

Host-age Structure and Parasitism in a Laboratory System of Two Hymenopterous Parasitoids and Larvae of *Zabrotes subfasciatus* (Coleoptera: Bruchidae)

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Environ. Entomol. 14: 507-511 (1985)

ABSTRACT Host-age structure of *Zabrotes subfasciatus* (Boheman) on larval parasitism by two hymenopterous parasitoids, *Heterospilus prosopidis* Viereck (Braconidae) and *Anisopteromalus calandrae* (Howard) (Pteromalidae), were examined in a series of laboratory experiments. Ages of the hosts offered to the parasitoids were varied and the number of host larvae successfully parasitized was monitored. The sex ratio of the resulting parasitoids was also monitored. A life-history refuge from parasitism by both parasitoids was found, consisting of the egg stage and the small, young larvae. The refuge length differed for both parasitoids. Host individuals were not parasitized efficiently by *A. calandrae* for the first 14-16 days, whereas they were not parasitized at all by *H. prosopidis* for the first 12 days. Host individuals were protected from attack during these refuge periods for up to 60% of their larval period. Host-age refuges were important in the stability of these two host-parasitoid systems. Stability increased with increasing length of the refuge period. The shorter refuge period in the *H. prosopidis*-host system may lead to further instability by creating asynchrony between the host and parasitoid life cycles. The age of the larval host also determined the sex ratio of the parasitoid populations. This factor may further destabilize the *H. prosopidis* populations, while having a lesser effect on *A. calandrae*.

A FACTOR ignored in most studies of populations, and especially in the construction of predator-prey models, is the effect of age structure of the prey on the predator-prey relationship. Theoretical biologists have considered the possibility that an effective refuge for the prey may result if the predator cannot attack a particular class of prey and concluded that such refuges may contribute to population stability (Hassell and May 1973, Murdoch and Oaten 1975, Hassell 1978). These refuges may be either physical, spatial, or temporal, or may simply result from invulnerable classes of prey. A number of field and laboratory studies have demonstrated that such refuges are important in the dynamics of predator-prey interactions (Gause 1934, Callan 1944, Huffaker 1958, Huffaker et al. 1963, Connell 1970, 1975). Smith and Mead (1974) examined how age structure affected stability in several simple simulation models and showed that stability tended to increase as the proportion of prey vulnerable to attack at equilibrium decreased. They concluded that the most stable system should be one in which only the younger stages are attacked by a predator.

Aside from attempts to determine the theoretical effects of age structure and resulting refuges on predator-prey systems, little experimental work has dealt with the effects host-age structure might have on parasitoid or predator populations. This

paper examines the relationship of host age (larvae of *Zabrotes subfasciatus* [Boheman]) with parasitism by two hymenopterous parasitoids, *Heterospilus prosopidis* Viereck (Braconidae) and *Anisopteromalus calandrae* (Howard) (Pteromalidae). I attempt to determine if an effective refuge for the host results from some age classes of host larvae being invulnerable to parasitism and if host-age utilization by the two parasitoid species is different. I then discuss the effect differences that refuge size might have on the stability of the two parasitoid-host systems. These experiments were designed to examine the differences in the stability of these two host-parasitoid systems, which have been described by Fujii (1983). All experimental conditions were the same in mine and Fujii's experiments, and thus my data may be used to explain the results of his multigeneration stability experiments. Based upon the conclusions of Smith and Mead (1974), the more stable populations should be those with the smallest proportion of prey vulnerable to attack at equilibrium population densities. Lastly, I discuss how differential host larval utilization affects the sex ratios of the parasitoid populations and the resulting effects this might have on the system stability.

Materials and Methods

Larvae of *Zabrotes subfasciatus* were used as hosts in all experiments. Females oviposit their transparent eggs on the surface of beans. The first

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instar bores into the seed after 5 days and, during this process, fills the egg with frass, giving the egg an opaque, white appearance. The larvae complete their life cycle, while feeding inside the bean, and emerge as adults after a minimum of 25 days. During the period from entrance (day 5) until emergence (day 25), the larvae are susceptible to parasitism by parasitoids. Both parasitoid species oviposit directly onto host larvae and develop as ectoparasitoids. The parasitoids have similar life cycles of ca. 14 days.

