Adaptive responses to local mate competition by the parasitoid, *Telenomus remus*

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Summary. The parasitic wasp, *Telenomus remus*, lays her eggs in discrete patches of moth eggs, where her offspring develop and mate before dispersal, satisfying conditions for local mate competition (LMC). In the presence of other ovipositing females, wasps lay a higher sex ratio (proportion males), as predicted by LMC theory, and achieve this by a combination of two mechanisms, (1) avoidance of superparasitism and a sequence of sex allocation initially biased towards males and (2) a direct increase in sex ratio in the presence of other wasps. On host patches previously visited by other wasps, sex ratio increases with the proportion of previously parasitized hosts, as predicted by LMC theory. In both cases, chemical traces left by foraging wasps are indicated as the stimuli causing wasps to increase the proportion of males allocated to hosts.

Introduction

Many parasitic Hymenoptera are arrhenotokous: males develop from unfertilized and females from fertilized eggs. Ovipositing females have a degree of control over fertilization, and hence over the sex ratio which they produce. Highly variable sex ratios are often found among parasitoid species, possibly as a result of natural selection acting on oviposition behaviour to produce sex ratios adaptive to different conditions (Waage 1986).

Over the last two decades, several evolutionary models have shed light on variable sex allocation in parasitoids (Charnov 1982). Of particular value has been the theory of local mate competition (LMC) (Hamilton 1967). This theory is applicable to a common parasitoid life history, where one or more females lay their eggs on discrete patches of resource (hosts or groups of hosts) on which the offspring develop and mate at random before dispersal to find new patches. The optimal sex ratio for an ovipositing female (proportion males) may be expressed in terms of the number of females colonizing a patch (*n*), and equals \((n-1)(2n-1)/n(4n-1)\) (Hamilton 1979). Thus, in an outbreeding population (*n* very large) the optimal sex ratio approaches 0.5, while as *n* decreases, sex ratio approaches zero. When LMC is complete (*n* = 1), a female should produce only enough sons to mate all her daughters on a patch.

A general prediction of this model is that sex ratio should be positively density dependent. This is true for many studies where parasitic wasps are confined on a patch of hosts in the laboratory (Salt 1937; Wilkes 1963; Wylie 1965, 1976b; Schwartz and Gerling 1974). However, another explanation of this density dependence is the selective survival of males in hosts which have received repeated attacks from conspecífics (superparasitism) and therefore contain too many eggs to allow the development of all offspring. This can occur at high ratios of parasitoid to host, and the developmental advantage of males in this situation is well documented (Grosch 1948; Wilkes 1963; Wylie 1966; Suzuki et al. 1984).

As a result of this complicating factor, there exist only a few unambiguous tests of LMC theory in parasitoids where effects of differential mortality have been investigated and excluded (Werren 1983; Waage and Lane 1984). Some other studies, while not specific tests of LMC theory, have revealed density dependent sex ratios under conditions
where differential mortality in superparasitism was shown to be unlikely (Jackson 1966; Wylie 1979; Viktorov and Kochetova 1973b).

These studies indicate that wasps do change sex allocation to host patches as a function of the number of colonizing females, but the behavioural mechanism behind this effect remains unclear. In *Trichogramma*, sex ratio shifts may occur without a change in the pattern of sex allocation (Waage and Lane 1984). Because females lay more male eggs early in an oviposition bout (Waage and Ng 1984), and because they also tend to avoid superparasitism, sex ratio increases at high n for a particular patch size because every female will lay proportionally fewer eggs. In other studies, changes in sex allocation with density have been attributed to physical interference between wasps (Wylie 1976a, 1979) and to chemical traces left by previous females (Viktorov and Kochetova 1973a). For the case of superparasitism in *Nasonia*, Wylie (1973) suggests that host death following parasitism provides the stimulus for sex ratio adjustment by the second wasp (but see Werren 1984).

