,b). The neonate larvae were obtained from eggs laid by adults from colonies established in the laboratory and maintained as previously described (Hanks et al., 1993a,b). Half of the larvae were introduced into incisions cut into one side of each log on the day after sealing with wax and the other half were introduced into the opposite side of each log on the following day (Joyce et al., 2002). Logs were incubated for 2, 3, 4, or 5 weeks in a greenhouse depending of the larval host size needed, at approximately $27 \pm 2\,°C$ and 50% RH.

Adult *S. lepidus* were obtained from an established laboratory colony maintained on both *P. recurva* and *P. semipunctata* (F.) larvae as described in Millar et al. (2002). Adult wasps from the colony were placed in large screen cages with logs containing host larvae at suitable developmental stages to allow both mating and oviposition. Logs were replaced within these oviposition cages every 7–10 days, placed in a greenhouse at $27 \pm 2\,°C$ for parasitoid development, and then placed in sealed cardboard boxes (60 cm × 60 cm × 45 cm) with a

1 liter clear glass jar attached to one side to collect the positively phototactic adults as they emerged. Adult wasps were collected from the jars twice daily.

2.2. Parasitoid choice experiment

At the beginning of the study, four logs (one log with each beetle larval age 2, 3, 4, and 5 weeks old) were placed in each of five oviposition cages (a cube 60 cm on a side) constructed of wooden frame and metal screen sides. Six adult *S. lepidus* (three of each sex) were placed in each cage. After a 3.5 day period (termed a sting session), logs were removed and replaced with a new set of logs. Before attempting to remove the logs, the cage was heavily misted with water which discouraged movement of adult wasps. Any wasps on the logs were carefully returned to the cage. The process of log replacement every 3.5 days was repeated for the life of the female parasitoids in each cage.

A total of 15 newly emerged (<24 h old) males and 15 newly emerged females were used at the start of the experiment. Males that died during the experiment were replaced with newly emerged males, marked with a drop of white liquid paper correction fluid (Gillette, Boston, MA) to distinguish them from the original group of males. Males were replaced to ensure that females always had continual access to mates, although it is not known whether female *S. lepidus* will mate more than once. Oviposition cages were checked daily for the survival of male and female parasitoids. Longevity of females and the first set of males was determined from these observations. Daily applications of streaks of honey and water mist to the roof of the cages served as a food and humidity source for the wasps.

Logs removed from the cage were enclosed individually in cardboard emergence boxes ($\sim 20 \times 20 \times 40$ cm). Logs were placed in the box horizontally with the ends supported by 1 cm diameter rods to provide a space around each log for adult parasitoids to emerge. The box was sealed with duct tape, and each box was labeled with the cage number, sting session, and age of the host larvae in the log. A 2 cm hole was punched into one end of the box and a 40-dram clear plastic vial lid with a corresponding 2 cm hole punched in it was stapled to the box, so that a 40-dram clear plastic vial could be fitted, removed, or replaced easily onto its lid. Emerging parasitoids were attracted to the light and collected in the vials twice daily. The total number of parasitoids that emerged from each box was recorded, and the gender and size (right hind tibia length) of each parasitoid was measured. Emergence boxes were maintained in a greenhouse at $27 \pm 2\,^{\circ}$C and 50% RH. Logs remained boxed for several months after parasitoids ceased to emerge to ensure that emergence was complete.

The age of the larvae was used as a proximate value for larval size in this study. Hanks et al. (2001) and Joyce et al. (2002) both clearly demonstrated that there was a highly significant correlation between larval weight and larval gallery width. After emergence of adult parasitoids had ceased, we removed the bark of logs with a chisel and measured the width of feeding galleries for host larvae that had been parasitized.

2.3. Data analysis

We determined the sex ratios of offspring (M:F) emerging from logs from each 3.5 day sting session, and the sex ratios of progeny produced over the lifetime of female parasitoids. Initially, each cage had three ovipositing females, but females died over the course of the experiment. In order to make similar comparisons, we compared data from cages that had the same number of living females. For the first four sting sessions, there were four cages with three ovipositing females, and for sting sessions 5 and 6 there were two females surviving in all cages. The chi-squared goodness-of-fit test was used to compare the frequency of the males and females to the expected frequencies (H_0: 1:1) for the first four sessions. Similarly, chi-squared tests compared observed with expected emerging wasps from sting sessions 5 and 6. Because no differences were found between the two tests, the data were pooled and reanalyzed using a heterogeneity chi-squared test (Steele et al., 1997).