All experimental conditions were the same as those of Fujii (1983). A plastic petri dish (15 by 100 mm), kept in an environmental chamber at 30°C and 70% RH, was the experimental unit. To obtain host larvae of different ages, I placed *Z. subfasciatus* adults on azuki beans (*Vigna angularis*) for 24 h. After the first instars entered the seeds the opaque, white eggs were used to sort the beans into classes with densities of one to eight host larvae per bean. The larvae were allowed to develop for 8–24 days (day 1 = oviposition) before being offered to the parasitoids. A total of 50 host larvae were placed into each experimental unit. Series of experimental units were set up, each consisting of hosts of the same age. Each experimental unit in the series consisted of hosts of different density classes. At host ages of 12, 17, and 22 for *H. prosopidis* and 14, 17, and 22 for *A. calandreae* a complete series of all densities from one to eight host larvae per bean was used, with from four to six replicates of each age–host density combination. At all other host ages (8–24 days) four replicates at each of two densities (two and four hosts per bean for *A. calandreae*; three and five hosts per bean for *H. prosopidis*) were used. For the analysis on host age, results from all replicates (e.g., different host densities) were combined to gain an overall view of host age effects on parasitism. The total number of replicates at each host age is shown in Fig. 1 (top).

One pair (male and female) of adult parasitoids was placed into each experimental unit with each age-class–density combination of host larvae for 24 h. Successful parasitism was determined by collecting the adult parasitoids after they had emerged from the bruchid larvae.

In a second set of experiments eight pairs of parasitoids were placed into each experimental unit. One replicate of each host age (8–26 days) was set up, with 110 total hosts per replicate with a mixed density of two and three hosts per bean.

Results

In the experimental systems under study there was a threshold host size below which the parasit-

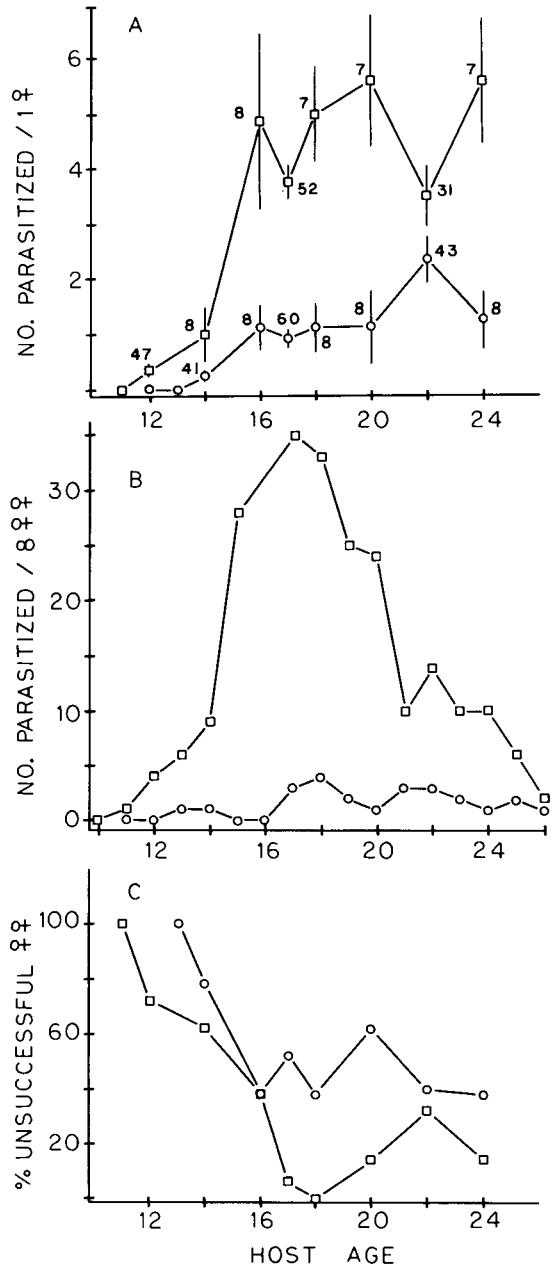


Fig. 1. Parasitism of larvae of *Z. subfasciatus* of different host ages by two hymenopteran parasitoids. *A.*

calandreae (○), and *H. prosopidis* (□). As host age increases above a threshold, parasitism of host larvae rapidly increases. Regardless of whether one (A) or eight (B) pairs of parasitoids are used, the threshold age for attack by *H. prosopidis* (11–12 days) is distinctly less than that for *A. calandreae* (14–16 days). A decrease in the number of parasitoid pairs not producing any offspring (C) corresponds closely with the increase in host utilization efficiency as host age increases. *H. prosopidis* is always more successful in utilizing hosts of any age, but the use of younger hosts than *A. calandreae* is proposed to be relatively more important in determining system stability. Values (A) are means and standard errors and the values in the figure are the number of replicates.

