

Rates of Parasitism by Natural Enemies of a Solitary Bee, *Dieunomia triangulifera* (Hymenoptera, Coleoptera and Diptera) in Relation to Phenologies

by

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ABSTRACT

Variation over three years in phenological patterns of parasites *Heterostylum croceum*, *Rhipiphorus solidaginus*, *Triepeolus distinctus*, *Zodion fulvifrons*, and a mutillid wasp (probably *Pseudomethoca sanborni*) which attacked brood, the stored food, or adults of a solitary ground-nesting bee, *Dieunomia triangulifera*, showed that the emergence of parasites was synchronized with the nest provisioning activity of their hosts in two years (1989 and 1991), but not in 1990 when bees delayed nest provisioning behavior due to unfavorable edaphic conditions. Overall rates of parasitism based on emergence trap data are not tightly correlated with emergence synchrony, nor with the relative abundance of adult parasites from the previous year.

Keywords: Solitary bees, parasitism, phenology, *Dieunomia triangulifera*, *Heterostylum croceum*, *Rhipiphorus solidaginus*, *Triepeolus distinctus*, *Zodion fulvifrons*, *Pseudomethoca sanborni*

INTRODUCTION

Numerous insects parasitize the immatures or stored food of solitary ground-nesting bees and wasps (Hymenoptera: Apoidea, Vespoidea), taking advantage of a host's absence to steal or appropriate unattended resources. Such cumulative losses are hypothesized to influence the evolution of various host traits, in particular those relating to mutualistic behavior (Lin & Michener 1972). Despite this presumed importance, the biology of most of these parasites is not well known.

Our three year study documents parasite-host phenological relationships and rates of parasitism to test the hypothesis that parasites with emergence patterns more closely synchronized to those of host females will have higher success rates than parasites not closely synchronized.

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We studied the following taxa of parasites; the first four taxa either parasitize the pollen masses stored by adult bees, or attack the immature bees, while the fifth taxon parasitizes adult bees.

Female *Heterostylum croceum* Painter (Diptera: Bombyliidae) fly above the nesting site and flick eggs into nest entrances, holes, and cracks; the eggs hatch and active first instar larvae crawl to a host cell (Bohart *et al.* 1960). *Rhipiphorus solidaginus* Pierce (Coleoptera: Rhipiphoridae) females deposit eggs on flower buds, which hatch into first instar larvae (triungulins); these larvae attach to foraging host bees for transportation back to a nest cell (Linsley *et al.* 1952). Mutillid wasp¹ (Hymenoptera: Mutillidae) females lay eggs in the bees' cells; eventually the egg hatches and a larva consumes the prepupa or pupa (Brothers 1972). The cleptoparasitic bee, *Triepeolus distinctus* Cresson (Hymenoptera: Nomadinae), deposits eggs in empty cells, and after hatching the larva kills the host larva or egg, and then consumes its provisions (Rozen 1989). *Zodion fulvifrons* Say (Diptera: Conopidae) females fly above the nesting site, pounce on female bees returning to the nests, and oviposit on or into the hosts' metasoma (abdomen) (Clausen 1940).

Host records are known for several of these parasites: *T. distinctus* has been reared from nests of *Dieunomia heteropoda* (Smith) (Wcislo 1993); *H. croceum* parasitizes *D. nevadensis* (Kerfoot 1964); *R. solidaginus* was associated with another population of *D. triangulifera* (Pierce 1904); and *Z. fulvifrons* sometimes parasitizes large numbers of worker honey bees (*Apis*) (Severin 1937). Scant host data for congeners suggests that none of these parasite species are likely to be highly host specific (Hull 1973; Linsley *et al.* 1952).

MATERIALS AND METHODS

We studied *Dieunomia triangulifera* and its parasites at large nesting aggregations on a farm along the Kansas River near Eudora, KS (Douglas Co.) (Minckley *et al.*, in press). There is a single generation of bees per year, and adult bee activity is approximately synchronized with the flowering phenology of an annual sunflower (*Helianthus annuus* L.), which is the primary pollen source for females.

