Effects of Water Mite Parasitism on Cenocorixa spp. (Heteroptera: Corixidae).

By

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ABSTRACT

The purpose of this study was to understand the mechanisms by which parasitic water mites exclude one species of sympatric water boatmen from low salinity, while a sibling species survives. Attachment of the larval water mite Eylais euryhalina Smith was studied in the laboratory on two species of flight polymorphic water boatmen, Cenocorixa bifida hungerfordi Lansbury and C. expleta (Uhler). After 24 hours of exposure, prevalence and abundance of mites did not differ significantly between host species or host morph (sclerotized versus non-sclerotized). From this, it was concluded that mites recruited to all host types at the same rate. By measuring prevalence and abundance of attached mites only, it was determined that the number of mites initially able to attach also did not differ significantly between hosts.

In analyzing the initial location of attachment of E. euryhalina on the four host types, no significant difference was found between species, but a significant difference was discovered between sclerotized and unsclerotized morphs. This effect was evident as a shift of mite attachment from the centre of abdominal segments 2, 3, and 4 on the non-sclerotized hosts, to the thoracico-abdominal membranes (T.A.M.) on the sclerotized hosts. It is speculated that the thickness of the flying hosts' sclerotized integument forces this change in location of mite attachment.

A six- to eight-day study of the morphs of each species that are predominant in the field found significant differences in mite prevalence between hosts. Non-flying C. expleta had significantly greater prevalence of mites than flying C. bifida. The number of engorging mites was also significantly greater on non-flying C. expleta. Location of attached and engorging mites followed the same trends as seen in one day experiments. Based on these findings and initial studies, it is argued that it is the sclerotization of C. bifida that causes a reduction in the
prevalence of mites over time, rather than a host species effect per se. Because on sclerotized hosts, mites can only engorge on the T.A.M., the number of engorging mites on these hosts is limited to 2 or less, whereas greater number of mites can feed on non-sclerotized hosts. As *C. expleta* is normally non-flying in the field, whereas *C. bifida* is predominantly flying, *C. bifida* has a competitive advantage where mites are present in abundances of greater than 2 mites per host.

Field collections of parasitized hosts showed the same patterns of spatial mite attachment as in the laboratory, except that sclerotized hosts often had mites attached directly through the abdominal terga. This must have been the result of mite attachment prior to host sclerotization. Abundances of mites in the field were greater than 2 mites per host in some collections. The predominance of the sclerotized, flying morph of *C. bifida* appears to allow this species to survive at low salinity where mites abound. *C. expleta* is excluded from these waters, but its predominantly non-sclerotized, non-flying condition allows better reproduction at moderate to high salinities in the absence of mites. The alternative methods by which these two closely related species of water boatmen have dealt with parasite pressure implicates mite parasitism as a possible impetus in their speciation process.
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INTRODUCTION

A. Description of Thesis

Waterboatmen (Heteroptera: Corixidae) are a common constituent of the insect fauna of ponds, lakes, and slow-moving rivers. The family is notable for its wide-ranging salinity tolerance: from fresh to highly saline waters (Scudder, 1976). Two morphologically similar species of the genus Cenocorixa are abundant in all but the most saline lakes of the British Columbia Interior, occurring in sympathy throughout much of their range. *C. bifida hungerfordi* Lansbury (hereafter *C. bifida*) occurs in lakes with conductivities of 20 to 20 000 μS cm⁻¹, whereas *C. expleta* (Uhler) normally lives in water with conductivities of 13 000 to 30 000 μS cm⁻¹. Scudder et al. (1972) found that the exclusion was not caused by *C. expleta*’s inability to osmoregulate at low salinity, in fact Cannings (1978) demonstrated that *C. expleta* could breed in freshwater in the lab. Nor was the exclusion attributable to differences in life cycle phenologies (Jansson and Scudder, 1974), or because *C. bifida* outcompeted *C. expleta* when in sympathy (Reynolds, 1974) (These studies are all reviewed by Scudder, 1983). The most plausible explanation so far forwarded is that of Smith (1977) concerning the effects of parasitic water mites (Acari: Hydracarina) on water boatmen. My thesis
is a continuation of this study.

