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# INTERACTIONS BETWEEN WATERSTRIDERS (GERRIDAE) AND TWO SPECIES OF EGG PARASITOIDS (TRICHOGRAMMATIDAE AND SCELIONIDAE)

by

NIDIA PRISCILA MORENO

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

DEPARTMENT OF ENTOMOLOGY

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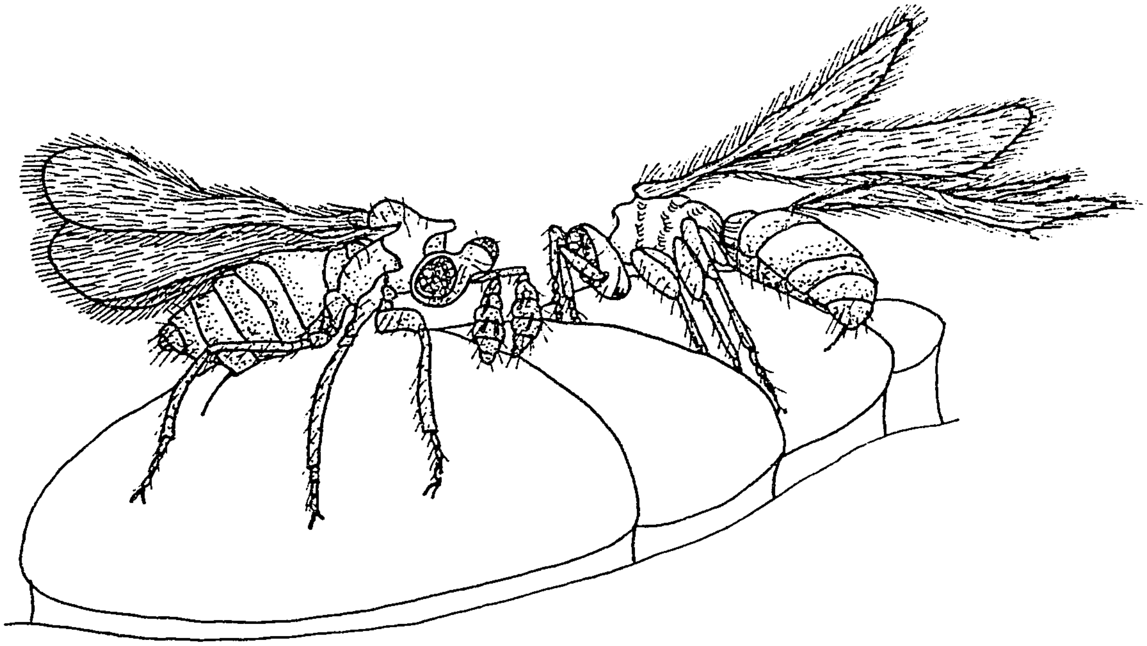

Frontispiece:

*Lathromeroidea* sp nova and *Tiphodytes gerriphagus* parasitizing *Limnoporus* eggs.

THE UNIVERSITY OF ALBERTA

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled "Interactions between waterstriders (Gerridae) and two species of egg parasitoids (Trichogrammatidae and Scelionidae)" submitted by Nidia Priscila Moreno in partial fulfillment of the requirements for the degree of Master of Science.

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A la memoria de Jorge Vega y los demás.

# ABSTRACT

The relationships between water striders (Heteroptera: Gerridae) and two hymenopterous egg parasitoids, *Tiphodytes gerriphagus* (Scelionidae) and *Lathromeroidea* sp nova (Trichogrammatidae), were investigated.

Influence of aquatic vegetation and adult gerrid presence on host location by *T. gerriphagus* was studied at two man-made ponds located at the George Lake Field Station (near Dunstable, Alberta). High densities of gerrid adults, of either sex, as well as presence of aquatic vegetation, were associated with increased parasitism. Visual cues or a combination of visual and chemical cues are important for host location in this species.

Phenology of *T. gerriphagus* was studied in 1990 using egg traps and field surveys of natural levels of parasitism. Data collected over nine years were used to test whether gerrid egg aggregations affected the intensity of parasitism. Proportions of gerrid eggs discovered by wasps varied significantly in each of three host egg aggregation classes, and between two periods of wasp activity. High values of parasitism were the direct result of wasp abundance. *T. gerriphagus* did not aggregate on patches of high host abundance, as expected according to the models of optimal foraging.

Behavior and use of gerrid eggs as hosts by *Lathromeroidea* sp nova were studied under laboratory conditions. Wasps parasitized eggs of two *Gerris* and four *Limnoporus* species. Eggs of the latter genus appear to be less suitable for wasp development. Size of gerrid eggs affected both weight and length of adult parasitoids, and the smallest wasps were recovered from the smallest host eggs. Male wasps emerged ahead of females, as expected for inbred populations, and under conditions of local mate competition. Sex ratios were strongly biased towards females. Field rates of parasitism indicate that *Lathromeroidea* sp nova parasitizes *Limnoporus* eggs when eggs of *Gerris* are not available, suggesting that there is resource partitioning between these two parasitoid species.

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# 1. INTRODUCTION

A parasitoid, as defined by Eggleton and Gaston (1990), is "an organism which develops on or in another single ("host") organism, extracts nourishment from it, and kills it as a direct or indirect result of that development". The insect parasitoid-host relationship is unique in two aspects. First, insect parasitoids usually belong to the same taxa as their hosts, therefore, their biologies, habitats, reproductive rates and dispersal capabilities are similar. Second, because the host does not survive the association, the parasitoid has to ensure the acquisition of sufficient energy to disperse and find suitable new hosts. This aspect poses a number of constraints on parasitoid-host relationships at the ecological, behavioral, immunological and physiological level (Boulétreau 1986).

Insect parasitoids exhibit diverse life histories (Askew 1971). For example, some species are solitary, others are gregarious; some develop inside the host (endoparasitoids), others develop outside the host (ectoparasitoids); many are specialists, but there are also generalists. Insect parasitoids have evolved strategies to exploit all stages of host development, from egg to adult.

Egg parasitoids appear to be among the most successful and least species-specific of parasitoids. Among the Hymenoptera Parasitica, a group that comprises at least 250,000 species (Gauld 1986), the families Mymaridae, Trichogrammatidae and Scelionidae are apparently composed exclusively of egg parasitoids (Strand 1986). Egg parasitoids are usually of small size and difficult to study under field situations, however, their natural histories and behavior are fascinating.

This thesis presents the work carried out with two “aquatic” egg parasitoids, the scelionid *Tiphodytes gerriphagus* Marchal and an undescribed trichogrammatid, *Lathromeroidea* sp nova. Both species exploit eggs of several species of water striders (Heteroptera: Gerridae) with varying levels of success, but apparently without competing for host egg resources.

## 1.1 Biology of the hosts

The family Gerridae comprises a large number of species inhabiting ponds, lakes and streams all over the world (Andersen 1982). Water striders are predators whose phenologies vary from strict univoltism to various patterns of multivoltism in temperate latitudes (Vepsäläinen 1978). Females oviposit on aquatic vegetation, and their egg outputs vary with temperature (Spence *et al.* 1980) and food availability (Kaitala 1987).

*Limnoporus dissortis* is one of the largest and most fecund pond-dwelling gerrid species. Its mating season in Alberta extends from May throughout mid August, depending on the production of summer generation reproductives (Spence 1989). It has the longest reproductive life, with diapause breeders laying approximately 720 eggs, and a mean reproductive rate of 12 eggs per day. Eggs are laid on floating vegetation, and production peaks during July. There are few direct breeders produced, and their fecundity is lower (Spence 1989). Univoltism may be selectively enforced, in part because many temporary habitats dry up during summer, levels. These two factors reduce the survival rates of young produced after mid-summer. Adults disperse readily between mid-April and early July, spreading reproduction of most females over several ponds (Spence 1986).

*Gerris comatus* breeds in more permanent. predictable habitats than those occupied by *L. dissortis*. Females lay few eggs underwater, but have retained the most primitive oviposition pattern (Andersen 1982), laying the eggs slanted, in regular rows along the edges of floating aquatic leaves. Post-diapause *G. comatus* females lay an average of 237 eggs over their lifetimes, twice as many eggs as those laid by direct breeders (Spence 1989).

Overwintered individuals of both *L. dissortis* and *G. comatus*, along with winged migrants from two other *Gerris* species, *G. pingreensis* and *G. buenoi*, recolonize the ponds early in May and constitute the breeding assemblage of gerrids. Among these four species, the first two are heavily attacked by *T. gerriphagus* because their oviposition behavior makes their eggs more accessible to wasps.

## 1.2 Biology of the parasitoids

*T. gerriphagus* was described by Marchal in 1900, and its biology and behavior studied by Martin (1927). The high levels of parasitism reported by Spence (1986) and Nummelin *et al.* (1988) on several gerrid species, reflect the tremendous searching capacity of this wasp. In laboratory experiments, Spence (1986) found that, although wasps were markedly affected by size of the egg species, females preferred to oviposit in smaller eggs of *Gerris* than in those of *L. dissortis*, which are protected by a jelly coat. In the field, concealed *Gerris* eggs. Spence suggested that the gelatinous matrix and egg placement are adaptations against parasitoid attack.

*Lathromeroidea* sp nova was first reported parasitizing gerrid eggs by Spence (1986), but he suggested that gerrids were not its primary host. Until now, there has been no information on the behavior and biology of this trichogrammatid.

### 1.3 Objectives of this thesis.

Much research has been carried out to understand how parasitoids find their hosts (see reviews by Lewis *et al.* 1976; Weseloh 1981; Vinson 1984; Alphen and Vet 1986), however aquatic habitats appear to have been neglected in those studies, and little is known about interactions between "aquatic" parasitoids and their hosts. Chapter 2 focuses on the ability of *T. gerriphagus* to find its host eggs following cues from adult hosts and the environment. To the best of my knowledge, this is the first study using field experiments in aquatic habitats to investigate host location.

Once the hosts are found, parasitoids may respond by searching mostly on those patches of high host density, a behavior called "non-random search" or "parasitoid aggregation" (Hassell and May 1974). Theoretical considerations have led many to expect that parasitoid aggregation produces density dependent parasitism (Hassell 1978). Results from field studies, however, have shown that inverse density dependence and density independence are common phenomena (Morrison and Strong 1980; Lessells 1985; Stiling 1987; Walde and Murdoch 1988; Pacala *et al.* 1990). Large aggregations of *L. dissortis* and *G. comatus* eggs, the result of many especially during mid-summer. This oviposition behavior is likely to influence the functional response of *T. gerriphagus.* In Chapter Three, I explore the relationship between host density and mortality caused by *T. gerriphagus* over a nine year period, and discuss my findings relative to the life histories of both parasitoids and hosts.

In Chapter Four, I sought to understand the influence of host species on life history parameters of *Lathromeroidea* sp nova. Gerrid eggs parasitized by these wasps were collected from the field early and late in the season. Through laboratory experiments I have shown that although the wasps are not very abundant in the field, they are able to parasitize several gerrid species in the laboratory. I further argue that there is partitioning of resources between *T. gerriphagus* and *Lathromeroidea* sp nova.

In Chapter Five, I present the conclusions of my study, and outline some possible directions for further research.

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# 2. HOST LOCATION IN THE GERRID PARASITOID
# *Tiphodytes gerriphagus* Marchal
# (HYMENOPTERA: SCELIONIDAE).

## 2. 1 SYNOPSIS

Host location mechanisms used by the scelionid egg parasitoid *Tiphodytes gerriphagus* to locate its gerrid host eggs were studied in the field using cage experiments. Parasitism was higher in treatments in which adults of *Limnoporus dissortis* were present than in cages devoid of gerrids. Higher densities of adult gerrids were associated with higher parasitism. The presence of aquatic vegetation influenced host finding, although there were no significant differences in observed parasitism between random, uniform and clumped vegetation patterns. Wasps may use visual cues, chemical cues, or a combination of both to locate their hosts. I discuss the possible influence of *T. gerriphagus* on the reproductive strategies of its *Limnoporus* hosts.

## 2.2 INTRODUCTION

Insect parasitoids have an impressive ability to locate their hosts in complex environments. After suitable habitat selection, the next step in successful parasitism is locating the host itself (Vinson 1975a, 1976, 1977; Lewis *et al.* 1976; Vinson and Iwantsch 1980; Saladin 1980). Host location is defined as the perception of and orientation to an appropriate host from a distance (Weseloh 1981). Host location may involve the use of long-distance orientation via chemicals, sound, or light; short-range intensive searching of host traces; and direct detection through integumentary chemicals or physical characteristics (Weseloh 1981; Vinson 1984a; Alphen and Vet 1986). Parasitoids respond to the aforementioned stimuli by fairly stereotyped behavioral patterns which have evolved in the context of increasing searching efficiency

Searching behavior has been studied in detail in parasitoids of various hosts associated with plants (Vinson 1975a; Roland *et al.* 1989; Lewis *et al.* 1990; Turlings *et al.* 1990). However, many parasitoids do not exploit phytophagous hosts, and these may use different cues and strategies to locate their hosts. Egg parasitoids are also special cases, since eggs do not appear to produce cues that can be used to locate them. Furthermore, searching for non-phytophagous host eggs may pose additional problems for parasitoids, especially if the hosts occur submersed or in contact with water.

The scelionid parasitoid *Tiphodytes gerriphagus* (Marchal) exploits eggs of a complex of water striders occurring in ponds and lakes throughout the Holarctic region (Masner 1972). Early studies by Martin (1927), and later by Spence (1986) focused mainly on how this wasp affects the population dynamics and community structure of its hosts. For example, this species has a dramatic effect on *Limnoporus dissortis* populations in ponds throughout Western Canada, where parasitism can reach 100% during the peak of gerrid egg production (Spence, 1986). Information about the specific strategies used by this parasitoid to locate its hosts is necessary to explain its successful performance in such complex environments.

This chapter focuses on how females *T. gerriphagus* locate their hosts. I sought to understand how the aquatic habitat and host behavior shape the wasp's ability to parasitize gerrid eggs which are laid on aquatic plant material (Spence 1986a). I used field experiments to study the parasitoid's response to changes in gerrid presence and densities, as well as vegetation densities and patterns.

## 2.3 MATERIALS AND METHODS

### 2.3.1 General

Host location experiments were carried out at the George Lake Field Site, operated by the Department of Entomology of The University of Alberta, and located *ca.* 100 km NW (114° 06'W, 53° 57'N) of Edmonton, Alberta (Figure 2.1).

Ponds Description. Studies were carried out at Experiment and Meadow Ponds, two man-made ponds chosen because of their accessibility and past history of wasp abundance (see Spence 1986a). The ponds are permanent throughout the summer, and seasonal variation of water levels depends on snowmelt, rainfall and evaporation. Both ponds harbor a diversity of aquatic insects but do not contain fish. Experiment Pond is 0.75-1.5 m deep throughout its main basin, with surface area varying between 945 and 1260 $m^2$. Meadow Pond has a surface area of 1583 to 1800 $m^2$, and its deepest point reaches 1.7 m, thus thorough egg collection can be more difficult in this pond.

Structure of ponds vegetation. The aquatic vegetation component differs between ponds. Vegetation at Experiment Pond consists of water plantain (*Alisma plantago-aquatica* L.), cattails (*Typha latifolia.* L.), and narrow-leaved bur-reed (*Spargangium angustifolium* Michx), along its margins. These plants are abundant during the summer, providing gerrids with adequate substrate for oviposition. Grasses, narrow-leaved bur-reed and cattails are very common throughout the summer along the pond's borders, and the long leaves of these species are especially favoured by *L.*

*dissortis* for oviposition. The pond is mostly free of plants in the middle area, except for some floating leaves of bur-reed and arrowhead (*Sagittaria cuneata* Sheld) towards its west side, and a central mat of Sago Pondweed (*Potamogeton pectinatus* L.) that develops in some years. The pond is shaded, especially towards its south shore, and it is surrounded by willow (*Salix* spp.) and trembling aspen (*Populus tremuloides* Michx).

Meadow Pond is surrounded by an open meadow. Its vegetation includes clumps of sedges (*Carex* sp) and rushes distributed at the margins, floating marigold *(Caltha natans* Pall) mainly along the west shore, pondweed (*Potamogeton natans* and *P. pectinatus*) and white water crowfoot (*Radunculus* sp) at the pond center, and abundant grasses along the south margin. Vegetation at this pond has been severely affected by the feeding of one muskrat, and as a result the number of oviposition sites for *L. dissortis* has been drastically diminished over the past two years and are mainly restricted to the south shore.

Gerrid Assemblages. Both ponds harbor a community of gerrid species that have been monitored for 10 years (Spence 1986a, 1986b, 1989). One species of *Limnoporus* (*L. dissortis*) and three species of *Gerris* (*G. buenoi, G. pingreensis* and *G. comatus*) inhabit the ponds. Adults of these four gerrid species colonize the ponds early in May, and each species may be partially bivoltine (Spence 1989). *G. buenoi* and *L. dissortis* are the dominant species in Meadow and Experiment Ponds.

The largest species, *L. dissortis*, has the highest fecundity and longest reproductive life in both overwintering and reproductive generations (Spence 1989). It is associated with densely vegetated temporary ponds, where females lay their eggs exclusively on floating plants. The eggs of this species are deposited superficially and lengthwise on the substrate, a type considered ancestral among the semiaquatic bugs (Cobben 1968; Andersen 1982). This oviposition behavior renders eggs more accessible to searching females of *T. gerriphagus*. Although the gelatinous coat that covers *L. dissortis* eggs interferes with parasitoid attack once the eggs have been located (Spence 1986a), high rates of parasitism, and even extinction of local populations, are not uncommon. Spence (1986) proposed that selection pressure exerted by parasitoids is associated with the use of temporary sites and the frequent flight observed among *L. dissortis* from mid-April to July.

Females of *G. comatus* oviposit both at the surface and underwater, and suffer high rates of parasitism by *T. gerriphagus*. Eggs of *G. pingreensis* and *G. buenoi* laid in rotting tissue and underwater respectively, are more difficult to find and are parasitized less frequently by the wasps (Spence 1986a). Underwater and sheltered oviposition are derived adaptations to secure a humid environment for the developing eggs (Andersen 1982), but Spence (1986) suggested that these *Gerris* species may have altered their oviposition behavior to reduce accessibility to parasitoids.

In all host location experiments, I used *L. dissortis* eggs produced in laboratory breeding cultures (19L:5D/24°C), by adult gerrids collected at Corners, Kirchner's East and Saloon Ponds, near the study site (see Figure 2.1). Protocols for the maintenance of gerrid cultures have been described elsewhere (Spence *et al.* 1980). *L. dissortis* females oviposited in the laboratory either on pieces of grass (10-20 cm long) collected from the ponds, or on styrofoam strips (10 cm long). Eggs were held at 5°C after oviposition and were discarded if not used for experiments within a week.

### 2.3.2 Location of surface vs. submersed eggs.

I tested the hypotheses that submersed eggs are harder to find by *T. gerriphagus* by using the following protocols. Styrofoam pieces each bearing *ca.* 50 *L. dissortis* eggs were fixed to wooden stakes with monofilament lines. Each set of eggs was submersed at a different depth (5, 10, 15 or 20 cm) by pushing the stake into the bottom among natural vegetation. Each stake was separated by at least 1.0 m. After three days, the eggs were collected, and taken back to the laboratory where they were held as above, and then scored for wasp presence under a dissecting microscope. This experiment was carried out twice at Meadow Pond and once at Experiment Pond during mid-July 1990.

### 2.3.3 Adult of *L. dissortis* as attraction cues.

Several experiments were carried out to test the hypotheses that wasps are attracted to potential host eggs by the presence of adult gerrids.

Continuous presence of adults *L. dissortis.* I first sought to establish whether the continuous presence of adult gerrids near an egg batch would attract wasps. Single dead adults of *L. dissortis* were attached (sewed) to pieces of styrofoam bearing *ca.* 80 *L. dissortis* eggs and placed in Meadow Pond during July 1990. The dead gerrids were of either sex, and were killed by freezing for one hour prior to the experiment. Similar styrofoam pieces bearing eggs but without gerrids were used as controls. Both control and treatment styrofoam strips were placed alternately at one meter intervals along the shore, where vegetation was more abundant. After three days of exposure to parasitoids, the styrofoam pieces were collected and scored for parasitism.