A chi-squared goodness of fit analysis was used to determine whether host size influenced the number of emerged adult wasps. After the overall analysis, differences between pairs of means were tested using chi-squared analysis.

An estimate of individual lifetime fertility was determined by dividing the total number of progeny that emerged by the number of ovipositing females used to begin the experiment. In addition, the mean number of progeny produced per sting session was determined by dividing the number of offspring produced by the number of living wasps in that sting session. Data from all five oviposition cages were included in this analysis.

The mean sizes of male and female parasitoids emerging from each larval host size were compared within gender using one-way analysis of variance (ANOVA), and a Tukey's test was run for separation of means (SAS Institute, 1996). Similar analyses were used to compare the mean gallery width from parasitized larvae from the four different sized larval hosts.

3. Results

3.1. Sex ratios

The numbers of male and female progeny that resulted from the oviposition bouts (sting sessions) and the sex ratios of emerging wasps are summarized in

Table 1
The sex ratios of *S. lepidus* progeny produced from *P. recurva* hosts in successive sting sessions

Sting session[*]	Female wasp age (days)	Total progeny produced		Proportion male
		Male	Female	
1	0–3.5	12	6	0.67
2	3.5–7	48	35	0.58
3	7–10.5	44	30	0.60
4	10.5–14	33	36	0.49
5	14–17.5	9	8	0.53
6	17.5–21	11	8	0.58
Total progeny		157	123	0.56

[*] Females were allowed to sting and oviposit on hosts for six sequential bouts of 3.5 days each.

Table 1. Because females died during the experiment, we initially compared the sex ratios produced among cages with three ovipositing females (sting sessions 1–4), and separately compared those from sting sessions 5 and 6. There were no significant differences in the sex ratios of progeny produced among the first four sting sessions ($\chi^2 = 6.92$, $df = 4$, $P = 0.14$). The sex ratios of progeny emerging from the last two sting sessions 5–6 were also not significantly different ($\chi^2 = 0.533$, $df = 2$, $P = 0.77$). When the data from sessions 1–6 were pooled for analysis, there were no significant differences in the sex ratios of progeny produced over the lifetime of the parasitoids ($\chi^2 = 7.453$, $df = 6$, $P = 0.28$). Thus, the age and previous experience of female wasps does not appear to affect the sex allocation of their progeny.

Because all logs used in the study were boxed separately, we were able to separate the progeny emerging from each log (i.e., each larval host size). The sex ratios emerging from all the logs of each host larval size from the entire study were compared using chi-squared analysis to determine whether oviposition in smaller hosts resulted in more male offspring than offspring produced from larger hosts, and results were significant ($\chi^2 = 12.77$, $df = 3$, $P = 0.005$) (Fig. 1). There were no differences in the ratios of male progeny emerging from 3, 4 or 5 week old larval hosts ($\chi^2 = 2.20$, $df = 2$, $P = 0.33$), but the 2 week old larvae produced a higher ratio of male wasps than the other host larval sizes.

3.2. Host size choice

There were significant differences in the number of progeny produced from each host size over the lifetime of the wasps ($\chi^2 = 81.63$, $df = 3$, $P < 0.001$) (Fig. 2). Subsequent pairwise combinations showed that more parasitoid progeny emerged from 3 week old host larvae than from 2, 4, or 5 week old larvae ($\chi^2 = 20.15$, $df = 1$, $P < 0.001$; $\chi^2 = 28.50$, $df = 1$, $P < 0.001$; $\chi^2 = 69.34$, $df = 1$, $P < 0.001$, respectively). The numbers of progeny produced from 2 and 4 week old larvae were not significantly different ($\chi^2 = 0.81$, $df = 1$, $P < 0.37$), but 2 and 4 week old hosts produced more wasps than did 5 week old larvae ($\chi^2 = 17.3$, $df = 1$, $P < 0.001$; $\chi^2 = 11.58$, $df = 1$, $P < 0.001$, respectively).