Smith (1977), studying the field distributions of C. bifida, C. expleta, and the water mites found that water mites occurred in all lakes below 13 000 μS cm⁻¹, but C. expleta was only found in abundance in lakes above 13 000 μS cm⁻¹. C. bifida, however, was abundant above and below 13 000 μS cm⁻¹. It was proposed that mite parasitism had a greater effect on C. expleta compared to C. bifida, resulting in the exclusion of C. expleta in waters below 13 000 μS cm⁻¹ (Smith, 1977).

Prevalence of mites in lakes where C. bifida and C. expleta co-occurred with the mites supported this theory. In the pond LE 3 (13 026 μS cm⁻¹ on Sept. 15-20, 1977) parasitism on C. expleta was greater than 40 per cent for 6 samples from July to October. Parasitism of C. bifida in these samples was consistently below 20 per cent. Round-up Lake (10 700 μS cm⁻¹ on Sept. 15-20, 1977) was similar, with more than 25 % parasitism of C. expleta, while less than 15 per cent of C. bifida were parasitized. Parasitism had a direct effect on host fecundity as dissections of field collected parasitized and unparasitized C. bifida showed significant reductions in egg production for the parasitized bugs.

With respect to the size of engorging mites on C. expleta and C. bifida, C. expleta was rarely found with fully
engorged mites, whereas fully engorged mites were often found on *C. bifida*. Smith (1977) concluded that the absence of *C. expleta* with fully engorged mites was because of high mortality of *C. expleta* prior to full mite engorgement, whereas *C. bifida* could survive even with fully engorged mites.

Laboratory studies by Smith (1977) corroborated the field observations. Larval *Eylais euryhalina* Smith were used to infect *C. bifida* from Long Lake (Chilcotin) (8.064 μS cm⁻¹ on Sept. 15-20, 1977) and *C. expleta* from Barnes Lake (15.197 μS cm⁻¹) in fresh, dechlorinated water. When equally exposed to *E. euryhalina*, over 90 per cent of the *C. expleta* were parasitized, whereas less than 25 per cent of the *C. bifida* were parasitized.

While there was good evidence that mites had a greater impact on *C. expleta* than on *C. bifida*, the actual mechanism behind this effect was not clear. More study was necessary on the corixid-mite interaction in the Chilcotin region to understand how and why *C. expleta* was more susceptible. The main objective of my study was to determine the exact mechanisms by which water mites limit *C. expleta* in low salinity lakes. In addition, the life history of the mite *Eylais euryhalina* Smith was examined in detail. (Data and observations about mite life history are given in Appendix
1.) To fulfill my main objective, 5 questions were asked regarding the attachment of the mite *Eylais euryhalina* Smith (formerly *E. infundibulifera* # 1) on *C. bifida* and *C. expleta*. To answer these questions, hypotheses were formed (see below) and experiments performed (see Materials and Methods). From these experiments, a greater effect of parasitism on one host type was concluded if

a.) more mites attached to one host type and/or 

b.) a greater susceptible area of mite attachment was found on one host (explained below: hypothesis 2b).

1.) Does species of host affect a.) quantity of mites initially attaching and b.) where mites initially attach?

1a.) Hypothesis (quantity of mites)

**There are significantly more mites attaching initially to *C. expleta* than to *C. bifida***.

This would corroborate the findings of Smith (1977) who reported more parasitism on *C. expleta* compared to *C. bifida* when equally exposed to four species of mites including *E. euryhalina*. More mites attaching to *C. expleta* initially, was predicted to lead to more engorging mites later, causing reduced fecundity and survival.
1b.) Hypothesis (location of mites)

There is no significant difference between the initial pattern of mite attachment on C. bifida and C. expleta (if host sclerotization is held constant).

No difference was expected because the exact position that the mites choose is governed only by the morphology of the air spaces surrounding the hosts' dorsal surfaces, and these regions are similar in both host species (Jansson, 1972).

2.) Does host sclerotization (wing morph) affect a.) quantity of mites initially attaching and b.) where mites initially attach?

2a.) Hypothesis (quantity of mites)

There are significantly more mites attaching to unsclerotized (non-flying) hosts than to sclerotized (flying) hosts.