Data was analyzed performing a Mann-Whitney *U* test on the Stat-View 512 (BrainPower Inc., Calabasas, CA, U.S.A.) package on a Macintosh computer.

Influence of male and female *L. dissortis* on egg location. I tested whether presence, density and sex of adult bugs provided cues for host location by *T. gerriphagus.*

Experiments were carried out during three summers (1989-91). I used rectangular, 2.0 $m^2$ cage exclosures (1.0 X 2.0 m), constructed on wooden frames and screened on four sides with fiberglass screen (mesh size 0.5 $mm^2$). Exclosures were supported by metal poles at each corner which were firmly anchored in the bottom. Water level inside the cages was kept at about 25 cm by adjusting the poles up and down on the corner posts.

Experiment 1. In these experiments I tested the hypotheses that living adult gerrids attracted wasps, and looked for differences in attraction between male and female *Limnoporus.* I divided each 2.0 $m^2$ exclosure to make four 0.5$m^2$ compartments and placed four exclosures along the margins of each Experiment and Meadow Ponds. After removing plants and gerrids from the exclosures using an aquatic net, two pieces of grass bearing 100 *L. dissortis* eggs were anchored 30 cm apart in each compartment. Adults of *L. dissortis* were added to each compartment after assigning one of the following treatments to each division: 1) 4 females; 2) 4 males; 3) 2 males and 2 females; and 4) no bugs present. Thus, all 2.0 $m^2$

exclosures had a density of 6 bugs/m$^2$. I prevented emigration by fusing the wings of each gerrid with a minute drop of cyanoacryllic glue, a procedure repeated each time adult *L. dissortis* were used in field experiments. Eggs were collected and taken back to the laboratory after three days of exposure. The experiment was carried out during July, 1989.

Experiment 2. In this experiment, I used four treatments similar to Experiment 1. However, the experiment was run using the full 2.0 m$^2$ exclosures as the unit of replication. Overall densities of *L. dissortis* adults were reduced to 2 bugs/m$^2$, thus the four treatments were 1) 2 males, 2) 2 females, 3) 1 male and 1 female, and 4) no bugs. Pieces of grass bearing each on average 100 laboratory eggs of *L. dissortis* were placed into each exclosure separated by 50 cm. Exposure time was reduced to 24 hours, and the experiment was carried out twice, on June 20 and July 19, 1990. Data from both trials was pooled for analysis.

Data from Experiments 1 and 2 was analyzed using a One-Way Analysis of Variance (ANOVA) on the Stat-View 512 (BrainPower Inc., Calabasas, CA, U.S.A.) package on a Macintosh computer.

Experiment 3. In these experiments, I studied seasonal variation in parasitism and the influence of gerrid densities on attraction cues for the wasps. As in Experiment 2, I used entire exclosures (2m$^2$) as experimental units for the following four treatments: 2, 4, 8 and 16 *L. dissortis* males. Three replicates of each density treatment were cast randomly over 12 exclosures along the margins of Meadow Pond. During each 3-day experiment, three pieces of styrofoam (a batch of 50 *L. dissortis* eggs in each), were placed in an exclosure separated 30 cm from one another.

Exposure time was varied to assess the extent of day to day variation in parasitism levels and the effectiveness of host location. Two egg blocks were exposed for one day, two for two days and one batch was exposed for three days in each exclosure (for a diagram of experimental design, see Figure 2.2). Eggs were collected and scored as above. The full experiment was repeated on: June 20, July 2 and July 23, 1991 (for statistical analysis, the dates of execution of experiment were called "periods").

Levels of parasitism for four different bug densities, at three levels of exposure, and during three periods were compared using a non orthogonal Two-Way ANOVA with a split-plot design. Total variance was split into treatment (3 df) and period effects (2 df) with a separate error term (11 df). Analysis was performed using SAS (SAS Institute Inc., Cary, NC, U.S.A) on the Mainframe Computer at the University of Alberta.

### 2.3.4 Experiments with aquatic vegetation.

Dispersion of floating vegetation. With these experiments I aimed to test whether different patterns of emergent aquatic vegetation influenced the searching behavior of females *T. gerriphagus.* Six of 15 cm grass pieces each bearing *ca.* 100 *L. dissortis* eggs were randomly assigned to 2m$^2$ exclosures in Experiment Pond using one of the following patterns: 1) randomly distributed vegetation, 2) regularly arranged vegetation, and 3) clumped vegetation. Experiment was repeated twice (on June 21 and July 5, 1990), with an exposure period of 24 hours. There were three replicates of each treatment in both dates. Two-Way ANOVA was performed on pooled data.

Presence of emergent vegetation. In a second experiment I studied the effect of presence or absence of bunches of emergent vegetation on host location by the wasps. Small cages constructed on 1 m wooden poles and screened with saran mesh (size 0.5 $mm^2$) on the four sides, were set close to shore in Experiment Pond, in areas without natural aquatic vegetation. Each cage constituted a replicate of two treatments (1) presence and (2) absence of emergent vegetation. Exclosures with vegetation contained entire grass mats firmly anchored to the pond's bottom. Grass leaves were long enough that they covered the upper edge of the exclosures' walls. A styrofoam strip (bearing *ca.* 100 *L. dissortis* eggs) was anchored into each exclosure. None of the treatments contained gerrids. Egg traps were exposed for three days on June 16, and July 23, 1991. Eggs were collected and scored as above. One-Way Analysis of Variance was performed on data for both experimental trials.

### 2.3.5 Experiments with *L. dissortis* adults and vegetation

The objective of this experiment was to evaluate the relative effect of gerrid and vegetation density in attracting wasps searching for eggs. Two densities (high=8/$m^2$, low=2/$m^2$) of each of the variables (gerrids and vegetation) were distributed in 2$m^2$ exclosures in Experiment Pond using a 2X2 factorial design. Only three of the grass leaves allocated to each exclosure bore *L. dissortis* eggs. Adult *L. dissortis* of both sexes were used in all treatments. The experiment ran for 24 hours on July 29, 1990. Eggs were scored as above, and the experiment was analyzed using a Two-Way ANOVA.

## 2.4 RESULTS

### 2.4.1 Location of surface vs. submersed eggs.

None of the *L. dissortis* eggs submersed underwater were parasitized by *T. gerriphagus,* although many eggs did not hatch suggesting that there may be some risk of mortality associated with oviposition underwater. *L. dissortis* eggs did not experience differential mortality at the depths tested (5, 10, 15 and 20 cm, $F$=1.067, $df$=3,16, $p$=0.4). Although mortality was higher in Meadow (26.46% ± 6.66, $n$=9, Mean ± S.E) than in Experiment Pond (18.09% ± 3.73, $n$=8) the differences were not significant ($t$=-1.13; $df$=15; $P$=0.5). Most dead eggs were swollen, however few (< 1%) were sucked out, suggesting predation.

### 2.4.2 Adult *L. dissortis* as attraction cues

Continuous presence of adult *L. dissortis* . Eggs on styrofoam strips with freshly killed *L. dissortis* attached, showed high rates of parasitism. There were significant differences in proportion parasitized between treatment and controls (Mann-Whitney *U* test, $U$(1), 4,5=19, $P$=0.027). Percent parasitism on strips with dead gerrids was 79.58 ± 4.65, about four times the rate observed on control strips (21.36 ± 16.81).

Influence of male and female *L. dissortis* in egg location

Experiments 1 and 2. Levels of parasitism were very high for all gerrid densities tested during 1989 (Figure 2.3), in relation to ambient levels for the same period (see Figure 3.1, Chapter 3). There were no significant differences in parasitism levels among the four treatments ($F$=2.04; $df$=3,31;

*p*=0.132). However, inspection of the data suggests that parasitism was higher and less variable in presence of female bugs alone.

Analysis of pooled data for Experiment 2 revealed marginally significant differences among the treatments (*F*=5.70; *df*=3,7; *p*=0.063). However, in contrast to results from Experiment 1, the simultaneous presence of both sexes of *Limnoporus* was associated with the highest parasitism.

Differences in parasitism levels between both experiments suggested that temporal and spatial scales had strong influence on searching behavior in *T. gerriphagus.* Eggs in Experiment 1, exposed for three days were more parasitized than eggs from Experiment 2, exposed only for one day. At the spatial level, it appears that wasps "perceive" adult gerrid densities over scales bigger than 0.5 $m^2$ but lower than 2.0 $m^2$.

Experiment 3. Parasitism rates were strongly influenced by variations in seasonal periods during *L. dissortis* egg production peak (*F*=7.25; *df*=2,11; *p*=0.01), and these effects may be explained by the relative abundances of both *T. gerriphagus* and gerrids during the months tested. The lowest levels of parasitism (13.88 ± 6.59 %) were observed in the third trial carried out the last week of July (Figure 2.4). These low levels coincided with the end of breeding season for *L. dissortis*, when only overwintering adults are emerging. Levels of parasitism for the first two trials of this experiment did not differ significantly (June 20: 31.72 ± 5.99; July 2: 28.85 ± 3.94), possibly because both wasps and naturally occurring hosts were more abundant.

Effects of different adult gerrid densities on parasitism rates were highly variable. It appears that the highest densities had the most significant effect on parasitism, especially on eggs exposed for three days (*F*=4.63; *df*=3,11; *p*=0.025). Results from the first trial in which the lowest gerrid densities had the most marked effect on parasitism rates are the exception. However, these reverse effects may possibly be explained by the high density of wasps present at the ponds during this period (see Chapter Three). The interaction between bug density and period at which experiment was carried out was not significant (*F*=1.72 *df*=6,11; *p*=0.206).

A second factor that had a significant effect on the levels of parasitism was egg exposure period. Analysis of variance showed that, as in previous experiments, longer exposure times were generally associated with higher parasitism (*F*=6.20; *df*=2,46; *p*=0.0073).

### 2.4.3 Effect of aquatic vegetation.

Dispersion of floating vegetation. Analysis of variance performed on pooled data from experiments using different patterns of vegetation showed no significant differences between clumped, regularly spaced or randomly distributed vegetation (*F*=0.39; *df*=2,7; *p*=0.69) (Figure 2.6).

Presence of emergent vegetation. Results of experiments carried out during June and July were not statistically different (*F*=0.99; *df*=1,12; *p*=0.34), suggesting that there were no temporal effect. Presence of vegetation did not have significant effects on parasitism (*F*=1.61; *df*=1,15; *p*=0.23) (Table 2.1), although parasitism was higher on exclosures with vegetation, suggesting that plants may play a role at orienting wasps towards potential oviposition sites for *L. dissortis*.

### 2.4.4 Effect of gerrids and aquatic vegetation.

Levels of parasitism increased drastically with gerrid density ($F=8.73$; $df=1,12$; $p=0.012$), but showed only marginal response to increasing density of aquatic plants ($F=3.74$; $df=1,12$; $p=0.077$) (Figure 2.6). There was no significant interaction of these factors on parasitism levels by *T. gerriphagus* ($F=1.66$; $df=1,12$; $p=0.222$).

## 2.5 DISCUSSION

Doutt (1964) and Vinson (1984a, 1984b) cited host habitat location and host location as the first steps required to achieve successful parasitism. These processes have been analyzed under field conditions in a variety of parasitoid species attacking all stages of insect development, but most studies deal with parasitoids in terrestrial habitats. To my knowledge, this is the first report on experiments about host location in an aquatic egg parasitoid.

Cues generated at three levels are important in host location for *T. gerriphagus* searching females. These are: (a) cues provided by aquatic plants, (b) cues provided by adult gerrids and, (c) potential cues provided by the host eggs themselves. These probably operate in a hierarchical order, each guiding parasitoids closer to susceptible hosts.

### 2.5.1 Aquatic vegetation as cues.

Plants play a major role in orienting many parasitoids to potential host communities (Vinson 1984a). Water striders, although not phytophagous, are associated with plants during oviposition, territorial displays and mating (Hayashi 1985; Spence and Wilcox 1986; Nummelin 1988). Because *L. dissortis* eggs are laid exclusively on floating vegetation, wasps should have evolved strategies that allow them to locate floating leaves. My results with experiments using pond vegetation showed a trend towards higher parasitism on *L. dissortis* eggs surrounded by clumps of sedges than on single floating egg batches, although treatments were not statistically different. Similarly experiments evaluating parasitism rates in exclosures with different vegetation patterns showed higher values when floating leaves were clumped together. These results showed that dispersion of pond vegetation is important as cues for the wasps, allowing them to orient more often towards clumped vegetation while flying.

In general, stimuli involved in the process of host location or host habitat location may be chemical or physical. Attraction to odor, color (Ma *et al.* 1992) and/or structure of vegetation (Lawton 1983; Casas 1989; Andow and Prokrym 1990; Stadler and Völkl 1991), and the situation in which plants developed (Sato and Ohsaki 1987) are important for habitat and host finding for several hymenopterous parasitoids.

Plant chemicals are important not only during host plant location by phytophagous insects (Prokopy and Owens 1983), but also for searching parasitoids (Altieri *et al.* 1981; Alphen and Vet 1986; Turlings *et al.* 1990). Phytophagous-induced damage produce volatiles that are used by some parasitoids to find hosts (Drost *et al.* 1988; Sheehan and Shelton 1989; Turlings and Tumlinson 1991), especially when odours can be learned previous to searching (Drost *et al.* 1988; Lewis and Takasu 1988; Sheehan and Shelton 1989; Turlings *et al.* 1990; Lewis and Takasu 1990). In the water strider system, however, plant chemicals induced by host feeding are not present. Aquatic vegetation is only used as substrate for oviposition, and the host stage targeted by the wasps does not induce damage to the plants.

### 2.5.2 Adult *L. dissortis* as cues.

Females of *L. dissortis* may oviposit alone or with a guarding, post-copulatory male in attendance (Spence and Wilcox 1986). Because male *L. dissortis* defend territories around oviposition sites (Wilcox and Spence 1986), one of the first hypotheses tested was that males protected the eggs against wasp attack (Spence and Wilcox 1986). Although parental protection of the young (subsocial behavior) has evolved many times in insects (Wilson 1971), and in the Heteroptera is known in at least 14 species (Bequaert 1935; Odhiambo 1959; Eberhard 1975), it has never been observed and recorded among semiaquatic bugs (Andersen 1982). Results of my experiments reject the parental care hypotheses for *L. dissortis* because the presence of adults was associated with high levels of parasitism. These results suggest that parasitoid pressure has little to do with the evolution of territorial behavior.

Reproductive behavior in several water strider species changes as the breeding season progresses. For example, in *Gerris elongatus* males establish territories during mid-season and attract females which oviposit with a male in attendance, but as the season progresses, many females oviposit alone (Hayashi 1985). Individual females of *G. najas* DeG and males of *L. rufoscutellatus* (Lt.) show shifts between territorial and non-territorial behaviors (Vepsäläinen 1985), and in *L. dissortis* many females lay their eggs without males in attendance (Spence and Wilcox 1986). Diversity in water striders reproductive strategies have been related to patterns of food use and mate acquisition, but at least in the case of *L. dissortis*, the evolution of ovipositing behavior in absence of male guards may have evolved to avoid parasitism, as suggested by Spence and Wilcox (1986).

I showed that egg parasitism was higher when adult *L. dissortis* of either or both sexes were present than when there were no gerrids. Female wasps commonly remain close to ovipositing bugs and attack eggs as soon as the female has moved away, indicating that wasps may be attracted to any adult gerrid. Thus, *T. gerriphagus* may orient toward immobile gerrids (either ovipositing females or territorial males).

The mechanisms used by *T. gerriphagus* wasps to orient towards gerrids may involve vision, sometimes in conjunction with host movement (Monteith 1956; Walker 1961; Herrebout 1969; Richerson and DeLoach 1972). For example, Eberhard (1975) demonstrated that scelionids use host adults as visual cues. Studying a case involving parental care in the stink bug *Antiteuchus tripterus limbativentris* Ruckes, Eberhard showed that females of two parasitoid species (*Trissolcus bodkini* and *Phanuropsis semiflaviventris* Girault), were successful in attacking host egg masses, despite constant maternal vigilance. When Eberhard removed the guarding mother, *Trissolcus* wasps attacked the eggs at the same rate. However, parasitism by *Phanuropsis* actually decreased. He concluded that presence of egg-guarding females served as a "beacon" to *Phanuropsis* to identify location of potential hosts, and that this response was visually mediated.

In addition to vision, chemicals emanating from the host or its products (kairomones) may also serve as cues to searching parasitoids (Vet 1985; Lewis and Tumlinson 1988; Lewis and Takasu 1990). The mechanisms by which parasitoids use kairomones are divided in two categories, long-range (olfaction) and close-range (contact chemorreception). The first enables a parasitoid to locate a host in a large area by attracting it to the host's vicinity; the second is important in intensive searches over small areas that eventually result in host contact (Weseloh 1981). Volatiles produced by *L. dissortis* scent glands seem to have toxic or repellent effects on other arthropods, especially predators (Andersen 1982), but they may act as long-range cues that guide the wasps towards adult gerrids. Laboratory studies using an olfactometer would be useful to study whether the wasps use products from the gerrid scent glands to locate hosts.

Once the wasps have located gerrids sitting on plants, short range cues may operate to guide them towards the eggs themselves. In several parasitoid-host systems, sources of contact cues may include host's food and host traces*. Host traces left by ovipositing females near eggs act as cues for a number of egg and egg-larval parasitoids (Laing 1937; Lewis *et al.* 1971, 1972, 1975; Jones *et al.* 1973; Vinson 1975b; Nordlund *et al.* 1977, Chiri and Legner 1982). However, to my knowledge, the existence of host

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* Here, the term "host traces" includes chemicals, feces, mandibular and labial secretions and other host products such as host marking pheromones. Weseloh (1981), however, uses the term only to refer to chemical substances deposited by the adult host near the eggs during oviposition.

traces has not been reported in gerrid species, although it is possible that oily secretions from females penetrate the leaf surface during oviposition.

### 2.5.3 Gerrid eggs as cues.

The ancestral oviposition state in water striders, in this study exemplified by *L. dissortis*, involves laying the eggs superficially, lengthwise on the substrate, embedded in a substance that protects them from dessication (Andersen 1982). Similar oviposition behavior is exhibited by *G. comatus* females, although eggs lack the jelly coat. Eggs of the two other *Gerris* species present in the study site are laid underwater, sometimes inserted into decomposing plant stems. Spence (1986a) showed that field parasitism rates by *T. gerriphagus* were greater in eggs deposited on the surface than those laid underwater. However, in Spence's two choice laboratory experiments, eggs lacking the jelly coat were preferred by the wasps. Thus, he suggested that both presence of the jelly matrix and underwater oviposition are adaptations against parasitoid attack.

After wasps have landed on plants, they may concentrate their searching efforts examining only leaves on which eggs are discovered, because time spent searching unprofitable leaves may affect the parasitoid's time budget. The theory of optimal foraging states that parasitoids should adopt the searching strategy that maximizes the number of parasitized hosts during their lifetime (Hubbard and Cook 1978). Therefore, parasitoids should search only those patches that gives them the highest rate of return to maximize efficiency. Ideas regarding the effects of host egg clumping on searching and optimal foraging by *T. gerriphagus* are examined in Chapter Three.

To find gerrid eggs, female parasitoids either have to search underwater or be able to detect their presence while antennating along the leaf. As described by Marchal (1900) and Martin (1927), female *T. gerriphagus* exhibit two different oviposition behaviors, either by submersing completely underwater, or by tilting the abdomen with the ovipositor fully extended to reach the eggs. They also search underwater by walking on the submersed face of the leaf, but I never observed wasps swimming in search of eggs. Also, my results with *L. dissortis* eggs submersed in the ponds failed to reveal parasitism, thus I conclude that these wasps are unable to find eggs submersed even a few centimeters underwater.

It is possible that wasps detect egg presence by sensing the jelly coat with their ovipositors while on the leaf, a behavior that was frequently observed in the laboratory before the wasp submersed completely. Newly laid *Limnoporus* eggs may be more susceptible to wasp attack since the gelatinous cover does not expand immediately, but after being in contact with water (Andersen 1982). Thus, a good strategy for wasps is to home in on ovipositing *L. dissortis.*

### 2.5.4 Spatial and temporal scale effects on parasitism.

Parasitism was higher in exclosures with high densities of *L. dissortis*, although the highest density of adult bugs used (8/m$^2$) are probably not common in field situations. Wasps appear to react to larger aggregations of hosts, perhaps perceiving the exclosure as a whole, without discriminating among the treatments.

