WATER MITE PARASITISM OF WATER BOATMEN (HEMIPTERA:CORIXIDAE)

by

BRUCE PAUL SMITH
B.Sc., University of Toronto, 1975

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE in
THE FACULTY OF GRADUATE STUDIES
DEPARTMENT OF ZOOLOGY

We accept this thesis as conforming to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA
September, 1977
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Department of Zoology

The University of British Columbia
2075 Wesbrook Place
Vancouver, Canada
V6T 1W5

Date Sept. 27, 1977
ABSTRACT

In this study the consequences of water mite parasitism on water boatmen were investigated, concentrating on two host species of the genus *Cenocorixa*.

It was established that mite parasitism severely restricted egg production in *Cenocorixa bifida* Hung.: whether this should be attributed to a nutritional drain or through hormonal intervention was considered. The possibility of mite interference in flight ability and post-imaginal flight muscle development was also investigated.

It was found that mite parasitism of *C. bifida* in the field varied considerably between habitats, salinity of the lake water influencing both the mite species involved and the prevalence of mite parasitism. When tested both in the field and laboratory, there was no apparent difference in parasitism rates based on the sex, morph or teneral development of the host. It was concluded that individuals of a species were equally susceptible to attack. There was, however, a very definite difference in susceptibility between host species based on equivalent exposure under laboratory conditions. When *C. bifida* and *Cenocorixa expleta* Uhler in particular were compared, *C. expleta* was significantly preferred by the four main mite species infecting *C. bifida*. This was substantiated in field data.

Considering the prevalence of mites on *C. bifida*, and the susceptibility of *C. expleta* to parasitism, the probability of the
latter being parasitized approaches 100% in lakes within the salinity tolerance range of mites. When parasitism of these two host species was further investigated, it became apparent that C. expleta cannot sustain mite parasitism and in most cases, died.

Past workers have noted the limited coexistence of C. expleta and C. bifida. Despite both species being physiologically fresh water insects, they only cohabit lakes in the upper salinity range of C. bifida. When the relative abundance of these two species was compared over the salinity range in which they coexist, C. expleta was rare until the upper salinity limit of mites was reached. There was a defined change in their relative abundance at this point, C. expleta being in the majority when salinity was above this limit.

It is evident that water mites severely reduce the reproductive success of C. expleta in low salinities. They are therefore instrumental in influencing the outcome of any biological interactions between C. expleta and C. bifida in these lakes.
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I. INTRODUCTION.

A. The Aim.

At present very little is known about mite-arthropod associations. Host-parasite records are about the only data available. There is some information on the effects of mites on economically important arthropods, such as scutacarid mite parasitism which causes the Isle of Wight disease in honey bees (Hirst, 1921), but the impact of mites on insects has largely been ignored. Further, the interrelationships of mite populations and their host populations are generally unexplored.

For the most part information on the effect of water mites on their hosts is largely speculative. There are very few accurate observations on the effects of water mite parasitism. For example, Abdel-Malek (1948) and Miyazaki (1936) showed that fecundity was reduced in parasitized mosquitoes, however Mullen (1974) states that the effects are not clear-cut. Davies (1959) concluded that mites may at times control Simulium decorum. Soar and Williamson (1925) recorded large numbers of dead parasitized Corethra sp. floating in lakes, and presumed the parasite load to be the cause of death.

In recent times, many workers have concentrated upon the Corixidae for studying the mite-insect interaction, with articles by Davids (1973), Harris and Harrison (1974), Davids and Schoots (1975), and Martin (1975). The corixid-water mite relation is ideal for study: the mites parasitic on corixids undergo the
greatest size increase on the host, and the final volume ratio of parasite to host is the largest recorded (Davids, 1973). It is therefore a logical association to study for an investigation of physiological damage to the host.

The aim of this study was to investigate the impact of mite parasitism on water boatmen, specifically the genus *Cenocorixa*. First physiologic damage to the individual was assessed in *C. bifida* (hung.), followed by an investigation of the ecological aspects of the relationship. In the ecology section the variation in parasitism between environments and between host species was studied. Finally an evaluation was made of the effect of parasitism on host populations and the influence of differential parasite pressure between host species.

B. The Study Area.

This research was conducted in the Fraser Plateau region of central British Columbia, with study sites in the vicinity of Williams Lake, Clinton, and Kamloops (Fig. 1). Most of the lakes selected for this research have previously been studied by Scudder (1969a, 1969b, 1975), Topping (1969), Cannings (1973), Reynolds (1974), and Topping and Scudder (1977). Consequently, a fund of information on physical, chemical, and biotic characteristics of these lakes was available. In the Williams Lake region, three study lakes (Boitano Lake, Westwick Lake, and SP 8) were located near Springhouse, while seven of the lakes (Round-up Lake, Phalerope Lake), Barnes Lake (Box 4), Lake Lye (Box 20/21), Near Pothole Lake, Barkley Lake (Opposite Box 4), Greer Lake
Figure 1. Research area.

A. Riske Creek Region
B. Springhouse Region
C. Clinton Region
D. Kamloops Region
(Box 89), and Long Lake (Chilcotin)) were located on Becher's Prairie near the town of Riske Creek. In the Clinton region, localities consisted of Long Lake (Clinton), Le 3, Le 4, and Le 5. As noted by Topping (1969), Le 1 and Le 2 have joined Long Lake (Clinton) as a result of a rise in the water table. A single lake, LB 2, was located in Kamloops on Bachelor's Range.

The lakes with *Cenocorixa* were selected so as to cover a broad range of salinity. Several extra lakes were studied in the salinity range where *C. bifida* and *C. expleta* (Uhler) coexist. Surface conductivity readings were taken in each lake during the study period and are listed in Table I. Conductivities are adjusted to 25°C for standardization, and conductivities quoted in the rest of this study will be maximum annual readings. These were comparable to records from previous studies. The ionic composition varies from lake to lake, fresher lakes being predominantly magnesium carbonate while in the higher salinity lakes sodium bicarbonate prevails (see Topping and Scudder, 1977). The lakes also varied in floral and faunal communities, which generally are inversely proportional in complexity to the ionic content of the water (Hammer et al., 1975). As noted by Reynolds and Reynolds (1976), the submergent vegetation is virtually non-existent in higher salinities (5,900 μmhos. and up in this study), while the bottoms of most fresher lakes are densely covered.

Temperature records were taken in several lakes using monthly chart recorders (Ryan model D-30, chart 380-4) and air temperature was recorded in the Williams Lake vicinity (Fig. 2). From past studies (Cannings, 1973; Jansson and Scudder, 1974; Scudder,
Table I. Salinity data 1976/77.

<table>
<thead>
<tr>
<th>LAKE</th>
<th>APRIL 17-19</th>
<th>MAY 4-6</th>
<th>JUNE 25-30</th>
<th>SEPT. 15-20</th>
<th>MAY 15-20</th>
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<td>LB 2</td>
<td>-</td>
<td>14130†</td>
<td>20470</td>
<td>20547</td>
<td>-</td>
</tr>
<tr>
<td>LONG LAKE (CLINTON)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>17058</td>
<td>-</td>
</tr>
<tr>
<td>BARNES LAKE</td>
<td>1321</td>
<td>10551</td>
<td>-</td>
<td>15197</td>
<td>10017</td>
</tr>
<tr>
<td>LE 3</td>
<td>-</td>
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<td>-</td>
<td>13026</td>
<td>4361</td>
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<tr>
<td>ROUND-UP LAKE</td>
<td>1867</td>
<td>7762</td>
<td>10446</td>
<td>10700</td>
<td>7357</td>
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<tr>
<td>LAKE LYE</td>
<td>859</td>
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<td>9704</td>
<td>8529</td>
<td>6574</td>
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<tr>
<td>LONG LAKE (CHILCOTIN)</td>
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<td>6884†</td>
<td>-</td>
<td>8064</td>
<td>6887</td>
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<tr>
<td>LE 4</td>
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<td>-</td>
<td>-</td>
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<td>WESTWICK LAKE</td>
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<td>BARKLEY LAKE</td>
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<td>343</td>
<td>503</td>
<td>581</td>
<td>504</td>
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Micromhos per centimeter surface conductivity, adjusted to 25°C.
Figure 2. Temperature data. Presented are daily temperature ranges for two of the lakes monitored, and for air temperature at Springhouse. Temperature recorders for the lakes were placed at a depth of 30 cm. Records are for April 1976 to June 1977, with winter represented by a break in the horizontal axis. Note that temperatures below 0°C are below the range of the temperature recorders.

A. Lake Lye water temperature.

B. Westwick Lake water temperature.

C. Springhouse (by Westwick Lake) air temperature.
1975), the water temperature is quite consistent between lakes and study sites, although Kamloops is slightly warmer and Clinton slightly cooler than the Williams Lake region (Jansson and Scudder, 1974). Compared to other years, the spring and summer of 1976 were below average in temperature, while the fall, winter, and following spring were above average.

C. The Corixidae.

Seventeen species of water boatmen can be found in the research lakes, however only a fraction of these are regularly encountered (see Appendix II). This study concentrates on *Cenocorixa bifida* and *C. expleta*, which were especially common in the region, and have been subjects for considerable previous work (Jansson and Scudder, 1974; Reynolds, 1974; Scudder, 1969b, 1971, 1975; Scudder, Jarial and Choy, 1972; Scudder and Meredith, 1972). The *Cenocorixa* species are bivoltive in high salinity lakes (a partial third for *C. expleta* in LB 2), and monovoltive in low salinity habitats (Jansson and Scudder, 1974; Scudder, 1975). They reproduce until the end of July or early August, then enter an ovarian diapause, presumably for nutritional reasons (Jansson and Scudder, 1974; Scudder, 1975). These two species exhibit a flight muscle polymorphism, consisting of a blockage in post-imaginal flight muscle development in the individuals forming the flightless morph (Scudder, 1971, 1975). A very high frequency of the non-flying morph is characteristic of *C. expleta*, while *C. bifida* exhibits this polymorphism to a lesser degree and only in moderately saline waters (Scudder, 1975).
The flightless morph develops in the fall, apparently only when temperatures remain below 15°C (Scudder and Meredith, 1972; Scudder, 1975). Other common corixid species of these lakes are Hesperocorixa laevigata (Uhler), Cymatia americana Hussey, Sigara bicoloripennis (Walley), Sigara decoratella (Hung.), and Callicorixa audeni Hung.