The rationale for proposing this hypothesis is that mites are able to pierce the integument of unsclerotized hosts more easily than sclerotized hosts, making prevalence higher on unsclerotized hosts. Since field populations of C. expleta are predominantly non-flying (unsclerotized), whereas C. bifida populations are predominantly flying (sclerotized), sclerotization could be a factor in the exclusion of C. expleta in areas where mites occur.
2b.) Hypothesis (location of mites)

Mites on unsclerotized hosts are uniformly spread over the entire dorsum, whereas mites on sclerotized hosts congregate on areas that remain unsclerotized throughout the host’s adult life span.

This was proposed because mites are predicted to be unable to pierce the hardened terga of sclerotized hosts, therefore, they will only attach on the small, permanently unsclerotized membranes of these hosts. A smaller susceptible area for attachment on sclerotized *C. bifida* was predicted to result in reduced overall susceptibility to mite parasitism compared to unsclerotized *C. expleta*. The rationale for this prediction is that crowded mites compete for space and do not extract as much energy from their hosts as a similar number of evenly spaced mites. Mitchell (1968) reported up to 50% mortality of *Arrenurus* spp. mites on the damselfly *Cercion hieroglyphicum* Brauer when mite crowding occurred.
3.) Does salinity affect a.) quantity of mites initially attaching and b.) where mites initially attach?

3a. Hypotheses (quantity of mites)

Low salinity (less than 300 µS cm⁻¹) does not significantly alter the quantity of mites initially attaching, on any host type, compared to attachment on the same hosts at moderate salinity. High salinity (above 18 000 µS cm⁻¹) prevents attachment on all hosts.

This question was asked to ensure that the effects of mites are the same throughout the salinity regime from which C. expleta is excluded, but significantly less above the salinity at which E. euryhalina is found (and C. expleta abounds). The rationale for proposing the first hypothesis is that both C. bifida and C. expleta were found to be able to regulate their body fluids at low salinity (Scudder et al., 1972). From this study, both species appear to have no physiological disadvantage at low salinity, so there is no reason to believe that low salinity would affect one species differently than the other with respect to mite parasitism. The hypothesis regarding high salinity is proposed because E. euryhalina is not found breeding in the field at this high salinity, and it may be because of inability to attach to their hosts.
3b. Hypotheses (Spatial Attachment)

Low salinity (less than 300 μS cm⁻¹) does not significantly alter the location of mite attachment from what would occur at moderate salinity on all host types. High salinity (above 18 000 μS cm⁻¹) also does not alter the location of mite attachment.

These hypotheses were proposed for the same reasons as above.

4.) When does the effect of mites occur, or more specifically does the effect occur initially and/or during mite engorgement for a.) quantity of mites and b.) location of mites?

4a.) Hypotheses (quantity of mites)

More mites attach and engorge on the predominant non-sclerotized morph of C. expleta than on the predominant sclerotized morph of C. bifida over a 6 to 8 day period.

In questions 1 and 2, the quantity and location of initial mite attachment was measured on different host types. By comparing the answers to these questions with that of question 4 (long term engorgement), the duration of the effect of mites could be determined. I formed the hypothesis of question 4a because I believed that the lack of
sclerotization in non-flying C. expleta would lead to a higher number of mites being able to attach and engorge compared to the flying C. bifida.

4b.) Hypotheses (location of mites)

Mites attaching and engorging on unsclerotized C. expleta are uniformly spread over the entire dorsum, whereas mites attaching and engorging on sclerotized C. bifida congregate on areas that remain unsclerotized throughout the host’s adult life span.

The rationale for proposing this hypothesis is as above (hypothesis 2b). Sclerotization gives C. bifida some protection from mite parasitism whereas C. expleta has no protection because it is predominantly unsclerotized.

5.) Are the data collected from one- and six-day laboratory experiments representative of mite parasitism in populations of field collected corixids for a.) quantity of mites and b.) location of mites?

