

Observations on superparasitism in a natural population of *Centrodora scolyppae* (Hymenoptera: Aphelinidae)

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ABSTRACT

Superparasitism was found to be an important mortality factor in a natural population of *Centrodora scolyppae* (Valentine), parasitising the eggs of *Scolypopa australis*. Levels of superparasitism varied between years and host plants. Progeny from the first oviposition suppressed the development of later individuals. *Centrodora scolyppae* females were shown to discriminate for oviposition sites between parasitised and nonparasitised eggs.

Keywords: *Centrodora scolyppae*, *Scolypopa australis*, superparasitism, discrimination.

INTRODUCTION

The genus *Centrodora* consists of 29 known species (Hayat 1974, 1981). Host records are known for 16 species (Hayat 1974). They differ from species in most other aphelinid genera in that virtually all are specialised egg parasitoids, attacking orthopteran and

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homopterous insects. One exception is *C. speciosissima* which parasitises pupae of dipterous, chalcid and proctotrupid insects.

Centrodora scolypopae (Valentine) was first found in the eggs of *Scolypopa australis* (Walker) (Homoptera: Ricaniidae) in New Zealand in 1962 (Cumber 1966). It was identified as a new species and the adult external morphology described by Valentine (1966). The biology and morphology of the immature stages has been described by Gerard (1989a).

Adult emergence commences between mid January and the end of February, depending on summer temperatures. One, more often 2, or very rarely 3 eggs are laid into the host egg. The first egg is always female and subsequent eggs always male. Fecundity is generally between 30-35. There are 3 larval instars with most reaching the overwintering prepupal stage in late April and May in the Waikato. Pupation occurs in January. A combination of diapause and subsequent temperature requirements synchronise parasitoid adult appearance to *S. australis* oviposition.

There is usually 1 generation per year. Two generations per year can occur in Northland. In hot summers in the Waikato, the oldest larvae pupate instead of entering the overwintering stage, but the onset of winter prevents completion of this second generation (Gerard 1985).

During a study of populations of *S. australis* and *C. scolypopae* (Gerard 1985), multiple oviposition scars were frequently observed on *S. australis* eggs. However, the number of *C. scolypopae* larvae in these host eggs did not appear greater than for single ovipositions. This paper reports on a study which investigated possible superparasitism or discrimination for oviposition sites by *C. scolypopae* and the survival of competing progeny.

METHOD

During August 1983, *S. australis* egg batches laid in bracken (*Pteridium aquilinum* var. *esculentum*) were collected along the length of 25 m paths, bisecting 4 sampling areas in a study site near Hamilton. The egg batches were taken from the vegetation between 0.75 and 1.25 m above ground level. Approximately 25 egg batches were collected per sampling area. The host eggs were extracted from within the twigs and the chorion cleared with 70% ethanol so that the parasitoids within the eggs were visible. *Centrodora scolypopae* leaves a small raised protuberance where the ovipositor was inserted in the egg. This is possibly a small amount of the host egg contents which exuded out and solidified. With the use of a low power stereomicroscope, these protuberances can be counted on the dorsal surface of the host egg. Because of the relatively large egg surface area and small size of the oviposition scar, the chance of 2 females ovipositing at exactly the same site was small. For each host egg viewed, the number of parasitoid oviposition scars, parasitoid progeny and stage of development was recorded.

The process was repeated during March 1984, when *S. australis* eggs in blackberry (*Rubus fruticosus* agg.) were sampled also, and again in June 1984.

RESULTS

The results from the 3 sampling times are presented in Tables 1-4. As there were no significant differences in the proportion of eggs with multiple oviposition scars between the 4 sampling areas, the results were pooled.