D. The Mites.

*Hydrachna* and *Eylais* are the only two genera known to contain species parasitizing water boatmen. The mites are parasitic only as larvae, the nymph and adult being free living predators (see Fig. 3). There are quiescent life history stages, calyptostases, separating the egg, larva, nymph, and adult stages. Peculiar to mites of Hydrachnidae and Eylaidae, the nymphochrysalis (between the larval and nymphal stages), is also associated with the host (Mitchell, 1957; Davids, 1973; Harris and Harrison, 1974).

*Hydrachna* differs considerably from *Eylais* despite the convergent life history strategy. *Hydrachna* as a nymph and adult is predatory on corixid eggs, and possesses an aquatic larva that actively hunts its host. *Eylais*, in contrast, is a predator of microcrustaceans, and its larvae walk upon the water's surface tension until a water boatman accidentally contacts the mite when replenishing its air supply. *Hydrachna* also differs in ovipositing within air chambers in the stems of aquatic plants, *H. skorikowi* Piersig being the only reported exception.

Before beginning this study it was necessary to survey the mite species occurring on corixids in this region, as all previ-
Figure 3. *Eylais-Hydrachna* life history. Calyptostases are quiescent developmental stages analogous to pupation in insects.
PFPion ON HOST — PERIOD OFF HOST

Calyptostases

Period on host

Period off host

Δ Calyptostases
ous studies had been conducted in Europe or upper New York State. It appears that the past tradition of applying the names or European species to North American counterparts is often not justified when larval characters are referred to. Several new species were encountered, and a detailed revision is in progress. A key to the larvae of mites encountered has been included (Appendix I), and it must be stressed that while I have used the European names in several instances, these are not necessarily the same species. Nine species of mites were found on corixid hosts in this region.
II. PHYSIOLOGY OF WATER MITE PARASITISM.

A. Introduction.

The effect of parasitism by water mites appears best recorded in the Corixidae. Leston (1955) suggested they could be a direct cause of mortality, while Crisp (1959) recorded interference with ovarian development. Harris (1970) suggested mites may interfere mechanically and physiologically with corixid flight, and proposed that respiration and copulation may be mechanically hindered. Davids (1973) studied the population dynamics and ecology of the mite *Hydrachna conjecta* Koenike and noted reduction in parasitism during winter on smaller hosts, and argued that damage to the host was a result of nutritional drain. More recently Davids and Schoots (1975) reported a direct correlation between host species, parasite species, and number of eggs in the host, and presumably the nutritional drain. Martin (1975) also studied mite induced host castration and suggested a hormonal rather than nutritional basis. In *Cenocorixa bifida* mite parasitism seems to prevent egg maturation in the flying form, but non-flying females can produce at least some mature eggs when parasitized (Jansson, 1971; Jansson and Scudder, 1974; Simpson, 1968). Young (1965a, b) presumed that the flightless morph had more room in the thorax for fat body, used little reserves for flight muscle development and maintenance, and had an increased metabolic efficiency. There is thus a good deal of circumstantial evidence for a nutritional drain by water mite parasites which has a detrimental effect on the host.
During their parasitic larval stage water mites feed on the host's haemolymph: in insects the haemolymph serves to transfer the nutritional reserves from the fat body to the host's organs (see Fig. 4). It has been shown with other haemolymph parasites of insects that there is a competition between the host's tissues and the parasite for these nutrients (Vinson, 1975). In Hemiptera the nutritional reserve is stored as triglyceride (Martin, 1969; Thomas, 1974). It is relayed to the organs via the haemolymph as diglyceride conjugated with haemolymph proteins (Chino and Gilbert, 1965; Gilbert, 1967; Gilbert and Chino, 1974; Thomas, 1974). It is reported that the long chain fatty acids in the tri- and diglycerides are necessary for ovarian yolk deposition and for both respiration and development of flight muscles (Chino and Gilbert, 1965; Thomas and Gilbert, 1967).

There appears to be evidence for shared use of this lipid reserve by flight muscle and ovaries, as flight muscle development is sometimes by-passed during ovarian development (for example in *Sigara nigrolineata*, Young, 1965b): it is well known in insects that dispersal and reproduction are temporally separated because of nutritional competition problems (Dingle, 1965; Johnson, 1953, 1969). If water mites exert a sufficient drain on the resources to compete with ovarian development in Corixidae, it is reasonable to expect competition with flight muscle development and flight, as these are the two other major energy expenditures for the adult.

In this section the relationship between mite parasitism and the three predicted areas of nutrient competition is investigated.
Figure 4. Summary of lipid transport and physiology.

A. Midgut: Passes lipids into haemolymph as Diglycerides (1). Can change chain length of fatty acid constituents.

B. Haemolymph: Transport system for nutrients. Brings Diglycerides and Phospholipids to points of development and respiration (5, 6, 7, 8) in conjugation with haemolymph proteins.

C. Fat Body: Locus of storage and conversion. Takes up surplus Diglycerides from the haemolymph (2) that originate at the midgut. Stores lipids as Triglycerides, converting them to Phospholipids and Diglycerides for release into the haemolymph (3, 4) as they are needed.

D. Flight Muscles: A major drain of Phospholipids during post-imaginal development (5), and of Diglycerides during flight (6).

E. Mite: Feeds on haemolymph and its nutrients in transport (7).

F. Ovaries: Demands large quantities of Diglycerides and Phospholipids during vitellogenesis (8).

Diglycerides: 1, 2, 4, 6, 7, 8.
Phospholipids: 3, 5, 7, 8.
SUMMARY OF LIPID TRANSPORT AND PHYSIOLOGY
The reported flightless morph advantage is looked at closely, and Martin's (1975) hypothesis that mites castrate their hosts hormonally in order to keep them in a dispersal state is considered. Evidence of a major impact of water mite parasitism on the physiology of *C. bifida* is sought.

Three separate experiments were carried out. In the flight experiment the aim was to determine if the flight ability of a corixid is modified by mite parasitism. By the nutritional competition hypothesis, we would expect a reduction in flight ability for parasitized hosts. If Martin's (1975) hypothesis was correct, the reverse would be true. The flight muscle development experiment was inspired by the presence in field samples of teneral corixids bearing mature nymphochrysalids. Using the nutritional drain hypothesis as a rationale, this test was designed to see if mite parasitism was associated with retarded flight muscle development. The third experiment was undertaken to examine the effects of parasitism on egg production. Egg production in hosts parasitized by the three major mite species was compared to that of unparasitized bugs. In addition, a further investigation was made into the reported difference in egg production between the two flight morphs when parasitized.

### B. Materials and Methods.

1. **Flight Experiment.**

   Flying form *C. bifida* were collected from Long Lake (Chilcotin) on May 5, 1977 and transported to the laboratory in insulated flasks. The bugs were then kept in dechlorinated water
without food and in darkness at 5°C until use. Insects were used during the first three days following their collection in the field. This was the standard procedure used for handling corixids for experimentation. Female corixids were undergoing ovarian development at this time. Individual male and female corixids were introduced into the flight chamber for a one-half-hour period during which their time spent in flight was recorded.

The flight chamber (Fig. 5) was constructed from a plastic bag 45.7 x 81.3 cm. held expanded by a wire ring. The bag was suspended by its closed end and the chamber's floor was formed by attaching a 45.7 cm. square of polyethylene sheet to the bag's open end. One side of the square was not attached for a 5 cm. distance to allow access to the chamber. This assembly was suspended so that the floor rested on the surface of a water bath held at 30°C, and a 40 watt incandescent light was placed several inches from the chamber's upper end. The chamber's design was based on the observations that a sudden change in light intensity and temperature are stimuli for flight in corixids (Fernando, 1959; Popham, 1952; Scudder, 1969). A flight mill cannot be used with most aquatic insects as suspending them in air induces a swimming behaviour rather than flight. Water boatmen that failed to fly were examined and if their wings were physically damaged the trail was discarded.

Forty C. bifida were tested; 10 parasitized and 10 unparasitized of each sex. Parasitized bugs used for the test carried one Eylais spp. larva of an intermediate stage of engorgement attached to the second, third or fourth abdominal tergum. The results
Figure 5. Apparatus for flight experiment.
FLIGHT CHAMBER

- Plastic bag 45.7 cm. x 81.3 cm.
- Wire ring
- Water bath
- Polyethylene sheet 45.7 cm. sq.
- Access port 5 cm.

40 W. lamp
for the two sexes were tested separately for significance with the Mann-Whitney U test.

2. Flight Muscle Development Experiment

For this experiment, teneral sexually immature C. bifida were collected from Long Lake (Chilcotin) on Sept. 10, 1976. They were transported to and maintained in the laboratory in the same manner as for the flight experiment (page 18). In addition, several reeds densely covered with egg masses of Eylais infundibulifera #1 (undescribed species) were collected from the same lake, and transported to the laboratory in an insulated flask filled with lake water. In the laboratory, the mite eggs were placed at room temperature in an open tray with enough lake water to keep the eggs submerged. To induce hatching, a 40 watt lamp was placed within 8 inches of the water's surface.

When sufficient numbers of mites had hatched, several flat, rectangular tissue culture bottles (8.5 cm. x 13 cm. x 13 cm.) were partially filled with lake water and inoculated with a number of mite larvae. Teneral C. bifida (Stage I by Scudder, 1971) were introduced in numbers to the tissue culture bottles, to which a square of window screening had been inserted to provide a substrate for the insects to cling to. The corixids were sampled at intervals until a large proportion were parasitized by mites. One hundred water boatmen were then selected, 50 unparasitized and 50 parasitized with one mite each, and placed in a round rearing dish 10 cm. high by 24 cm. in diameter. These corixids were maintained at 20-24°C in dechlorinated water provided with constant aeration. They were cleaned and fed frozen
brine shrimp daily.

After 18 days the surviving corixids were preserved and sorted with respect to flight muscle development. Scudder's (1971) stages of teneral development were used as the criterion, Stages I-III representing the undeveloped class. The results were tested with a Fisher Exact Probability test for statistical significance.