5a.) Hypotheses (quantity of mites)

In field collections, more mites are found on C. expleta than on C. bifida. More mites are found on unsclerotized hosts than sclerotized hosts.
This question was asked to verify that the findings in my laboratory studies had some bearing on the exclusion of *C. expleta* in the field. Overall, I predicted the quantity of mites on field-collected host types to follow the same trends as seen in the one- and six-day laboratory experiments. The hypothesis regarding species of host is based on the study of Smith (1977). He found more mites attaching to *C. expleta* than *C. bifida* in several lake samples in which the two host species occur in sympatry with *E. euryhalina*. I predicted that more mites would be found on unsclerotized hosts in the field because of their greater surface area that is susceptible to attachment (see hypothesis 2a).

5b.) Hypotheses (location of mites)

In field collections, there is no difference in the spatial attachment patterns of mites on *C. expleta* and *C. bifida* (field collections are similar to laboratory data, hypothesis 1b). Mites found on unsclerotized hosts are uniformly spread over the entire dorsum (field collections are similar to laboratory data, hypothesis 2b). Mites found on sclerotized hosts are also spread over the entire dorsum (field collections differ from laboratory data, hypothesis 2b).
The hypothesis concerning species of host was predicted because the interspecific differences are not great enough to cause differences in spatial mite attachment (see hypothesis 1b). Field-collected unsclerotized hosts were predicted to have the same mite attachment as in the laboratory because they remain unsclerotized their entire adult life, therefore presenting the same attachment area to mites as the unsclerotized hosts in one and six day experiments. The sclerotized field-collected hosts were predicted to be different from laboratory experiments because in the laboratory, the attachment of mites occurs after sclerotization (by design), whereas in the field, attachment may occur prior, during or after sclerotization. Mite attachment prior to sclerotization could occur anywhere on the host’s dorsum, causing potential differences in predicted attachment patterns between field and laboratory infected sclerotized hosts.

B. Overview of Water Mite Parasitism

Larval water mites form an ecological group known as the Hydracarina (= Hydrachnellae = Hydrachnidia). According to the classification of Prasad and Cook (1972), they belong to the Subclass Acari, Order Acariformes, and Suborder Parasit-engona although the higher classification of the Acari is
I. M. Smith and Oliver (1986) have reviewed the literature on larval parasitic water mites and their hosts. At Becher’s Prairie, 6 species of mites from 2 genera have been recorded parasitizing water boatmen (Smith, 1977) (See Table 1). Of these, only *Eylais discreta* Koenike (Acari: Eylaidae) and *Hydrachna cruenta* Muller (Acari: Hydrachnidae) are Old World species. The *Eylais* species found in North America are described in Smith (1986), and the *Hydrachna* species are described in Smith (1987). My investigation is the first since the initial description of the ecology of one of these species: *Eylais euryhalina* Smith.

The distribution of water mites at Becher’s Prairie extends from the freshest ponds to waters of about 13 000 μS cm⁻¹ (moderate salinity) (Smith, 1977) although only two species, *E. euryhalina* and *H. barri* Smith are present in moderate salinity. *E. euryhalina* is the only species of mite that occurs in both fresh and moderately saline water, therefore making it the best candidate for a study across a range of salinities.

Members of the genus *Eylais* parasitize long-lived adult aquatic insects such as those of the family Corixidae. They also parasitize other Hemiptera including giant water bugs (Belostomatidae) (Lanciani, 1969) and backswimmers (Notonectidae) (Stout, 1953), as well as aquatic beetles of
Mites

*Eylais euryhalina*  
B  B  B  B  B

*Eylais lancianii*  
?  B

*Eylais discreta*  
B  B  B  b

*Hydrachna davidsi*  
B  B  B  B

*Hydrachna barri*  
B  B

*Hydrachna cruenta*  
?  B

Corixidae

*Cenocorixa bifida*  
B  B  B  B  B  B  B  b

*Cenocorixa expleta*  
?  R  R  b  B  B  B


| Box 27 | Barkley | Greer | Near Pothole | Long (Chil.) | Lye | Barnes | Round-up |

Bodies of Water

Increasing Salinity

Table 1. Mites recorded from Becher’s Prairie plotted with respect to salinity (extracted from Smith, 1977).