In this paper, we investigate sex allocation and LMC in the solitary scelionid egg parasitoid, *Telenomus remus* Nixon. This species attacks the egg batches of *Spodoptera* spp. (Lepidoptera, Noctuidae) which can vary greatly in size: for *S. litura* (F.), for example, batches can range from 50–1000 eggs (Braune 1982). Fecundity of the adult female wasps is variable; in the strain used in these studies the mean was about 140 eggs (S. Ravendranath, pers. comm.). Hence, large batches of moth eggs in the field may be colonized by more than one female. Unlike some other scelionids (Waage 1982), *T. remus* tolerate the presence of other ovipositing females on an egg batch (Schwartz and Gerling 1974), and avoid superparasitism by marking parasitized eggs (C.R.L. van Welzen, unpublished data). Male progeny emerge first and mate females as they emerge.

Thus, the biology of *T. remus* satisfies those conditions under which we would expect LMC to operate. Previous studies on scelionids have shown that sex ratio variation between species fits prediction of LMC theory (Waage 1982) and that *T. remus* does produce higher sex ratios at higher parasitoid-host ratios, although this might be due to superparasitism and differential mortality (Schwartz and Gerling 1974).

We examine sex allocation by *T. remus* under two situations likely to be encountered by wasps in the field. First, we consider wasps parasitizing an egg batch simultaneously with other wasps. Second, we consider wasps parasitizing a batch previously parasitized by another female, consisting of various proportions of parasitized and unparasitized eggs. Both experiments were observed continuously to identify the possible stimuli which elicit changes in sex allocation during oviposition.

**Methods**

*Telenomus remus* was collected in Barbados in January 1984 from eggs of *Spodoptera frugiperda* Smith, and reared in the laboratory on *S. littoralis* (Boisd.). This host was reared on the artificial diet described by Hoffman et al. (1966) but without sinigrin. Adult moths were kept in 35 cm by 24 cm cages and fed a 50% honey solution. Eggs were collected daily and stored at 10 ± 1°C until 1 h before the experiment. All stages of the host were cultured at 25 ± 1°C and 70 ± 5% RH, while wasps were cultured at 26 ± 2°C. For all experiments, one day old hosts and 2–3 day old wasps were used. At that time, the wasps have the maximum number of eggs in their ovarioles (S. Ravendranath, pers. comm.).

Wasp for experiments were allowed to mate at emergence on a host batch. On the next day, wasps were placed individually in a gelatin capsule (2.5 × 0.8 cm) with a drop of honey as food and kept overnight. Prior to the experiment, five host eggs were introduced into the gelatin capsule for 15 min to give the wasp ovipositing experience and to ensure, by subsequent rearing, that the wasp was mated. Data from unmated individuals were discarded. Wasps were then left for 0.5 to 2.5 h before experimentation.

In the first experiment, a batch of 20 eggs was placed at 25 ± 2°C under a Wild M7A dissecting microscope fitted to a Sony time-lapse video recorder. Wasps were placed on the batch at densities of 1 (7), 2 (7) and 4 (6) (no. replicates in parentheses). Their behaviour was recorded on magnetic tape until all eggs were attacked at least once. Wasps were then removed and the egg batch was reared at 30 ± 1°C and 60 ± 5% RH. After seven days, when wasp development was nearly completed, eggs were separated into individual tubes. Parasitoids were sexed in emergence.

For each wasp, the video tapes were analyzed to determine the sequence in which eggs were parasitized and specific behavioural events which preceded oviposition in each egg attacked. These events will be described below. When superparasitism occurred, the superparasitized egg and the eggs which were subsequently parasitized by that wasp were excluded from the analysis.

In the second experiment, a wasp was placed at 24 ± 3°C on a batch of 20 eggs and removed after it had parasitized 5 (6), 10 (16) or 15 (19) of these eggs (number of replicates in parentheses). Then, a second individual was introduced to the same batch after 1–5 min and allowed to parasitize the remaining unparasitized host eggs, 15 (11), 10 (14) and 5 (22), respectively. Differences in replication between first and second wasps arose because all eggs attacked by one wasp sometimes collapsed before parasitoid emergence, and were excluded from the analysis. Each wasp was observed continuously through a dissecting microscope to record the sequence in which eggs were parasitized. The experiment was terminated when the second wasp began to superparasitize hosts. Eggs superparasitized by the first or second wasp were not included in the analysis. Wasps were reared and sexed as in the first experiment, and the parasitoids were sexed upon emergence.

The separation of parasitized eggs, which was necessary for determining sex ratio sequence may have damaged some eggs, but the relatively high level of egg collapse was largely...