Emergence phenologies, and relative abundance of parasites, were obtained for each of 3 years (1989-1991) by placing three 0.9 X 0.3m, and one 1 X 1m emergence traps over areas where nests were abundant the previous year. Our sample is biased towards high host densities, which may be significant since host density and distribution can influence parasites' success (Wcislo 1984; Rosenheim 1990). The area covered by the traps (~1.9 m²) is a tiny fraction of the areas where bees nested (>30,000m²), but we believe they give a reasonable representa-

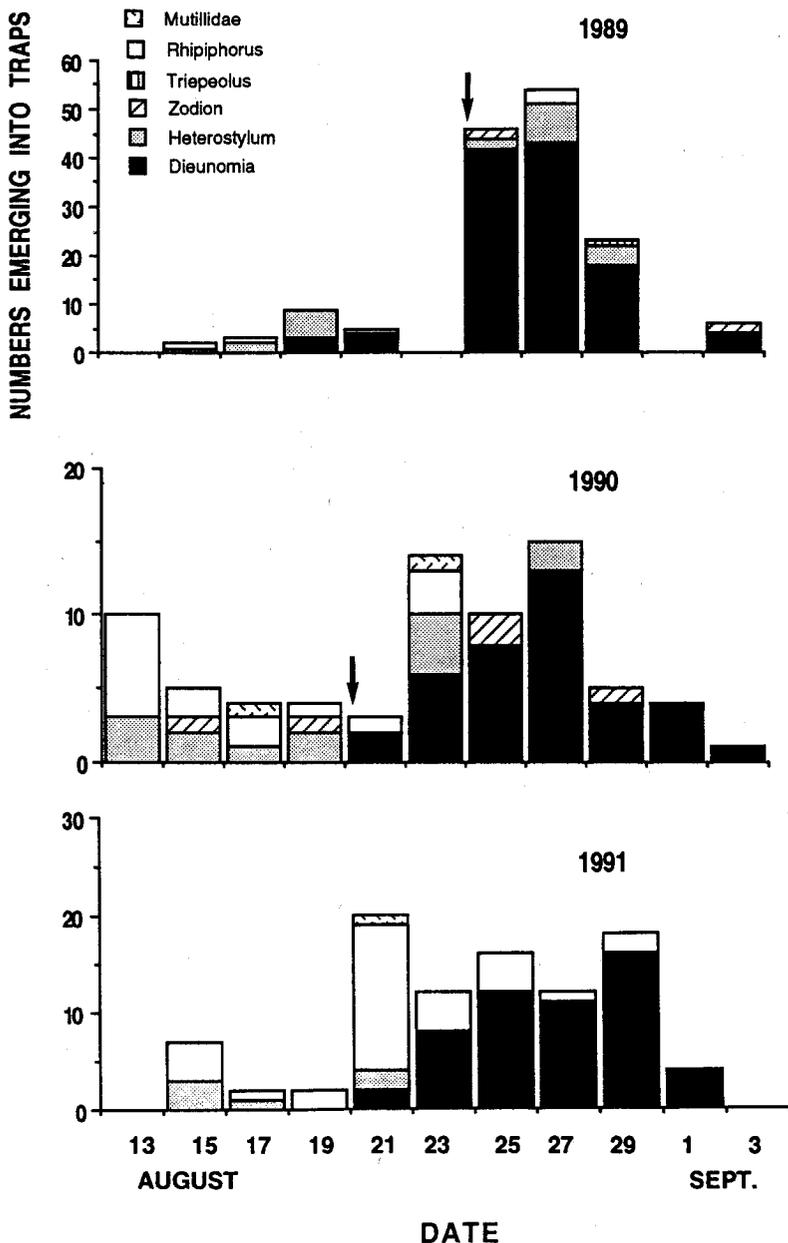


Fig. 1. Emergence phenologies of female *Dieunomia triangulifera* and associated insect parasites for the years 1989 (a), 1990 (b), and 1991 (c). The arrows (1989 and 1990) indicate the start of the bees' provisioning periods.

tion of activity patterns over the entire nesting aggregation, based on subjective impressions during daily visits to the nest site. Relative rates of parasitism during the years 1988 - 1990 were obtained from the emergence trap data collected from 1989 - 1991.