On the temporal scale, the longer the eggs are exposed in the field, the higher the probability of being found by parasitoids, thus the chances of parasitism increase. Also, although the jelly coat possibly evolved as protection against parasitoid attack, it does not act as an efficient mechanical barrier, even after it has completely expanded with water.

In conclusion, wasps were attracted towards the presence of both adult *L. dissortis* and vegetation. Both adult gerrids and the structure of plant community are important for the wasps to locate potential oviposition sites. Gerrid-emitted cues could be chemical, although this needs to be studied further. Visual cues are likely to be used by the wasps especially regarding host location after using plant stimuli.

**Table 2.1**. Mean values of *Limnoporus dissortis* eggs parasitized by *Tiphodytes gerriphagus* during experiment testing presence or absence of vegetation.

| Date of Experiment | Treatment | % Parasitism (Mean ± S.E) |
|---|---|---|
| 23-26 June | | |
| | Vegetation absent | 42.37 ± 16.13 |
| | Vegetation present | 50.69 ± 17.41 |
| 16-19 July | Vegetation absent | 14.98 ± 13.20 |
| | Vegetation present | 46.36 ± 16.54 |

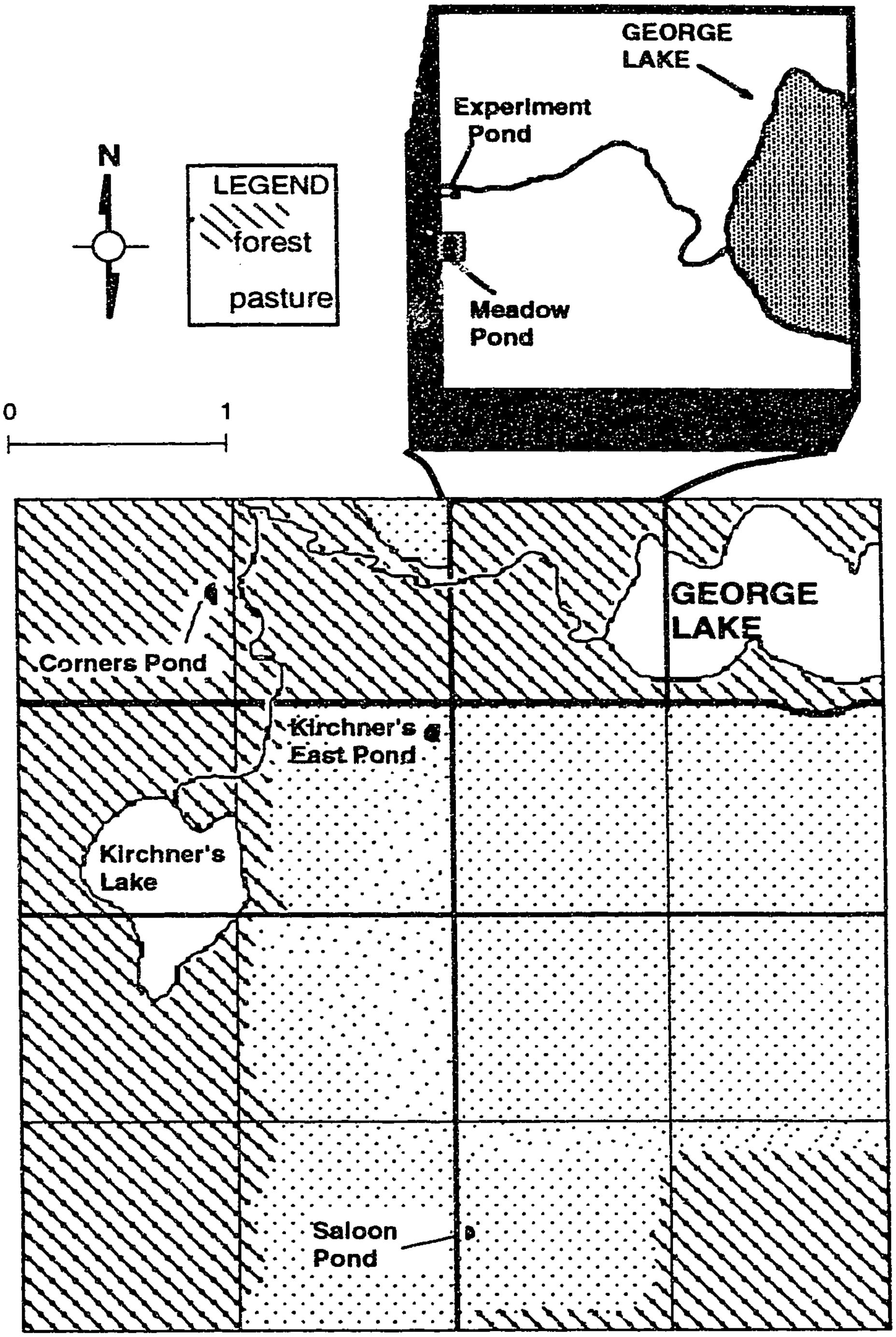

**Figure 2.1** Relative locations of ponds studied at George Lake Field near Dunstable, Alberta.

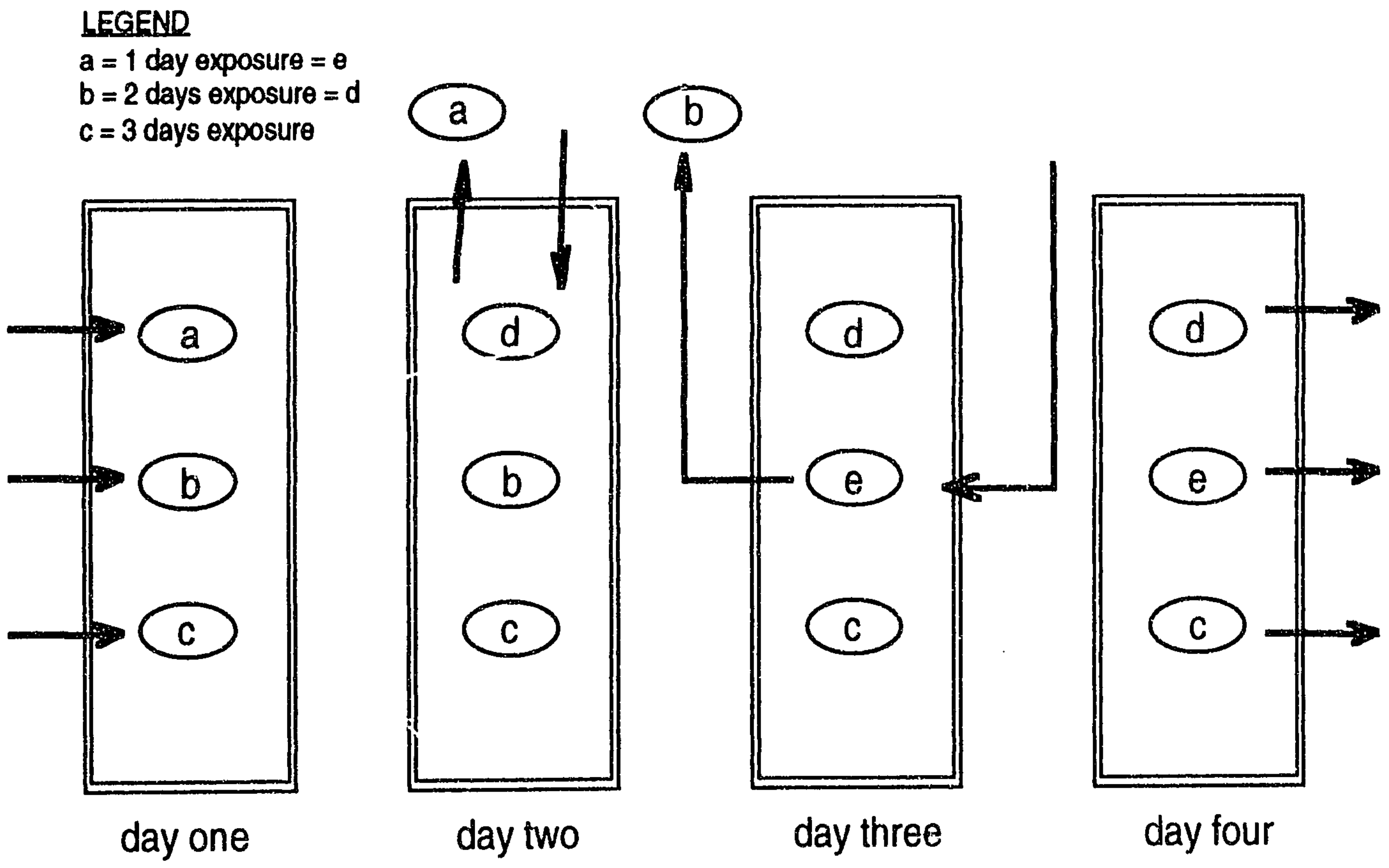

**Figure 2.2** Experimental design for exposure periods of eggs of *Limnoporus dissortis* during 1991 experiment.

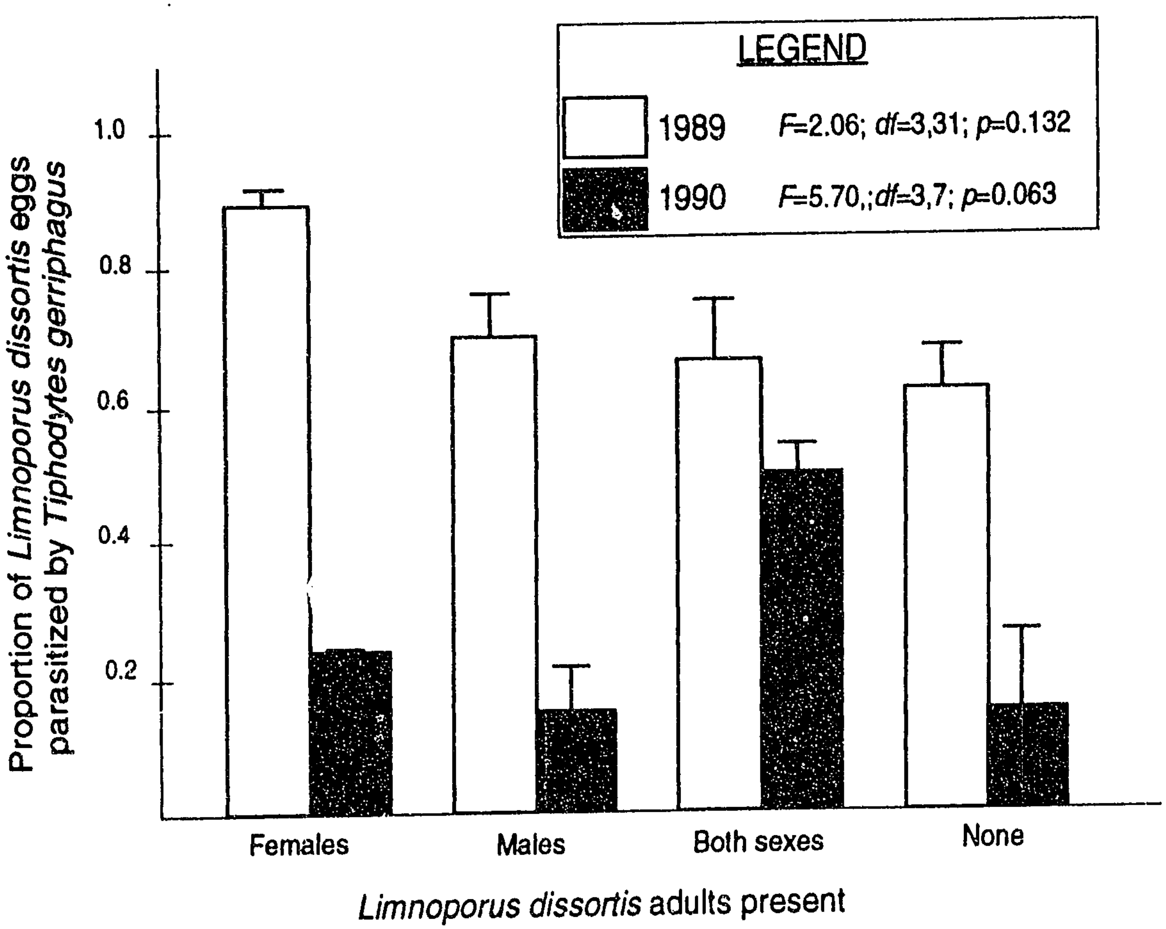

**Figure 2.3** Influence of presence of *Limnoporus dissortis* adults of both sexes on levels of parasitism by *Tipnodytes gerriphagus*. 1989 and 1990. (Error bars represent ± One Standard Error).

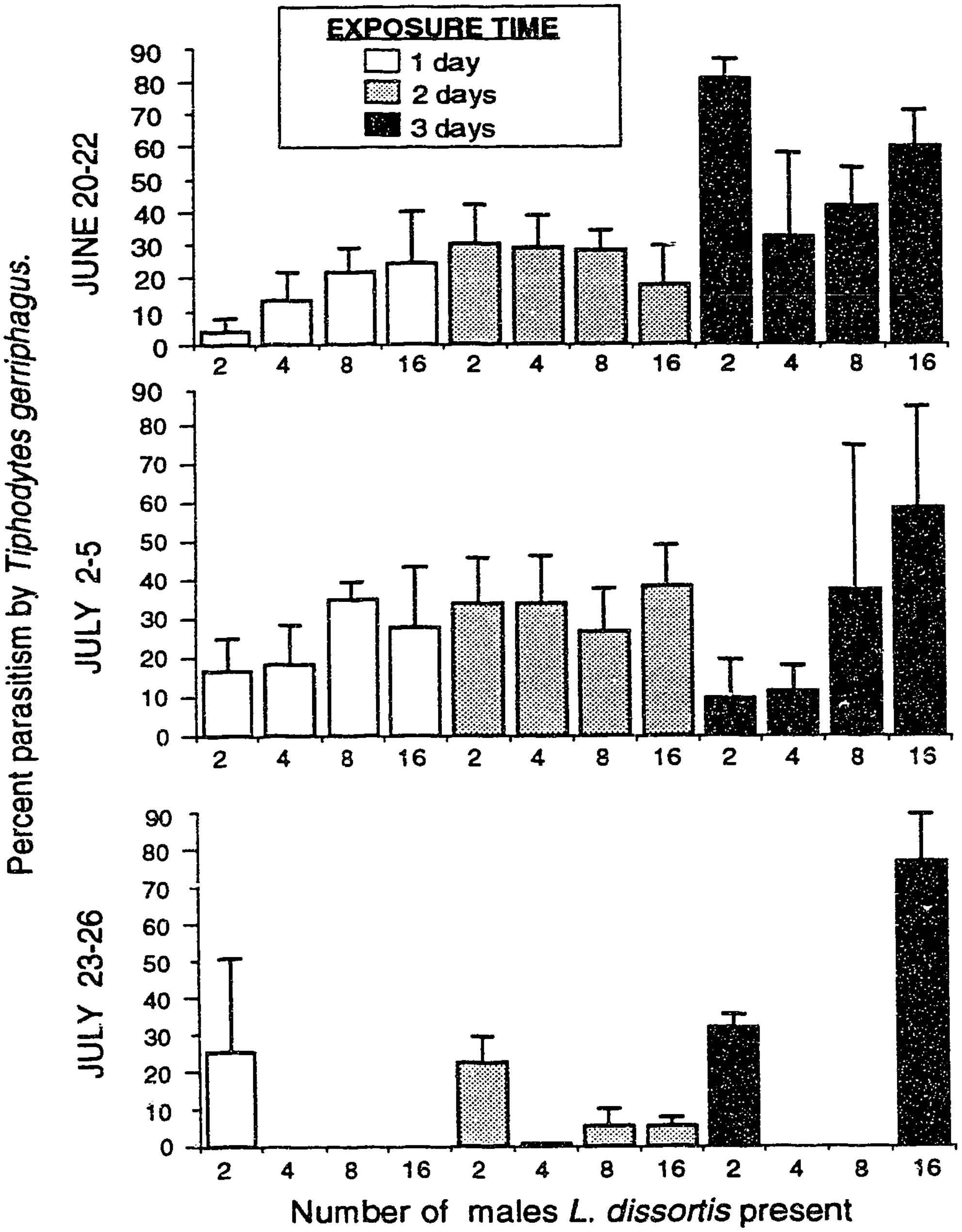

**Figure 2.4** Levels of parasitism by *Tiphodytes gerriphagus* for experiments with *Limnoporus dissortis* males. 1991. (Error bars representa ± One Standard Error).

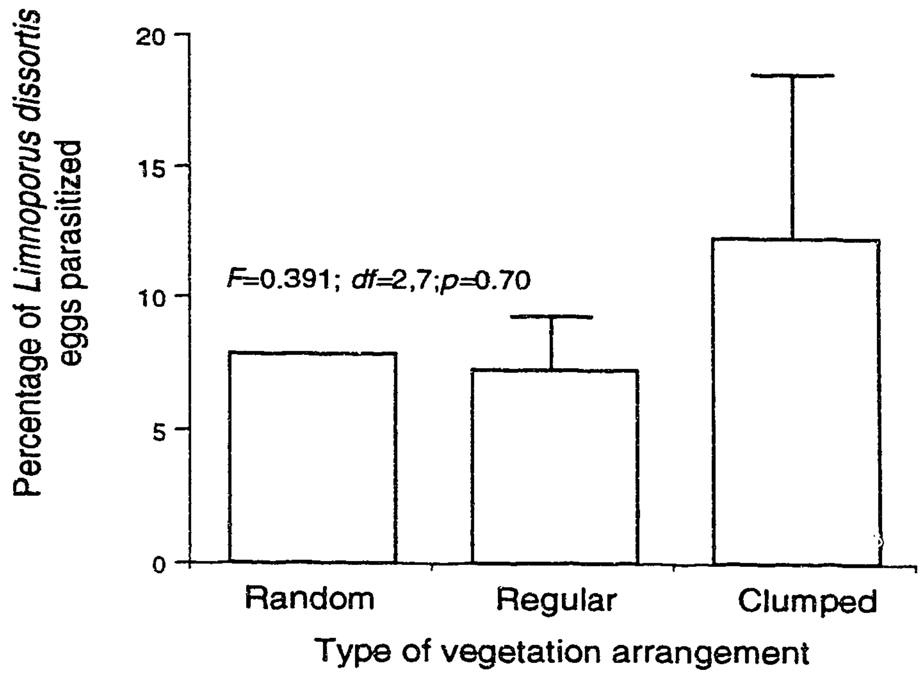

**Figure 2.5** Effect of different vegetation patterns on percent parasitism by *Tiphodytes gerriphagus*. Experiment Pond. 1990.