3. Egg Production.

The relationship between parasitism and egg production was investigated in two lakes, using spring 1977 collections of C. bifida made for the ecological study (page 36). Samples were taken on April 22, May 4, May 20, and June 2. Greer Lake was one lake chosen as the three main parasites of C. bifida bred in this lake and heavily parasitized the corixid species. Long Lake (Chilcotin) was also chosen, as this was one of the only lakes possessing non-flying C. bifida.

The corixids were dissected and the number of mature chorionated eggs per bug was recorded. The water boatmen from Greer Lake were grouped as to whether they were unparasitized, parasitized by one of each of the three mite species (Eylais infundibilifera #1, Eylais discreta Koenike, Hydrachna conjuncta) or bearing an empty nymphochrysalid membrane from one of the mite species. Long Lake dissections were grouped with regard to flight morph, then further split into unparasitized, parasitized with one E. infundibilifera #1, or one E. infundibilifera #1 membrane. In addition, the length of the mite was measured for Long Lake samples using a calibrated eyepiece graticule.
C. Results.

1. Flight Experiment.

Flight duration varied considerably, ranging from almost two minutes to no attempt. The mean flight duration (Fig. 6) was significantly less for male parasitized bugs (P<.05) but not significant for females. The results for the males and females were not combined as a significant sexual difference was present.

2. Flight Muscle Development Experiment.

In this experiment the parasitized group had fewer individuals with flight muscle development past stage III, but a significance level of only P=.07 (see Table II). The relatively high mortality in the experiment reduced the power of the test, only twenty bugs surviving. At termination, several mites had recently completed their host associated development, and were free swimming nymphs.

3. Egg Production.

A reduced mean egg number per bug was observed in all parasitized groups. In Greer Lake, all species of mite found on C. bifida were associated with a significant reduction (Fig. 7). However, E. discreta differed from E. infundibulifera #1 and H. conjuncta in that the E. discreta parasitized corixids produced some eggs in early May. It was also noticed that E. discreta was consistently smaller than E. infundibulifera #1 when both were present as engorging larvae. In June there was a partial recovery of ovarian development in water boatmen bearing mite nymphochrysalid membranes, although mean egg number was still less. Corixids bearing E. infundibulifera #1 membranes appeared
Figure 6. Results for flight experiment.
The difference between mean flight time of parasitized and unparasitized male *C. bifida* is significant at \( P<.05 \) for a Mann-Whitney U Test. The difference between the two female groups is not significant. Parasitized hosts carried one *E. infundibulifera* #1 mite each.

Table II. Flight muscle development and parasitism.
The number of *C. bifida* that had completed flight muscle development is compared to the number that had not. Fisher Exact Probability = .07 for the null hypothesis of no difference with respect to parasitism. Parasitized hosts carried one *E. infundibulifera* #1 mite each.
Table: Flight Duration

<table>
<thead>
<tr>
<th></th>
<th>Female</th>
<th>Male</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parasitized</td>
<td>0.30</td>
<td>0.20</td>
</tr>
<tr>
<td>Unparasitized</td>
<td>0.20</td>
<td>0.10</td>
</tr>
</tbody>
</table>

Female: Parasitized vs. Unparasitized

Male: Parasitized vs. Unparasitized

Parasitized Unparasitized

<table>
<thead>
<tr>
<th>Flight</th>
<th>4</th>
<th>7</th>
</tr>
</thead>
<tbody>
<tr>
<td>Teneral</td>
<td>7</td>
<td>2</td>
</tr>
</tbody>
</table>

Fisher Exact Probability = 0.07
Figure 7. Egg production by *C. bifida* in Greer L. with respect to parasitism. Mean egg numbers are graphed, with the sample sizes and 5% confidence limits above each group. The 'm' subscript indicates hosts bearing an empty nymphochrysalid membrane. Each parasitized host carried one mite.
U = UNPARASITIZED
I = INFUNDIBULIFERA
D = DISCRETA
C = CONJECTA
m = MEMBRANE

MAY 4

MAY 20

JUNE 3

AVERAGE EGG NUMBER

0 10 20
to be fastest in recovery, followed by *E. discreta* and *H. conjecta*, but the only statistically significant difference was between *H. conjecta* and the two *Eylais* spp.

In Long Lake (Chilcotin) there was a non-flying morph advantage while the mites were on the host (see Fig. 8). Significantly more eggs were produced by parasitized non-flying bugs in comparison to the flying form, but there was no difference in un-parasitized corixids. This trend for a non-flying morph advantage was however reversed once the mites had dropped off their hosts; the flying form recovered its ovarian development first. The average length of mites from non-flying bugs was significantly less than on flying forms (Fig. 8), and this suggests that the difference in egg production was due to mites on the non-flying morph being in an earlier stage of engorgement.

D. Discussion.

In general these results support the hypothesis of nutritional competition between the mite parasites and the host's organs. The flight experiment was only significant in the males, but this is not too surprising. As mites compete with ovarian development, they probably obtain a large proportion of their required nutrients from those intended for egg production. In essence, the mite development replaces egg development, and in a female host the mite only competes against flight metabolism for the further energy it needs. As male insects do not normally have energy stores comparable to those needed for egg production (Fast, 1964; Gilbert, 1967), the flight metabolism and other systems are under
Figure 8. Average egg production by *C. bifida* in Long L. (Chilcotin) with respect to *Eyelais* spp. parasitism and flight morph. Included above each bar is the 5% confidence interval, and below each bar is the sample size. The difference between morphs of unparasitized hosts on May 20 is significant, as well as for the parasitized hosts on April 22, May 20, and June 2. Mean mite length is significantly different in both cases. Each parasitized host carried one mite.
a heavier competition. In any event, we cannot accept the hypothesis by Martin (1975) that the mite suppresses ovarian development in order to increase the likelihood of migration. By his theory the mites should be associated with an increased flight activity, which by this experiment is clearly not the case.

While the results of the flight muscle development experiment were not significant at P=.05, I feel it should not be disregarded, due to the small sample size and a probability of P=.07. Also, water boatmen of Stage II or III development can be found in July carrying mature mite nymphochrysalids. Flight muscle development takes an estimated 4 to 15 days, depending on temperature (Scudder, 1971), while at 20-24°C mites were associated with their hosts at least 17 days, longer at lower temperatures. The presence of these Stage III corixids bearing mite nymphochrysalids would be impossible if flight musculature was not retarded.

The egg development study demonstrated that all three major parasites of *C. bifida* influence egg development. Total egg production was greatly reduced, but the bugs were not permanently sterilized: with all species examined there is a recovery of egg production after mite drop off. This was also recorded by Martin (1975) working with *Sigara falleni*. However, when any of these three mite species were in the final stages of association with the host, there were no eggs produced. It was noticed that the life cycle of *E. discreta* is slightly staggered in comparison with *E. infundibilifera #1*, being smaller in early spring, and becoming
a nymphochrysalid and dropping off the host slightly later (see also page 65). This was reflected in egg production, as some water botamen bearing *E. discreta* contained mature eggs on May 4, unlike *E. infundibulifera* #1 parasitized bugs, but were behind *E. infundibulifera* #1 in ovarian recovery, although this difference was not statistically significant in this study. Davids and Schoots (1975) encountered a comparable situation with *H. conjecta* and *H. cruenta* on *Sigara striata*.

Differences in relative mite development appear also to be a factor in comparing parasitized non-flying and flying hosts. When a mite is delayed in development, the host can produce a few eggs in early spring, but is later in regaining ovarian development. It is not surprising that the mites on the non-flying morph are behind those on the flying morph hosts; the former host develops only in late fall and the mites attaching to them have very little time for engorgement before winter. It has been established that mites do not engorge significantly over the winter (Davids, 1973; Davids and Schoots, 1975), so that mites of non-flying morph hosts are behind in development relative to those of flying morph hosts. It therefore appears the non-flying morph does not gain any selective advantage under parasitism in this case.

The nutritional hypothesis for host detriment appears to be adequate for explaining the parasite induced effects on corixid hosts. While this does not discount an interference in the host's hormonal balance by the mite, it is unnecessary for our present understanding of this relationship. There is no evidence for alteration of secondary sexual characters as is so often
associated with hormonal castration (Askew, 1971). When we consider that in certain mite/corixid combinations eggs can still be produced in reduced numbers (Davis and Schoots, 1975), endocrine castration is unlikely. There appear to be conflicting views in general as to whether a parasite castration in insects is due to parasitic intervention in the endocrine system (Rockstein, 1973), or nutritional drain (Engelmann, 1970). It is likely that both occur, but to ascribe all cases to one or the other is an overly simplistic view.

In summary, the effect of mite parasitism on corixids appears to be severe, interfering with dispersal, possibly retarding flight muscle development, and reducing fecundity of a parasitized female to a small fraction of its normal production. It can be predicted that if the incidence of parasitism is high, mites would have a considerable impact upon the fitness of the host population.
III. ECOLOGY OF WATER MITE PARASITISM.

A. Introduction.

Several authors have in the past recorded population dynamics of water mite parasites and their hosts. For example, McCrae (1976) and Mullen (1974) surveyed mosquito parasitism, Davies (1959) worked with blackflies, and Marples (1962) studied Hydrachna sp. on the notonectid Anisops assimilis. The only such works on mites parasitizing Corixidae were done by Davids (1973), and Harris and Harrison (1974).

There has not been any study to date, however, that considered the variation in parasitism between different habitats. In this study area, the lakes form natural gradients in salinity, and thus is an obvious and convenient parameter to study. The only author to have considered variation of parasitism for a given corixid species was Davids (1973), who tested for differences between the two sexes of host.

Variation in intensity of parasitism between different host species has often been recorded (Davids, 1973; Davies, 1959; Harris and Harrison, 1974; Martin, 1975; Mullen, 1974). While such possible reasons as differences in host microhabitat, behaviour or size, as well as differences in mite preference have been suggested, there have not been any tests of these hypotheses to date. Martin (1975) suggested different levels of parasitism may in turn affect competitive advantage between different host species, but this has not been investigated further.
In this section I shall examine variation in mite parasitism of *C. bifida* within populations, between habitats, and compare the parasitism of *C. bifida* with other available hosts. While host behaviour and microhabitat are undoubtedly at least in part responsible for differences between host species, I shall only be concerned with testing differences in mite susceptibility under equivalent exposure. In addition, the possible results of differences in parasite pressure between the two *Cenocorixa* spp. will be examined. As *C. bifida* and *C. expleta* have a broad overlap in food, microhabitat and general ecology (Scudder, 1969b; Reynolds, 1974), I feel a comparison of the relative impact of parasitism on their success is meaningful.

