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Infection of gerrid eggs (Heteroptera: Gerridae) by the parasitoid *Tiphodytes gerriphagus* Marchal (Hymenoptera: Scelionidae) in Finland

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The scelionid wasp *Tiphodytes gerriphagus* parasitizes the eggs of at least four Finnish waterstrider species: *Gerris lacustris*, *G. odontogaster*, *G. paludum*, and *Limnoporus rufoscutellatus*. Observed rates of parasitism were lowest (3–5%) for *G. odontogaster* and highest in one population of *G. lacustris* (84%) (although no evidence of parasitoids was found in another population). In general, gerrid species that lay their eggs on floating vegetation were affected more than those that oviposit in rotting vegetation. Early in the season egg parasitoids were less abundant in temporary habitats, and none were found associated with gerrid populations in the Baltic archipelago.

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1. Introduction

Although *Tiphodytes gerriphagus* has been known to infect waterstrider eggs since the beginning of the century (Marchal 1900, Bradley 1902, Matheson & Crosby 1912, Martin 1927, Hoffmann 1932), all reports [except that of Hoffmann (1932)] were incidental and egg parasitism was thought to be an interesting but relatively unimportant aspect of gerrid biology. Recent findings in Canada (Spence 1986) now suggest that egg parasitism is a significant evolutionary force shaping life history patterns and behavior (Spence & Wilcox 1986) of waterstriders. Rates of parasitism for many populations of two *Limnoporus* species reached 95–100% by mid-July. Although *Gerris* species were generally less affected in the field they were preferred hosts in laboratory trials. These data suggest that both the jelly coat around *Limnoporus* eggs and the spatial patterns of oviposition that characterize pond-dwelling *Gerris* species have evolved as anti-parasitoid adaptations (Spence 1986). In addition, Spence suggested that differential rates of parasitism have important influences on the structure of local gerrid assemblages.

Although *Tiphodytes gerriphagus* is a Holarctic species originally described from France (Marchal 1900), the only published records of host use that we are aware of for Europe are for *G. lacustris* (Marchal 1900, Henriksen 1918). Furthermore no quantitative data about the effect of this parasitoid on European gerrid populations have been published. In the Nearctic region, the parasitoid uses a wide variety of gerrid hosts and rates of parasitism can be impressively high (Martin 1927, Spence 1986). In this study we surveyed eggs of six Finnish gerrid species for egg parasitism. Our data can be used to test several hypotheses about host use proposed by Spence (1986) based on work in western Canada. This preliminary report should encourage further studies of the interaction between egg parasitoids and gerrids in Europe.

Table 1. Gerrid species present at the study sites. Species name in parentheses when the species was present but no eggs were found. See text for more detailed description of habitats.

Site	Habitat type	Species present
1	ditch, temporary	*L. rufoscutellatus*, (*G. lacustris*, *G. odontogaster*)
2	pond, permanent	*G. odontogaster*, (*G. lacustris*, *G. argentatus*, *L. rufoscutellatus*)
3	rock pools	*G. thoracicus*
4	rock pools	*G. thoracicus*
5	pond, permanent	*G. argentatus*
6	ditch, temporary	*G. lacustris*, (*G. lateralis*)
7	lake, permanent	*G. paludum*, *G. lacustris*, *L. rufoscutellatus*, (*G. najas*)

Table 2. Parasitism of gerrid eggs by *Tiphodytes gerriphagus* at several sites during the summer of 1987.

Gerrid species	Site	Date	Eggs number	Eggs parasitized (%)
L. rufoscutellatus	1	08.06.	175	0 (0)
		27.06.	127	1 (1)
		17.07.	139	21 (25)
		04.08.	94	41 (44)
	7	10.06.	315	121 (38)
G. paludum	7	28.06.	261	0 (0)
		11.07.	101	12 (12)
		25.07.	196	80 (41)
G. lacustris	6	18.07.	995	0 (0)
		28.07.	101	0 (0)
		21.08.	168	0 (0)
	7	25.07.	56	47 (84)
G. odontogaster	2	09.06.	164	5 (3)
		27.06.	69	3 (4)
		17.07.	54	1 (2)
		04.08.	40	2 (5)
G. argentatus	5	14.07.	66	0 (0)
G. thoracicus	3	10.06.	11	0 (0)
		01.09.	91	0 (0)
	4	20.07.	205	0 (0)