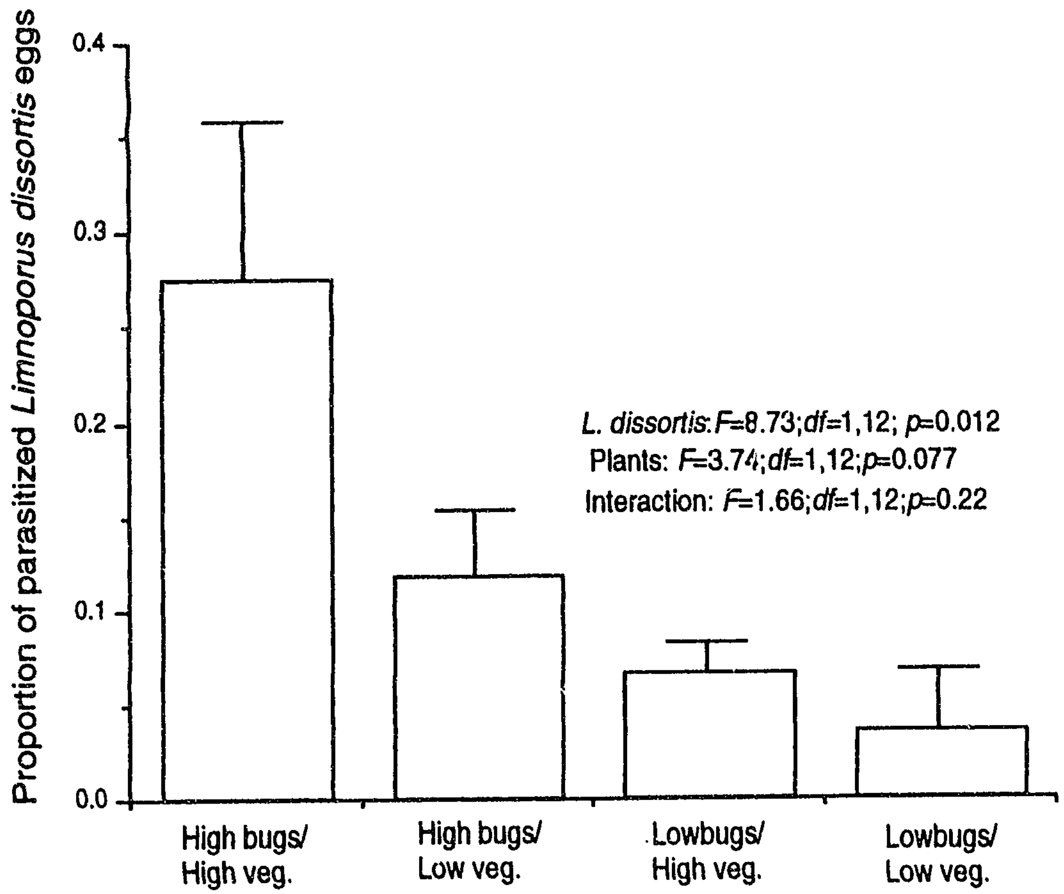

**Figure 2.6** Effect of gerrid and vegetation densities on percent parasitism by *Tiphodytes gerriphagus*. Experiment Pond. 1990.

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# 3. STUDY OF PARASITOID PHENOLOGY AND THE EFFECT OF HOST AGGREGATION ON PARASITISM BY *Tiphodytes gerriphagus* Marchal (HYMENOPTERA: SCELIONIDAE)

## 3.1 SYNOPSIS

Seasonal distribution of *Tiphodytes gerriphagus* was studied using egg traps and field surveys of natural levels of parasitism. The relationship between host aggregation and intensity of parasitism was investigated using data from a nine year period. The probability of parasitism was estimated by the proportion of sites discovered by the wasps in each category, and the proportion of hosts actually parasitized in each site. The proportion of discovered gerrid eggs varied significantly in each of three host egg aggregation categories (1-20, 21-40 and greater than 40 eggs), and between two periods of wasp activity (early and late season). *T. gerriphagus* does not aggregate in response to host density, as predicted by the models of optimal foraging. The observed high values of parasitism were a direct result of wasp abundance.

## 3.2 INTRODUCTION

Relationships between host density and mortality caused by parasitoids are central to an understanding of parasitoid-host interactions, especially in the context of biological control (Murdoch 1975, Murdoch *et al.* 1984). Many laboratory studies have shown that parasitoids concentrate their searching efforts in areas of high host density, a behavior referred to as "parasitoid aggregation" or "non-random search" (Hassell and May 1973, 1974; Rogers and Hubbard 1974; Hassell 1978; Mishra and Singh 1991). Parasitoid aggregation can lead to density-dependent mortality and it is thought to regulate natural host populations. Optimal foraging theory suggests that parasitoids (and predators) should aggregate in order to maximize their rates of oviposition (or prey capture) when exploiting patchily distributed hosts (Comins and Hassell 1979; Sutherland 1983). Field studies, however, have revealed inverse density-dependence (Hirose *et al.* 1976, Brown and Cameron 1979; Morrison *et al.* 1980; Hassell 1982; Stiling and Strong 1982), and density independence (Lyons 1962; Weseloh 1973; Dowell 1979; Sharov 1979) in several parasitoid-host systems.

The aquatic parasitoid *Tiphodytes gerriphagus* causes high mortality to eggs of *Limnoporus dissortis* and *Gerris comatus*, two water strider species that oviposit on floating vegetation (Spence 1986a). Eggs of these two species are frequently laid in large aggregations because gerrid mating systems concentrate oviposition around male territories (Spence and Wilcox 1986). Therefore, it should be expected that parasitoids aggregate on sites of high host density, producing the high parasitism rates observed in nature.

In this chapter, I describe the phenology of *T. gerriphagus* in eggs of *Limnoporus dissortis*. I also present the results of a long-term study (1983 to 1991), to determine whether parasitism is strongly density-dependent within small ponds that are the usual habitat of *L. dissortis* and *G. comatus*.

## 3.3 MATERIALS AND METHODS

### 3.3.1 General

I chose Experiment and Meadow Ponds (see Figure 2.1, for exact pond locations) for the study of wasp phenology because the dynamics of the gerrid species inhabiting them are well understood (Spence 1986b, 1989), and because a parasitoid population has been sampled in these ponds for at least nine years (Spence 1986a). The biological and physical attributes of both ponds were described in the previous chapter.

Parasitism by *T. gerriphagus* was studied in the field using two species of gerrids, *L. dissortis* and *G. comatus*. The reproductive season of both gerrid species extends from May to mid-August. Females of these species lay their eggs on floating plant material (Spence and Wilcox 1986), and therefore experience more parasitism by *T. gerriphagus* than species that lay their eggs deeper in the water (Spence 1986a). This oviposition behavior facilitates data collection and makes assessments of parasitism levels more accurate.

### 3.3.2 Phenology of *Tiphodytes gerriphagus*.

"Egg traps". I set out fresh, healthy *L. dissortis* eggs obtained in the laboratory as described in Chapter Two. Fifteen egg traps bearing approximately 100 eggs each were transported to Meadow Pond in plastic containers filled with tap water. They were anchored at least 50 cm apart among the vegetation in the near shore area. After an exposure period of four days, the egg traps were collected, brought back to the laboratory and held at 19L:5D/24°C until wasp emergence was complete. Eggs were counted and the numbers of parasitized and dead eggs were recorded by sorting the eggs under a dissecting microscope. Parasitized eggs were recognized by the presence of a developing wasp, or if a round hole indicating wasp emergence was evident at one end of the host egg. Eggs from which gerrids had successfully emerged were recognized by distinctive longitudinal slits made by the emerging nymph. Eggs were scored as dead if after three weeks neither *L. dissortis* larvae nor wasps had emerged. Egg traps were set out from the first week of May through October, 1990.

The purpose of using egg traps was to obtain a weekly indicator of wasp activity that was not confounded by variation in host availability. Use of egg traps measures parasitoid activity more accurately than do surveys of naturally occurring parasitized eggs (Driesche 1983).

Weekly egg surveys. Additional data about parasitoid phenology were collected in weekly surveys of both ponds from May to August 1990. Samples of gerrid eggs were collected by searching the pond margins for floating vegetation bearing *L. dissortis* and *G. comatus* eggs. Whole leaves bearing one or more batches of gerrid eggs were collected from sites separated by at least one metre. These egg-bearing substrates were taken to the laboratory and held at 19L:5D/24°C for a week after the last wasps had emerged. The number of parasitized, unhatched wasps, dead and healthy *L. dissortis* eggs were recorded using the same criteria as above. After scoring the eggs, wasps and gerrids were taken back to the pond to minimize effects on their natural densities.

### 3.3.3 Effect of host aggregation on parasitism by *Tiphodytes gerriphagus*

Spatial variation in intensity of parasitism by *T. gerriphagus* was studied as part of a long-term project initiated by John Spence (unpublished) in 1983. At least 15 oviposition "substrates" were collected periodically throughout the gerrid reproductive season from both Experiment and Meadow Ponds (although fewer substrates were collected early and late in the season, because of low host abundance). A '"substrate" was defined as any floating piece of vegetation that carried recently oviposited eggs of *L. dissortis* or *G. comatus*. Fertile gerrid eggs are distinguishable because they show a brownish coloration indicative of the early stages of gerrid development. Parasitized eggs show the necrotic puncture made by the female's ovipositor two days after oviposition has occurred, and eggs become whitish at first and larval feeding movements may be observed during the first week of parasitoid development. Only leaves that bore fertile parasitized eggs were collected during the surveys. At sites where a plant with more than one leaf bearing eggs were encountered, only one leaf was collected. Sites were separated by a minimum distance of 2 m. Substrates were transported to the laboratory and held at long day photoperiod (9L:5D) and 24°C, and scored as described above. Emerging wasps as well as gerrid nymphs were returned to the ponds upon hatching. Egg sampling was carried out every second week during 1983 and 1984, and weekly between 1985 and 1991.

*L. dissortis* and *G. comatus* eggs are laid in batches of different sizes, commonly from 17 to 33 eggs in the laboratory, although batches with fewer eggs were frequently found in the field. Many substrates, however, bore more than one batch of eggs, the output of several ovipositing females, and finding leaves with their perimeters completely covered by eggs was not uncommon, especially during the peak of gerrid egg production.

To study whether rates of parasitism were density-dependent at the scale of oviposition sites, data from each year were first categorized as follows: (1) sites bearing 1 to 20 eggs, (2) sites bearing 21 to 40 eggs and, (3) sites with more than 40 eggs. These categories were chosen on the basis that a *T. gerriphagus* female is able to parasitize *ca.* 20 eggs a day (Spence 1986), and thus batches in category 1 could be completely parasitized given the activity of a single parasitoid, category 2 of two parasitoids, and category 3 of many ovipositing female wasps.

To evaluate the probability of parasitism given the egg density in a patch, I followed the hierarchical method of Morrison and Strong (1981). Thus, the probability of parasitism at a site depended on a) the proportion of patches in each site category discovered by the wasps, and b) the proportion of hosts actually parasitized in each patch. The latter measure is the probability of parasitism for any eggs present at a site, given discovery. First, I calculated the proportion of sites in each category discovered by searching parasitoids per sampling date. A "discovered patch", as defined by Morrison and Strong (1981) is "any leaf on which parasitism occurs". Second, the percentage of eggs parasitized at each site was calculated. Correlation Coefficients between number of host eggs in a patch and percent parasitism were calculated for each sampling day in each pond.

To study potential temporal variation in parasitism levels for each site category, each year was divided in two periods, early season (15 May to 30 June), and late season (1 July to 15 August). These periods correspond approximately to the activity periods of first and second generation wasps, respectively. Proportion of sites discovered by wasps in each sampling period and for each egg density category was calculated, and a factorial analysis of variance (3 egg density classes X 2 seasons X 9 years) was performed on ranked data after arc sine transformation, using SYSTAT (SYSTAT Inc., 1990) on a IBM compatible computer. This analysis was run mainly for exploratory purposes because, even after transformation, the data were clearly heteroscedastic. Interpretation of significance tests should be done with this in mind.

## 3.4 RESULTS

### 3.4.1 Phenology of *Tiphodytes gerriphagus*.

Eggs were searched for starting the first week of May, but the first gerrid eggs were found on May 30 at both ponds, and some of these had already been parasitized (Figure 3.1). The recovery of parasitoids from egg traps a week before the first naturally occurring parasitized eggs were detected by the surveys, indicates that wasps were actually present somewhat earlier in the season. Levels of parasitism remained low the first few weeks of June in Meadow Pond, but increased steadily to reach a maximum of 68% by July 16. Subsequently, parasitism levels decreased until no more parasitized eggs could be found by mid-August. At Experiment Pond, parasitism increased rapidly to reach values higher than 80%, and except for one date during mid-June, were constantly high from early June through mid August. After this date, levels dropped sharply to zero by the end of the season (August 21), when few gerrid eggs were available.

There were differences between ponds in availability of oviposition sites for gerrids. Floating vegetation at Experiment Pond was more abundant, offering more oviposition sites to female bugs, and thus a higher number of host eggs were available. In Meadow Pond, suitable substrates for egg-laying were scarce throughout most of the season during 1990, and batches found contained few eggs. There was also a heavy thunderstorm on July 17, that raised the pond water level by at least 10 cm and submersed virtually all floating vegetation at Meadow Pond. Subsequently most adults of *L. dissortis* disappeared from the pond, contributing to the collapse of the host population during 1990.

Data from egg traps suggests that there were two generations of parasitoids in the field, the first reaching its peak during mid-June, and the second by late-July. The last egg traps that were parasitized by the wasps were collected on the first week of September indicating that wasps were present and searching past the normal period of egg production by gerrids. Adults obtained from the last parasitized egg traps, kept under long-day photoperiod and 24°C, produced non-diapausing offspring in *L. dissortis* eggs in the laboratory.

Rates of parasitism estimated using data from egg traps are probably more accurate than the estimates provided by egg surveys because they give a more exact measurement of wasp activity over a three-day exposure period in healthy host eggs.

### 3.4.2 Effect of host aggregation on parasitism by *Tiphodytes gerriphagus.*

The number of gerrid eggs collected fluctuated during the years of study at both Experiment and Meadow Ponds (Figure 3.2), but these values may be considered as good indicators of relative host egg availability in the three different classes. Sites with 1 to 20 eggs were the most abundant throughout the study period at both ponds. Sites comprised of more than forty eggs were more numerous on the long floating leaves of *Spargangium angustifolium* commonly only at Experiment Pond, showing that local habitat structure can have important effects on the spatial arrangement of host patches.

Proportions of discovered sites for both season periods are presented in Figure 3.3. An exploratory analysis suggests that there were highly significant differences between the proportion of sites discovered by the wasps in three gerrid egg density categories (*F*=20.69; *df*=2,88; *p*=0.0001). Sites bearing 1 to 20 eggs were clearly discovered less frequently by wasps in both ponds (Experiment: 0.66 ± 0.19, *n*=9; Meadow: 0.65 ± 0.16, *n*=8; Mean ± S.D). Substrates bearing more than 20 eggs were heavily parasitized at both ponds, both early and late in the season (see Table 3.1 and 3.2 for yearly mean proportions of discovered sites at Experiment and Meadow Ponds respectively).

Differences in discovery rates between early and late season were also marked (*F*=23.56; *df*=1,88; *p*=0.0001). During the second period, the proportion of sites discovered was high for all three host abundance classes. Clearly the parasitoid population was so high during July that most oviposition sites were found and consequently parasitized, regardless of number of host eggs present. Because none of the possible interactions approached significance (*p*>0.05), the importance of the two main effects ("host density class" and "season") seems assured. The strength of these patterns and the lack of interaction are clearly illustrated in Figure 3.3.

There were no strong relationships between number of eggs at a site and percentage of eggs parasitized by *T. gerriphagus* whether data were pooled across years or analyzed separately for each year (see Figure 3.4 for Experiment and 3.5 for Meadow Ponds). Only 4 Correlation Coefficients between percent parasitism and egg abundance were significant, and they were negative (*n*=120).

The limited data for May suggest that high rates of parasitism are not achieved with larger numbers of eggs. However, as both wasp and gerrid populations build up during June, there is no apparent effect of egg density on the percentage of eggs parasitized at a site, apart from the lower probability of discovery for sites with few hosts. During June, most sites were discovered and parasitized at some degree, with many large sites exhibiting 100% parasitism. Data from July suggest a weak, positively density-dependent relationship at Experiment Pond (Figure 3.4), because few sites with more than 40 eggs escaped heavy parasitism during this month. Eggs that escaped parasitism were mostly located in small aggregations up to *ca.* 20 eggs, but this was mostly a function of them not being discovered. This pattern of density-dependence is less clear at Meadow Pond (Figure 3.5). During July, the wasp population also reached its maximum (See Figure 3.1), and the high average parasitism rates are probably a function of wasp abundance. The high parasitism values in those two months and the few sites that actually were not discovered by the wasps, are consistent with my estimates of wasp activity discussed earlier. Fewer host eggs were laid in August because most adult gerrids are in reproductive diapause (Spence 1989). However, rates of parasitism were high in the few eggs found. Most of the batches that escaped were located in small aggregations.

## 3.5 DISCUSSION

### 3.5.1 Phenology of *Tiphodytes gerriphagus.*

Adequate estimates of parasitism rates for multivoltine parasitoid species, or those whose hosts have overlapping life stages are difficult to obtain. Marston (1980) discussed some sources of bias in data derived from traditional sampling methods, and several improved methods have been proposed to estimate parasitism in the field with greater accuracy (Southwood 1978, Groden *et al.* 1990). Driesche (1983) proposed the use of "trap hosts" as a superior technique to measure the timing and intensity of parasitoid oviposition in the field. Data from such traps are not affected by variation in the population of hosts that enter the stage susceptible for parasitism (Driesche *et al.* 1991). Furthermore, all parasitoids reared from such traps clearly represent oviposition events that occurred during the trapping period. I used this method to analyze parasitoid phenology. However data from weekly surveys were used for the long-term study of host aggregation effects on parasitism, so that the results could be interpreted in the context of natural, spatio-temporal distributions of hosts.

The egg traps detected wasp activity a week before parasitism was measurable by the egg survey, and late in the season when no eggs were being produced by gerrids. Thus, wasps are active beyond the normal reproductive period of gerrids in Alberta. In early season, there is limited availability of *L. dissortis* eggs, therefore wasps probably exploit eggs of *G. pingreensis* and *G. buenoi*, which are also suitable hosts (Spence 1986a). Late in the season, competition between female wasps for resources is probably more intense because there are few gerrid eggs available (Spence

1989), thus superparasitism probably becomes a frequent event. It is also possible that *T. gerriphagus* uses alternate hosts when gerrid eggs are not being produced. Because there are high numbers of parasitized *L. dissortis* and *G. comatus* eggs found in August and September, Spence (1986a) suggested that wasps overwinter in gerrid eggs. The possibility that parasitoids overwinter in alternate hosts can not be rejected.

There was a clear pattern of parasitism showing two peaks of wasp activity, the first during June and the second during mid-July. This pattern is consistent with observations on the parasitoid's biology (Spence 1986), since the period between the two peaks is roughly equivalent to the development time of *T. gerriphagus*. However, this pattern is not seen in he survey data probably because of large variation in the age of eggs parasitized in field samples.

Habitat perturbations probably caused the different patterns of parasitism observed between the two ponds (Figure 3.1). At Meadow Pond, potential oviposition sites were eliminated by muskrat grazing and a heavy rainstorm. Grazing has a strong impact in the pond vegetation, because of the steady decrease in accessible plants used for oviposition by gerrids. This change in the habitat may have caused *L. dissortis* adults to disperse to neighboring ponds, a common phenomenon in several gerrid species (Vepsäläinen 1978; Kaitala 1987). Dispersal of reproductive adults reduces accessibility to local abundance of primary hosts to searching parasitoids, and may have favoured the evolution of plasticity in host selection and acceptance in *T. gerriphagus*.

### 3.5.2 Effect of host aggregation on parasitism by *Tiphodytes gerriphagus*

The pattern. The main problem addressed in this chapter is the relationship between the intensity of parasitism and host aggregation. Parasitoid aggregation in areas of high local host density is thought to enhance stability in parasitoid-host systems (Ullyett 1953; Hassell and May 1973, 1974; Murdoch 1975; Hassell 1978; May 1978; Beddington *et al.* 1978; Hassell 1980; May and Hassell 1981; Murdoch *et al.* 1984). Recently, however, Hassell and Pacala (1990) demonstrated theoretically that population regulation can be enhanced as much by density-independence as by density-dependence heterogeneity. He showed that the more scattered the data of percent parasitism against local host density, the more stable the population is likely to be.

Density dependence brought about by concentration of individual parasitoids searching in patches of high host density has been demonstrated (Wylie 1958; Hassell 1968; Kfir 1983; Driessen and Hemerik 1991). However, clear patterns of inverse density-dependence have been shown in several parasitoid-host relationships (Anderson and Kaya 1973; Hirose *et al.* 1976; Münster-Swendsen 1980; Morrison and Strong 1981; Hassell 1982; Stiling and Strong 1982), and density independence is also common (Eikenbary and Cox 1968; Weis 1983a; Strong 1989; Stiling *et al.* 1991; Cronin and Strong 1990; Romstöck-Völkl 1990). Also, different species of parasitoids that attack the same host show variable responses to host aggregation (Heads and Lawton 1983; Murdoch *et al.* 1984). Morrison and Strong (1980), and Strong (1986), suggested that for the majority of parasitoid species, levels of parasitism are not clearly affected by variation in host density.