3.3. Reproductive biology

The 15 ovipositing female *S. lepidus* produced a total of 327 progeny during their lifetimes (~22 offspring per female). Fertility peaked during sting sessions 3–5, which corresponded to days 7–14 of the wasps' lifespan (Fig. 3). Sting session 7 only produced 1 progeny, and
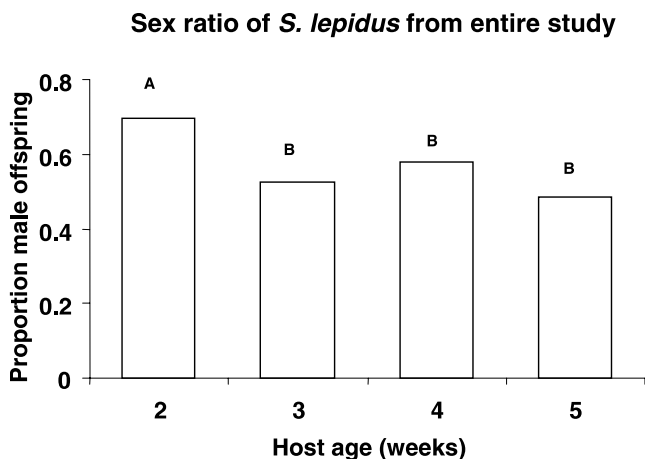
Fig. 1. Sex ratio of all *S. lepidus* progeny emerging from each of four different size classes of *P. recurva* larval hosts.
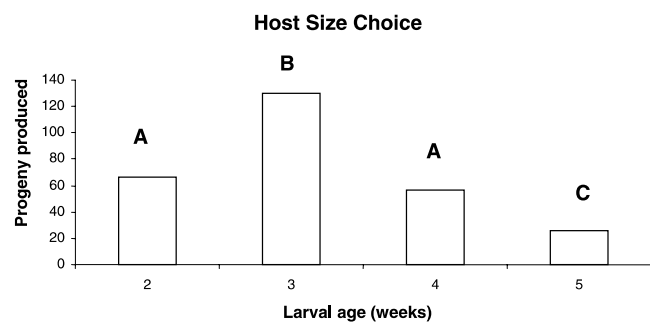
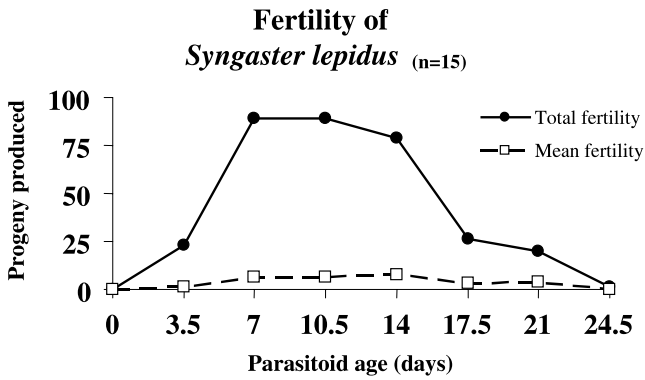Fig. 2. The total number of *S. lepidus* progeny emerging from each host size.

Fertility of Syngaster lepidus (n=15)

Fig. 3. Lifetime total number of progeny of S. lepidus, and mean number of progeny per "sting session."

consequently was not included in the above analyses of sex ratios. Females lived an average of 25 ± 2.42 days (range 14–30, $N = 13$), whereas male longevity was significantly shorter, averaging 12.85 ± 2.63 days (3–34, $N = 13$) ($t = 3.40$, $P = 0.001$) (Fig. 4).

3.4. Parasitoid size and gallery size

The larval gallery widths reflect the sizes of the concealed larvae that created them while feeding on the phloem, cambium, and outer layers of xylem tissues. Larval gallery widths were significantly different for the different host larval age classes ($F = 16.47$, $df = 3, 252$, $P < 0.001$) (Fig. 5). The sizes of both sexes of progeny parasitoids increased significantly as host size increased (male, $F = 12.54$, $df = 3, 182$, $P = 0.0001$; female $F = 5.08$, $df = 3, 132$, $P = 0.0009$) (Fig. 6). There was a trend for wasp size to increase with host age (gallery size) with the largest wasps being produced from the largest hosts, smallest wasps emerging from the smallest hosts, and intermediate size wasps emerging from medium sized hosts. This pattern was particularly strong for males. The smallest males were produced from 2 week old hosts, there was no difference in sizes of male
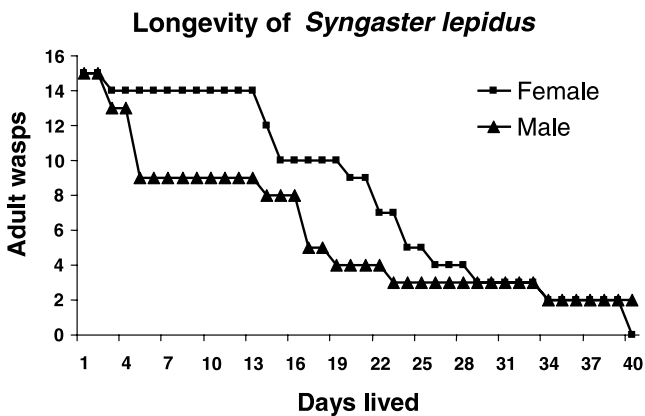
Gallery width of parasitized hosts