Each emergence trap consisted of a pyramid-shaped frame made of PVC^R tubing covered with screen; a screen cone passed through a hole in a wooden platform atop the pyramid. A strip of foam was glued to the perimeter of this platform, and a plastic collecting container was held snugly against the foam with clamps, which prevented the escape of any emerging insects. Emerging insects walked up the sides of the trap, crawled through the cone, and were trapped in the container.

Emergence traps were placed in the fields prior to the start of the active seasons, and traps were checked daily or, rarely, once every other day until bee activity ceased. The numbers of bees and parasites emerging into the container were counted, and the containers were then emptied and replaced. Since no insects emerged during inclement weather, data are pooled for periods of two days to smooth the distributions.

Voucher specimens of bees and associated parasites, except the mutillid wasp⁴, are deposited in the Snow Entomological Museum, University of Kansas, Lawrence, KS.

RESULTS

Dieunomia triangulifera emerged in early- to -mid-August (Fig. 1), and females provisioned nests through mid- to late-September. The following dates are for 1989 and 1990, respectively. Males began emerging on 16 and 17 August, and females did so on 20 and 19 August. Females began excavating nests on 21 and 19 August, and began provisioning cells with nectar and pollen when sunflowers first bloomed (24 and 21 August). The start of the provisioning phase is probably most relevant to the life-history of the brood parasites. The estimated relative size of the bee population varied from 52,660 (1989) to 154,961 (1990) to 116,383 (1991).

In 1989 the emergence phenologies of the parasites were generally synchronized with that of their host (Fig. 1a), and overall approximately 11% of the *D. triangulifera* cells were parasitized (Table 2). Our sample sizes for most of the parasites are too small to meaningfully compare the higher moments of their emergence distributions, but some facts point to their importance. In 1990 (Fig. 1b), for example, the emergence and

⁴The species in this study is probably *Pseudomethica sanborni*, but voucher specimens were misplaced prior to positive identification.

Table 1. Relative abundance of adult parasites at a nesting site of *Dieunomia triangulifera*, based on the percent cumulative numbers of hosts and parasites emerging from the soil into traps throughout the nesting season.

| RELATIVE ABUNDANCE (%) OF ADULT PARASITES | | | |
|---|------|------|------|
| SPECIES | 1989 | 1990 | 1991 |
| <i>Zodion fulvifrons</i> | 11 | 14 | 0 |
| <i>Heterostylum croceum</i> | 69 | 40 | 15 |
| <i>Rhipiphorus solidaginus</i> | 18 | 40 | 83 |
| <i>Triepeolus distinctus</i> | 2 | 0 | 0 |
| Mutillidae sp. | 0 | 6 | 3 |

Table 2. Percentage of the total *Dieunomia triangulifera* brood cells which were parasitized by individuals of different brood parasitic species over a three-year period. Data were collected from emergence traps (year is indicated in parentheses), reflecting rates of brood parasitism by adult parasites active the previous year. The total number of cells is the cumulative number of parasites emerging into traps, plus the numbers of males and females of *Dieunomia triangulifera* (i.e., the total number of viable brood cells; N = 212, 159, and 134, in 1988, 1989, and 1990, respectively).

| SPECIES | 1988 (1989) | 1989 (1990) | 1990 (1991) |
|--------------------------------|----------------|----------------|----------------|
| <i>Heterostylum croceum</i> | 8 | 9 | 4 |
| <i>Rhipiphorus solidaginus</i> | 2 | 9 | 25 |
| <i>Triepeolus distinctus</i> | 0.4 | 0 | 0 |
| Mutillidae sp. | 0 | 1 | 1 |

nesting activity of most bees was delayed due to a drought producing unfavorable conditions for nest excavating. Consequently, emergence of the parasites occurred prior to nest provisioning. Parasites such as *Zodion* apparently did poorly because we did not catch them in emergence traps the following year (Fig. 1c, 1991).