B = breeding in abundance  
b = breeding, but not in abundance

R = recorded, but not necessarily breeding

*Cenocorixa* spp. of corixids shown for reference to salinity.  
Round-up Lake was lower in salinity than Barnes Lake before 1979, but has increased in salinity more than the other lakes in the area, and now has no breeding mites and is home to almost exclusively *C. expleta*. 
the families Dytiscidae (Aiken, 1985), Gyrinidae and Noteridae (Piatakov, 1916 quoted from Smith and Oliver, 1986), Hydrophilidae and Hydraenidae (Lanciani, 1970b), and Haliplidae (Nielsen and Davids, 1975).

The general parasitic water mite life cycle is depicted in Figure 1 (adapted from Harris and Harrison, 1974). In temperate zones, parasitic water mites overwinter as larvae on their hosts. In the spring, the partially engorged larvae continue their engorgement until they reach a critical size at which time they cease engorgement and pupate into a sessile nymphocrisalis (protonymph) on the back of their host. After a brief period (relative to the larval stage), the developed protonymph breaks through the larval cuticle in which it pupated becoming a free-living deutonymph. The immature nymph actively feeds on ostracods and cladocerans (corixid eggs for the genus Hydrachna) for a short time until it once more pupates, this time on a submerged substrate, forming a teleiochrysalis (tritonymph). The fully developed tritonymph breaks through its nymphal cuticle emerging as a dioecious, octopod adult.

Nymphs and adults of the genus Eylais can be identified by their bright red colour, relatively large size (up to 16 mm in length), and their habit of trailing the fourth pair of legs behind them when they swim (Lanciani, 1969). Copulation
Figure 1. Typical Water Mite Life Cycle. The length of arrows approximates the duration of the respective life stages based on the life cycle of *E. euryhalina* during the spring and summer of 1991. For comparison, the adult stage was approximately 1 month in duration during June and July, 1991.
takes place shortly following emergence after which, the males die and the females begin to oviposit. The bright, red eggs are laid in masses on submerged substrates (See Materials and Methods: Section A. 2.). A single female may lay over 10,000 eggs in this manner over a number of weeks (Davids, 1973 for *E. discreta*).

The eggs develop to active prelarvae within their shells and hatch as hexapod larvae after 24-38 days at room temperature (Nielsen and Davids, 1975 on *E. infundibulifera* Koenike). The positively phototactic larvae swim to the water surface and skate across the top surface in search of an appropriate host. (*Hydrachna* spp. mites hunt actively for their hosts or cling to the underneath of the water surface.) Hosts coming to the surface for air are mounted, and after finding a suitable attachment site, the larval mites pierce the insect's integument and begin engorgement. Engorgement can take weeks or months depending on the temperature, but most species of *Eylais* on corixids appear to be bivoltine in temperate regions (Lanciani, 1970a). The summer generation is associated with the host for less than 2 months, whereas the overwintering generation attaches for much longer. *Eylais* spp. show the largest increases in size during engorgement of any water mite (Lanciani, 1971b).
Larvae of the genus *Eylais* are not truly aquatic, requiring a constant air supply while engorging. They attach only to areas such as on the thoracic and abdominal dorsum covered by the forewings (subelytral air space), the hindwings or underside of the forewings (which are also in the subelytral air space), or occasionally in the air space between the head and prothorax (Davids et al., 1977). In contrast, many families of mites are truly aquatic in their larval stage (e.g., the family Hydrachnidae). Larval *Hydrachna* spp. can utilize dissolved oxygen in the water allowing attachment to all surfaces of their host including the exterior of the wings, head and legs (Harris and Harrison, 1974 on *H. elongata* Smith formerly *H. cruenta*). Attachment to immature hosts is possible for *Hydrachna* spp., although full engorgement may not occur before host moulting, causing death of the mite. In contrast, some species of mites can attach to an immature host, transfer to the newly moulted adult after host ecdysis, and subsequently begin to engorge (Abro, 1982 for *Arrenurus* spp. on the damselfly *Enallagma cyathigerum* Charp.). (*Hydrachna* spp. and *Eylais* spp., are incapable of movement once attachment has occurred.)