2. Materials and methods

We searched for gerrid eggs in nature by scanning through floating and submersed vegetation. Gerrid eggs were first identified according to their similarity to related Canadian species and with respect to laboratory observations about oviposition habits of the gerrid species present in the local habitat. All eggs found were brought into the laboratory, counted and initially scored for parasitism under a binocular microscope. The appearance of parasitized eggs is well described by Martin (1927). Eggs were kept immersed in plastic basins until the gerrid larvae had hatched. Identification of gerrid species was verified from first-stage larvae using the key of Vepsäläinen & Krajewski (1986). Final counts of parasitized eggs were made after all gerrid larvae had hatched (1–4 weeks from date of collection). Eggs were classified as parasitized under a dissecting microscope if a developing wasp was visible in the egg or if a round hole was evident at one end. Such holes are characteristically left by wasps biting their way out of host eggs. A hatching gerrid opens the eggs with a longitudinal slit. Unfertilized or aborted eggs that yielded neither striders nor parasitoids were eliminated from our data set for further analyses.

We studied gerrid populations at seven field sites several times during the summer of 1987. The summer was exceptionally cool and rainy and even unstable gerrid habitats retained water for most of the season. Sites 1–5 are located in the vicinity of the Tvärminne Zoological Station (University of Helsinki) on the south coast of Finland (59°48′N, 23°06′E). Site 6 (Henriksberg) is located on Hanko Peninsula, 6 km west from the Zoological Station. Site 7 is in Pojo, about 40 km NNE of Tvärminne (60°10′N, 23°30′E). A list of gerrid species present at each site is provided in Table 1. The sites are individually described as follows:

Site 1. Ditch about 1.5 m wide, crossing open fields. The ditch dries during some summers. Eggs of *L. rufoscutellatus* were collected along a 100 m stretch, mainly from floating *Sparganium* leaves.

Site 2. Man-made pond (c. 50 m^2) in a field c. 20 m from site 1. This is a relatively permanent habitat and supports a dense growth of *Typha latifolia*. Eggs of *G. odontogaster* were found mainly in pieces of rotting *Typha*.

Site 3. Rock pools on the island of Brännskär in the Gulf of Finland. These are highly unstable habitats, most of them drying out at least once during each summer. Eggs of *G. thoracicus* were found mainly under floating *Sparganium* leaves.

Site 4. Rock pools on the island of Långskär, 3 km off the mainland in the Gulf of Finland. Habitats and gerrid species as at site 3.

Site 5. A large, stable pond on the island of Långskär (c. 2000 m^2). Eggs of *G. argentatus* were collected mainly from small crevices in rotting *Typha*.

Site 6. Ditch about 2 m wide, crossing fields and forest. This habitat may dry out during some summers. Eggs of *G. lacustris* were collected under floating leaves of *Potamogeton natans*.

Site 7. The large Lake Hemträsket (c. 0.5 km^2), surrounded by fields, forest and open rock. Eggs were collected at the mouth of a brook discharging into the lake. Eggs of *L. rufoscutellatus* and *G. lacustris* were found mainly under floating leaves of *Sparganium*, and those of *G. paludum* were found mainly attached to floating leaves of *Carex*.

3. Results and discussion

We found egg parasitoids infesting eggs of four of the six gerrid species sampled (Table 2). In addition to confirming that *T. gerriphagus* infects *Gerris lacustris* in Northern Europe, we provide new host records for *G. paludum*, *G. odontogaster* and *Limnoporus rufoscutellatus*. Thus, as in the Nearctic region (Spence 1986), this parasitoid uses a number of gerrid hosts.

In general, rates of parasitism observed in Finland were lower than those observed by Spence (1986) for *L. dissortis* and *L. notabalis* in western Canada. However, even our preliminary data set suggests that parasitism may be locally intense in Finland (e.g. 84% for *G. lacustris* at site 7), and the cool, rainy summer may have depressed parasitism below normal rates in other populations. In general, our results are consistent with those of Spence (1986) in suggesting that eggs laid in groups at the surface (*G. lacustris*, *G. paludum*, and *L. rufoscutellatus*) are subject to higher rates of parasitism than those laid in rotting vegetation (*G. odontogaster*). Rates of parasitism observed for *G. odontogaster* (2–5%) were conspicuously lower than Spence (1986) observed for its Nearctic equivalent *G. buenoi* (31%). This suggests that the habit of laying eggs in rotting vegetation, as observed for the Tvärminne population of *G. odontogaster*, is an even more effective way of avoiding parasitism than is laying single eggs on submersed vegetation as reported for *G. buenoi*. In Canada, Spence found that *G. pingreensis* which lays its eggs in rotting *Typha* suffered lower rates of parasitism than did *G. buenoi* on the same pond. The relatively high rates of parasitism observed for *L. rufoscutellatus* at site 1, just a short distance from site 2, emphasize that the low parasitism rates observed for *G. odontogaster* were not simply a matter of low local wasp population size.