Patterns of abundance did not correlate well with subsequent successful parasitism (as estimated by the relative numbers of adult parasites which emerged the following year) (for brood parasites only, Pearson's $r = 0.58$, $P > 0.05$, $N = 8$; also not significant with Kendall's tau). For example, in 1989 the bee fly *H. fulvifrons* was the most

abundant parasite (Table 1), and nearly all these flies emerged during the same period as did female *D. triangulifera* (Fig. 1a), yet their relative abundance decreased the following year. In 1990 most bee flies emerged earlier than their hosts, and the following year their relative abundance did not change.

The percentages of *D. triangulifera* cells attacked by different brood parasites over a 3 year period is given in Table 2. These percentages were calculated by dividing the number of individuals of each brood parasitic species by the total number of individuals (excluding *Zodion*) emerging into traps (i.e., the total number of viable cells). Overall, the mean percentage of brood mortality due to parasites increased slightly in each year, and differences between years were significant ($X^2 = 14.2$, $P < 0.05$).

DISCUSSION

Parasites are often responsible for substantial losses of productivity for bees (Schmid-Hempel & Schmid-Hempel 1988; Weislo 1990). Bee flies usually were the most abundant parasite at our site, accounting for 4-9 % of all parasitized cells. For other host species, the incidence of bee fly parasitism varies greatly among localities and years (Frick 1962; Batra 1965; Krombein 1967; Packer 1986). Bohart *et al.* (1960), for example, report that *H. robustum* parasitized greater than 90% of all cells at a large aggregation (>500,000 nests) of *Nomia melanderi*; the following year the bee population was reduced by half, and rates of parasitism fell to ~50%; the third year the bee population was stable, while parasitism rates fell again to 30%. Other bee aggregations have been extirpated by parasites (Batra 1966). Despite the potential for such high rates of parasitism, some bee aggregations can persist for many years (Malyshev 1935), including the *D. triangulifera* site, where bees have been present at least since 1972 according to a local farmer (Mr. Gregory Shipe, pers. comm.).

Dieunomia triangulifera females are markedly less fecund (producing fewer than six offspring, on average; Minckley *et al.*, in press) than the parasites, as inferred from dissections of the parasites' congeners. Frick (1962), for example, reported that *H. robustum* females had a mean of 169 ova, while Linsley (1952) states that female *Rhipiphorus smithi* contained up to 853 eggs. Alexander & Rozen (1987) showed that parasitic bees are more fecund than solitary free-living relatives. Since *D. triangulifera* are philopatric, and have nested in the same area for at least 20 years, the higher expected intrinsic growth rate of the parasites should lead to ever increasing numbers of parasites, until the parasite load is too great and the host population crashes, as described above for *N. melanderi*. Bohart *et al.* (1960) believed that two factors are primarily

responsible for the failure of parasites to extirpate their hosts. First, they hypothesized that bees which do not nest within aggregations avoid the heaviest attacks when parasites are abundant, although they did not address the point that such selection should lead to the evolutionary loss of aggregating behavior (Wcislo 1984). Secondly, they hypothesized that some bees emerge late, and so begin nesting after the adult parasites have already died. In this case, selection should shift the emergence distribution of the bee population, unless countered due to phenological differences with respect to blooming periods of its pollen plants, or between-year variation in parasite emergence phenologies.

The second hypothesis of Bohart *et al.* highlights the presumed importance to parasites of phenologies synchronized with their hosts' activity, at least in a general way (Robertson 1926; Wcislo 1987; Price 1980). Rashad *et al.* (1979) show a seasonal correspondence between pollen provisioning behavior of *Nomia unidentata* and abundance of a cleptoparasitic bee, *Pasites* sp. (Nomadinae), although they provide no evidence to confirm this host association. Coordinated phenologies presumably ensure that potential hosts have stored enough resources to support the developing parasites. We know nothing, however, about the costs associated with deviations away from synchronized activity with particular hosts, which should vary with the degree of dependency on a given host.

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