The location of attachment is usually species-specific. Resource partitioning has been demonstrated for the genus *Eylais* such that species that could compete, parasitize
different hosts, different locations on the host, or at different times of the year (Lanciani, 1970a). The exact location of attachment on the dorsum or wing by Eylais spp. has been documented by Nielsen and Davids (1975) for E. discreta on Sigara striata (L.) and Cymatia coleoptrata (Fab.). They found that on S. striata, E. discreta preferred tergum 3 followed by terga 2 and 4, while on C. coleoptrata, E. discreta preferred tergum 2, and then 3. Such exact plotting of mite attachment positions is important in understanding the effects of mites on their hosts, and the co-evolution of sympatric host-parasite systems.

The effects of water mites on their hosts was reviewed by Smith (1988) and Lanciani (1983). Following Smith (1988), the levels of effects can be classified as follows:

1. Effects on individuals.
2. Effects on populations.
3. Effects on communities.

1. Effects on individuals.

On an individual basis, the effects range from being apparently harmless as for Hydrachna conjecta Koenike on the water boatman Sigara falleni (Fieb.) (Davids, 1973) to being lethal as demonstrated by Lanciani (1975) on the mite-induced reduction in survival of marsh treader (Heteroptera:
Hydrometridae). The causes of mortality have been linked to upset of water balance caused by parasitism (Smith and McIver, 1984c), and rupturing of the integument in cases of superparasitism of mites on damselflies (Mitchell, 1968).

Other important effects of parasitic mites on aquatic insects include reduction in the fecundity of females (Davids and Schoots, 1975; Martin, 1975; Smith, 1977), reduction in the rate of nymphal growth (Lanciani and May, 1982), and reductions in male mating success (Forbes, 1991).

2. Effects on Populations.

The effects of mortality on individuals can be witnessed at the population level by comparing field samples to a negative binomial distribution (Crofton, 1971). Lanciani and Boyett (1980) demonstrated that on the mosquito Anopheles crucians Wiedemann there was significant mortality of hosts from the mite Arrenurus pseudotenuicollis Wilson when abundance of mites was greater than 11 mites per host. (The negative binomial predicted that there would be more hosts with 11 or more mites than were found in field samples.) Direct observations of populations have drawn the same conclusions. Fernando and Galbraith (1970) reported the absence of the water strider Gerris comatus Drake and Hottes almost 2 months earlier than usual, in years when early collections detected high levels of parasitism by Limnochares
aquatica L. Similarly, early mortality because of mites has been inferred by the absence of old-aged hosts with high prevalence of mites, despite a high mite prevalence on younger hosts (McCrae, 1976 on mosquitoes).

Mites may also affect other groups of individuals within a population. Mitchell (1967) found higher mite parasitism on male dragonflies compared to females suggesting that mite parasitism can skew the sex ratio of a population. Martin (1975) found that non-flying Sigara falleni had more Eylais spp. mites on them than flying morphs, implying that parasitism could alter the frequencies of morphs.

Finally, the location of a population in its habitat can be altered by mite parasitism. Apart from the work of Smith (1977) on the exclusion of C. expleta from low salinity, Wiegert and Mitchell (1973) have shown a similar habitat restriction with respect to temperature. The brine-fly Paracoenia thermalis Viets inhabits thermal pools. It can only optimize its fitness in areas that are not too hot to allow reproduction, but not too cold or stable to allow parasitic water mites to reach high abundances.

3. Effects on Communities.

Because parasitic water mites often attach to a wide range of hosts, they can affect the community composition of their hosts through differential effects. Minchella and Scott
(1991) review the importance of parasites (including water mites) in determining community structure. Gledhill et al. (1982) found differential effects of mites on blackflies (*Simulium* spp.). They determined that one species of host is less affected by mite parasitism than two other species because of a defensive covering on the pupa. Other studies found that the pupae of the mosquito *Aedes cinerus* Meigen decrease parasitism by *Arrenurus* spp. mites through violent shaking behaviour, whereas *Aedes communis* (Degreer) and *Aedes punctor* (Kirby) do not shake and are more susceptible to mites in laboratory experiments (Smith and McIver, 1984a). A field study, however, demonstrated the complexity of community interactions between these mites and their hosts. In the field, *Aedes cinerus* is the most parasitized because *A. communis* and *A. punctor* develop later in the year, and in so doing, avoid mite parasitism almost entirely (Smith and McIver, 1984b). From these studies, it can be speculated that mite parasitism may cause alterations in the seasonal phenology of its hosts.