Fig. 5. The mean gallery size of four age classes of P. recurva larvae parasitized by S. lepidus.
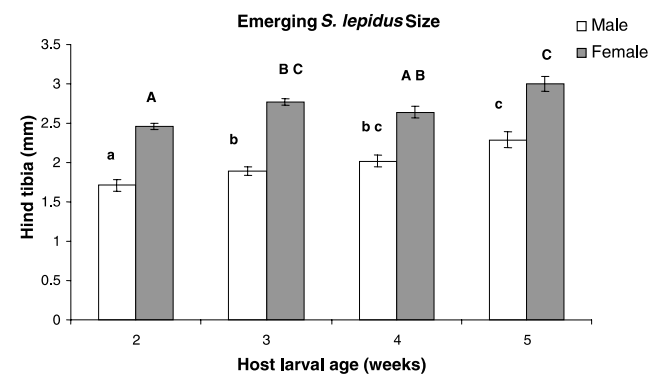
Emerging S. lepidus Size

Fig. 6. The mean size of male and female S. lepidus emerging from different sizes of P. recurva host larvae.

progeny emerging from 3 and 4 week old hosts, and no difference between males emerging from 4 and 5 week old hosts. The pattern was not as clear-cut for females. Although female wasps emerging from 5 week old hosts were significantly larger than those emerging from 2 week old beetle larvae, there were no differences in the sizes of females emerging from 3 and 5 week old hosts or 3 and 4 week old hosts.

4. Discussion

Although a few S. lepidus females lived as long as 39 days, there was minimal reproduction after they were 21 days old. Total fertility was greatest during the second week (days 7–14) of adult life. Although oviposition was lower during the first and third weeks, the progeny sex ratios remained constant over the lifetime of females. Females were presented with a variable reproductive environment (a range of host sizes available simultaneously) and responded to that environment by producing progeny with a constant sex ratio. It is not possible to determine whether changing the proportion of available hosts in the different size classes would have resulted in a changed sex ratio.

Longevity of Syngaster lepidus

Fig. 4. Longevity of male and female S. lepidus adults in oviposition cages.

In accordance with the predictions of Charnov et al. (1981), the proportion of male progeny was greatest from the smallest size class of hosts. However, this result contrasts somewhat with the results of a previous study (Joyce et al., 2002) in which only males were produced from the smallest hosts when females were not given a choice of size classes. In both studies, larvae in each size class were available to ovipositing females in numbers that would exceed by more than 50% the number of eggs that could be laid during the oviposition time interval. Consequently, it was not possible for the most preferred host size to be exhausted, forcing females to select from the remaining less preferred sizes. It is not clear why females having a choice of laying female eggs in larger hosts would choose to use the smallest hosts instead when, in the absence of a choice, they chose not to lay female eggs (Joyce et al., 2002). There remains the possibility of differential mortality between male and female progeny in the smallest hosts, although this does not seem to have been a critical factor in other systems (Heinz and Parrella, 1990; King, 1990; Opp and Luck, 1986). The results, however, do confirm that it is possible for female progeny to complete development on small hosts.