B. Materials and Methods.

1. Field Sampling.

Faunal samples were taken from the end of July 1976, shortly after mites had begun attaching to their hosts, to early June 1977, when over 80% of the mites had dropped off their hosts. Collecting was terminated in mid-October 1976 at freeze up, and resumed in late April 1977 within days of the ice break-up.

Samples were taken at a constant depth and location within the lake, but no attempt was made to estimate density. A "D" frame aquatic net (Wards Scientific, Monterey, California) was used throughout the study, and a white photographic developing tray facilitated sorting water boatmen from the net sweepings. Sample size was kept as large as possible (up to a limit of approximately 750 bugs per sample).
Corixids were preserved in 95% ethyl alcohol and identified under a dissecting microscope to species and sex, and the number and species of associated mites and mite nymphochrysalid membranes was recorded for each host. When the species identification of a mite or nymphochrysalid membrane was in doubt, it was mounted on a slide for examination by interference contrast microscopy. In addition, mites were regularly examined under the interference contrast microscope to check the accuracy and consistency of dissecting microscope identifications.

For C. bifida, the prevalence (percentage parasitism), mean number of mites per host, variance of mites per host, and mean number of mites per parasitized host were calculated for each mite species in each sample. These parameters were graphed for C. bifida for each lake in which mites bred. In only four cases were the sample sizes for C. bifida below 50, the average sample consisting of approximately 250 of this species. Over 42,000 C. bifida were sorted. These parameters were also calculated for other corixid species when sample sizes were sufficiently large. Whenever possible, differences between the sexes and between teneral and fully sclerotized bugs in percent parasitism and mites per parasitized host were tested for significant differences. As well, the observed number of interspecific multiple parasitisms (two or more species of mites on one host) were compared to the

1The following sample sizes were below 50: SP 8, July 20, 1976, N=46; SP 8, October 10, 1976, N=42; Boitano Lake, July 30, 1976, N=36; LE 4, July 26, 1976, N=48.
expected value when the expected frequency of parasitism was sufficiently large to be tested statistically.

When plotting mite distributional data, the presence of teneral or non-flying morph corixids with a given mite species was the only proof accepted for that mite successfully breeding in the lake. Attention was also paid to the frequency of parasitism by mites not breeding in the lake, which proved to be a very useful indicator of immigration.


Host preference experiments were used to try and determine: 1) if a subset (sex or teneral stage) of the host population was susceptible to parasitism, 2) if mites avoided a previously parasitized host, 3) if the variance in parasitism between several host species was due to differences in susceptibility or just an artifact of habitat differences within a lake, 4) if differences in susceptibility are real, how do C. bifida and C. expleta compare when exposed to the common C. bifida parasites?

The procedures used in these experiments were similar. Corixids for experimentation were transported and maintained until use in the standard method described earlier (page 18), and larval E. infundibulifera #1, when used, were obtained from field collected eggs as mentioned previously (page 22). Unless stated otherwise, the procedure outlined in the flight muscle development experiment (page 22) was used for subjecting water boatmen to mite larvae and determining exposure time. If one tissue culture bottle was too small for the experiment, a round plastic rearing dish (10 cm. high x 24 cm. in diameter) was substituted.
Water boatmen used in an experiment were introduced to the test container simultaneously, and the water was changed several times at the end of the experiment to exclude any unattached mites. Exposure time was thus kept consistent for bugs of a given experiment. Percent parasitism and mites per host were calculated and compared in each experiment, using contingency tables and chi-square tests respectively to establish statistical significance. Specific details and any deviations from the standard method are described below.

i. Differences in mite preference for morph or sex groups. For this experiment fifteen teneral females, sixteen teneral males, eight flight form females, and fifteen flight form males of _C. bifida_ were exposed to _E. infundibulifera #1_. Both the water boatmen and mite eggs were collected from Long Lake (Chilcotin). The results were tested with a non-parametric ANOVA test.

ii. Mite avoidance of parasitized hosts. _C. bifida_ and _E. infundibulifera #1_ were also used in this experiment, collected from Long Lake (Chilcotin). Twenty-seven unparasitized and thirty-five corixids parasitized with one _E. infundibulifera #1_ each were used in this comparison. Results were again tested for significant differences with a non-parametric ANOVA.

iii. Differences in mite susceptibility for four corixid species. This test was to establish if differences in intensity of parasitism between species is in fact due to differences in attachment rates. _Cymatia americana, H. laevigata_ (both collected from Greer Lake), _C. expleta_ (from Barnes Lake), and _C. bifida_ (from Long Lake, Chilcotin) were simultaneously exposed to _E._
infundibulifera #1 for a 24-hour period.

iv. Comparison of susceptibility to parasitism between C. bifida and C. expleta. This experiment was in fact four separate tests, using a different mite species in each case. C. bifida for the tests were collected from Long Lake (Chilcotin) and C. expleta from Barnes Lake. Eggs of E. infundibulifera #1 were obtained as mentioned previously, while eggs for H. skorikowi and H. conjecta were obtained from adult mites collected in the field and kept in the laboratory at 20°C without food. E. discreta larvae for the test were collected in the field by skimming the surface water of SP 8.

3. Comparison of E. infundibulifera #1 Growth on C. bifida and C. expleta.

Round-up Lake was chosen for this study as it possessed the largest population of C. expleta co-occurring with an endemic E. infundibulifera #1 population. The corixids used were those collected in the field sampling (page 36). Measurements were made using a dissecting microscope equipped with a calibrated eye-piece graticule.

C. Results.

1. Mite Distribution on C. bifida.

   i. Field data. Twelve of the fifteen lakes supported breeding populations of mites. The analysis of mite parasitisms on C. bifida for these twelve lakes is presented in Figures 9 to 20. Five mite species were found on C. bifida, however, H. cruenta #1 (undescribed species) and H. skorikowi were too few to calculate any meaningful statistics. E. infundibulifera #1, E. discreta,
Figure 9. Parasitism parameters for *E. infundibulifera* #1 on *C. bifida* in LE 3 for the 1976/77 season. The winter break is indicated by a dotted line breaking the horizontal axis. The upper curve for the percent parasitism in late May and June represents the percentage of hosts bearing empty mite nymphochrysalid membranes.
Figure 10. Parasitism parameters for *E. infundibulifera* #1 on *C. bifida* in Round-up L. for the 1976/77 season. The winter break is indicated by a dotted line breaking the horizontal axis. The upper curve for the percent parasitism in late May and June represents the percentage of hosts bearing empty mite nymphochrysalid membranes.
Figure 11. Parasitism parameters for *E. infundibulifera* #1 on *C. bifida* in Lake Lye for the 1976/77 season. The winter break is indicated by a dotted line breaking the horizontal axis. The upper curve for the percent parasitism in late May and June represents the percentage of hosts bearing empty mite nymphochrysalid membranes.
Figure 12. Parasitism parameters for *E. infundibulifera* #1 on *C. bifida* in Long L. Chilcotin for the 1976/77 season. The winter break is indicated by a dotted line breaking the horizontal axis. The upper curve for the percent parasitism in late May and June represents the percentage of hosts bearing empty mite nymphochrysalid membranes.
Figure 13. Parasitism parameters for *E. infundibulifera* #1 on *C. bifida* in LE 4 for the 1967/77 season. The winter break is indicated by a dotted line breaking the horizontal axis. The upper curve for the percent parasitism in late May and June represents the percentage of hosts bearing empty mite nymphochrysialid membranes.
Figure 14. Parasitism parameters for *E. infundibulifera* #1 on *C. bifida* in LE 5 for the 1976/77 season. The winter break is indicated by a dotted line breaking the horizontal axis. The upper curve for the percent parasitism in late May and June represents the percentage of hosts bearing empty mite nymphochrysalid membranes.
Figure 15. Parasitism parameters for *E. infundibulifera* #1 on *C. bifida* in Boitano L. for the 1976/77 season. The winter break is indicated by a dotted line breaking the horizontal axis. The upper curve for the percent parasitism in late May and June represents the percentage of hosts bearing empty mite nymphochrysalid membranes.
Figure 16. Parasitism parameters for mites on *C. bifida* in Near Pothole L. for the 1976/77 season. Statistics for the three mite species (*Eylais infundibulifera* #1, *E. discreta* and *Hydrachna conjecta*) are figured. The winter break is indicated by a dotted line breaking the horizontal axis.
PERCENT PARASITISM

MITES PER PARASITIZED HOST

MITES PER HOST

VARIANCE

0 10 20 30 40

0 0.5 1 1.5

J A S O M J

INFUNDIBULIFERA NOI

DISCRETA

CONJECTA
Figure 17. Parasitism parameters for mites on *C. bifida* in Greer Lake for the 1976/77 season. Statistics for the three mite species (Eylais infundibulifera #1, *E. discreta* and *Hydrachna conjecta*) are figured. The winter break is indicated by a dotted line breaking the horizontal axis.
Figure 18. Parasitism parameters for mites on *C. bifida* in Westwick Lake for the 1976/77 season. Statistics for the three mite species (*Eylais infundibulifera* #1, *E. discreta* and *Hydrachna conjecta*) are figured. The winter break is indicated by a dotted line breaking the horizontal axis.
Figure 19. Parasitism parameters for *Hydrachna conjecta* on *C. bifida* in Barkley L. for the 1976/77 season. The winter break is indicated by a dotted line breaking the horizontal axis.
Figure 20. Parasitism parameters for mites on C. bifida in SP 8 for the 1976/77 season. Statistics for the three mite species (Eylais infundibulifera #1, E. discreta and Hydrachna conjecta) are figured. The winter break is indicated by a dotted line breaking the horizontal axis.
and *H. conjecta* were very similar in their population dynamics. Attachment began in late July, often with a sudden peak period causing a very high prevalence, a large number of mites per host, and high variance. The attachment rate then rapidly dropped and the various parameters levelled off to an equilibrium. Mite attachment continued throughout August, September and into October, but there was no evidence of mites attaching in spring. A very small second generation was evident as *E. infundibulifera #1* and *H. conjecta* were dropping off their hosts in small numbers during late July and early August, but the vast majority of mites remained on their hosts until spring. *E. infundibulifera #1* were slightly earlier than *E. discreta* and *H. conjecta* in dropping off their hosts, which took place in May and early June.

