

Reproductive Strategy of *Trissolcus euschisti* (Hymenoptera: Scelionidae) Under Conditions of Partially Used Host Resources

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ABSTRACT *Trissolcus euschisti* (Ashmead), a scelionid parasitoid of stink bug eggs, did not alter its sex ratio in response to chemical traces left by previously ovipositing wasps as had been predicted by published local mate competition models. Female *T. euschisti* generally oviposited male offspring early in an ovipositional sequence. Consequently, stink bug egg masses that have been parasitized by more than one female should produce a higher male/total wasp sex ratio than those parasitized by single females as suggested by Waage (1982) for certain other scelionid parasitoids. Thus, the apparently adaptive outcome of higher sex ratios when more than one foundress oviposits in a patch may be the same as that predicted by local mate competition theory but does not involve local mate competition because of a relatively fixed pattern of sex allocation. Female *T. euschisti* rejected heavily parasitized egg masses more frequently than they rejected host egg masses of a similar size that were only lightly parasitized.

KEY WORDS Insecta, sex allocation theory, parasitoids, local mate competition

FACTORS INFLUENCING SEX RATIOS of offspring in parasitoid wasps have been thoroughly discussed (King 1987). One of these factors, increasing female wasp density, resulted in a higher sex ratio of males to total offspring in 11 of 13 species studied. Hamilton's (1967) theory of local mate competition predicts a female-biased sex ratio in inbreeding populations where sons of a parent compete with each other for mates, rather than competing with the sons of other mothers as happens in large, randomly mating populations. For haplodiploid organisms, the predicted optimal sex ratio (frequency of males) is $(n - 1)(2n - 1)/n(4n - 1)$, where n is the number of females colonizing discrete patches of a resource (Hamilton 1979). Thus, under conditions of total sibmating a female should produce the minimal number of sons necessary to fertilize her daughters. As more females contribute to that local mating group, the sex ratio produced should increase until it approaches that of outbreeding populations, 0.5. Fisher (1930) predicted this ratio for a randomly mating population in which the cost of producing male or female offspring is equal.

Haplodiploid sex determination, where unfertilized eggs develop into haploid males and fertilized eggs develop into diploid females, is common among the Hymenoptera. This feature allows us to test predictions of sex ratio theory, because female wasps may have the potential of adjusting their sex ratio in response to local conditions by controlling fertilization (Charnov 1982). Under conditions where a resource patch can be exploited by two parasitoids, the optimal strategy for a second

foundress should be a function of the number of eggs she lays relative to the number of eggs produced by the first foundress (Werren 1980). Werren's (1980) model for a two foundress situation where brood sizes can vary relies on the reasonable assumptions that females mate with males from their own host (little male movement between hosts occurs), first and second broods emerge synchronously and mate randomly, the second brood does not suffer increased mortality, there is no inbreeding depression, and the second wasp can vary her sex ratio. When a second foundress oviposits relatively few eggs into the host, she should produce a greater number of males and ensure a higher proportion of matings with the female-biased progeny of the first foundress. The optimal proportion of sons that a second female should produce in order to maximize numbers of grandchildren should decrease as oviposition opportunities increase relative to number of offspring produced by the original foundress.

To show a facultative sex ratio response to varying levels of local mate competition, a female parasitoid must be able to recognize a situation in which more than one foundress has colonized a host and to assess either her brood size relative to that of the first foundress or her own absolute brood size (Werren 1987). Facultative sex ratio response also presumes a high degree of flexibility in, and control over, the fertilization process determining the sex of a female's offspring. We can expect that not all parasitoids will use facultative sex ratio strategies. Waage (1982) suggested a fixed pattern of sex allocation that will result in the production of an

adaptive increase in sex ratio with increasing foundress numbers. The early placement of male offspring in an ovipositional sequence will result in an increased proportion of males produced by each colonizing female as oviposition opportunities become limited. To say with certainty that a particular species possesses facultative sex ratio control, we must first rule out the possibility that increases in the male to female sex ratio are produced merely as a result of a fixed sequence in which the sexes are oviposited.