Although the results from the smallest hosts support the predictions of Charnov et al. (1981), there was no difference in sex allocation among the three larger host size classes. Two of the fundamental assumptions of Charnov's predictions are that larger hosts will produce larger offspring and that this difference in host size is important in potential reproductive fitness of females. The trend for increased progeny size with greater host size was strong for male *S. lepidus*, but less clear for females. Males are significantly smaller than females (Joyce et al., 2002), and thus it would be expected that sex allocation would be biased towards males in the smallest host sizes. For the larger host size classes, there may be alternative selection forces responsible for the deviation from the predictions. For example, there appears to be a tradeoff between host age and the number of progeny produced, with significantly fewer parasitoids being produced from hosts in the two oldest age classes. Furthermore, it is possible that female parasitoids are not egg-limited, but rather, the effort in locating and successfully parasitizing a host limits lifetime reproductive output. Observations of ovipositing females in the field and in the laboratory indicate that it takes a substantial time for a female wasp to orient to the spot precisely above a hidden host, before beginning the lengthy (frequently >1 h, T.D.P and J.G.M, pers. obs.) and arduous process of drilling through 5–15 mm of bark to sting and parasitize the host. These factors are reflected in the small number of progeny produced by females throughout their lifetimes (∼22 per female), an average of less than one offspring per day.

Female progeny emerging from 3 and 5 week old hosts were of similar size in this study, but significantly greater numbers of progeny emerged from the 3 week old hosts. Field studies conducted in Australia on the parasitoid species complex that use *Phoracantha* larvae as hosts have demonstrated that larger larvae are preferred by *Callibracon limbatus* (Brulle) (Hymenoptera: Braconidae), *Jarra phoracantha* Austin, Quicke, and Marsh (Hymenoptera: Braconidae), and *Jarra painei* Austin and Dangerfield (Hymenoptera: Braconidae) whereas smaller larvae are preferred by *S. lepidus* (Hanks et al., 2001; Paine et al., 2000). Male *S. lepidus* developed on the smallest hosts, but there was significant overlap in the host sizes used by progeny female *S. lepidus* and both male and female progeny *C. limbatus* (Hanks et al., 2001). Conceivably, this partitioning of the available host resource may represent a tradeoff between acquiring adequate resources to maximize female fertility while minimizing interspecific competition for host resources.

There also appears to be tradeoffs for the beetles between the risk of being parasitized and successful colonization of logs. In Australia, *P. semipunctata* and *P. recurva* utilize downed trees, broken branches, or standing stressed trees as the larval food resource. Adults may disperse over considerable distances to locate oviposition sites (Hanks et al., 1998), which they locate by using volatile chemical cues produced by suitable larval host material (Chararas, 1969; Drinkwater, 1975; Gonzalez-Tirado, 1987; Hanks et al., 1993a,b; Ivory, 1977). However, if beetles colonize host tissue when it is too fresh, the relatively high water content of the inner bark may be detrimental to survival of neonate beetle larvae (Hanks et al., 1991a, 1999). Beetles colonizing fresh, suitable logs may initially have a higher rate of survival, but they are subject to increased rates of parasitism (Paine et al., 2001). On the other hand, older, desiccated cambium tissue represents poor quality host material that is also less favorable for larval development (Paine et al., 2001). Furthermore, neonate larvae attempting to colonize older host material may have to contend with increased inter- and intraspecific competition from older larvae that are already well established in the host resource (Hanks et al., 1991b, 1993a,b; Ivory, 1977; Mendel, 1985; Powell, 1978, 1982). However, beetles colonizing older and more desiccated logs are subject to lower rates of parasitism (Paine et al., 2001).

Although it has not been specifically studied, it is likely that parasitoid orientation to potential host habitat is mediated by volatile chemical cues released from recently fallen trees and branches. There appears to be a distinct advantage for *S. lepidus* to arrive relatively early in the development of the host larvae, before the arrival of potential competitors. Results from the present study suggest that preferential utilization of hosts during their

third week of development does not reduce the allocation of progeny to females or result in reduced adult size. Selection of the smaller, younger larvae may result in reduced interspecific competition within the parasitoid guild and, consequently, increased reproductive output for the early arriving females.

Given a choice of host sizes, sex allocation by female *S. lepidus* deviated somewhat from the predictions of Charnov et al. (1981). When denied a choice of host sizes, the observed sex allocation much more closely followed the predicted pattern (Joyce et al., 2002). The availability of different host sizes simultaneously, however, more closely reflects field conditions, in which a female parasitoid may have a choice of different trees under different stages of colonization. The resulting sex allocation patterns may reflect a balance between the interacting selection factors on progeny survival and reproductive fitness.

Acknowledgments

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