Corixids bearing mites not known to breed in a given lake were uncommon until after early September (Table III), which corresponds with the fall/spring dispersal (Popham, 1952; Fernando, 1959; Scudder, 1969b). As these stray mites were so frequent at this time, considerable mixing of water boatmen populations must have occurred and should be considered when interpreting the data.

Taking the early September samples as the latest reliable data, we can compare the distribution of mite parasitism over the salinity gradient (see Fig. 21). *E. infundibulifera #1* was the major parasite of *C. bifida* in high salinity, that is in lakes up to 13,000 µmhos. conductivity. A definite peak in parasitism (as high as 35% parasitism) occurred for this mite around 7,000 to 8,000 µmhos. but in lakes of lower salinity this mite was of
Table III. Parasitism rates of *C. bifida* by non-resident mite species (pooled).

<table>
<thead>
<tr>
<th>DATE</th>
<th>LAKE LYE</th>
<th>ROUND-UP LAKE</th>
<th>LONG LAKE (CLINTON)</th>
</tr>
</thead>
<tbody>
<tr>
<td>JULY 31, 1976</td>
<td>0.0</td>
<td>0.0</td>
<td>-</td>
</tr>
<tr>
<td>AUG. 10-13, 1976</td>
<td>0.73</td>
<td>0.77</td>
<td>0.72</td>
</tr>
<tr>
<td>AUG. 24-26, 1976</td>
<td>0.58</td>
<td>1.30</td>
<td>2.01</td>
</tr>
<tr>
<td>SEPT. 7-9, 1976</td>
<td>1.17</td>
<td>1.18</td>
<td>4.81</td>
</tr>
<tr>
<td>SEPT. 23-24, 1976</td>
<td>2.66</td>
<td>6.92</td>
<td>24.77</td>
</tr>
<tr>
<td>OCT. 10, 1976</td>
<td>7.81</td>
<td>11.91</td>
<td>17.23</td>
</tr>
<tr>
<td>APRIL 22, 1977</td>
<td>6.18</td>
<td>8.02</td>
<td>-</td>
</tr>
<tr>
<td>MAY 4, 1977</td>
<td>7.81</td>
<td>7.28</td>
<td>-</td>
</tr>
<tr>
<td>MAY 20, 1977</td>
<td>11.48</td>
<td>7.79</td>
<td>-</td>
</tr>
<tr>
<td>JUNE 3, 1977</td>
<td>13.92</td>
<td>8.19</td>
<td>-</td>
</tr>
</tbody>
</table>
Figure 21. Distribution of mites parasitic on *C. bifida* with respect to salinity. The vertical axis is the percent parasitism for the various mites from samples taken Sept. 8, 1976. The horizontal axis represents the Sept. 15-20 surface conductivity readings for the various sample lakes. Mites not breeding in a given lake (as defined by absence of parasitized teneral hosts) have been excluded. An 'X' represents the record of a mite breeding in the lake, but that none were found in the Sept. 8 collection.
PERCENT PARASITISM

E. infundibulifera no.1  E. discreta  H. conjecta  H. skorikowi  H. cruenta no.1

CONDUCTIVITY IN \mu mhos.

0 0'000 0'00 strikthrough 0'00 strikthrough 0'00 strikthrough 0'00 strikthrough
lesser importance, and rarely attained even 5% prevalence. *H. skorikowi* also was more successful in high salinity, but never reached even 1% prevalence. The upper salinity limit for this species was also 13,000 µmhos. *E. discreta* and *H. conjecta* only bred in lower salinity lakes, up to 5,000 µmhos. *E. discreta* was found to exist on teneral water boatmen in two lakes of higher conductivity, but on only a small fraction of one percent of the hosts. *Eylais* spp. were notably absent from Barkely Lake, which was especially overgrown with submergent macrophytes. *H. conjecta* was very successful in this lake (over 40% of *C. bifida* were parasitized), and this was the only lake in which *H. cruenta* #1 was found. *H. cruenta* #1 was, however, rarely found on *C. bifida*, being primarily a parasite of *Cymatia americana*.

In terms of total percentage of corixids bearing mites, *C. bifida* was under a heavy parasite pressure in the fresher waters (total parasitism up to 45%), with a second, lesser peak in the range of 7,000-8,500 µmhos. There was a low percent parasitism of *C. bifida* in lakes at the transition between dominant mite species (5,000-6,000 µmhos.). Over 8,500 µmhos. the percent parasitism was around 10-15% until the upper limit for mites of 13,000 µmhos. No mites were found to breed in Barnes Lake, Long Lake (Clinton), or LB 2 during this study.

ii. Differences in mite preference for morph or sex groups. From the field data, comparisons between sexes and between teneral and fully sclerotized hosts for both percent parasitism and mites per parasitized host frequently showed statistically significant differences. These differences, however, were not consis-
tent in direction of preference even within a given lake or sample date. It was therefore evident that testing field data would not give a trustworthy answer to this question.

When this question was tested in the laboratory, there were differences in mean number of mites per host between the different groups (Table IV), the rates for male flight and teneral groups being considerably different. There was, however, little difference for the females. When teneral development was not considered and the groups were lumped, there was no sexual difference in mean mites per host. These results were tested with a non-parametric ANOVA test, and the results were not significant (P>.99). This test takes into account the numbers of mites on each individual host, and thus I attribute the variation in mean mites per host to chance.

iii. Mite avoidance of parasitized hosts. The expected frequencies of interspecific multiple parasitisms for the field data were rarely large enough to test for significance, despite very large sample sizes. There is the requirement that an expected frequency must be five or more to use a chi-square test. There was rarely a significant difference when these tests were possible, and the direction was inconsistent.

When avoidance of attaching to a parasitized host was tested in the laboratory, there was a trend towards higher attachment rates on parasitized hosts (Table V). This was, however, not significant (P=.20). It is possible that some individuals are more susceptible to mite parasitism and thus are attacked at a higher rate, or that the presence of a mite increases susceptibil-
Table IV. Mean numbers of mites per host with respect to flight muscle development and sex.

Table V. Mean numbers of mites per host with respect to previous parasitism.
<table>
<thead>
<tr>
<th></th>
<th>MALE</th>
<th>FEMALE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flight</td>
<td>3.7</td>
<td>4.7</td>
</tr>
<tr>
<td></td>
<td>N = 15</td>
<td>N = 8</td>
</tr>
<tr>
<td>Teneral</td>
<td>6.5</td>
<td>4.9</td>
</tr>
<tr>
<td></td>
<td>N = 16</td>
<td>N = 15</td>
</tr>
</tbody>
</table>

Non-parametric ANOVA $P > .99$

<table>
<thead>
<tr>
<th></th>
<th>Parasitized</th>
<th>Unparasitized</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>0.6</td>
<td>0.2</td>
</tr>
<tr>
<td></td>
<td>N = 21</td>
<td>N = 15</td>
</tr>
<tr>
<td>Female</td>
<td>1.1</td>
<td>0.3</td>
</tr>
<tr>
<td></td>
<td>N = 14</td>
<td>N = 12</td>
</tr>
</tbody>
</table>

Non-parametric ANOVA $P = .20$
ity by weakening the host. The hypothesis for avoidance of multiple parasitism is therefore rejected, and while a higher attachment rate to parasitized hosts is possible, I reject it as the significant level was too low.

2. Variation in Parasitism Between Corixid Species.
   i. General. Strong differences in intensity of parasitism were noticed between corixid species in the field samples (see Table VI). In low salinity, *Cymatia americana* was the major host for *E. infundibulifera #1*, while *C. bifida* was only lightly parasitized. The reverse was true, however, for *E. discreta*. *Sigara bicoloripennis* was also heavily parasitized by *E. discreta*, but the mites showed no signs of engorgement, and resulted in a large black spot on the host's cuticle. *C. bifida* appeared to sustain the heaviest parasitism by *H. conjecta*, although *C. americana*, *H. laevigata*, and *S. bicoloripennis* were also strongly affected. *H. conjecta* also did not appear to engorge on *S. bicoloripennis*. In terms of total mite parasite pressure, *C. bifida* appeared to be under the heaviest parasite load, followed by *C. americana*. *H. laevigata* and *S. bicoloripennis* were both infected by their own species of mites (*E. infundibulifera #2* on *H. laevigata*, *E. infundibulifera #3* and *Hydrachna SP#1* on *S. bicoloripennis*) that were not found on any other host species.

The results of the laboratory experiment for differences in mite susceptibility for four corixid species were significant at \( P < .001 \) in terms of both percent parasitism and mites per host (Fig. 22). Both *C. expleta* and *Cymatia americana* suffered
Table VI. Comparison between host species of parasitism parameters.