Trissolcus euschisti (Ashmead), a scelionid parasitoid of pentatomid eggs, provides an excellent opportunity to study the predictions of sex ratio theory. In Kentucky, *T. euschisti* and another scelionid, *Telenomus podisi* Ashmead, are probably the most abundant parasitoids of stink bug eggs (Yeargan 1979). Both species are polyphagous parasitoids that attack 19–20 species of pentatomids in the Nearctic region (Johnson 1984a,b). Pentatomid hosts deposit their eggs in widely dispersed discrete clusters, thus making local mate competition in *T. euschisti* likely. Male *T. euschisti* emerge approximately 1 d before females, remain on the host egg mass, and mate with sibling females as they emerge. Only one parasitoid develops and emerges for each host egg. Scelionids, including *T. euschisti*, usually mark their host eggs after oviposition and thus may reduce superparasitism (Rabb & Bradley 1970, Okuda & Yeargan 1988). *T. euschisti* that arrive at a previously parasitized egg cluster should, therefore, be able to recognize and determine the amount, if any, of resource that remains unparasitized. Sex ratio shifts in favor of males in response to the presence of other females or the presence of trace pheromones have been demonstrated for the scelionid *T. grandis* Thomson (Viktorov 1968, Viktorov & Kochetova 1973). We wanted to determine whether shifts in *Trissolcus euschisti* sex ratios occurred in response to chemical traces left by a conspecific on a host egg mass, or alternatively, as a result of a fixed ovipositional sequence (Waage 1982, Waage & Lane 1984).

Materials and Methods

The parasitoids used in these experiments were the F_1 progeny of *T. euschisti* collected from the field by placing egg masses of the spined soldier bug, *Podisus maculiventris* (Say), on hackberry (*Celtis occidentalis* L.) leaves along the border of a small woodlot. Female *T. euschisti* were collected by aspirating them from the egg masses placed in the field. Egg masses removed from the field and egg masses, which were later exposed to field-collected females in the laboratory, were incubated at 24°C until the parasitoids were ready to emerge. Mated females were isolated and held individually in plastic cups with a source of free water and access to a 10% honey solution.

Three-day-old, mated female parasitoids, which had access to four host eggs 24 h before the ex-

periment (to give them the opportunity for uniform experience in parasitizing hosts), were exposed to a stink bug egg mass that had been reduced to 10 eggs. Females were allowed to oviposit in and mark a variable number (from 1 to 9) of host eggs. We recorded the sequence in which a particular female oviposited on a map of the egg mass. The first female *T. euschisti* was then removed, and a second female was allowed to parasitize the remaining eggs. We also recorded her sequence of oviposition. Time between the removal of the first parasitoid and introduction of the second parasitoid ranged from 2 to 4 h. Chemical markings left by *T. euschisti* remain effective for up to 4 d after they are deposited (Okuda 1986).

Parasitized host eggs were incubated until the first male had emerged (about 13 d at 24°C, Yeargan 1983), which indicated that development was nearly completed. Upon emergence of the first male, the host egg masses were frozen. Subsequent dissection of host eggs and comparison with previously prepared maps of ovipositional sequence allowed us to determine the sex of each parent female's offspring. Male and female *T. euschisti* are easily distinguished, because females have clubbed antennae and male antennae are filiform. In this way, we determined the sequence in which male and female offspring were deposited by each set of foundresses. No superparasitized egg masses were included in analyses. The proportions of sons produced by the first and second foundresses also were compared (Fisher's distribution-free sign test, Hollander & Wolfe 1973).

Certain hymenopterous parasitoids, including another scelionid, *Gryon atriscapus* Gahan, have a tendency to deposit males early in an ovipositional sequence (Waage 1982, Waage & Lane 1984). We could determine the sequence of oviposition of male and female offspring in a relatively small egg mass by using the studies outlined above. To be certain that a smaller-than-average size egg mass did not influence the ovipositional sequence, we placed 10 female parasitoids, of the same age and ovipositional experience as above, on an average-sized *P. maculiventris* egg mass (17 eggs per mass, Yeargan 1982) and mapped the sequence in which they oviposited. Egg masses were then incubated, frozen, and dissected as described above.