The differential effects of mites not only affect the parasitized generation, but may also affect the offspring. Decreased or delayed fecundity of parasitized females can cause a smaller and/or later following generation which may affect competitiveness (Martin, 1975 on water boatmen). In
cases where food or other resources are limiting, such an effect could be critical to the survival of one host species in a community.

C. Overview of the Corixidae

The corixids of Becher's Prairie are the most conspicuous insects in the lakes. At times, especially near dusk, one sweeping sequence can yield more than 500 corixids, usually constituting more than 90 per cent of the total fauna collected (personal observation in Barnes Lake).

In all, 13 species of corixids from 7 genera have been recorded at Becher's Prairie (Smith, 1977) (See Table 2). This study deals exclusively with *Cenocorixa bifida* and *C. expleta*, but *Hesporocorixa laevigata* (Uhler), *Cymatia americana* Hussey, and *Callicorixa audeni* Hung. are also abundant and have been studied with respect to parasitism (Smith, 1977). The taxonomic differences between *Cenocorixa bifida hungerfordi* and *C. expleta* have been determined morphologically (Jansson, 1972) and through acoustic differences in male pre-mating stridulatory patterns (Jansson, 1973).

The life cycles of *C. bifida* and *C. expleta* are described by Jansson and Scudder (1974) and are typical of corixids in temperate regions. Adults overwinter with the females undergoing ovarian diapause until spring. The males are
<table>
<thead>
<tr>
<th>Corixidae</th>
<th>Bodies of Water</th>
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<tbody>
<tr>
<td>Cenocorixa bifida</td>
<td>B B B B B B B B</td>
</tr>
<tr>
<td>Cenocorixa expleta</td>
<td>? R R b B B B B</td>
</tr>
<tr>
<td>Cymatia americana</td>
<td>B B B B R R R R</td>
</tr>
<tr>
<td>Hesperocorixa laevigata</td>
<td>B B B B</td>
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<tr>
<td>Hesperocorixa vulgaris</td>
<td>b b R R R R R</td>
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<tr>
<td>Hesperocorixa atopodonta</td>
<td>R</td>
</tr>
<tr>
<td>Hesperocorixa michiganensis</td>
<td>? R</td>
</tr>
<tr>
<td>Callicorixa audeni</td>
<td>B b b b R R R</td>
</tr>
<tr>
<td>Arctocorisa sutilis</td>
<td>? b b? R R</td>
</tr>
<tr>
<td>Dasycorixa rawsoni</td>
<td>b? b?</td>
</tr>
<tr>
<td>Sigara bicoloripennis</td>
<td>R b R</td>
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<tr>
<td>Sigara decoratella</td>
<td>R B b b R R</td>
</tr>
<tr>
<td>Sigara penniensis</td>
<td>? R R</td>
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</tbody>
</table>

Increasing Salinity -------->

Table 2. Corixids recorded from Becher's Prairie plotted with respect to salinity. (Modified after Smith, 1977).

- **B** = breeding in numbers
- **b** = breeding, but not in numbers
- **R** = recorded, but not necessarily breeding

N.B. Because the salinities of the lakes have changed since Smith (1977), some of the breeding records may now be in error. I have tried to integrate my findings of 1990 and 1991, with that of Smith (1977).
sexually mature by late winter and copulation occurs shortly after ice break-up. Eggs are laid on submerged rocks and vegetation (Scudder, 1966). Nymphs hatch in late May (depending on temperature) and progress through five instars becoming adults by the middle of June. At the latitudes of Becher's Prairie only two generations are usual. However, further south a partial third generation may occur (eg. C. expleta in the high salinity lake LB 2 near Kamloops).

Water boatmen (including Cenocorixa bifida and C. expleta) often exhibit wing muscle polymorphism. Associated with wing muscle development is a hardening and darkening process (Young, 1965a). This process is most evident on the notum and abdominal segments, although the head and forewings (hemelytra) are also affected. The hardness of the corixid notum and tergum is of direct importance to my investigation because these are the susceptible areas for attachment of Eylais spp. mites (See Introduction, Question 2).