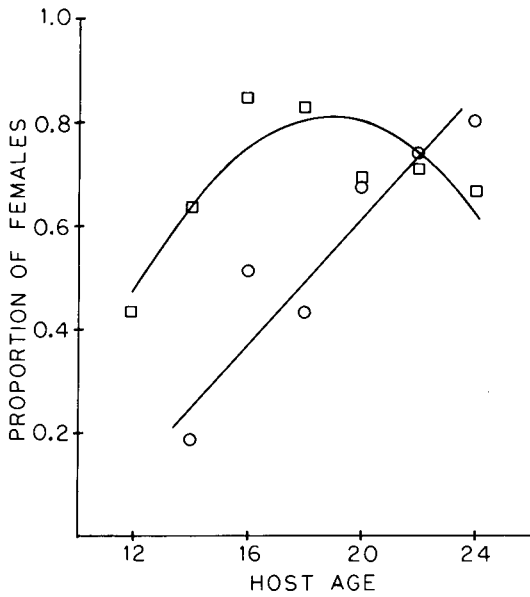


Fig. 2. Change in sex ratio of *A. calandrae* (O; $y = 0.613x - 0.618$, $r^2 = 0.925$) and *H. prosopidis* (□; $y = -0.00726x^2 + 0.2743x - 1.781$, $r^2 = 0.763$) as the age of the host larvae increases.

oids were not able to parasitize the hosts. At host ages below 11–12 days for *A. calandrae* and 13–14 days for *H. prosopidis*, the parasitoids were unable to parasitize the host larvae (Fig. 1 top and middle). Since the host eggs hatched on day 5, the resulting larvae were safe from parasitism by *H. prosopidis* during the first 6 days and from *A. calandrae* during the first 8 days of larval life. The adult weevils began to emerge on day 25 and so during 44–52% of the lifetime of the hosts, the parasitoids were unable to attack the hosts. *A. calandrae* was unable to consistently parasitize hosts until they were older than 16 days. This provides an effectively larger refuge from parasitism for 64% of the host's developmental period. However, *H. prosopidis* was able to relatively effectively parasitize hosts (Fig. 1 middle) as young as 12 days, resulting in a relatively smaller refuge for only 48% of the host's developmental period.

There was a clear increase in both the ability of the parasitoids to parasitize hosts (Fig. 1 bottom) and the total number of hosts parasitized as the age (size) of the host larvae increased, which reached a maximum at around a host age of 18 days (Fig. 1 top and middle). The rate of parasitism by the wasps then remained high until ca. day 24. The hosts most heavily parasitized are those in the age range of 16–24 days. This range appears roughly to correspond to the last several instars and perhaps the pupal stage, since hosts begin to emerge at 25 days. Within this range of host ages, *H. prosopidis* parasitizes significantly more larvae in 24 h than *A. calandrae* (4.97 ± 3.34 versus

1.55 ± 1.50 ; pooled Student's t test, $df = 52$, $t = 4.313$, $P < 0.001$).

As the size of the host larvae increased with age, the female wasps also tended to vary the sex ratio of their offspring (Fig. 2). This will not affect the prey death rate directly but will affect the number of female wasps in the next generation and so will play some part in the dynamics of the systems. The parasitoids tendency to lay female eggs also indicates that it is advantageous for both wasp species (and perhaps hymenopterans in general, Wilson 1975) to produce mostly female offspring.

Discussion

Host-age structure has been hypothesized to provide a refuge from predation. In this study, host age appeared to play a significant part in the parasitoid-*Z. subfasciatus* systems. Other factors such as population dynamics of the host, functional responses of the parasitoids, mutual interference, and parasitoid age are also relatively important in these systems (Kistler 1979). *H. prosopidis* was potentially able to parasitize larvae during <50% of the host's larval period, whereas *A. calandrae* was able to parasitize larvae during <40% of the host's larval period. The host larvae thus not only have an effective refuge for a large proportion of their life span, but the refuge size varies with parasitoid species.

The proportion of the host's life span during which it is protected from parasitism is closely related to the searching ability of the parasitoid species. Thus, *A. calandrae* did not parasitize hosts until they were several days larger than the minimum size, which could be parasitized by *H. prosopidis*, even though the smaller size of *A. calandrae* might allow it to parasitize these smaller hosts successfully.

These refugia should bring some stability to the host-parasitoid interaction (Smith and Mead 1974). The longer the refuge period, the fewer the number of hosts that will be available to parasitoids at any time. The result will be a slower rate of increase for the parasitoids and a greater stability for the parasitoid-host populations. Based on this prediction, the *A. calandrae*-*Z. subfasciatus* system should be more stable than the *H. prosopidis*-*Z. subfasciatus* system, because of the longer refuge period. The stability of systems of *H. prosopidis*-*Z. subfasciatus* and *A. calandrae*-*Z. subfasciatus* on different host resource beans has been described by Fujii (1983). On azuki beans, *H. prosopidis* destabilizes populations of the host, whereas *A. calandrae* stabilizes host-population dynamics. On blackeye beans (*Vigna unguiculata*) both *H. prosopidis* and *A. calandrae* destabilize the host populations, resulting in rapid extinction of the parasitoid or host. As predicted, the systems found to possess longer refuge periods were more stable. This difference in host-size utilization (or refuge size) might be one reason why the *A. calandrae*-

Z. subfasciatus system was more stable in the experiments by Fujii (1983) than the *H. prosopidis*-*Z. subfasciatus* system. This also may partially explain the greater instability which he found exhibited in the *A. calandrae*-*Z. subfasciatus* system when the host resource was the blackeye bean. In the blackeye system, *A. calandrae* females can successfully attack hosts that were as young as 9 days (Kistler 1979). Thus, as the size of the host refuge decreases and younger hosts are able to be parasitized, the stability of the parasitoid-host system seems to also decrease. This study agrees with that of Smith and Mead (1974). It provides experimental evidence that age-related refugia may increase the stability of host-parasitoid systems.