To determine if female *T. euschisti* respond to previously parasitized egg masses in some manner other than by altering their sex ratio, we recorded the behavior of female parasitoids that were offered either lightly or heavily parasitized egg masses. Female parasitoids were presented with an egg mass of 10 eggs in which either 2 or 8 eggs had been parasitized by another *T. euschisti* female less than 2 h earlier. They were then placed in the center of a large (l × w × h, 31 by 31 by 41 cm) arena. After thorough inspection of the egg mass by the female, parasitoid response was recorded as acceptance if the female remained and parasitized at least one egg or rejection if she left the egg mass

Female parasitoids offered host egg masses that were only lightly (20%) parasitized usually responded by accepting that egg mass and staying to further parasitize it. *T. euschisti* antennated and then left a lightly parasitized egg batch in only 5 of 20 cases. In contrast, females offered heavily (80%) parasitized egg masses more frequently rejected them and left without ovipositing (13 out of 21 cases). Of the 8 cases in which a female accepted a heavily parasitized egg mass, five females parasitized host eggs that had already been parasitized and marked by a previous visitor, which is an infrequently observed behavior for this species. Marking substances left by a parasitoid usually serve to deter oviposition in the same host either by that same parasitoid or by another female of the same species (Okuda & Yeargan 1988). These data indicate a clear difference in behavior ($\chi^2 = 5.56$, $P < 0.025$) of female parasitoids when confronted with heavily versus lightly parasitized host resources. Whether this difference is simply a reflection of the probability of encountering a parasitized egg when an egg mass is discovered is unknown.

Discussion

Werren (1980, 1983), in his work with *Nasonia vitripennis* (Walker), a chalcidoid parasitoid of dipteran pupae, found that females of this species did alter their sex ratios in a manner consistent with the local mate competition theory. Optimal sex ratio of the second female to attack a host depends on the brood size of the second female relative to that of the first female. Frank (1985) presented data suggesting that the sex ratio of fig wasps, *Blutophaga psenes* (L.), decreases with increasing amounts of inbreeding and local mate competition. Observed sex ratios were, however, lower than those predicted by existing models and new predictive models were presented. Current sex ratio theory, however, fails to explain the high degree of variation in second sex ratios (those produced by the second females to attack the hosts) (Orzack 1986, Orzack & Parker 1986). Other research suggests that female parasitoids may not exert fine control over their sex ratios or may fail to accurately assess relative brood size (Orzack 1986, Werren 1987).

Behavioral analysis of *Trichogramma evanescens* Westwood, attacking the eggs of the moth *Mamestra brassicae* L., suggested that wasps did not respond to the presence of other wasps on the patch (Waage & Lane 1984). Instead, adaptive changes in sex ratio were due to the sequence in which male and female progeny were oviposited. Waage (1982), in his discussion of sex ratio strategies in scelionid wasps, suggested that the tendency to deposit a male early in an ovipositional sequence would result in an increase in the sex ratio when an increasing number of females oviposit in a patch, because each female lays fewer eggs and therefore proportionately more males.