As pointed out by Cappuccino (1991), most studies showing density-dependence caused by parasitoid aggregation deal with phytophagous hosts in outbreak situations. In these situations density-dependence may be expected given the large host densities. In the present study, I examined the effect of host density on parasitism rates by *T. gerriphagus*, in aquatic habitats in which the parasitoid-host interactions may have evolved with a different degree of complexity. If parasitism were density-dependent in this system, substrates with large gerrid eggs aggregations would be strongly parasitized, and those with small host concentrations would escape wasp attack.

Spence (1986a) suggested that *T. gerriphagus* may be responsible for local extinctions of *L. dissortis* populations. This could be brought about if adults of this species frequently disperse during summer as a consequence of parasitoid pressure. In such a system, stability of regional host populations may be maintained because gerrids disperse among ponds every summer.

I could find no evidence that *T. gerriphagus* caused consistent density-dependent mortality of gerrid hosts at either of the two ponds over the course of nine years and at least 18 generations of both parasitoids and hosts. Even at probability levels of 0.1, correlation coefficients between percentage of parasitism and egg abundance were rarely significant across several periods. Recently, Cappuccino (1991) showed that significant density-dependence occurred in only 11% of interactions between natural enemies and phytophagous insects of goldenrod (*Solidago altissima*). In Cappuccino's system there was a trend towards density dependence, but for the interactions between gerrids and *T. gerriphagus*, most correlations are negative.

Choosing the correct scale is as important as understanding parasitoid behavior for the detection of spatial density dependence in parasitoids (Stiling *et al.* 1991). Because *T. gerriphagus* wasps are active fliers and probably disperse between adjacent ponds, I believe that the small pond scale is appropriate for investigation of density-dependence. However, field observations on the wasp behavior are required to determine whether the observed patterns of density-independence respond to one or several of the mechanisms proposed. For example, handling time (i.e. rejection if hosts are already parasitized), and parasitoid egg and time limitations may be responsible for the results observed in the study. Until these constraints are investigated under field conditions, our understanding of how parasitism operates in this system will not be complete.

Interactions with host behavior. Eggs of *L. dissortis* and *G. comatus* are patchily distributed in the ponds. The majority of eggs sampled were in small batches (1-20 eggs), however large accumulations of more than 40 eggs were common, especially during gerrid egg production peak. These large batches occur at particular locations around the pond which seemed to be favoured sites of territorial males. Thus host resources were concentrated in relatively small areas, even though suitable oviposition sites did not seem to be limited in principle. For example, at Experiment Pond, long leaves of bur-reed and grasses were abundant throughout the season without accumulating any gerrid eggs.

Aggregations of individuals can function against predation by reducing the number of groups and the frequency of encounters between groups and predators (Brock and Riffenburgh 1960). Large aggregations, however, also increase the chance of detection by predators. In large groups, the risk of predation is the same for all equally vulnerable individuals (Jones 1983; Weis 1983b; Weis et al. 1985; Price and Clancy 1986; Price 1988), as is the case of *L. dissortis* and *G. comatus* eggs. Gerrid eggs laid in large concentrations seem to escape parasitism only during early-season (see Figure 3.4 and 3.5) perhaps because the few wasps present have utilized all their eggs before all host are parasitized. Thus, there seems to be an advantage of laying in large groups when the parasitoid population is low. As the season progresses and parasitoid numbers increase, aggregation provides little protection from parasitoids because densities of wasps are so high that most eggs will be found, regardless of the size of the batch in which they were laid.

In summary, overall spatial and temporal patterns of parasitism in field populations of gerrids show that the parasitoid's impact on eggs of *L. dissortis* and *G. comatus* is independent of host distribution and density. The intensity of parasitism is a function of how many sites with host eggs are found. Eggs oviposited in large aggregations are protected against parasitism early in the season, but during the peak of wasps and gerrid eggs production, parasitoids are so numerous that most hosts are found.

**Table 3.1.** Proportion of sites discovered by *Tiphodytes gerriphagus* wasps for three egg density categories. Experiment Pond. Data from 1983 to 1991.

EXPERIMENT POND

| | 1-20 eggs | 21-40 eggs | >40 eggs |
|---|---|---|---|
| MAY - JUNE | | | |
| 1983 | 0.75 | 0.75 | 1.0 |
| 1984 | 0.67 | 1.0 | 0.88 |
| 1985 | 0.5 | 0.71 | 1.0 |
| 1986 | 0.67 | 0.83 | 1.0 |
| 1987 | 1.0 | 1.0 | 1.0 |
| 1988 | 0.64 | 0.81 | 0.96 |
| 1989 | 0.83 | 1.0 | 1.0 |
| 1990 | 0.38 | 0.6 | 0.58 |
| 1991 | 0.5 | 0.82 | 0.88 |
| Mean ± S.dev | 0.66±0.19 | 0.84±0.14 | 0.92±0.14 |
| JULY-AUGUST | | | |
| 1983 | 1.0 | 1.0 | 1.0 |
| 1984 | 0.71 | 1.0 | 1.0 |
| 1985 | 0.78 | 1.0 | 1.0 |
| 1986 | 1.0 | 1.0 | 1.0 |
| 1987 | 1.0 | 0.83 | 1.0 |
| 1988 | 1.0 | 1.0 | 1.0 |
| 1989 | 0.88 | 1.0 | 1.0 |
| 1990 | 0.89 | 0.97 | 1.0 |
| 1991 | 0.81 | 1.0 | 1.0 |
| Mean ± S.dev | 0.9±0.11 | 0.98±0.06 | 1.0±0 |

**Table 3.2**. Proportion of sites discovered by *Tiphodytes gerriphagus* wasps for three egg density categories. Meadow Pond. Data from 1983 to 1991.

| | MEADOW POND | | |
|---|---|---|---|
| | 1-20 eggs | 21-40 eggs | >40 eggs |
| MAY - JUNE | | | |
| 1983 | 0.67 | 1.0 | 1.0 |
| 1984 | 0.77 | 0.9 | 1.0 |
| 1985 | 0.86 | 1.0 | 1.0 |
| 1986 | 0.41 | 0.86 | 0.73 |
| 1987 | 0.77 | 0.94 | 0.75 |
| 1989 | 0.75 | 0.83 | 1.0 |
| 1990 | 0.47 | 0.61 | 0.83 |
| 1991 | 0.52 | 0.82 | 0.89 |
| Mean ± S.dev | 0.65±0.16 | 0.87±0.13 | 0.9±0.12 |
| JULY-AUGUST | | | |
| 1983 | 1.0 | 1.0 | ---- |
| 1984 | 0.65 | 1.0 | 1.0 |
| 1985 | 0.83 | 1.0 | 1.0 |
| 1986 | 0.91 | 1.0 | 1.0 |
| 1987 | 0.94 | 1.0 | ---- |
| 1989 | 0.71 | 1.0 | 1.0 |
| 1990 | 0.75 | 1.0 | 1.0 |
| 1991 | 0.45 | 0.67 | 0.67 |
| Mean ± S.dev | 0.78±0.18 | 0.96±0.12 | 0.95±0.13 |

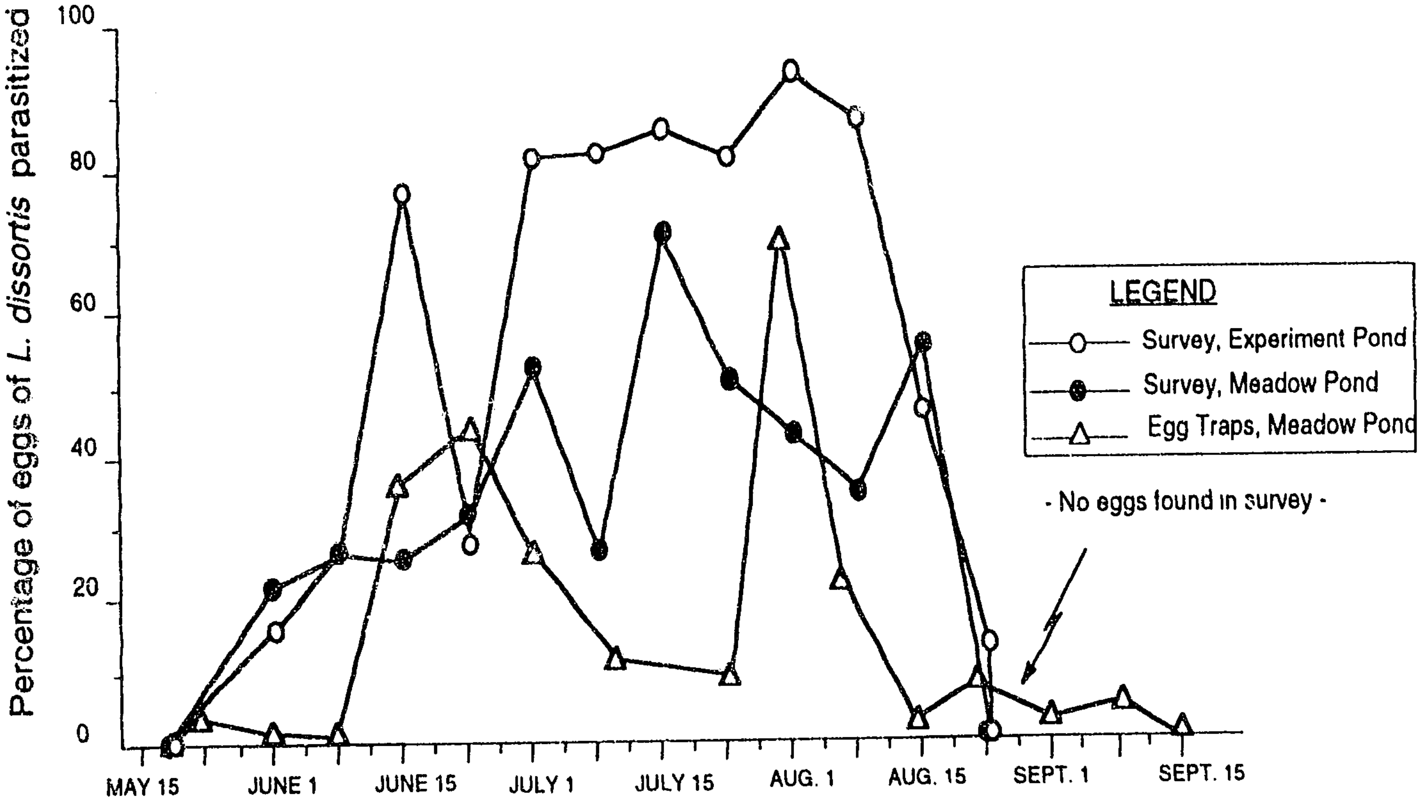

**Figure 3.1** Phenology of *Tiphodytes gerriphagus*. Data from Meadow and Experiment Ponds. Egg surveys and egg traps. 1990.

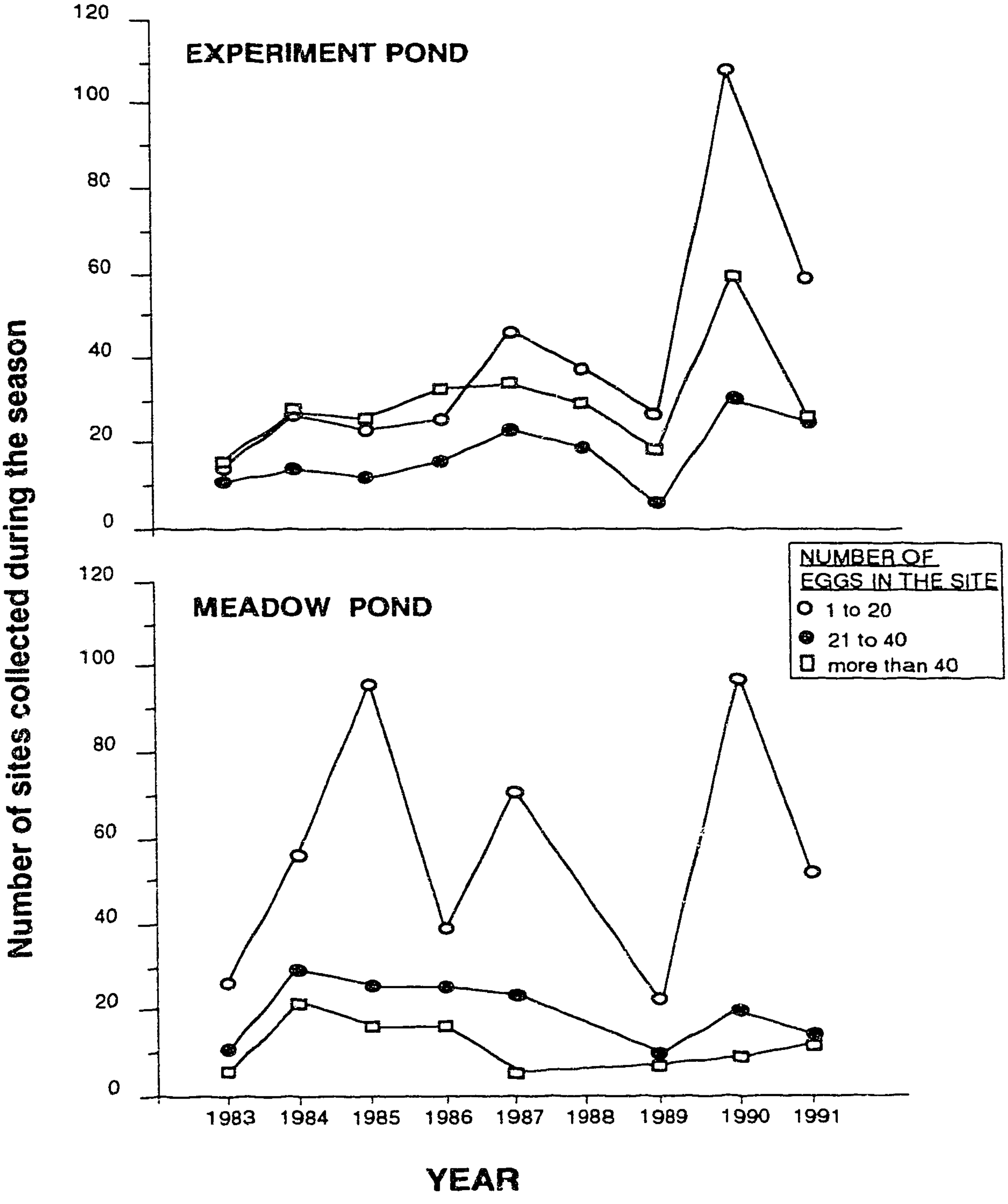

**Figure 3.2** Numbers of substrates bearing gerrid eggs collected from 1983 to 1991 at Experiment and Meadow Ponds.

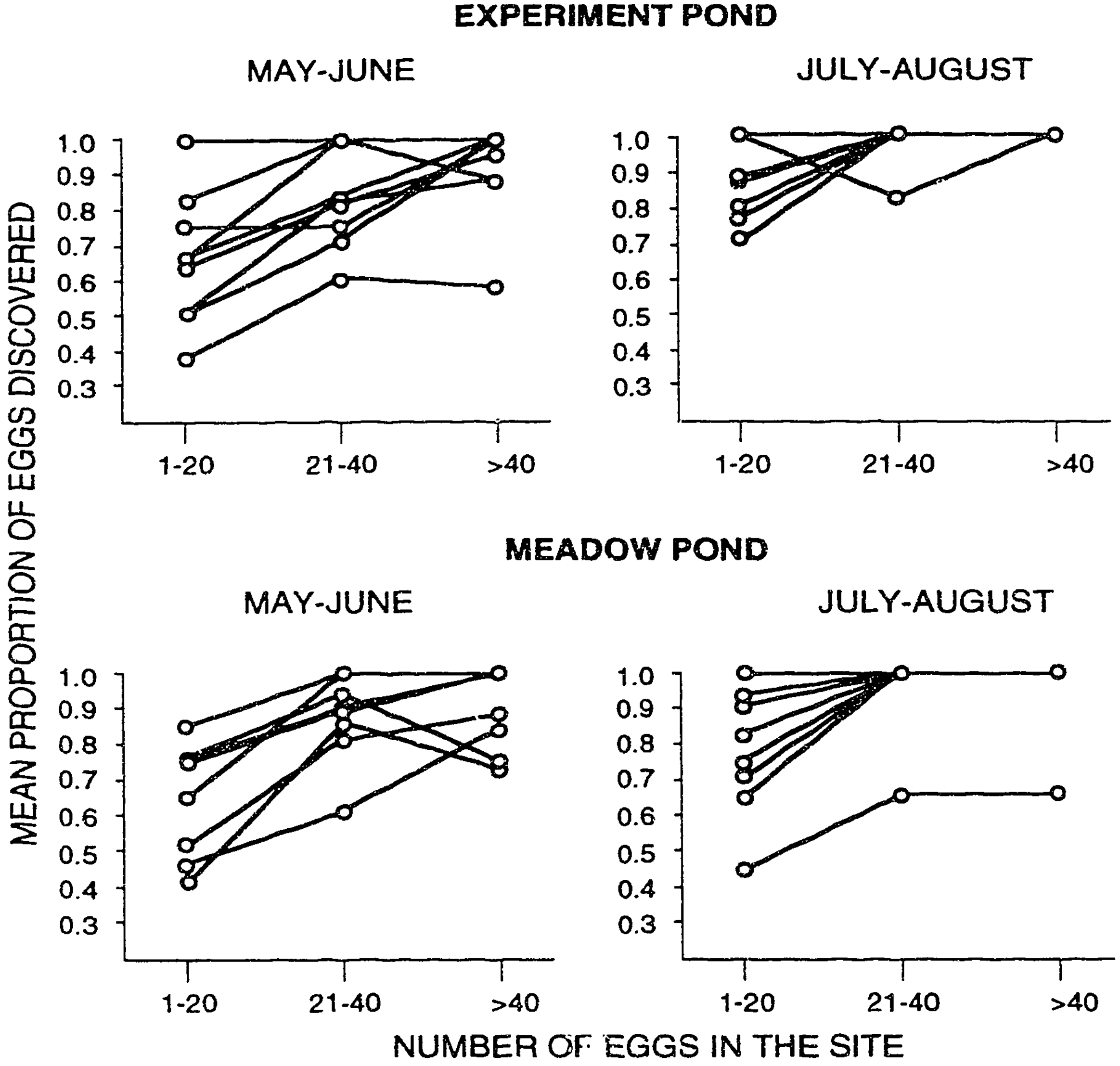

**Figure 3.3.** Mean proportions of sites discovered by *Tiphodytes gerriphagus* females, for three egg abundance categories. Results plotted as mean discovery probabilities observed yearly, 1983-91.