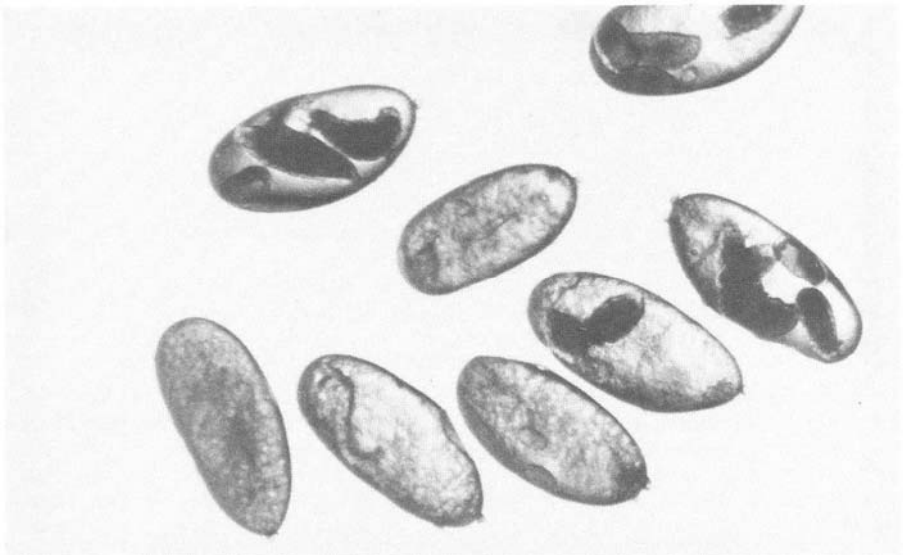
Table 1: Numbers of *C. scolypopae* oviposition scars and larvae in *S. australis* eggs in bracken, August 1983.

	Oviposition scars			
	1	2	3	4
Parasitoids/egg	44	21	8	1
	88	57	17	6
	0	6	3	0
	0	2	1	0
Total	132	86	29	7
Mean parasitoids/egg ± SE	.65 ± .04	1.87 ± .07	1.90 ± .13	1.86 ± .14

Table 2: Numbers of *C. scolypopae* oviposition scars and larvae in *S. australis* eggs in bracken, March 1984.

	Oviposition scars					
	1	2	3	4	5	
Parasitoids/egg	1 2 3 4 5	92 131 3 0 0	7 34 45 23 0	0 4 2 6 7	1 0 1 1 0	1 0 0 0 0
Total		226	110	25	3	1
Mean parasitoids/egg \pm SE		1.61 \pm .03	2.80 \pm .07	4.36 \pm .28	2.67 \pm .88	1
Mean larvae/oviposition \pm SE		1.61 \pm .03	1.40 \pm .04	1.45 \pm .09	0.67 \pm .22	0.2

In August 1983, the mean numbers of parasitoid larvae found in host eggs with 2 or more oviposition scars were significantly greater than in those with one ($P < .01$) (Table 1) indicating that superparasitism occurs. The March 1984 results (Table 2), demonstrate this more clearly with almost twice the mean number of parasitoid larvae being found when there are 2 oviposition scars and 3 times the mean number with 3 oviposition scars compared with that from a single oviposition. All stages of parasitoid development were found from eggs to fully mature larvae. Because of the rapid larval development, progeny from successive ovipositions within a single host egg could be distinguished easily by size in most cases (Plate 1). This provides visual evidence of superparasitism.

**Plate 1:** Sample of *S. australis* eggs showing occurrence of superparasitism by *C. scolypopae*. (Magnification 50X).

On examination of the approximately 500 superparasitized eggs in this study, it was apparent that progeny from the first oviposition inhibited the development of later individuals. Parasitoid eggs laid into host eggs already containing 3rd instar larvae failed to hatch, the contents becoming transparent and the chorion soft, so that the remains were sometimes twisted or folded. Eggs laid into hosts already containing 1st or 2nd instars hatched but the larvae failed to thrive and gradually assumed a dwarfed dense white

appearance, then eventually disintegrated. Only when all individuals were the same age did they all appear healthy at the time of the March 1984 sampling.

At this time, comparison of number of parasitoids found with the number of oviposition scars on each host egg showed that there was lower survival of parasitoids in host eggs with multiple oviposition scars than in those with a single scar (Table 2). Also at this time, eggs containing 3rd instar larvae were more likely to have multiple scars ($1.78 \pm .03$) compared to the population as a whole ($1.48 \pm .03$; $P < .001$).