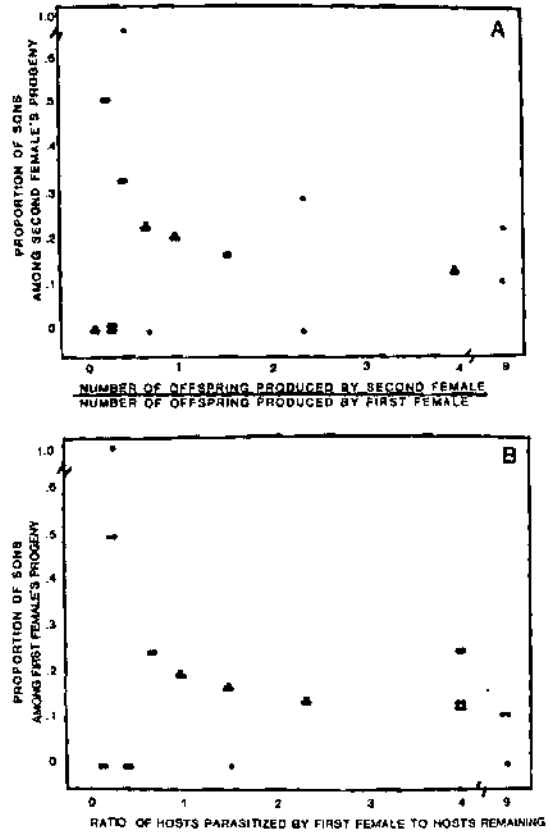


Fig. 3. Proportion of sons produced by either the second (A) or first (B) parasitoid foundress in relation to brood size (n = 28 female pairs).

Trissolcus euschisti females do not appear to alter their sex ratio in response to traces left by previously ovipositing wasps. However, the tendency to deposit male eggs early in an ovipositional sequence would be expected to result in higher sex ratios when fewer hosts are available. This strategy alone will produce an increase in sex ratio when individual females parasitize small egg masses as compared with large egg masses, or when more than one female oviposits in a mass. There is no evidence that *T. euschisti* alters its sex ratio in response to local mate competition.

Trissolcus euschisti females tend to reject heavily parasitized host egg masses rather than investing time and offspring in a resource already dominated by another female's offspring. Bakker et al. (1985) suggested that it might benefit a parasitoid to superparasitize a patch of resources (e.g., a mass of eggs) that has already been largely or totally parasitized by conspecifics, even though only a few of her offspring are likely to survive. This depends on the likelihood of survival of her offspring in superparasitized eggs and the probability that she will be able to locate other, unparasitized hosts before she dies. The latter is, of course, dependent on the abundance and spatial distribution of unparasitized hosts and the costs (e.g., time and risks

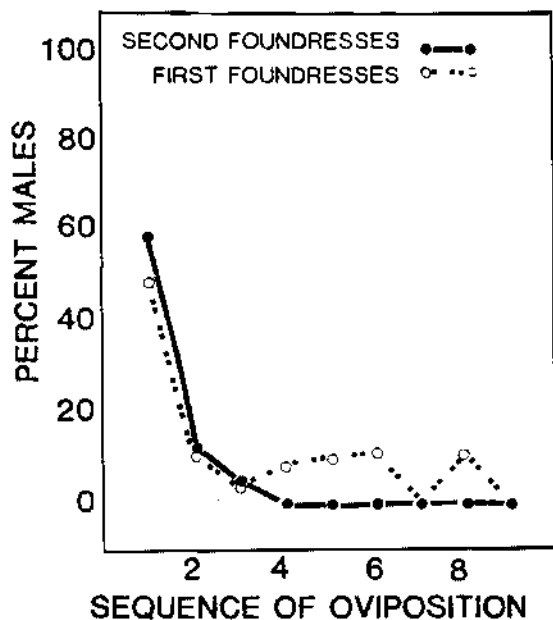


Fig. 1. Sequence of oviposition of male offspring by first and second parasitoid females to attack pentatomid masses of 10 eggs ($n = 28$ female pairs).

and traveled as far as one edge of the arena. Differences in acceptance of lightly versus heavily parasitized egg masses were determined by χ^2 . Voucher specimens of *T. euschisti* are located in the museum in the Entomology Department at the University of Kentucky, Lexington.

Results

The sequential pattern in which *T. euschisti* females oviposit male offspring (Fig. 1 and 2) is similar to that of the scelionid *Gryon atriscapus* reported by Waage (1982). In Fig. 1, the cumulative sex ratio for the first egg reflects oviposition by all females tested, and the sample size decreases as number of hosts increases. Number of females contributing to the calculation of frequency of males produced in host eggs 1 through 9 for first and second foundresses were, respectively, egg 1 (28, 28), egg 2 (25, 26), egg 3 (19, 23), egg 4 (16, 21), egg 5 (12, 19), egg 6 (9, 16), egg 7 (7, 12), egg 8 (5, 9), and egg 9 (2, 3).