Spence (1986) suggested that extremely temporary habitats may provide a refuge from egg parasitoids for gerrids. The wasp is thought to overwinter in gerrid eggs at the bottom of ponds and when a habitat dries out local wasp populations may go extinct. Our data from Finland are consistent with this hypothesis. Rates of parasitism were high for *L. rufoscutellatus* early in the season at a permanent lake (Table 1, site 7) but no parasitoids were found at the temporary site 1 in samples from about the same time. Rate of parasitism did rise over the season at site 1, presumably the result of recolonization of the habitat by wasps. Unfortunately, despite two additional sampling visits, no eggs of *L. rufoscutellatus* were collected from site 7 later in the season. The breeding population of *L. rufoscutellatus* at site 7 may have collapsed partly due to the effects of egg parasitism. This could be produced in two ways: First, high rates of parasitism reduce production of summer-generation reproductives. Second, breeders may fly away from sites where they experience high encounter rates with wasps. As the species is univoltine in Finland, only the latter mechanism is a plausible one there.

The effect of habitat permanence is clearly manifested in data about *G. lacustris* (Table 2). Most eggs of this species collected at the permanent site 7 were parasitized, but none of the 1259 eggs of this species collected during three visits to site 6 yielded parasitoids. This latter site is an isolated and quite unstable habitat.

Populations of *G. argentatus* and *G. thoracicus* from the Baltic archipelago were apparently not parasitized (Table 2). Because no wasps were found in gerrid eggs collected from the islands we cannot be certain that wasp populations exist there. We found that *G. argentatus* oviposits in small crevices in rotting *Typha* on Långskär, suggesting that this species is better than other species protected against egg parasitoids in mainland habitats with the wasp. Given that *G. argentatus* is the smallest of Finnish gerrids, and that host egg size has a profound effect on body size of emerging *T. gerriphagus* (Spence 1986), it will indeed be interesting to see if this species is parasitized. However, further studies are necessary to establish that *T. gerriphagus* exists on the Baltic islands.

In Finland, *G. thoracicus* is found only in the Baltic archipelago, in rock pools and on sheltered, brackish bays in the sea (Vepsäläinen 1978). Because the rock pools dry up frequently, it is unlikely that the small parasitoids would be able to recolonize them rapidly enough to maintain populations associated with *G. thoracicus* populations. Furthermore if they hold water, rock pools freeze to the bottom during winter possibly eliminating any overwinter survival of wasps. It is unknown where sea-dwelling *G. thoracicus* lay their eggs, because we did not sample these populations. However, it is known that these habitats are isolated, and unsuitable for gerrid reproduction in some summers (Vepsäläinen et al. 1985). Thus it is doubtful that associations between *G. thoracicus* and *T. gerriphagus* can be maintained in Finland. In middle Europe where *G. thoracicus* is a common species occurring along with other gerrids, its oviposition habits suggest that it will be heavily parasitized, except perhaps in the most temporary habitats.

We have provided data about egg parasitism for populations of six of nine Finnish species. We were unable to sample eggs of *G. lateralis*, *G. sphagnetorum* and *G. najas*. We predict that *G. lateralis* populations will harbour parasitoids because its oviposition habits seem to be similar to other *Gerris* species. There is no clear prediction for the rare bog-living *G. sphagnetorum*. Heavy parasitism pressure is expected on grounds of high species numbers and densities of other gerrids (Vepsäläinen 1973 and later unpublished observations). But the exceptionally robust fore-femora of *G. sphagnetorum* females could enable oviposition deep in between the *Sphagnum* mosses with which the species strictly associates.

Gerris najas is known to dive and oviposit at the bottom of river beds (Brinkhurst 1960, our own unpublished observations in the laboratory). Although there is a large population of this species on the brook discharging into Lake Hemträsket, we were unable to find eggs. In North America, *G. remigis* has similar oviposition habits but Spence (1986) did not find parasitoids in a sample of *G. remigis* eggs taken from a site with a large wasp population. This suggests that underwater oviposition may provide defense against egg parasitoids.

Thus the picture that emerges from our preliminary study of gerrid egg parasitism in Finland resembles that presented by Spence (1986) for the situation in western Canada. Stability and isolation of aquatic habitats, time of season, and oviposition habits of the gerrid species all seem to affect rates of parasitism by the scelionid wasp, *T. gerriphagus*. More intensive studies of these relationships are underway.

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