As in August 1983, there were significantly greater mean numbers of parasitoid larvae in host eggs with 2 or 3 oviposition scars than in those with 1 in June 1984 ($P < .001$; Table 3). However, the mean number of larvae in host eggs with multiple oviposition scars was considerably lower than found in the same population 3 months earlier (Table 2). In both years, the parasitoids in host eggs containing 3 or more individuals were small 3rd instar larvae. These larvae had unusual large clear globules in their gut, which also had a curdled appearance. Also, these larvae barely filled half the available volume compared with healthy individuals which completely filled the host egg. Although still alive, the poor state of these larvae would make it unlikely that they would mature. The occasional exceptions were eggs containing a female and 2 male larvae resulting from a single oviposition. These were healthy and filled the entire egg volume. Previous laboratory observations indicated that these larvae mature to viable, albeit small adults. Table 4 shows the parasitoid oviposition scar distribution on host eggs laid in blackberry, the only other significant plant species in the trial site.

Table 3: Numbers of *C. scolypopae* oviposition scars and larvae in *S. australis* eggs in bracken, June 1984.

	Oviposition scars			
	1	2	3	4
Parasitoids/egg				
1	84	27	14	4
2	128	62	14	2
3	0	6	0	0
4	0	5	2	0
5	0	0	0	0
6	0	0	1	0
Total	212	100	31	6
Mean parasitoids/egg \pm SE	$1.60 \pm .03$	$1.89 \pm .07$	$1.81 \pm .20$	$1.33 \pm .21$

Table 4: Numbers of *C. scolypopae* oviposition scars and larvae in *S. australis* eggs in blackberry, March 1984.

	Oviposition scars			
	0	1	2	3
Total	152	84	19	3
Mean parasitoids/egg \pm SE	0	$1.79 \pm .05$	$3.07 \pm .22$	$2.36 \pm .3$

The level of superparasitism varied from year to year. In 1983, 48% of parasitised eggs in bracken were superparasitised (Table 1). In the following year, 38-39% of eggs in bracken and 21% of eggs in blackberry were superparasitised.

Host discrimination can be analysed by comparing actual parasite distribution within a host population with a random (Poisson) distribution (Lenteren *et al.* 1978).

When oviposition scar distribution was compared with the distribution that would be expected if females oviposited at random, the two were significantly different ($P < .005$; Fig. 1.). Most notable was the higher than expected number of single ovipositions which indicated that *C. scolypopae* females can discriminate between parasitised and nonparasitised host eggs.

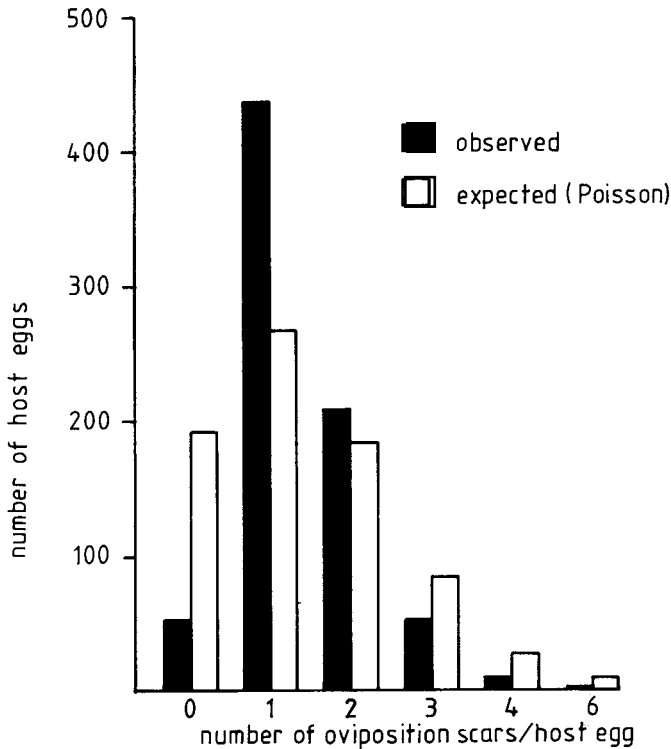


Fig. 1: Comparison of observed parasitoid oviposition scar distribution and distribution expected if oviposition occurred at random (Poisson distribution).