Fig. 2 reflects the proportion of males produced by 10 females in masses of 17 host eggs where all 10 females oviposited 17 times with no superparasitism. Overall sex ratio for this size host egg mass was 0.127. *T. euschisti* females tend to deposit male offspring very early in an ovipositional sequence, a behavior that should result in a higher proportion of males produced when less of the host resource (fewer unparasitized eggs) remains. The sequences in which the 28 parasitoid pairs (first and second foundresses) in this study deposited male and female offspring were very similar (Fig. 1), suggest-

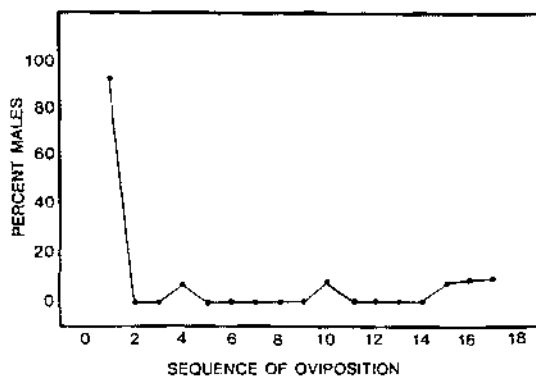


Fig. 2. Sequence of oviposition of male offspring by *T. euschisti* in an average-sized *P. maculiventris* mass of 17 eggs ($n = 10$ females).

ing a relatively fixed sequence of sex allocation regardless of previous parasitism by a conspecific. This tendency to deposit males early in an ovipositional sequence appears to become even more pronounced as the size of the host egg mass increases, i.e., the proportion of males in the first host egg increased from about 60% to about 90% as the size of the host egg mass increased from 10 eggs to 17 eggs. This trend also was apparent in results reported for *G. atriscapus* (Waage 1982).

The observed proportion of sons produced by the first or second females as a function of their relative brood size was quite variable (Fig. 3A and B), particularly when few hosts were parasitized. These results indicate that *T. euschisti* females do not alter their sex ratio in response to chemical traces left by previously ovipositing wasps. The first female in each case was presented an unparasitized egg mass and allowed to parasitize a varying number of host eggs (1-9). The proportion of sons produced by the first female (Fig. 3B) was, in fact, remarkably similar to the proportion of sons produced by the second female, indicating that the second female did not alter her sex ratio in response to previous parasitism of a portion of the egg mass. Analysis of sex ratios produced by the parasitoid females that first colonized the egg masses in comparison with the subsequent colonizers showed no statistical difference ($P > 0.5$) between the two groups.

The possibility that females deposited their male offspring during the preconditioning period (24 h before the experiment), thereby affecting these results, is unlikely. Female parasitoids used to determine ovipositional sequence on a large egg mass also were allowed to gain ovipositional experience before testing and still produced males early in an ovipositional sequence on subsequently offered egg masses (Fig. 2). Furthermore, parasitoids that were offered newly laid, unparasitized host egg masses of 25 eggs on a daily basis during fecundity experiments continued to deposit males in those egg masses (K.V.Y., unpublished data).

involved in searching) associated with finding new, unparasitized resources. We do not have the information necessary to assess the relative costs and benefits of superparasitism in *T. euschisti*. It is noteworthy that in experiments on interspecific competition, Okuda (1986) found that when either *T. euschisti* or *T. podisi* oviposited in host eggs that had been parasitized 2 d earlier by the other species, survival of the second parasitoid was low. Although this does not directly address the issue of intraspecific interactions, it suggests that efforts by *T. euschisti* to superparasitize eggs already parasitized by conspecifics are not likely to be productive.

Yeargan (1979) found that when *Euschistus* spp. egg masses were parasitized by scelionids in the field, about 98% of the eggs in a mass were parasitized. Egg masses of those species are similar in size to those of *P. maculiventris* (Yeargan 1982). This implies that when a parasitoid discovers a previously parasitized egg mass of these pentatomid species, there is little chance that a significant number of eggs remain unparasitized. Thus, unless a parasitoid quickly discovers an unparasitized egg upon encountering an egg mass, it may be more profitable for her to leave that egg mass and continue searching.

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