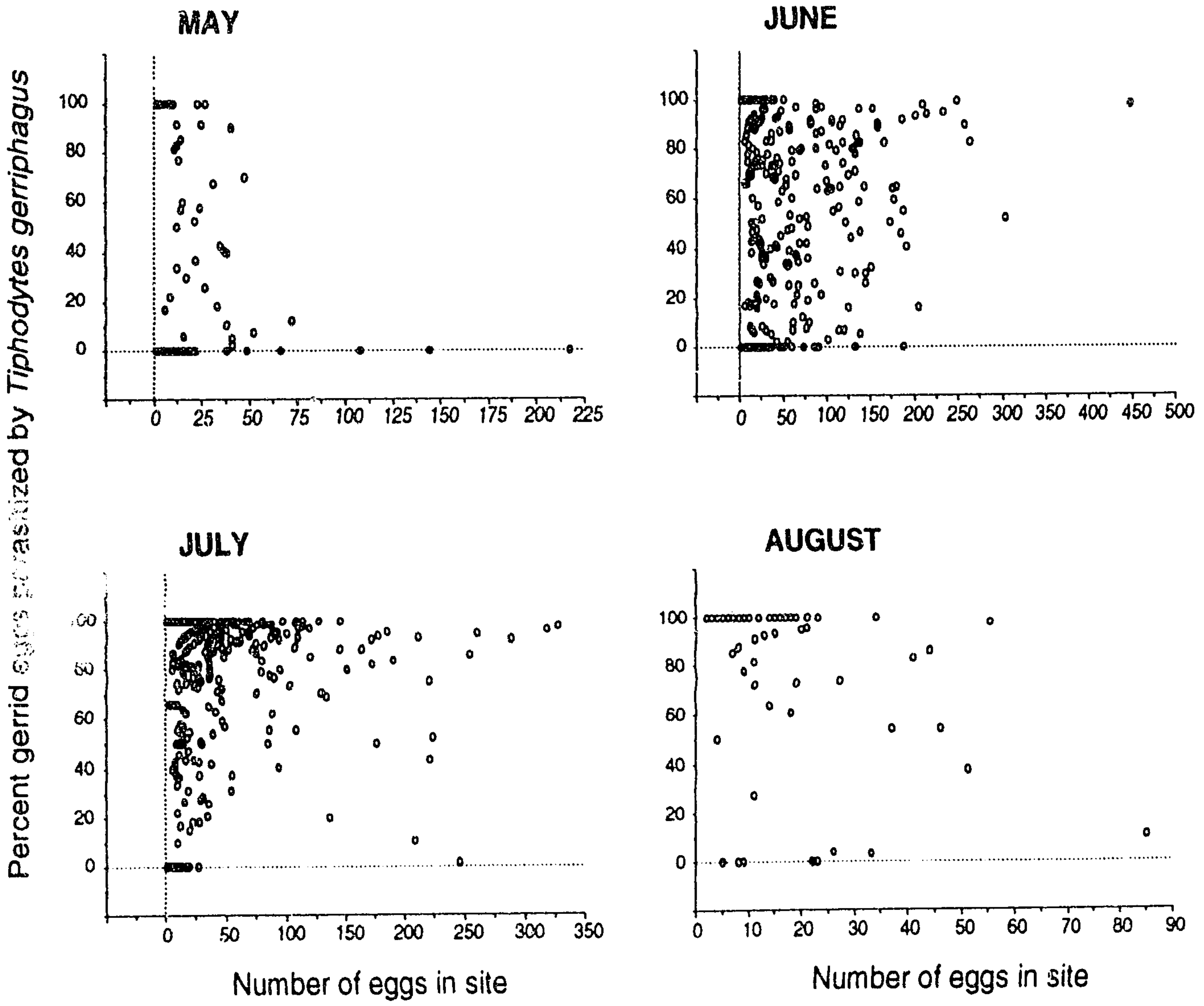

**Figure 3.4.** Percentages of eggs of *Limnoporus dissortis* and *Gerris comatus* parasitized by *Tiphodytes gerriphagus* in Experiment Pond per month. Pooled data from 1983 to 1991.

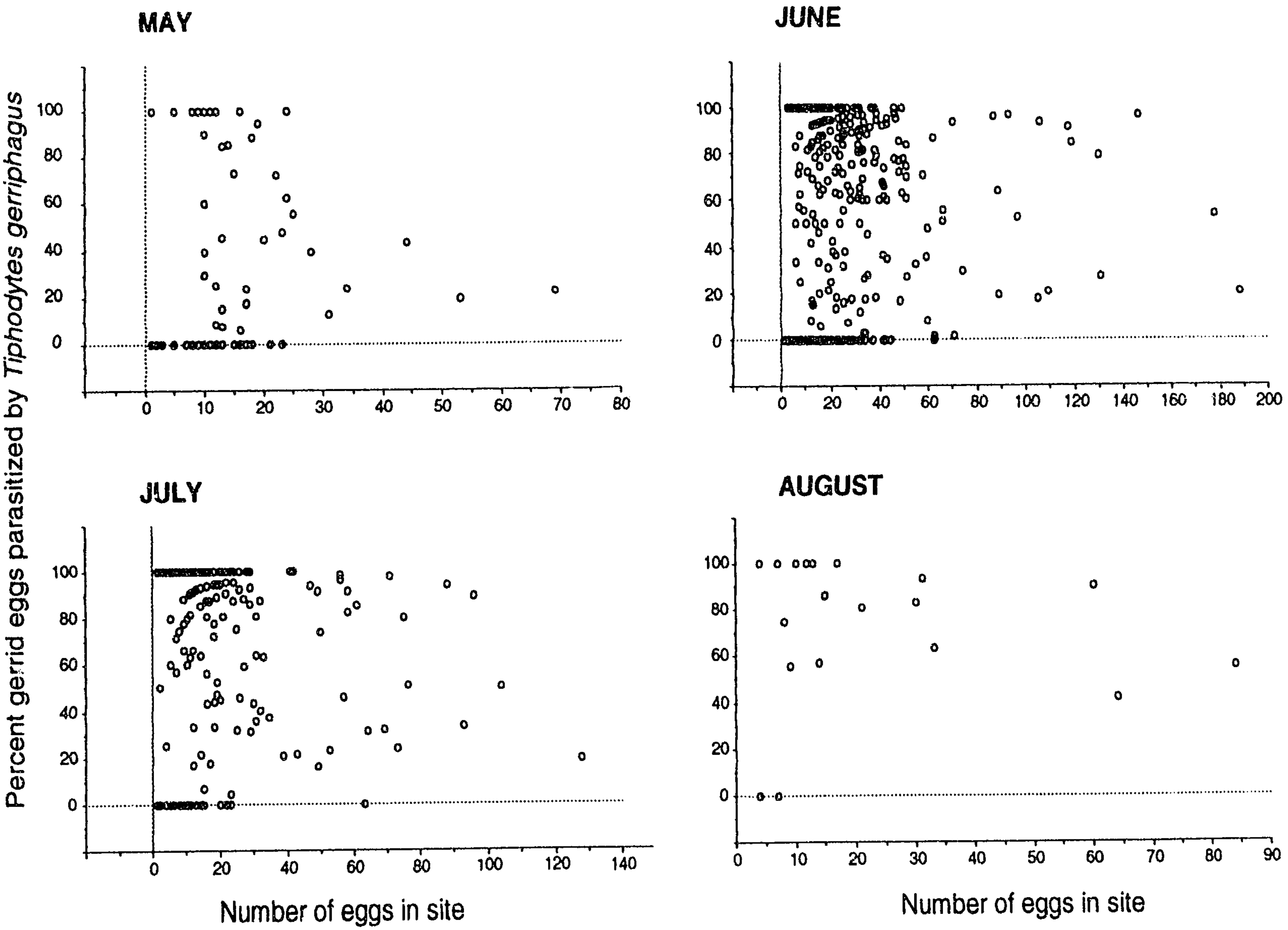

**Figure 3.5.** Percentages of *Limnoporus dissortis* and *Gerris comatus* eggs parasitized by *Tiphodytes gerriphagus* in Meadow Pond per month. Pooled data from 1983 to 1991.

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# 4. STUDIES OF *Lathromeroidea* sp nova (HYMENOPTERA: TRICHOGRAMMATIDAE), A PARASITOID OF GERRID EGGS.

## 4.1 SYNOPSIS

This study describes the behavior and use of gerrid hosts by the solitary egg parasitoid *Lathromeroidea* sp nova. Wasps parasitized four species of *Limnoporus* (*L. dissortis, L. notabilis, L. rufoscutellatus* and *L. esakii*), and two of *Gerris* (*G. buenoi* and *G. pingreensis*). In laboratory trials, more wasps emerged from eggs of *Gerris* than from *Limnoporus*, suggesting that species in the former genus are more suitable hosts. Resources provided for wasp development (host size) affected both weight and length of adult parasitoids. Smaller adult parasitoids were obtained from smaller host eggs and vice-versa. Sex ratios were female biased, with males emerging ahead of females, as expected for inbred populations, and under conditions of local mate competition. This study provides some evidence of resource partitioning between *Tiphodytes gerriphagus* (Scelionidae) and *Lathromeroidea* sp nova. Field observations showed that *T. gerriphagus* is a very effective parasitoid of *L. dissortis* eggs during middle summer; while *Lathromeroidea* sp nova seems to attack *L. dissortis* mainly when eggs of its presumed primary hosts (*Gerris*) are scarce.

## 4.2 INTRODUCTION

For a parasitoid to be successful, it must first ensure the dispersal of its propagules to new hosts. Parasitoids achieve this through active searching, using mechanisms that allow them to utilize cues emitted by their hosts (Alphen and Vet 1986). However, host searching exposes parasitoids to a series of environmental hazards, including predation. Therefore it is to the parasitoid's benefit to have a wide host range.

Strictly monophagous insect parasitoids appear to be rare (Zwölfer 1971), and polyphagy has been reported among species attacking all life stages of hosts. Egg parasitoids in particular, appear to be very successful in attacking more than one host species. These parasitoids do not have to overcome hosts defences, since eggs seem to lack a developed encapsulation response (Salt 1970; Askew 1971). Most strains of *Trichogramma*, for instance are able to recognize and parasitize a wide assortment of host species (Salt 1940; Taylor and Stern 1971; Pinto *et al.* 1978; Schulten and Feijen 1978; Burks 1979; Jennings and Houseweart 1983; Houseweart *et al.* 1984).

Some trichogrammatids attack aquatic insect eggs, usually found in plant tissue (e.g., *Hydrophylita* and *Brachista* spp are parasitoids of odonate eggs). But, although some "aquatic" trichogrammatids have been described, few have been studied in detail. Thus, little is known on the influence of aquatic habitats in shaping life histories and behavior of egg parasitoids.

The genus *Lathromeroidea* (Trichogrammatidae) comprises five species, from which only *L. odonatae* Ashmead is known from North America (Doutt and Viggiani 1968). The North American species was originally described from individuals obtained from eggs of *Lestes* (Ashmead 1900; Girault 1911; Kryger 1919), but the biology of the species is unknown. Wasps belonging to this genus were recently collected in Alberta from eggs of *Limnoporus dissortis* Drake and Harris and two *Gerris* species (Spence 1986). There is no doubt that the wasps belong to the genus *Lathromeroidea*, but it is apparently an undescribed species (J. Pinto and D.L.Vincent, pers. com.), therefore I will refer to this parasitoid as *Lathromeroidea* sp nova.

In this chapter I summarize my findings on the biology of *Lathromeroidea* sp nova. I tested the hypothesis that *Lathromeroidea* sp nova was capable of parasitizing a range of gerrid host eggs. I also report the results of host use and suitability experiments, and describe host effects on progeny using various gerrid eggs as hosts. Finally, I made observations on courtship, mating and oviposition behavior and report data about the parasitoids fecundity.

## 4.3 MATERIALS AND METHODS

### 4.3.1 Cultures

I established a laboratory breeding culture of *Lathromeroidea* sp nova using parasitized eggs of *L. dissortis* collected from leaves of *Spargangium angustifolium* (Sparganiaceae) at Kirchner's East Pond (Dunstable, Alberta) (Figure 2.1). Four batches collected towards the end of summer 1990, showed symptoms of parasitism differing from those observed in eggs parasitized by *Tiphodytes gerriphagus* (Marchal). These eggs were taken to the laboratory, examined under a dissecting microscope, and placed into a translucent container (9 cm deep, 8 cm in diameter) with 200 ml of tap water. Eggs were held at 24°C under long-day photoperiod (19L:5D) until wasps emerged.

Breeding cultures of *L. dissortis* were maintained at 24°C under long-day photoperiod (19L:5D), as described by Spence *et al.* (1980), to provide host eggs for the laboratory cultures of *Lathromeroidea* sp nova. Both fertile and infertile eggs were harvested daily from the cultures. If not required immediately for wasp oviposition, eggs were kept in an incubator at 19L:5D/5°C for a maximum period of five days, to slow development. After this period, unused eggs were discarded.

Cultures of *Lathromeroidea* sp nova were started with two male and four female wasps that emerged from one of the field collected batches of *L. dissortis* eggs. These wasps were placed into a 500 ml wide mouth jar with a group of *ca.* 100 eggs of *L. dissortis*, to allow oviposition. Wasps were offered a new batch of eggs daily until all adult wasps were dead. Dead wasps were preserved in 70% ethyl alcohol and identified subsequently as *Lathromeroidea* sp nova (John Pinto, pers. com.). Cultures were maintained at 24°C under long-day photoperiod (19L:5D) until wasps emerged.

New cultures were subsequently established by placing two male and six female lab-reared wasps with a group of 50 to 100 *L. dissortis* eggs. This method was used to keep the wasps breeding continuously. Also, ten virgin and ten mated females emerging from the same batch of eggs were used in trials for testing whether the species was arrhenotokous. They were separated into glass jars, each was offered a batch of 50 *L. dissortis* eggs. All cultures were handled as described above.

### 4.3.2 Behavioral Observations

Observations were made on wasps held under long-day photoperiod (19L:5D) at 24-26°C. Females were observed in a covered petri dish (50 mm diameter), partially filled with tap water and containing a floating piece of grass. One pair of wasps that had emerged within five hours previous to the observations, were placed on the leaf with a fine paintbrush. Courtship and mating were observed under a dissecting microscope. Observations ceased after males were successful in mating, or if there had been no encounters after 30 minutes. To confirm that mating occurred, the female spermatheca was dissected. Ten couples were observed, of which only seven mated.

Searching and oviposition behaviors were observed under the dissecting microscope. However, I observed only four of six females actually ovipositing perhaps because it was necessary to turn the leaf to observe oviposition subjecting the wasps to the bright light from the microscope.

### 4.3.3 Host use and Suitability

Fecundity and female survivorship. On the morning of eclosion, fourteen 5th generation females of *Lathromeroidea* sp nova were transferred individually to plastic microcentrifuge tubes with attached lids (30 X 8 mm). Each female was paired with a male of approximately the same age. Pairs were allowed to mate and kept in the tube for a period of 24 hours before the experiment, without access to food. Mated females were then separately transferred to a wide mouth jar containing *ca*. 200 ml tap water. Each female was offered an egg batch of *ca*. 50 eggs of *L. dissortis.* Every female was checked daily for survival and, if alive, transferred to a new jar with fresh host eggs.

Parasitized eggs were then held as above until the wasps hatched. The sex of each emerging adult was determined by examining external genitalia with a dissecting microscope under 50X. A sample of 20 hosts with dead parasitoids were dissected to check for the presence of superparasitoids.

Host suitability. Eggs of four species of *Limnoporus* (*L.dissortis*, *L. notabilis* Drake and Hottes, *L. rufoscutellatus* Latreille and *L. esakii* Miyamoto) and two of *Gerris* (*G. buenoi* Kirkaldy and *G. pingreensis* Drake & Hottes) were offered as hosts. Eggs used were five days old. Female wasps used for these experiments had emerged from laboratory cultures within 12 hours and were mated as described above.

Four mated female wasps were placed into circular 500 ml wide mouth jars filled wit *ca.* 200 ml of tap water. A styrofoam strip with 70 eggs of one host species was added to the jar. As far as possible each treatment was replicated at least 10 times (except for *G. pingreensis*, with 5 replicates and *L esakii,* with 6). Experiments lasted until all females were dead (4-[illegible] days). The number of wasps emerging from parasitized eggs was recorded. After all wasps had emerged (16 to 24 days, depending on host species), eggs that either did not hatch or showed signs of parasitism were dissected and checked for presence of parasitoid larvae.

I also tested whether the wasps parasitize damselfly eggs. Floating stalks of various aquatic plants were collected from the field and scanned for odonate eggs. Stalks that contained eggs (most likely of the genus *Lestes*) were cut in pieces measuring approximately 5 cm. Each piece contained 15 to 20 eggs. Three or four pieces were placed in 500 ml jars with tap water. Five mated females were confined with the eggs until they died. There were seven replicates. A week after experiment started, eggs were checked for symptoms of parasitism. Eggs were dissected after damselfly larvae had emerged.

*Effect of host species on development and reproductive output.* Five different species of gerrid eggs were provided as hosts for one-day old mated females without oviposition experience. I chose as hosts the large-bodied species *L. dissortis* and *L. notabilis* (from Canada), the small-bodied *L. esakii* (from Japan), and two species of *Gerris* (*G. buenoi* and *G. pingreensis*) which are common in Western Canada (Spence 1989). I initiated experiments by placing mated couples of *Lathromeroidea* sp nova into 500 ml glass jars each with a batch of 50 to 100 eggs. Egg batches were exchanged for new ones every day until females died. Adult wasps were not fed.

All emerged adult were killed and preserved in 70% ethanol, their sex and development times recorded, and individually measured at 50X using a dissecting microscope fitted with an ocular micrometer. Individual wasps were each placed in single glass tubes and oven-dried at 45°C for a minimum of 24 hours. Dried wasps were weighed using a Cahn model 26 automatic electrobalance. In addition, length and dried mass of twenty five eggs of each host species were recorded as described.

Statistical analysis were done using the Stat-View 512 (BrainPower Inc., Calabasas, CA, U.S.A.) package on a Macintosh computer. Two-way Analysis of variance were performed using SAS (SAS Institute Inc., Cary, NC, U.S.A) on the Mainframe at the University of Alberta.

## 4.4 RESULTS

### 4.4.1 Behavioral Observations

Arrhenotoky was confirmed in *Lathromeroidea* sp nova using eggs of *L. dissortis.* Unmated females ($n$=10) produced only male progeny, mated females ($n$=10) produced an offspring sex ratio of 1:2.20 males to females.

In *Lathromeroidea* sp nova, mating occurs soon after adults emerge. Courtship and mating occurred either on the water surface or on vegetation.

Males of *Lathromeroidea* sp nova emerged approximately. 24 hr before females and groomed themselves with their forelegs. They remained inactive on the water surface or the vegetation until females emerged. Courtship was initiated by the male, soon after a female's presence was detected. Males approached females while antennating and walking on the water surface. In both sexes the wings remained folded over the abdomen. Females usually remained immobile while males approached. A male mounted by grasping a female's pronotum, orientating his body parallel to the female's, and positioning his protarsal claws on the females' compound eyes. During mounting, females kept their antenna extended downward. When the male's antennal club touched the female's, with short alternate snaps, the female either accepted the male by remaining immobile, or rejected him by pushing the male's meta and mesolegs with their own hind legs. Copulation followed. Mating lasted 66 ± 11 secs (mean±SE, $n$=7) from mount to dismount.

I also noted that males attempted copulation with the same female after mating once, and that they also attempted to mate with previously mated females. However, no female that I observed (*n*=7) accepted a second mating. Many females that were not receptive or had already mated simply kept walking while a male tried unsuccessfully to copulate.

One virgin female, after two mating attempts by a male, submersed herself. She formed an air bubble between the wings and body, by pressing the wings against the abdomen with her metathoracic legs. She first introduced her head into the water and finally succeeded in submersing her whole body. The male immediately followed her into the water using the same method. They remained submersed and upside down for twenty minutes but there were no mating attempts while they remained underwater. After being submersed for twenty minutes, the female climbed to the water surface, head first, remained there for a few seconds, and submersed again. A few minutes later, both wasps left the water but the female kept her abdomen in the water, making mating impossible despite male's attempts. Both abandoned the water and walked on the vegetation, where the male attempted to copulate twice without success. I stopped the observations after 30 minutes of wasp inactivity.

Most inseminated females began searching for host eggs soon after mating. Females walked on floating vegetation, actively antennating the leaf surface. When eggs were discovered, possibly through use of chemical cues, females walked straight to the leaf border, pulled themselves underwater and began oviposition. Once the eggs were contacted with the antennae, a female positioned herself on the egg, bent her abdomen with the ovipositor fully extended to reach the chorion through the gelatinous covering of *Limnoporus* eggs. Females did not feed on the puncture holes made by the ovipositor, as has been reported for other parasitoids.

Wasps of both sexes used their wings to swim if accidentally submersed. However, I did not observe females swimming underwater in search of eggs. Also, neither males nor females flew readily, although individuals of both sexes have well developed wings. They mostly moved about by walking on the water surface with occasional short flying leaps.

### 4.4.2 Host use and suitability

Fecundity and female survivorship. Not all females tested laid eggs every day, but the analysis of daily oviposition rates also included data from those wasps that did not oviposit, because they also affect population growth. Female wasps parasitized 39 ± 3.77 (Mean ±SE) host eggs during their lives (Figure 4.1.A, Table 4.1), but only 27.43 ± 3.71 parasitoids developed and hatched. Oviposition began during the first day of exposure to gerrid eggs, and peaked on day three (10.07± 3.16, $n$=14). Minimum value of parasitism was recorded on day six (3.17 ± 1.35, $n$=6). Females started to die after day 3, and all were dead by day 8 (Figure 4.1.B).