DISCUSSION

The examination of parasitised eggs during March 1984, at the end of the parasitoid oviposition period, gave clear evidence that superparasitism occurs in *C. scolyopae*. Even though there were significantly less eggs per oviposition in superparasitised eggs (Table 2), it is probable that superparasitising females do not greatly reduce the number of eggs deposited.

Host eggs containing 3rd instar larvae were more likely to be superparasitised than the rest of the population. In most cases, these larvae had completely eliminated all traces of the later parasitoid eggs laid in each host egg. This is apparent in the results for the 4 and 5 oviposition holes per egg in Table 2.

The progeny from the first oviposition were dominant. Larval combat is unlikely as 1st instar larvae lack mandibles and those of the 2nd instar are rudimentary (Gerard 1989a). Younger individuals are most likely eliminated by physiological suppression. A variety of possible mechanisms have been suggested. Early writers proposed a toxin (Timberlake 1910; Muesebeck 1918; Spenser 1926; Thompson & Parker 1930; Johnson 1959). Tremblay (1966) hypothesized that older larvae withdraw nutrients from the host haemolymph that are essential to the development of the younger larvae. Fisher (1971) suggested that the respiratory requirements of the younger parasitoids are not satisfied in hosts already containing older larvae so that the younger larvae die of oxygen starvation. A combination of mechanisms is possible with *C. scolyopae*. Certainly almost all traces of competitive younger larvae are eliminated by July and August. The production of 3 healthy larvae from the occasional single 3 egg oviposition but the suppression of newly hatched larvae by 1st instars only a day or so older indicates an allelochemical toxin may exist.

Mortality of parasitoids is a common result of superparasitism in parasitic wasp species, particularly in solitary species when only a single offspring can develop in a host (Vinson 1976; Lawrence 1981). In many such cases superparasitism may present an adaptive advantage for the parasitoid population as only the fittest individuals survive (Labeyrie & Rojas-Rousse 1985). However, as progeny from the first oviposition were always dominant, superparasitism does not play this role in *C. scolypopae* populations.

Initially it appeared that *C. scolypopae* females showed little discrimination at oviposition. However, the difference between the expected random distribution and actual parasitoid oviposition scar distribution shows that discrimination does occur. Observations of *C. scolypopae* behaviour show that females usually take about 10 minutes examining the vicinity of a prospective host egg with their antennae before commencing oviposition. The ovipositor plays no role in discrimination as once it is inserted, eggs are always laid (Gerard 1985).

Superparasitism resulted in the wastage of approximately 65% of the parasitoid eggs laid in bracken in 1983, and 47-52% in bracken and 24% in blackberry in 1984. This was the largest mortality factor in the parasitoid population in these 2 years (Gerard 1985). The differences between the 2 plant species arises because eggs laid in blackberry are at a greater depth and much less vulnerable to parasitism than those in bracken (Gerard 1989b). This in turn reduces the level of superparasitism in blackberry.

The high level of superparasitism found may result from several factors. First, both in 1983 and 1984, the population of *C. scolypopae* was high compared to the number of host eggs available. On some bracken fronds, parasitism reached 100%. A searching female may have an increasing urge to oviposit and when only finding parasitised hosts, resorts to superparasitism. Salt (1934) recognized this phenomenon and attributed it to a failure of restraint.

Second, discrimination may have to be learned (van Lenteren & Bakker 1975; van Lenteren 1976). In some species, only after encountering and ovipositing in unparasitised hosts do the wasps avoid superparasitism. Until then they readily oviposit in already parasitised hosts. As the *C. scolypopae* population was high, the later emerging females would have reduced opportunities of finding unparasitised hosts early in their adult life, and thus lay higher proportions of their egg complements in already parasitised hosts.

Third, the *C. scolypopae* oviposition period is over 6 weeks long but many marking pheromones are water soluble and do not last long (Roitberg & Mangel 1989). As the function of marking lies in the benefit to the ovipositing female herself (van Alphen & Visser 1990), the marks of *C. scolypopae* females are only needed for the duration of adult life of up to 10 days. As her progeny can then eliminate any subsequent competitors, it is unlikely the mark is of a persistent nature. Finally, the host egg is laid below the surface of woody materials. This gives a relatively large area to search and through which drilling can occur. A female could miss another's mark on this rough surface.

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