Lake SP 8, 1976 - Field data

<table>
<thead>
<tr>
<th>Date</th>
<th>Host</th>
<th>E. infundibulifera #1</th>
<th>E. discreta</th>
<th>H. conjecta</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>%P M/Par.H</td>
<td>%P M/Par.H</td>
<td>%P M/Par.H</td>
</tr>
<tr>
<td>Aug. 25</td>
<td>Hesperocorixa laevigata</td>
<td>6.8 1.07</td>
<td>7.8 1.13</td>
<td>4.4 1.11</td>
</tr>
<tr>
<td></td>
<td>Cenocorixa bifida</td>
<td>5.9 1.00</td>
<td>22.6 1.52</td>
<td>34.3 1.51</td>
</tr>
<tr>
<td></td>
<td>Sigara bicoloripennis</td>
<td>2.9 1.00</td>
<td>29.8 1.68</td>
<td>1.0 4.00</td>
</tr>
<tr>
<td>Sept. 8</td>
<td>H. laevigata</td>
<td>18.3 1.05</td>
<td>2.5 1.33</td>
<td>19.2 1.48</td>
</tr>
<tr>
<td></td>
<td>Cymatia americana</td>
<td>40.9 2.07</td>
<td>1.5 1.00</td>
<td>16.7 1.18</td>
</tr>
<tr>
<td></td>
<td>C. bifida</td>
<td>2.4 1.00</td>
<td>22.5 1.45</td>
<td>30.6 1.81</td>
</tr>
<tr>
<td></td>
<td>S. bicoloripennis</td>
<td>2.7 1.00</td>
<td>17.8 1.92</td>
<td>13.7 1.20</td>
</tr>
<tr>
<td>Sept. 22</td>
<td>H. laevigata</td>
<td>3.3 1.00</td>
<td>10.9 1.20</td>
<td>9.7 3.44</td>
</tr>
<tr>
<td></td>
<td>C. americana</td>
<td>33.3 1.23</td>
<td>6.4 2.20</td>
<td>9.0 2.14</td>
</tr>
<tr>
<td></td>
<td>C. bifida</td>
<td>3.3 1.00</td>
<td>25.2 2.00</td>
<td>32.5 1.98</td>
</tr>
<tr>
<td></td>
<td>S. bicoloripennis</td>
<td>1.1 1.00</td>
<td>13.7 1.62</td>
<td>15.8 1.87</td>
</tr>
</tbody>
</table>

%P = Percent Parasitism; M/Par.H = Mites Per Parasitized Host.

Note: As identification of infundibulifera species depends on a character that is often lost in mounting engorged mites, I have lumped them into one group. C. bifida is parasitized by species #1 only, and S. bicoloripennis only by species #3. H. laevigata, however, is parasitized by both #1 and #2.
Figure 22. Comparative susceptibility of four host species to parasitism by *E. infundibulifera* #1. Both results are significantly different at $P<.001$ using Chi-square tests.
extremely high percentages of parasitized hosts, and while the mean number of mites per host were high for both species, C. expleta was much more susceptible. H. laevigata and C. bifida were attacked at much lower rates, H. laevigata having a higher percent parasitism than C. bifida but a lower mean number of mites per host. It is therefore accepted that there are interspecific differences in mite susceptibility even in equivalent exposure.

ii. Comparison of mite parasitism between C. bifida and C. expleta. In the field results, C. expleta is evidently under a much higher parasite pressure from E. infundibulifera #1 in terms of every parasitism parameter (see Figs. 23 and 24. Note that in four samples for LE 3 there was a sample size of less than 50 for C. expleta2'). The percent parasitism is approximately tenfold greater for C. expleta over C. bifida during initial mite attachment, dropping to approximately fourfold in later samples. H. skorikowi was the only other mite species coexisting with C. expleta to any extent, but H. skorikowi was never at a high enough prevalence for meaningful statistics to be calculated.

When the two Cenocorixa species were exposed to four mite species in the laboratory, C. expleta was significantly preferred in all cases (see Fig. 25). The results were most impressive for the two Eylais species, mites per host being significant at

2The following collections from LE 3 had sample sizes less than 50: July 26, 1976, N=19; Sept. 7, 1976, N=39; Sept. 24, 1976, N=48; Oct. 7, 1976, N=35.
Figure 23. A comparison between parasitism parameters for *C. bifida* and *C. expleta* in Round-up Lake. Winter is denoted by a dotted line splitting the horizontal axis.
Figure 24. A comparison between parasitism parameters for *C. bifida* and *C. expleta* in LE 3. Winter is denoted by a dotted line splitting the horizontal axis. Variance of load has been omitted as it was excessively high for *C. expleta*.
Figure 25. A comparison of susceptibility to parasitism between *C. bifida* and *C. expleta*. There were significant differences between these two species at $P<.05$ for each mite species tested. Chi-square tests were used.
PERCENT PARASITISM

SAMPLE SIZE

E. infundibulifera no.1  40  40
E. discreta  69  81
H. skorikowi  20  20
H. conjecta  60  76

MITES PER HOST

E. infundibulifera no.1  3
E. discreta  3
H. skorikowi  2.5
H. conjecta  2
P<.001, as well as for the difference in prevalence for *E. infundibulifera* #1. *H. skorikowi* and *H. conjecta* preferred *C. expleta* as well, but the difference was less dramatic (percent parasitism for both species was P<.05, mites per host was P<.001 for *H. skorikowi*, P<.05 for *H. conjecta*).

An interesting relationship is evident when the ratio of *C. expleta* to *C. bifida* is plotted for the lakes where they coexist ranked in regard to increasing conductivity (Fig. 26). A distinct break in the graph occurred when the mites' salinity limits was reached, with *C. expleta* being much more abundant relative to *C. bifida* when mites are absent. When mite prevalence is in the 10-15% range on *C. bifida*, *C. expleta* is moderately successful, but when around 25% on *C. bifida*, *C. expleta* is barely detectable. The relative abundance of *C. expleta* is thus related to the success of endemic mite populations and salinity. This graph was based on the early September samples, just prior to the period of fall migration (see Table III).

The comparison of *E. infundibulifera* #1 growth on *C. bifida* and *C. expleta* showed that the mites begin engorgement in the same manner on both hosts, but most mites fail to grow past a certain point on *C. expleta* (see Fig. 27). By spring, virtually all mites on *C. expleta* are unengorged, while *C. bifida* bears mite nymphochrysalids.
Figure 26. The ratio of *C. expleta* to *C. bifida* versus salinity. The ratio of these two species (expressed as percent *C. expleta* of the total *Cenocorixa* spp. present) was plotted against Sept. 15-20th conductivity readings for the various sample lakes. The corixid samples were made Sept. 8, 1976. Percent parasitism of *C. bifida* by mites on this sample date have been included.
Figure 27. A comparison of mite growth between the two *Cenocorixa* species. Mites are grouped in size classes expressed as percent of total number for the particular host species.
<table>
<thead>
<tr>
<th>MITE SIZE CLASS</th>
<th>0.75-1.25</th>
<th>1.25-1.75</th>
<th>&gt;1.75 mm.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sample Size</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>July 31</td>
<td>10</td>
<td>32-23</td>
<td>63-15</td>
</tr>
<tr>
<td>Aug. 12</td>
<td>72-34</td>
<td>36-43</td>
<td>51-31</td>
</tr>
<tr>
<td>Aug. 26</td>
<td>20</td>
<td>20</td>
<td>15</td>
</tr>
<tr>
<td>Sept. 9</td>
<td>14</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>Sept. 23</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oct. 10</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>April 22</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>May 4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>May 20</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

LEGEND
- BIFIDA
- EXPLETA

% OF MITES
D. DISCUSSION

When we examine the yearly population cycle we see that while fluctuations occur, there tends to be an equilibrium level in each lake for the various parasite parameters (i.e. Boitano Lake, Fig. 15; Lake Lye, Fig. 11; LE 3, Fig. 9). The cycle often begins with a sudden flurry of parasitism, resulting in superparasitism, and a high variance in loading (Long Lake, Chilcotin, Fig. 12; Greer Lake, Fig. 17). However, these superparasitized insects rapidly disappear, presumably having died (Davids, 1973). Both in this study and in that of Davids (1973), dead mites were found to remain on their hosts, so the disappearance of superparasitism cannot be attributed to mites dying and dropping off. The number of mites per parasitized host at the end of engorgement is invariably close to 1.0, parasitized hosts carrying only one, rarely two mites each. Presumably this is the maximum loading that \textit{C. bifida} can endure.

While in this study winter die-off noted by Davids (1973) did not occur, there was in some cases a sudden drop in the various parameters in the April 22nd to May 4th interval, when \textit{E. infundibulifera} \#1 underwent a sudden growth surge (i.e. Long Lake, Chilcotin, Fig. 12; Round-up Lake, Fig. 10). Whether this is an artifact of migration or death due to a sudden energy drain is not known. It is possible that this corresponds to the winter die-off reported by Davids (1973). There was only a partial second generation of \textit{H. conjecta}, \textit{E. discreta} and \textit{E. infundibulifera} \#1 during 1976, while Davids (1973) with \textit{H. conjecta} and
Lanciani (1969) with *E. discreta* and *E. infundibulifera* #2 reported two generations. It is likely that both differences in latitude and an unseasonably cold spring and summer of 1976 are responsible for the difference. Davids (1973) and Harris (1970) showed that mite developmental time was correlated with temperature. Mites dropped off their hosts a week or two earlier in 1977 than 1976, and in the summer of 1977 there was a large second generation of *E. infundibulifera* #1 in the Clinton lakes. It thus appears that there can be a considerable variation between years. Onset of ovarian diapause in *C. bifida* appeared to correspond with the termination of the second generation in mites, so it could be that the host's physiology is the cue to prepare for winter.

Davids (1973) concluded that there was no difference in attachment rates on the two sexes based on field results similar to those of this study. Mitchell (1967), however, found a most pronounced difference in *Arrenurus* parasitism of odonates. One could have predicted a preference for males in corixids, as there is no apparent decrease in reproductive capability when parasitized, but the probability of host contact is probably too low to allow choice. There was no evidence that teneral corixids were preferred over flight forms (Table IV), although mites may take advantage of hosts immobilized during final ecdysis. It is therefore concluded that there is no major difference in attachment rates within a species, and that we can consider a population to be homogeneous in susceptibility to parasitism.
While there were definite upper salinity limits for the various mite species (Fig. 21), the life history stage in which the salinity is limiting is not evident. If a mite species bred in a lake, the larval mites were found to attach to the hosts throughout the summer and fall. There was no observed tailing off in attachment rates as the season progressed and the salinity increased. It was not the adult or nymphal stages that were affected, as they were present even into October in lakes such as Barnes Lake, where no mites reproduced. For *H. conjecta* one could suggest that as its limit of 5,000 \( \mu \text{mhos} \) (Fig. 21) coincides with the limit of submerged macrophytes with air-chambered stems (in which they lay their eggs), that it is a lack of suitable oviposition sites that limit them. Davids (1973) stresses the importance of this behaviour to ensure oxygenation of the eggs. In lakes of higher salinity *H. conjecta* were found to lay eggs in reed and rush stems, but whether these are suitable substrates is not known. The only other *Hydrachna* species that was distributed widely enough for consideration was *H. skorikowi*, which will not lay eggs in plants even if they are available. It is the only *Hydrachna* species to extend past the salinity limit of submergent macrophytes (Fig. 21).