The analysis by Smith and Mead (1974) predicted that stability is more likely if a predator attacks younger age classes, but these data indicate that stability can also occur if the parasitoid attacks the older ages preferentially. This is perhaps the case for many ectoparasitic hymenopterans. Larger hosts should be easier to find, especially where the larvae are inside seeds, as is the case in most Bruchidae. This will probably not be the case where defense mechanisms, either physical or chemical, make parasitizing larger hosts more difficult as a result of increased handling time (Thompson 1978). My results indicate that the overall length of the refuge is more important than where the refuge occurs in the life cycle, at least in determining whether the effects resulting from the refuge will be stabilizing.

Developmental refugia may also cause instability in host-parasitoid systems in which the host and parasitoid do not have synchronized life cycles. The refuge from predation by *H. prosopidis* is longer than the life span of an average adult parasitoid (<10 days in these laboratory systems). Intense parasitism may deplete all hosts in age classes from 12-24 days, creating 12-day periods in which no hosts will be available for parasitism. The resulting asynchrony is probably the factor that brings about the eventual extinction of *H. prosopidis* by increasing the magnitude of the oscillations in the multigeneration systems of Fujii (1983), but allows for the continued existence of the host despite very intense levels of parasitism. This asynchrony is less important in the *A. calandrae*-*Z. subfasciatus* system. The refuge period was larger and less time was available for *A. calandrae* to deplete any age class of the host completely. Also, *A. calandrae* is less efficient at parasitizing hosts than *H. prosopidis* and is less likely to deplete any age class of hosts totally. This lower efficiency in itself need not lead to increased stability, because if very small hosts could be attacked (i.e., a shorter refuge period) the dynamics of even this inefficient parasite would most likely be much less stable, due to the removal of the most available hosts and the resulting increase in asynchrony between the host and parasite populations.

The age structure of the host also partly determines the sex ratio of the parasite, which will in turn determine the predator's rate of increase in the next generation. The parasitoids tended to lay unfertilized eggs, which develop into males, on small hosts and fertilized eggs, which develop into females, on the larger, older hosts. Sex determination occurs in many hymenopterous parasitoids and is probably a consequence of haplodiploidy (Flanders 1956, Wilson 1975). The size of the host indirectly determines the size of the emerging parasitoid and large size is more crucial to the female offspring, since it is probable that size is directly related to fecundity. The production of adequate amounts of sperm is probably not as dependent on size. Thus upon discovering a small host, a female parasitoid would be better off under most circumstances not to move off to search for a larger host for her offspring but to lay a male egg on such small hosts (Jones 1982). If hosts are always parasitized as soon as they become large enough to be attacked then there will be a majority of male offspring, which will decrease the effective parasitoid density in the next generation. This might either stabilize or destabilize the system, in that as large hosts disappear, the number of females in the next generation will be small. The host population will thus have an opportunity to recover from the parasitism. However, the numbers of female parasitoids might be reduced to levels near extinction. The stabilizing effect should be most marked in the *A. calandrae* system, which showed the greatest change in sex ratio as the host age decreased. Alternately, the proportion of female *H. prosopidis* was almost always >50% except on very young hosts, which were not parasitized in these experiments (Jones 1982). The production of mostly female offspring will most likely be destabilizing, since this increases the effective population density of parasitoids.

The age structure of the host appears to play an important role in these parasitoid-host systems, by providing a refuge for the host larvae. This leads to increased stability in the *A. calandrae*-host system, due mainly to the length of the host-refuge period and sex-ratio effects. The refuge may actually decrease the stability of the *H. prosopidis*-host system, due to a shorter host-refuge period, an asynchrony of the host-parasitoid life cycles, and the effects caused by sex determination by female *H. prosopidis*.

Acknowledgment

I thank C. D. Johnson, K. Fujii, M. Hetz, K. Paige, K. Mobley, and P. Waser for reviewing this manuscript or one of its earlier versions. Suggestions by P. W. Price and three anonymous reviewers helped to clarify the manuscript and were very much appreciated. This work was supported by National Science Foundation grant No. 7620333.

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Received for publication 29 May 1984; accepted 13 May 1985.