A high percentage of parasitoid larvae obtained in this experiment did not complete development. In those eggs, all parasitoid larvae had developed to the last instar but did not pupate. Dissection of those eggs, however, did not reveal any evidence that superparasitism was the cause of the failure to develop. Only one of twenty eggs dissected contained more than one parasitoid larva. *L. dissortis* eggs appearing to contain dead larvae have been observed in the field, usually towards the start and end of the summer.

The percentage of emerging wasps increased with day of oviposition through day 6 (R X C Test of Independence, $G=61.03$, $df=6$, $P<0.05$) with hatching success of fifty to one hundred percent (Table 4.2).

Host suitability. All six gerrid species offered as hosts were parasitized by *Lathromeroidea* sp nova (Figure 4.2). Analysis of variance performed on data after arc sine transformation, showed only marginal differences between the species in respect to percent parasitism ($F=2.04$; $df= 5,95$; $p=0.079$). However, there were significant differences among the host species tested in respect to emergence of adult wasps ($F=5.97$; $df=5,95$; $p=0.0001$). Proportionately more wasps emerged from *Gerris* eggs than from *Limnoporus*, suggesting that suitability differs between these two genera. All wasp larvae that died in *Limnoporus* eggs had developed to the last instar but did not reach pupation.

*Lathromeroidea* sp nova females did not parasitize damselfly eggs offered in the laboratory experiments. There was 96% larval hatching success for the odonates, and eggs that did not hatch contained either malformed damselfly embryos or were infertile.

Effect of host species on development and reproductive output. Eggs of the five gerrid species used as hosts differed in the amount of resources provided for parasitoid development, as indicated by significant differences in both weight ($F=254.42$; $df=4,120$; $p=0.0001$. Figure 4.3) and length ($F=201.47$; $df=4,120$; $p=0.0001$. Figure 4.4).

Host size affected both weight and length of wasps. Weight (dry mass) of males and females was not statistically different, but host size did have a strong effect on weight of adult parasitoids ($F=138.70$; $df=4,959$; $p=0.0001$). As expected, the largest host (*L. notabilis*) produced the heaviest wasps, and the smallest host (*L. esakii*), the lightest wasps (Figure 4.3). Only *G. buenoi* and *G. pingreensis* did not show significant differences (Scheffe's test following a significant one-way Anova, $p<0.05$).

Two-way analysis of variance showed that wasp length was affected by both sex of emerging wasp ($F=68.44$; $df=1,958$; $p=0.0025$) and host species ($F=9.20$; $df=4,958$; $p=0.0001$). Males were considerably larger than females, although there were no differences in weight. The largest hosts produced [illegible]gest wasps (Figure 4.4). There was no significant Interaction between host and wasp's sex with respect to length of adult wasps.

A Nonparametric one-way analysis of variance showed significant differences in development times for wasps obtained from the five species ($F=32.3$; $df= 4,959$; $p=0.0001$. Figure 4.5). Male wasps developed faster than females in *L. dissortis*, *L. notabilis* and *G. buenoi*, as is expected in sibling mating systems. Males emerge usually one day ahead of females. Development times at 24°C and long-day photoperiod ranged from 17 days in eggs of *L. esakii* to 20.5 days in eggs of *G. pingreensis*.

Overall, *G. pingreensis* and *L. esakii* were the least favorable as hosts for the development of *Lathromeroidea* sp nova. *L. esakii*, the smallest host tested, had the greater influence in wasp size, perhaps because it is possibly a novel host. Although offspring survival was not considered in this study, casual observations suggest that these small wasps do not live as long as wasps emerging from *L. dissortis* or *L. notabilis*.

Parasitoid sex ratios were significantly biased towards females among all host species but varied only slightly among larger sized species [*L. dissortis*: 1:2.31 ($X^2$=20.16, *df*=1, *P*=0.0001), *L. notabilis:* 1:2.38 ($X^2$=45.78, *df*=1; *P*=0.0001)]. There was more variation between the smallest *Gerris* species [*G. buenoi*: 1:1.84 ($X^2$=28.77, *df*=1; *P*=0.0001), and *G. pingreensis:* 1:2.38, ($X^2$=13.44, *df*=1, *P*=0.0002)]. Although sex ratios obtained from eggs reared from *L. esakii* were also biased towards females (1:1.38), results are not statistically significant, suggesting that more males came from the smaller eggs of this host.

## 4.5 DISCUSSION

The family Trichogrammatidae comprises a large number of species, all of which are parasitoids of insect eggs. Although most described species attack terrestrial insects, several parasitize insects in freshwater habitats. *Hydrophylita* spp (Matheson and Cosby 1912) and *Trichogramma* spp (Juliano 1981), for example, parasitize eggs of Odonata and aquatic Diptera respectively. Eggs of semiaquatic Heteroptera were not known to be attacked by these chalcids until recently.

Parasitization of gerrid eggs by *Lathromeroidea* sp nova was first reported by Spence (1986), in two species of *Gerris* collected near Dunstable, Alberta. Because wasps were initially though to be *L. odonatae*, whose only known hosts are damselfly eggs, Spence hypothesized that gerrids were not its primary hosts. However, I have shown that (1) the species is found in field collected gerrid eggs, (2) it can be easily reared using eggs of several gerrid species in the laboratory, and (3) wasps did not parasitize damselfly eggs when they were offered in the laboratory. Based on this evidence and on confirmation that the wasps are not *L. odonatae* (J. Pinto, pers. com.), I offer the following hypotheses about host use by this parasitoid.

*Lathromeroidea* sp nova uses gerrid eggs as its primary hosts. My laboratory studies showed that more wasps completed development in eggs of *Gerris* than in those of *Limnoporus*, suggesting that *Gerris* eggs are more suitable hosts. Field data indicates that eggs of *Limnoporus* are depleted more than those of *Gerris* by *T. gerriphagus* (Spence 1986). Therefore these two parasitoid species may not be competing for hosts eggs. The obvious next step is to study the levels of parasitism by *Lathromeroidea* sp nova in *Gerris* eggs under field conditions. In this study, I did not consider field parasitism in *Gerris* eggs, which are laid in vegetation underwater and are harder to sample than those of *Limnoporus*.

### 4.5.1 Mating and oviposition

*Lathromeroidea* sp nova is a solitary egg parasitoid. It is arrhenotokous, that is, mothers (foundresses) can control their offspring's sex ratio by controlling fertilization. Although field sex ratios are unknown, female biased sex ratios (28% males) were produced under laboratory conditions. Such female biased sex ratios were predicted for sib-mating systems by Hamilton (1967). In highly inbred systems, foundresses produce only enough sons to fertilize their daughters (Hamilton 1979; Werren 1980), because competition between male sibs impairs the reproductive success of the foundress (the sibs' mother). A test of that prediction was made by

Waage (1982) for several species of scelionid parasitoids. He found that males and females are assigned non-randomly to egg masses, ensuring mixing broods in the proper proportions. Female biased sex ratios have been recorded for a wide range of parasitoid species, including *T. gerriphagus* (Spence 1986) and the parasitoid of aquatic Diptera, *Trichogramma* nr *californicum* (Juliano 1982).

*Lathromeroidea* sp nova males developed ahead of females, emerging through a hole made on the host egg, and climbed the vegetation in search for mates. Searching for mates occurred on the water surface, a behavior probably more common in solitary parasitoids, such as *T. gerriphagus* (Martin 1927; Spence 1986). In most gregarious trichogrammatid species, potential partners are present from the beginning, thus finding mates does not seem to pose a problem (Suzuki and Hiehata 1985). In *Caraphractus cinctus* (Mymaridae), a gregarious parasitoid of dytiscid eggs (Jackson 1958) for example, males also emerge ahead of the bulk of females but remain submersed awaiting the emergence of their sisters.

Courtship and copulation time was short which may contribute to high mating success in both sexes, because males can serve several females as they are emerging from the eggs. In the laboratory, mating occurred soon after emergence, as seems to be the case in many parasitoid species (Price 1975) and it seems likely that males do not disperse away from emergence sites. Both males and females walk readily on water or pond vegetation, but few wasps fly, even though they are macropterous.

In the field, only a few individual eggs in batches of *L. dissortis* are parasitized, and given these low levels of parasitism, obtaining mates may be a problem for wasps. Parasitism in solitary eggs of *G. buenoi* pose the same limitations. In this species, finding mates may involve the use of short-distance pheromones. More field observations are necessary to establish whether *Lathromeroidea* sp nova males form aggregations that attract females. Male swarms have been observed in a number of solitary parasitoid species (Southwood 1957; Jervis 1979). These swarms emit long-distance signals attractive to virgin females. Such chemical cues have been identified and have been reported for several species of wasps, mostly ichneumonids and braconids (Lewis *et al.* 1971; Eller *et al.* 1984).

Inseminated female wasps search for host eggs by walking along leaf margins and antennating intensively. They probably find the eggs using chemical cues. Once the appropriated cues were found, wasps submersed using their wings to form an air bubble in order to reach the hosts. Although there are reports of aquatic parasitoids that swim underwater in search for host eggs (Jackson 1958, 1963), females *Lathromeroidea* sp nova did not exhibit this behavior.

### 4.5.2 Host use and suitability

*Lathromeroidea* sp nova is extremely polyphagous, parasitizing eggs of all gerrid species offered under laboratory conditions. The host in which the wasps developed may induce morphological variations in emerging adults. For example these variations in morphology have been reported for species of Eulophidae (Hansson 1985), Scelionidae (Johnson *et al.* 1987), and Aphelinidae (Woolley and Browning 1987). Morphological variations within parasitoid species are widespread but may not be taken into account sufficiently by many taxonomists when they describe new species. The mymarid *Anaphes iole*, for example, was redescribed by studying host-induced intraspecific variations (Huber and Rajakulendran 1988).

More wasps reached adulthood in *Gerris* than in *Limnoporus* eggs. High parasitoid mortality in *Limnoporus* eggs may be due to their inferior quality, rendering them less suitable. Host nutritional suitability (Flanders 1937; Salt 1938; Vinson 1980), often has a profound effect on sex ratios, size, development times, fecundity and longevity of the parasitoid (see Vinson and Iwantsch 1980 for a review). Among the factors that influence host nutritional suitability are nutrient level and quality, as well as availability and presence of correct titers of accessory growth factors. Juvenile hormones and ecdysteroids, for example, are present in substantial amounts in eggs of various insect species (Bergot *et al.* 1981; Mizuno *et al.* 1981; Lagueux *et al.* 1981; Scalia and Morgan 1982; Gharib and de Reggi 1983). Egg parasitoids are directly exposed to the *in vivo* endocrine milieu of host embryos and may interact with it.

Sex ratios were female biased, however, more male parasitoid developed in the smallest *L. esakii* eggs. Analogous findings with *T. gerriphagus* (Spence 1986) suggest that both parasitoid species allocate more males in smaller hosts. In both species, host size influenced sex allocation, as outlined in Charnov's models (1979, 1982). Production of male progeny from small hosts and females from large hosts is a common observation in solitary parasitic wasps (Clausen 1939; Charnov 1982; King 1987).

Usually only one wasp develops from each gerrid egg, although superparasitism did occur under high parasitoid densities in the laboratory and occasionally in the field. In these cases, a maximum of two small wasps developed to maturity and emerged, but their adult life span was significantly reduced. Field superparasitism may occur because of the wasps decision to stay longer in a batch in presence of competitors (van Alphen and Vet 1986). This behavior could be adaptive when transit times between potential hosts are long. In the laboratory, it is possible that many *Limnoporus* embryos may have died from multiple punctures.

*Lathromeroidea* sp nova and *T. gerriphagus* are similar in regard to host use and behavior. Females of both species initiated oviposition one day after mating, on the first day of exposure to gerrid eggs, and their life spans were similar (4-8 days). They have also developed analogous strategies that allow them to exploit hosts located underwater (*i.e.* the ability of submerse to contact gerrid eggs). Although fecundity was lower in *Lathromeroidea* sp nova than in *T. gerriphagus*, individual patterns of egg production were similar for members of both species.

Body size and development rate of *Lathromeroidea* sp nova were affected by host species. The larger hosts produced the largest wasps, a result also found in *T. gerriphagus*. Host effects on parasitoid morphology have been recorded in various families comprised of egg parasitoids; Tichogrammatidae (Salt 1940; Martson and Erlte 1973; Sengonca *et al.* 1990), Braconidae (Kumar and Ballal 1990), and Mymaridae (Meyerdirk and Moratorio 1987). Male body was larger than female in adults of *Lathromeroidea* sp, although there was not difference in weight. A positive correlation between host size and wasp size has been demonstrated for some solitary endoparasitoids. In several species, the percentage increase in size from small to large hosts is greater for females than for males (Jowky and Smilowitz 1978; Samson 1984; Spence 1986), but in several cases this increase in size is independent of sex (Legner 1969; Nealis *et al.* 1984; Hurlbutt 1987). Wasps developed slower in eggs of the smallest host species tested, a result also found in several species, including the egg-larval parasitoid *Chelonus blackburni* (Braconidae) (Kumar and Ballal 1990).

There are few well-known case studies of "aquatic" Hymenoptera, and all are egg parasitoids. Here I have presented new information about parasitism of gerrid eggs by *Lathromeroidea* sp nova, an undescribed species. Wasps are abundant in the field especially towards August, where they can be collected by picking them from floating vegetation, but overall levels of parasitism in *Limnoporus* eggs are low. I have shown that the wasps cause high mortality to eggs of various gerrid species in the laboratory. Because they appear to develop more successfully in eggs of *Gerris*, it is likely that resources are partitioned between this trichogrammatid and *T. gerriphagus* which is considered to be the most important mortality factor of *Limnoporus* eggs. Overall, my results show that gerrid-parasitoid systems can be more complex than previously thought.

**Table 4.1.** Mean values of *Limnoporus dissortis* eggs parasitized by *Lathromeroidea* sp nova.

| Day | Mean±SE | Number ovipositing females | Minimum eggs laid | Maximum eggs laid |
|---|---|---|---|---|
| 1 | 20.0±3.2 | 6 | 11 | 28 |
| 2 | 18.6±5.5 | 7 | 2 | 43 |
| 3 | 14.1±3.7 | 10 | 2 | 35 |
| 4 | 8.6±2.4 | 8 | 1 | 20 |
| 5 | 7.2±4.1 | 5 | 1 | 21 |
| 6 | 4.8±1.4 | 4 | 1 | 8 |
| 7 | 10.0±0.6 | 3 | 9 | 11 |

**Table 4.2.** Frequencies of hatching and dead larvae of *Lathromeroidea* sp nova at various days after oviposition.

| Day of Laying | Emerging Ovipositing | Dead | Total | %Emerging | mothers |
|---|---|---|---|---|---|
| 1 | 61 | 60 | 121 | 50.4 | 6 |
| 2 | 108 | 22 | 130 | 83.1 | 7 |
| 3 | 92 | 49 | 141 | 65.2 | 10 |
| 4 | 61 | 8 | 69 | 88.4 | 8 |
| 5 | 27 | 9 | 36 | 75.0 | 5 |
| 6 | 18 | 0 | 18 | 100.0 | 4 |
| 7 | 17 | 13 | 30 | 56.7 | 3 |
| Total | 384 | 161 | n=545 | | |

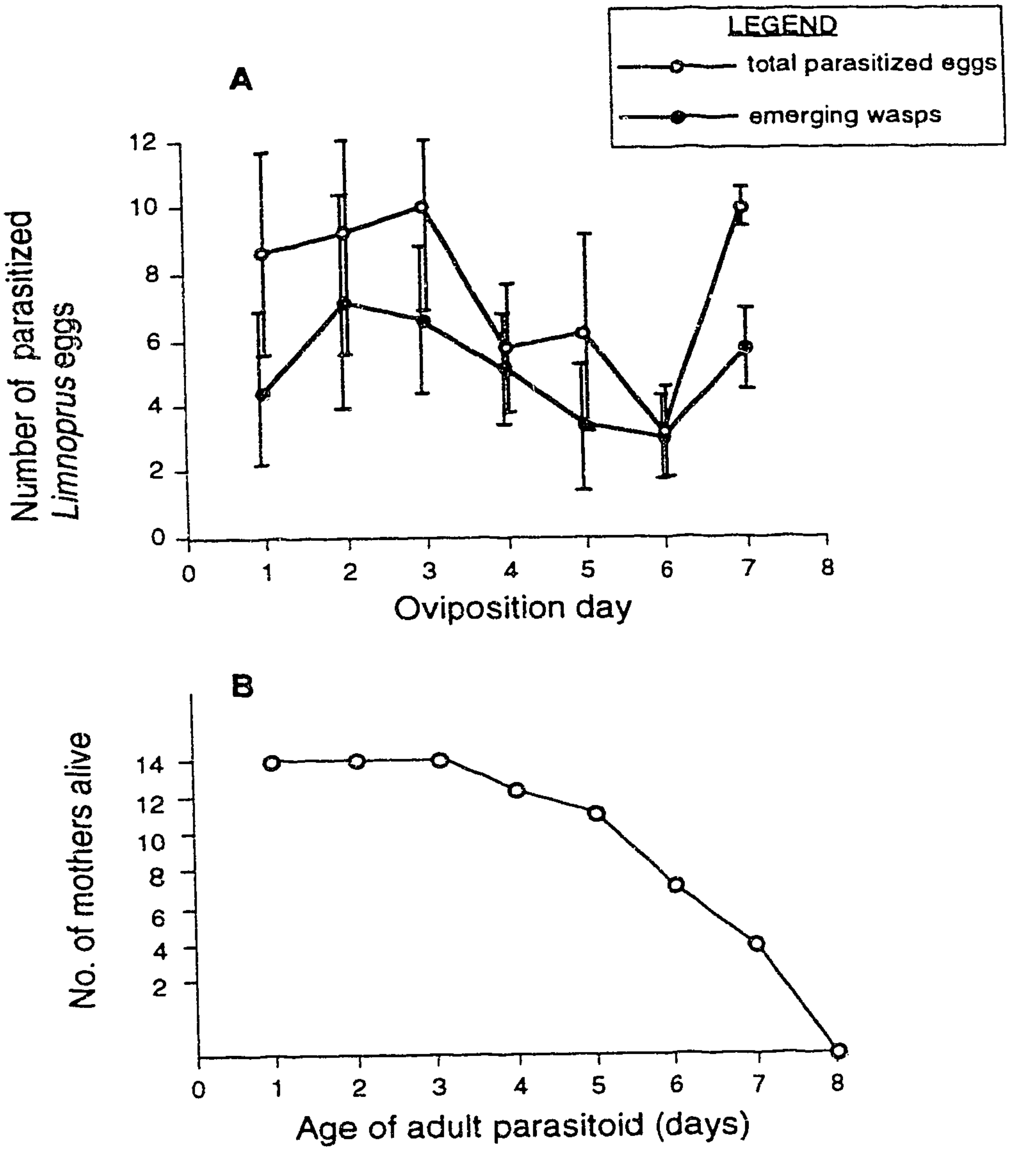

**Figure 4.1** A) Mean fecundity of individual wasps (total parasitized eggs and total emerging wasps) and, B) Survivorship of females of *Lathromeroidea* sp *nova* over time at 24 °C. (Error bars indicate ± one standard error).