There is, therefore, considerable variation in parasitism between habitats. Salinity has an obvious correlation with mite distribution, and we consequently can group the lakes studied as to salinity and parasitism. In the salinities above 13,000 \( \mu \text{mhos} \) there were no mites breeding, represented by lakes LB 2, Long Lake (Clinton), and Barnes Lake. Barnes Lake sometimes supports
a population of mites, and is thus a borderline to this classification. In the 6,000 to 13,000 \( \mu \)mhos. range there are essentially only two mite species found, namely \( H. \) skorikowi and \( E. \) infundibulifera \#1. The former is characteristically only present in low prevalence rates (0-1%), but the latter goes through a considerable range (5-35%), and this class can be subdivided using prevalence of \( E. \) infundibulifera \#1 as the criterion. The 8,500 to 13,000 \( \mu \)mhos. range is characterized by a 10-15% prevalence, while at 6,500 to 8,500 \( \mu \)mhos. there is a peak prevalence of \( E. \) infundibulifera \#1 at 15-35%. Five thousand to 6,500 \( \mu \)mhos. is a transition state: \( E. \) infundibulifera \#1 has dropped to a low prevalence (5-10%) characteristic of waters below 6,500 \( \mu \)mhos., but it is still too saline for the mite species characteristic of low salinity.

Waters below 5,000 \( \mu \)mhos. tended to have a low \( E. \) infundibulifera \#1 prevalence rate in \( C. \) bifida populations, but high rates for \( E. \) discreta and \( H. \) conjecta (up to 25% and 40% respectively). These range from characteristically \( E. \) discreta lakes (shoreline with open water patches, i.e. Westwick Lake, Fig. 18) to \( H. \) conjecta lakes (densely populated with \( M. \)yriophylum and other submergent plants, i.e. Barkely Lake, Fig. 19).

Waters of over 13,000 \( \mu \)mhos. conductivity thus serve as a refuge from mite parasitism, while in waters of 6,500 to 8,500 and 0 to 4,500 \( \mu \)mhos. there are considerable parasite loads.

\( E. \) infundibulifera \#1 evidently shifts from \( C. \) bifida as its major host in high salinity waters to \( C. \)ymatia americana in low
salinity (Fig. 21 and Table VI). Considering the choice experiment (Fig. 22) a change in relative abundance of the mite would be sufficient to cause this. As *Cymatia americana* is much more susceptible than *C. bifida* (approximately 4 to 5 fold in the attachment experiment Fig. 22), the abundance of *E. infundibulifera* #1 in lower salinities could be a small fraction of its abundance in higher salinity, and therefore avoid superparasitizing *Cymatia americana*. There may be some degree of partitioning of the corixid resource between mites when we consider species associations (Appendix III). Such corixids as *S. bicoloripennis* have their own species of mites while suffering little or no parasitism by other mite species. As well, only rarely would more than one species of mite have a high enough prevalence on the same host in the same lake to result in strong competition (Fig. 21). If two species of mite were at 20% prevalence on the same host, the expected overlap is still only 4%. As mentioned, *Hydrachna* is predominantly a mite of thick vegetation, while *Eylais* does not fare well in this situation (i.e. Barkely Lake) and prefers open waters. We therefore would expect habitat preferences to reduce the possibility of competition.

There was no evidence of the interspecific multiple parasitism rate being less than the expected value in the field results. A lower rate would have been an indication of avoidance of interspecific competition. Furthermore, in the laboratory experiment (Table V, page 70) there was no decrease in the likelihood of attachment to a previously parasitized host. Considering the likelihood of host discovery, it is probably a better strategy to
attempt to outcompete the previously attached mite. It appears that interspecific competition is not a strong selective pressure in this system, probably reduced because of host and habitat differences. Lanciani (1970) and Harris and Harrison (1974) discuss partitioning of attachment sites on water boatmen by the mites, but I do not feel this is justified. A corixid rarely supports more than one mite for full development, and if a large enough number of mites attack it to warrant space competition, the corixid is not likely to survive. Such a discussion should be restricted to parasites that have a small or imperceptible effect on the host, and thus can exist in large numbers.

The observed differences in parasitism of different hosts in the field (Table VI) is at least partially due to differential attachment rate. Under equivalent exposure, there were definite differences in susceptibility between host species (Fig. 22). Host size appeared to be insignificant, as the larger *H. laevigata* was much less parasitized than were the smaller *C. bifida* or *Cymatia americana* (Fig. 22), despite being almost twice the size. The exact reason why one host is preferred over another under equivalent exposure is not clear. Habitat differences, as pointed out by Harris (1970), are also likely to be important. For example, *Cymatia americana* and *H. laevigata* are predominantly associated with submerged plants, while *C. bifida* and *S. bicolori-pennis* are most abundant in shallows with a mud substrate.

When *C. bifida* and *C. expleta* were compared in terms of parasitism rates, it is evident *C. expleta* must be under a much heavier attack (Figs. 23 and 24). When we consider the rate of
C. bifida parasitism in the field by E. infundibulifera #1 (10-35%, Fig. 21) and the strong preference for C. expleta (approximately 7.5:1, Fig. 25), the probability of C. expleta being parasitized approaches 100% in lakes of 7,000 to 13,000 μmhos. maximum surface conductivity. This would have disastrous effects on the breeding potential of C. expleta, assuming host effects comparable to C. bifida: it could cause the elimination of C. expleta.

It appears, however, that these two corixid species are not equally affected. Engorgement begins in the same manner on both hosts (Fig. 27), but C. expleta with completely engorged mites are rarely found: The vast majority of C. expleta in the spring only carry mites that failed to begin engorgement. During August through October many dead C. expleta were found floating with partially engorged mites attached. It was also noticed that in a cage located in Lake Lye used for holding C. expleta for experimentation, six out of twenty-two bugs found dead were parasitized, while in a sample of forty-eight live corixids, only two were parasitized (chi-square P<.05). Of forty-one parasitized C. expleta taken from the cage in late August, forty had at least one mite with some stage of engorgement, only six carried an unengorged mite. In spring field samples, only four out of sixty-two parasitized C. expleta bore mites with some stage of engorgement (compared to 35 of 41 in cage, chi-square P<.001). I conclude that E. infundibulifera #1 can begin engorgement on C. expleta, but the host is killed in the vast majority of cases. It cannot be attributed to the stylosome effect as found by Davids (1973), for in that case no mites began engorgement, as
was found in this study with *E. discreta* on *S. bicoloripennis*. As mentioned earlier, dead mites remain on the host, so that possibility that mites die and drop off *C. expleta* is remote. If parasitism is fatal to the vast majority of *C. expleta*, coexistence with *C. bifida* in the presence of mites would decimate a population of *C. expleta* before its impact on the breeding potential could be realized.

When we observe the ratios of *C. expleta* to *C. bifida* over the salinity range they coexist in, the sudden break in the distribution at the upper salinity limit for mites is understandable (Fig. 21). From 7,000 to 8,500 µhmhos. (LE 5, LE 4, Long Lake, Chilcotin) *C. expleta* is just marginally detectable, despite breeding in lakes of this range. Considering the parasitism rates of *C. bifida* in these waters (Fig. 21), and the host preference (Fig. 25), *C. expleta* would probably soon be eliminated from these lakes if it were not for immigration. In the 8,500 to 13,000 µhmhos. waters (Lake Lye, Round-up Lake, LE 3), *C. expleta* is present in moderately low numbers, the lower parasitism rates allowing some of the population to escape parasitism. Once the mites upper salinity tolerance has been reached (between 13,000 and 15,000 µhmhos.), then the relative abundance of *C. expleta* soars (Long Lake Clinton, Barnes Lake). This is well below the maximum salinity level for *C. bifida* (20,000 µhmhos., Scudder, 1969b). The limited coexistence of *C. bifida* and *C. expleta* has been recorded previously (Scudder, 1969b). While the upper salinity limit for coexistence is set by *C. bifida*'s salinity tolerance (20,000 µhmhos. in *C. bifida* compared to 29,000 µhmhos.)
in *C. expleta*, Scudder, 1969b), *C. expleta* is physiologically a fresh water insect (Scudder, Jariah, and Choy, 1972) and can be bred successfully in fresh water (Cannings, 1978). As they have broad overlaps in habitat and food requirements, biological interactions were suggested to be possible limiting factors to coexistence (Reynolds, 1974; Scudder, 1976). Reynolds (1974), however, failed to demonstrate food resource partitioning, but noticed a decrease in relative abundance of *C. expleta*, but not *C. bifida*, when these two species coexist.

Since *C. bifida* would act as a reservoir for mite infections, attempts at coexistence in the two *Cenocorixa* species in salinities under 15,000 µmhos. could mean the extinction of *C. expleta*. High salinity, therefore, serves as a refugium for *C. expleta*. *C. expleta* were found in virtually every lake during the spring, but in lower salinities (under 6,000 µmhos.), females did not contain eggs. However, I do not suggest that mite parasitism is the only factor keeping *C. expleta* out of fresher waters, but is of fundamental importance from 7,000 to 13,000 µmhos., where the two species and mites coexist. It is a potential problem to *C. expleta* should the latter every reproduce in fresher waters. In the present range of coexistence of these *Cenocorixa* species, *E. infundibilifera* #1 is the only mite present in large enough numbers to have an effect. In lower salinities, it is likely *E. discreta* could have the same effect, based on the mite susceptibility (Fig. 25) and prevalence (Fig. 21).

The chances of a dispersing *C. expleta* landing in waters under 13,000 µmhos. or over 29,000 µmhos. is far greater than
finding water that lies between. Few water bodies in the research area fall within this salinity range. As well, corixids are apparently attracted to any shiny surface, and seem to be unable to discriminate between suitable and unsuitable habitats before landing (Popham, 1964; Scudder, 1969b, 1976). Cannings (1977) has shown that it may be disadvantageous for corixids to fly from high salinity waters to low salinity (but not the reverse), for physiological reasons. With these factors in mind, it could well be that the high proportion of non-flying morph in *C. expleta* (Scudder, 1975) is related to its slim chance of successful dispersal to suitable waters. *C. bifida*, by comparison, has a wide range of acceptable lakes, very few in this region exceed its tolerances. While at times *C. bifida* may have large proportions of non-flying individuals (Scudder, 1975), in the past two springs there have been less than 1% in every lake studied. No advantage could be established for this morph under parasitism (page 29), and presumably if it were at an advantage it would be in higher proportion. Presumably flight muscle polymorphism in *C. bifida* must have some other benefit.

The concept of parasites mediating the outcome of competition is not new (Park, 1948). Barbehenn (1969) suggested that parasites of mammals could be a mechanism for partitioning habitats, regardless of the actual competitive advantages of the species involved. By his logic, if Parasite #1 of Host #1 has a greater detrimental effect on alternate Host #2, and a reciprocal arrangement occurs with Parasite #2 of Host #2, then the coexistence of Host #1 and Host #2 would be limited. If we designate *C. bifida*
and *C. expleta* as Host #1 and Host #2 respectively, and replace Parasite #2 with salinity and Parasite #1 is *E. infundibulifera* #1, then the hypothesis would fit the proposed situation in *Cenocorixa*. The two *Cenocorixa* species would not necessarily have to be ecological homologues, as long as their habitat preference was the same and the reaction of the two host species to the salinity and parasitism was as described.

It appears that mite parasitism can be a major impact on corixid ecology. Parasitism rates in the field were regularly over 10% prevalence, occasionally over 40%. Considering egg production is reduced approximately 75% for a parasitized female (Figs. 7 and 8), mite parasitism represents a considerable load on the host population. By the works of Davids (1973) and Davids and Schoots (1975), as well as this study, we can extrapolate this load to most water boatmen. The differences in loading and host effect among corixid species would influence their relative successes, and a bug under especial pressure would have to either develop defences (i.e. stylosome effect, *Sigara falleni*; Davids, 1973), avoid habitats in which mites were abundant, or suffer the burden of a substantially lowered fitness.


APPENDIX I.

A KEY TO THE WATER MITE LARVAE FOUND ON CORIXIDAE IN THE FRASER PLATEAU REGION OF B.C.

1(A). Six leg segments (excluding coxal sclerites); gnathosome small, less than 1/4 of total body length (unengorged larvae); aerial larvae by Mitchell (1957) definition, weakly sclerotized, with long legs and bearing many long setae; attaches to the dorsal region of the host's abdomen, usually on the second or third tergites, very rarely to the wings or pronotum in the airspace behind the head..................2. Eylais spp.

1(B). Five leg segments (excluding coxal sclerites); gnathosome large, making up 1/3 or more of the body length (unengorged larvae); aquatic larvae by Mitchell (1957) definition, heavily sclerotized with short stocky legs, with few short body setae and natatory leg setae; attaches to the host on the inside and outside surfaces of the hemielytra, to various external regions (head, metaxyphus, legs) but never dorsal abdominal regions of Corixidae.................................5. Hydrachna spp.

2(A). Second and third coxal sclerites separate, not fused; larger mite with long legs; bearing a bifid tibial claw on the palp; dorsal plate bearing pores joined by the longitudinal furrow, the third pair of pores joined by the transverse furrow; wide range of hosts, including most corixid species present in
Figure 28. *Eylais* species parasitic on Corixidae.

A. *Eylais discreta* (ventral view)
   palp = p.

B. *Eylais discreta* (dorsal shield)
   longitudinal furrow = lf
   transverse furrow = tf
   pores on dorsal shield are numbered.

C. *Eylais infundibulifera #1* (ventral view)
   first coxal sclerite = e1
   second coxal sclerite = e2
   third coxal sclerite = e3

D. *Eylais infundibulifera #2* (dorsal shield)

E. *Eylais infundibulifera #1* (dorsal shield)

F. *Eylais infundibulifera #3* (dorsal shield)

Leg setae omitted for clarity.
Figure 29. *Hydrachna* species parasitic on Corixidae.

A. *Hydrachna skorikowi* (ventral view)
B. *Hydrachna conjecta* (coxal sclerites)
C. *Hydrachna SP#1* (ventral view)
   gnathosome = g.
D. *Hydrachna cruenta #1* (ventral view)
E. *Hydrachna cruenta #2* (coxal sclerites)

Legs and swimming setae omitted for clarity.
fresher waters (under 5,000μmhos. maximum annual conductivity)

2(B). Second and third coxal sclerites fused; small mite with short legs; palp lacking tibial claw; dorsal plate with the longitudinal furrow medial to pore rows, transverse furrow absent; species with relatively restrictive host specificity but collectively exploiting most host species present and over a wide salinity range.............3. E. (Syneylais) spp. Figure 28 (C).

3(A). Longitudinal furrow extending from pores 1 or 2 to beyond pore 6, never starting after pore 2; in this region only reported from Hesperocorixa spp., but reported by Lanciani (1969) from Sigara spp. in New York State; found in fresher waters (under 4,000μmhos. maximum annual conductivity).

3(B). Longitudinal furrow starting between pores 3 and 5, never before pore 3, and extending beyond pore 6; in this region recorded from most corixid species available..................4.

4(A). Longitudinal furrow usually starting at pore 3, occasionally mid-way between pores 3 and 4 but always closer to pore 3 (note: when discrepancy between the two furrows of one specimen, accept the longer one); reported from Cenocorixa spp., Dasycorixa rawsoni, Hesperocorixa laevigata, and Cymatia americana in this region; found in a wide salinity range, up to 15,000μmhos. maximum annual conductivity........E. infundibulifera #1. Figure 28(E).

NEW SPECIES.
4(B). Longitudinal furrow beginning at pore 4 or between pores 4 and 5 in region of 4, extending to beyond pore 6; to date only recorded on *Sigara* spp. in fresh waters (under 1,000μmhos. maximum annual conductivity).....*E. infundibulifera* #3. Figure 28 (F). NEW SPECIES.

5(A). Median margin of E 3 (third coxal sclerite) 1½ times or more as long as that of E 1 (first coxal sclerite).............6.

5(B). Median margin of E 3 (third coxal sclerite) less than or roughly equal length to that of E 1 (first coxal sclerite).....7.

6(A). Anterior margins of E 1 form an angle of less than 90°; median margin of E 1 clearly shorter than lateral margin; seta EB 3 long and hairlike, originating from the anterior margin of E 3; larvae attach to the inner surface of the hemielytra, very rarely to the underside of the pronotal disc; reported from a wide variety of hosts; present in fresher waters (under 5,000 μmhos. maximum annual conductivity)....*H. conjecta* Figure 29 (B). NEW SPECIES.

6(B). Anterior margins of E 1 form a straight line; median margin of E 1 clearly longer than lateral margin; seta EB 3 short and peg-like, inserted before the middle of E 3; larvae attach to the exterior of the hemielytra, to the eyes, head, and legs, rarely to the ventral body; reported from *Cenocorixa* spp., *Dasycorixa rawsoni*, and *Hesperocorixa laevigata*; recorded from high salinity waters (8,000 to 15,000μmhos. maximum annual conductivity) but may occur in fresh waters as well....*H. skorikowi* Figure 29 (A). NEW SPECIES.
7(A). Gnathosome long and tapered, approximately twice as long as basal width; posterior margin of E 3 without a thornlike process; recorded only from *Sigara bicoloripennis* to date; only attaches to the external surface of the hemielytra; occurs in fresh water (under 1,000μmhos. maximum annual conductivity).

......................... *Hydrachna* SP.#1. Figure 29 (C).

7(B). Gnathosome short and stocky, approximately as long as the basal width; prominent thornlike process on posterior margin of E 3; these two species have never been recorded attached to the hemielytra; recorded primarily *Cymatia americana* but one species occasionally found on other hosts........8. *H. cruenta* complex.

8(A). Only attaches to the metaxyphus or coxal bases in close proximity to the metaxyphus; primary host is *Cymatia americana*, but has been found on *Cenocorixa bifida* and *Hesperocorixa laevigata*; only recorded from fresh waters (under 1,500μmhos. maximum surface conductivity)........... *H. cruenta* #1. Figure 29 (D). NEW SPECIES ‡

8(B). Only attaches to the distal leg segments (tarsi); so far only reported from *Cymatia americana*; only found in fresh water (under 1,000μmhos. maximum surface conductivity).

......................... *H. cruenta* #2. Figure 29 (E). NEW SPECIES ‡

‡ Note: In this work I have considered these to be separate species, but their distinction is not clear. Morphologically they
are virtually identical, but there is a very striking site specificity difference, with no overlap whatsoever. As these two groups were in different lakes, this discontinuity was evident. However, until an accurate morphologic distinction can be found, the possibility of these being different populations of the same species must be considered.
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<tr>
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<th>LE 3</th>
<th>Round-up L</th>
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<th>LE 5</th>
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**Mites**

**Legends:**
- **R** = Proceed but not breeding
- **R** = Proceed, but few breeding in numbers
- **B** = Breeding

**Legend:**

- *Sigaera stolenta*
- *Sigaera grossistriata*
- *Sigaera pennisetata*
- *Sigaera concolorphila*
- *Sigaera decoratella*
- *Sigaera pennisetata*
- *Dasycorethra hybrida*
- *Dasycorethra reahornii*
- *Arctocoecella stulta*
- *Calicothra australis*
- *Hepterothra victoriana*
- *Hepterothra acioponora*
- *Hepterothra ocellaris*
- *Hepterothra lepispira*
- *Cymatella americanana*
- *Cenocoecella expilata*
- *Cenocoecella pilosa*
- *Water Boaemen*
- *Hydrachna sp. 1*
- *Hydrachna curvata #2*
- *Hydrachna curvata #1*
- *Hydrachna skrokom *
- *Hydrachna curvata*
- *Eptesicus diserta*
- *Eptesicus undulatissima #3*
- *Eptesicus undulatissima #2*
- *Eptesicus undulatissima #1*

**Distribution of Mites and Water Boaemen Encountered**

**Appendix II**

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### APPENDIX III.

**HOST-PARASITE ASSOCIATION RECORDS**

<table>
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<th>Host Species</th>
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**Legend:**

X indicates a recorded attachment, but not necessarily successful engorgement.