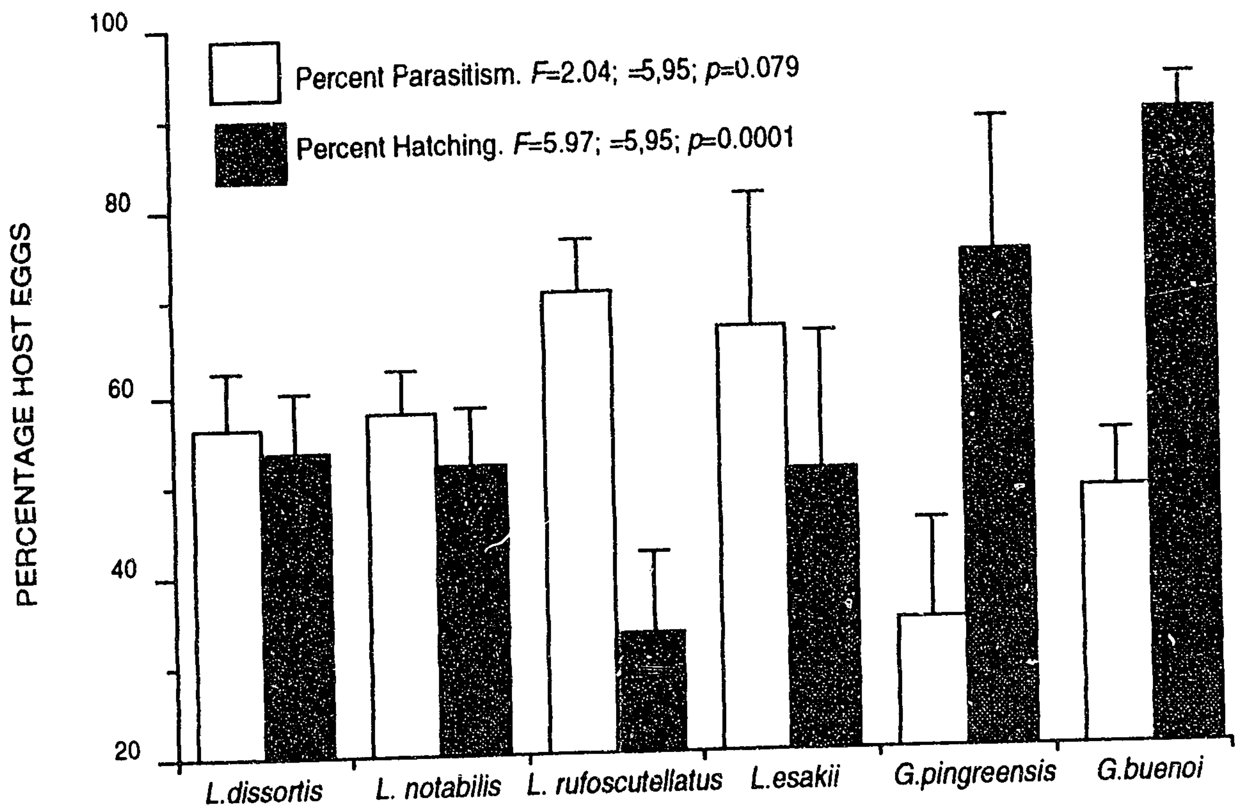

**Figure 4.2** Percentages of parasitism and hatching wasps of *Lathromeroidea* sp *nova* reared from six gerrid host eggs (Error bars indicate ±one standard error).

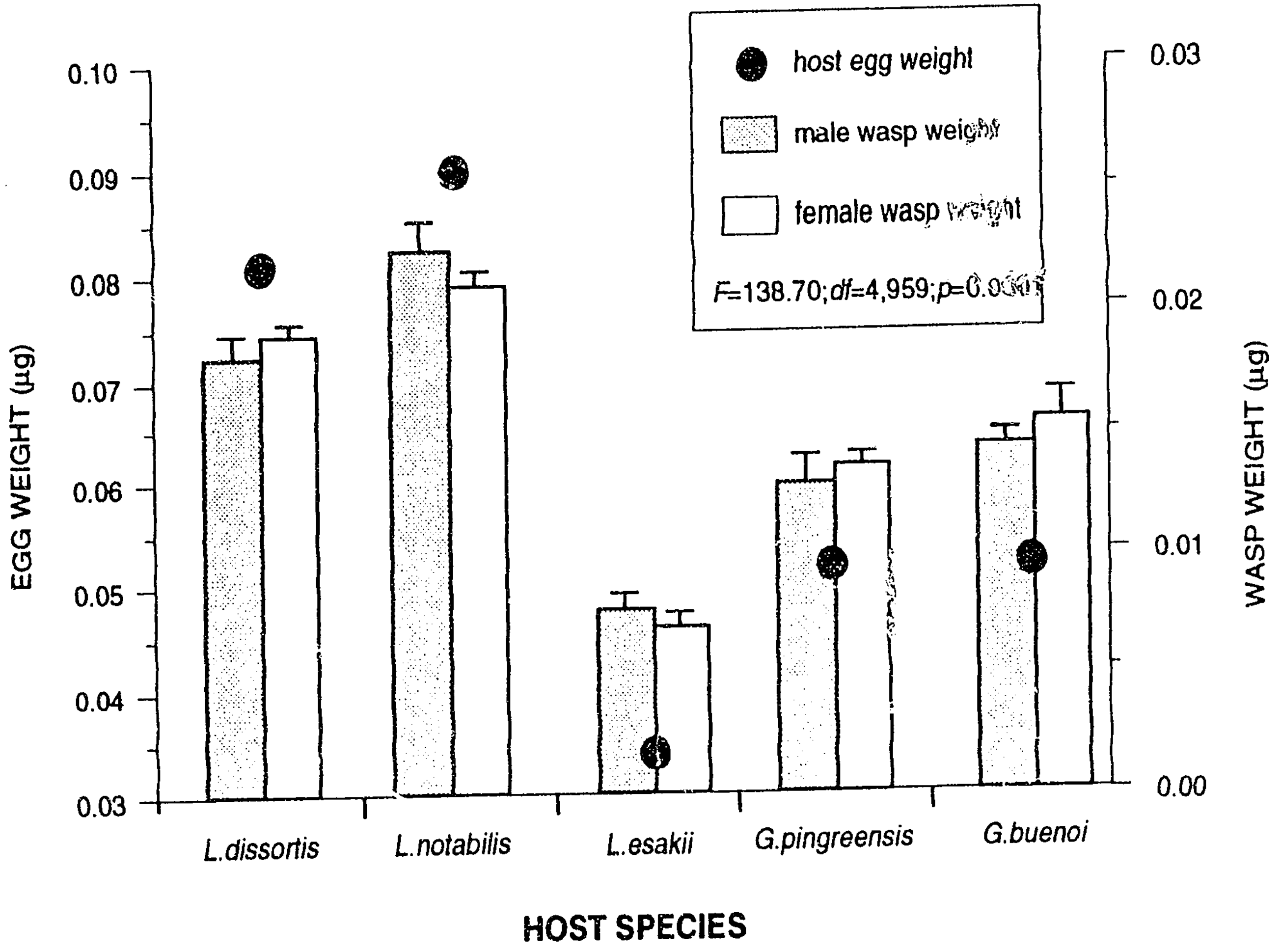

**Figure 4.3** Weight of host eggs and wasps of *Lathromeroidea* sp *nova* of both sexes reared from those eggs (Error bars represent ± one standard error).

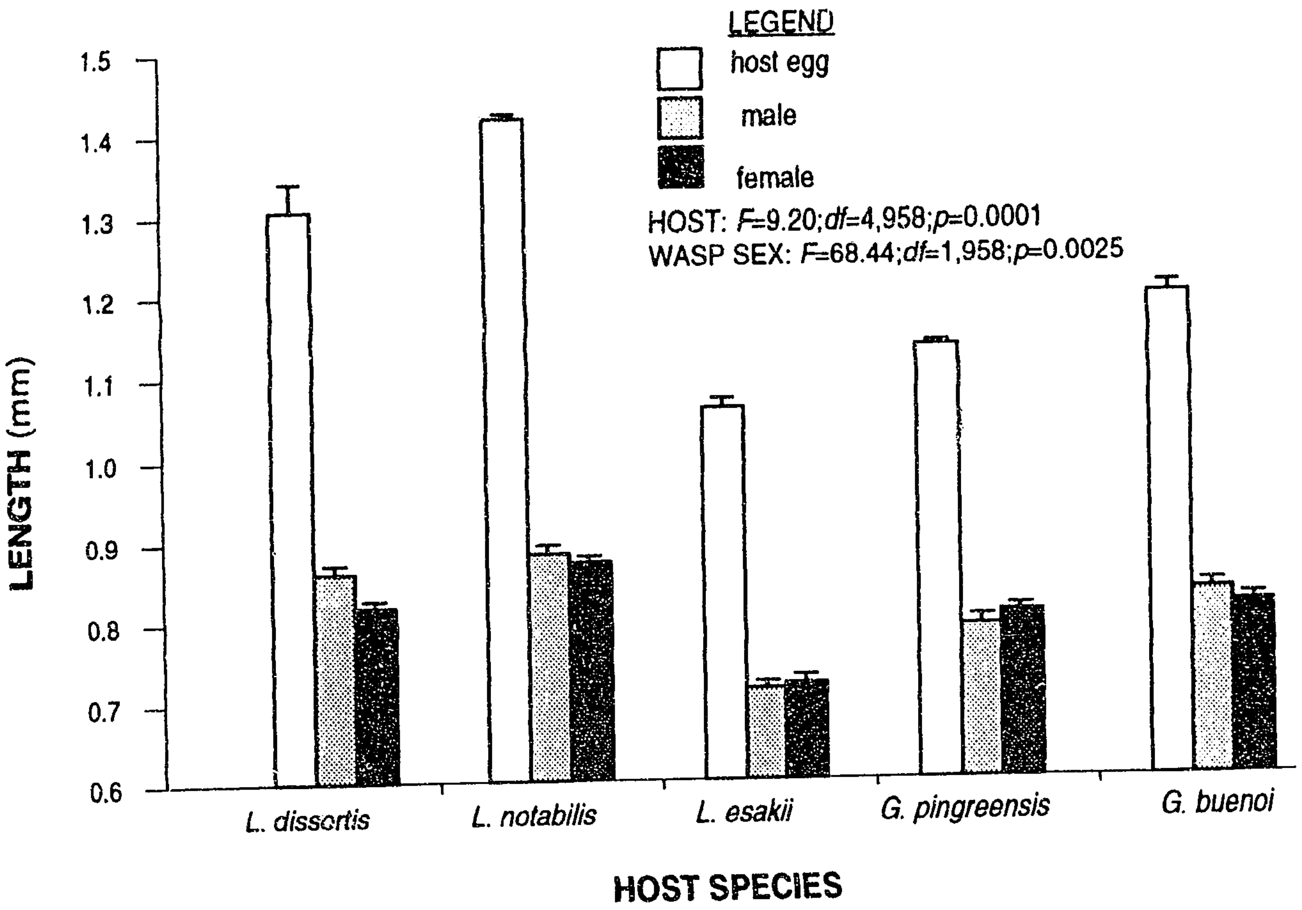

**Figure 4.4** Lengths of gerrid eggs and *Lathromeroidea* sp *nova* wasps of both sexes reared from five host species (mean ±SE).

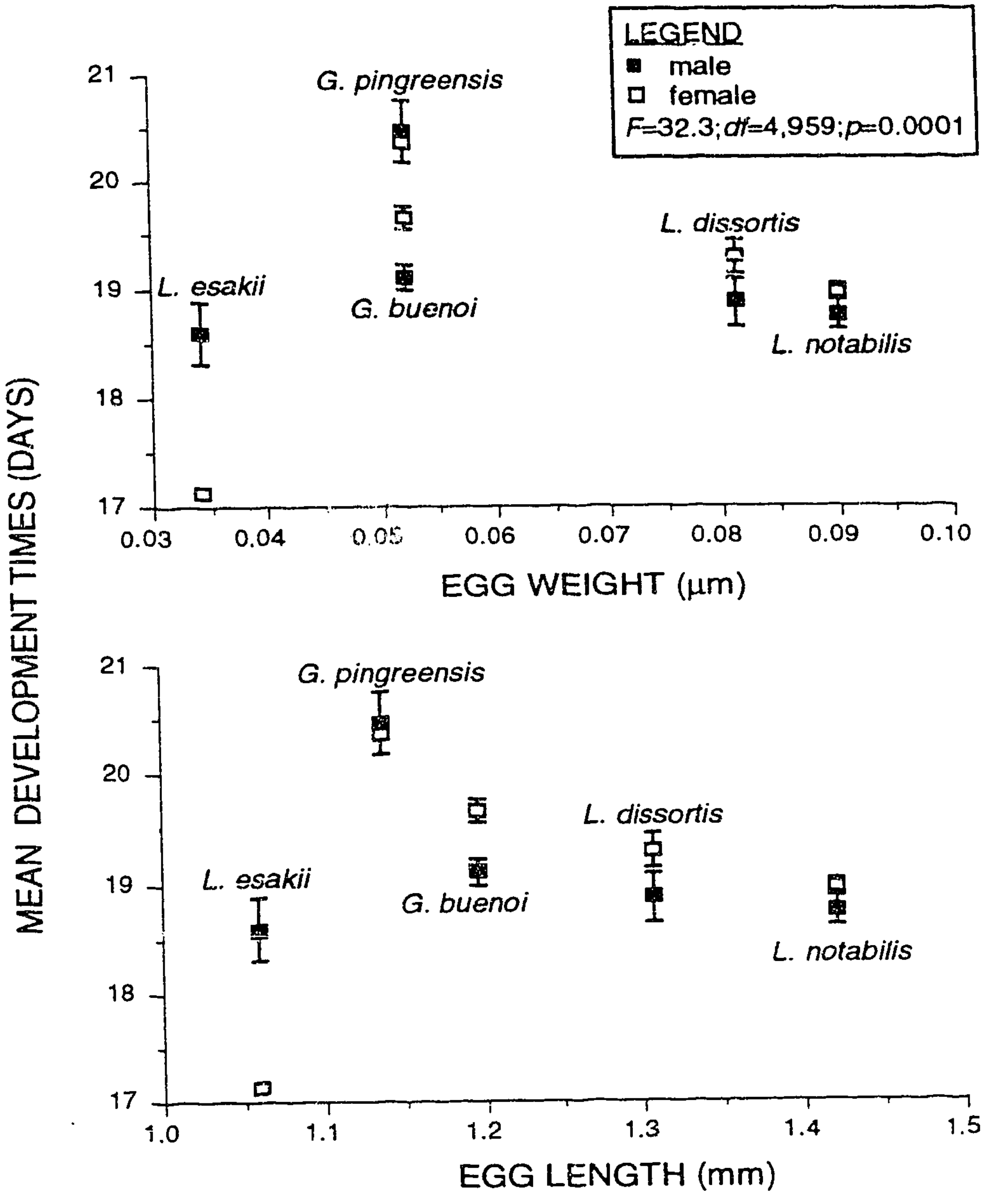

**Figure 4.5** Dimensions of host eggs and development times of *Lathromeroidea* sp *nova* wasps of both sexes reared from five gerrid species (Mean ±SE).

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# 5. CONCLUSIONS

## 5.1. Summary.

The relationships between insect parasitoids and their hosts are complex, and often involve extensive coevolution. Three levels of selection affect the evolution of parasitic associations. These are ecological (or behavioral), physiological, and immunological levels (Boulétreau 1986). A primary constraint on parasitism occurs at the ecological level, because habitat and microhabitat of both partners need to overlap. The presence of parasitoids in the same habitat as their hosts, however, is also a direct result of active searching. Thus, not only have parasitoids evolved mechanisms that allow them to search efficiently, but also to effectively exploit the hosts once they have been located. At the physiological and immunological levels, the suitability of a host for parasitoid development depends on numerous biochemical, nutritional and endocrinal factors (for a review see Vinson and Iwantsch 1980). These constraints must be overcome by parasitoids to obtain sufficient resources to complete development. In the preceding chapters I have examined several aspects of selection at the ecological level using the association between two micro-hymenopterous egg parasitoids and their gerrid hosts.

*Tiphodytes gerriphagus* is the most important mortality factor on eggs of *Limnoporus dissortis* and *Gerris comatus* in central Alberta (Spence 1986). Because of the direct link between host searching and wasps reproduction, parasitoid searching behavior is strongly influenced by natural selection (Alphen and Vet 1986). To understand the adaptive nature of this parasitoid's foraging behavior, it is necessary to understand how habitat in which wasps forage shapes their ability to find host eggs. In Chapter 2, I showed that three levels of stimuli may influence the ability of the wasps to find host eggs. First, vegetation provides wasps with visual cues about potential oviposition sites. Second, wasps use cues form adult gerrids to locate substrates where gerrids oviposit. My results showed that parasitism is much higher in exclosures where adult *L. dissortis* were present than in exclosures from which bugs were excluded. Cues provided by adult gerrids are probably visual, although I suggest that non-polar, close range kairomones may exist, and that these could provide wasps with information about placement of host eggs. Third, after being attracted to adult bugs, there may be chemicals discharged by female gerrids during oviposition which guide the wasps to the eggs. These three levels of aggregation may operate in hierarchical order.

In Chapter 3 , I showed that parasitism rates observed in eggs laid at the surface are not associated with the number of host eggs present in a patch. Rather, rates of parasitism are a result of the high densities of wasps foraging at the ponds. This was clearly shown during June and July when wasp activity peaked. Data collected over a nine-year period did not provide evidence that parasitoid aggregation produced higher parasitism at patches of high host density. It has been proposed that density-dependent parasitism should lead to stability in parasitoid-host systems (Hassell and May 1973, 1974; Hassell 1978; May 1978). Hassell (1986) suggested that regulation depends on the relative strengths of density-dependent and density-independent parasitism. I have argued that in the system studied, stability at the pond level is maintained by the constant recruitment of new members into the population of gerrid adults that disperse between ponds during the summer months. Adults of this species colonize temporal ponds covered with dense vegetation that may seem unsuitable for their locomotion. *T. gerriphagus* has modified the adaptive response of its *L. dissortis* hosts to the pond environment, as was suggested by Spence (1986, 1989).

Spence (1986) reported the first *L. dissortis* eggs parasitized by *Lathromeroidea* sp nova, but he suggested that gerrids were not the primary hosts and that its impact on gerrid populations was minor. In Chapter 4, I showed that wasps can develop, with varying levels of success, in four species of *Limnoporus* and two of *Gerris.* I studied the influence of these gerrid species on the fitness of *Lathromeroidea* sp nova, and suggested that the eggs of *Gerris* were more suitable hosts. As in many egg parasitoids, weight and length of adult wasps were affected by the amount of resources provided for development. As expected for highly inbred parasitoid populations, sex ratios were female biased, and males developed faster than females. This study provides evidence of resource partitioning between *T. gerriphagus* and *Lathromeroidea* sp nova. I suggest that the latter species attacks eggs of *Limnoporus* when eggs of *Gerris* are not available.

## 5.2 Importance of studies on Parasitoid-Host systems.

Parasitoids can have an important role in the population regulation of their host species. For both theoretical and practical reasons considerable scientific effort has been devoted to the understanding of such systems.

Until recently, most research was in the context of biological control. Levels of parasitism and composition of parasitoid complexes were often recorded in agricultural monocultures, where pest populations have increased beyond their natural limits. Under these circumstances, data obtained are likely to be a poor reflection of the "natural" situation in which evolutionary adaptations have occurred (Askew and Shaw 1986). Recently more attention has been paid to understand how parasitism affect systems commonly found in nature (Cappuccino 1991).

For the aforementioned reasons, I believe that to begin to understand the processes that govern parasitoid-host interactions, more effort should be devoted to the study of natural, undisturbed systems. An adequate knowledge of the distribution of the host and parasitoid species, both in space and time, and information about the effect of competitors and the risk of predation, is necessary to make accurate assumptions about the way in which parasitoids interact with their hosts. This is also of primary importance for making predictions about the outcome of such interactions.

### 5.3 Future directions for research.

There are many questions that remain unanswered regarding the relationships between gerrids and their parasitoid complex.

To fully understand how *T. gerriphagus* locate their hosts eggs, laboratory experiments are necessary to establish if there are chemicals (kairomones) emanating from gerrid adults or their eggs. Trials using an olfactometer can be designed to test for the presence of such chemicals. This can be complemented with studies of the parasitoid's sensilla involved in the recognition of such chemicals.

Although their small size makes it almost impossible to make rigorous behavioral observations in the field, wasp behavior could be investigated in laboratory settings. To determine whether host aggregation has an effect on parasitism rates caused by *T. gerriphagus*, laboratory trials using several densities of host eggs could be carried out. The ability of females of both species to "learn" information from their hosts and microhabitat that allows them to search more efficiently could be studied in the laboratory (Lewis and Takasu 1990; Lewis and Tumlinson 1988).

A detailed survey of *Gerris* eggs is necessary to establish natural parasitism rates for *Lathromeroidea* sp nova. As well, information about possible secondary hosts and overwintering in this trichogrammatid could be obtained from these surveys.

Nothing is known about the interactions between *T. gerriphagus* and *Lathromeroidea* sp nova. Laboratory experiments testing the outcome of competition between females of both species should provide a better understanding of the patterns of parasitism observed in the field. Furthermore, experiments could be designed to test sex allocation theory under local mate competition, as well as under resource competition between females of both species.

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