Wing muscle polymorphism is generally believed to be found in species that have stable habitats for at least part of their life cycle (Young, 1961). Those that live in ephemeral habitats will usually have a flying morph only. The control of wing muscle development seems to depend on the environment in which the newly eclosed (teneral) adult develops (Scudder and Meredith, 1972). Factors that may be involved include
temperature, photoperiod, availability of food, and crowding. For Cenocorixa expleta, 1.5 or more days at 15 °C gives rise to the flying morph, meaning that this morph only occurs in the late summer when the lakes have warmed. In the field, populations of C. expleta are predominantly non-flying. C. bifida, however, is usually predominantly flying. Scudder (1975) proposed that it is the high percentage of C. bifida’s population that develops at warm temperatures that makes it mostly flying. He documented the percentages of flying versus non-flying C. bifida for 1962-63 and 1966 to 1969 for 8 lakes of varying salinities. These data and other unpublished records are shown in Table 3. These records may be compared to the data of 1991 (See Results, Table 18).

Scudder (1971), following the methods of Young (1965a), classified the development of the wing muscles of Cenocorixa spp. based on the darkening of the mesonotum. For convenience, I used this method in my study. The teneral adult (freshly eclosed) is designated as stage 0 (uncoloured notum). Non-flying individuals exhibit up to stage 2 darkening (partial darkening of mesonotum), while flying individuals progress through stages 3 (more area darkening than stage 2) to 6 (completely dark mesonotum). The abdominal segments usually darken in correspondence to the notum and are completely dark by stage 6. Overwintered non-
Table 3. Percentages of *C. bifida* flying and non-flying in studied lakes from 1962 to 1969. Extracted from Scudder (1975) and unpublished data.

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<tbody>
<tr>
<td></td>
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<td>Female (n)</td>
<td>Male (n)</td>
<td>Female (n)</td>
<td>Male (n)</td>
<td>Female (n)</td>
<td>Male (n)</td>
<td>Female (n)</td>
</tr>
<tr>
<td>Lye</td>
<td>F 80 (50)</td>
<td>66 (35)</td>
<td>79 (70)</td>
<td>78 (40)</td>
<td>F 59 (112)</td>
<td>58 (101)</td>
<td>51 (126)</td>
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<td></td>
<td>NF 20 34</td>
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<td>22 (40)</td>
<td>NF 41 42</td>
<td></td>
<td>49 (49)</td>
<td>48 (48)</td>
</tr>
<tr>
<td>Barnes</td>
<td>F 79 (34)</td>
<td>71 (24)</td>
<td>89 (46)</td>
<td>83 (59)</td>
<td>F 54 (78)</td>
<td>59 (101)</td>
<td>96 (69)</td>
<td>92 (134)</td>
</tr>
<tr>
<td></td>
<td>NF 21 29</td>
<td></td>
<td>11 (11)</td>
<td>17 (17)</td>
<td>NF 46 41</td>
<td></td>
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<td>8 (8)</td>
</tr>
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*F* = Flying

*NF* = Non-flying
flying Cenocorixa spp. sometimes have fully darkened abdomens despite mesonotal darkening characteristic of Scudder (1971) stage 2 development.
MATERIALS AND METHODS

A. Study Site

Research was conducted in the Chilcotin region of south-central British Columbia, Canada (Figures 2 and 3). Locally, the region is known as Becher's Prairie and is situated about 300 km north of Vancouver and 45 km west of Williams Lake. The area is a plateau above the Fraser River at approximately 1 000 m elevation, and is typified by small bunchgrass prairies amid lodgepole pine and Douglas fir forests. Because of the rolling, post-glacial topography and solid bedrock formations, many small, pothole lakes without inflow or outflow are present, with varying salinities dependent on the composition of the underlying strata. In the summers of 1990 and 1991, air and lake temperatures were similar to previous studies (Smith, 1977; Lancaster, 1985) with lake temperatures ranging from 10 to 20 °C for May to September, and air temperature fluctuating from 0 to 35 °C for the same period. Precipitation in the area for 1990 was higher than usual with 450.1 mm, while 1991 was slightly above average (343.2 mm). The lakes in the area have been studied extensively since the 1950's. Chemically, the low salinity lakes are magnesium or sodium bicarbonate-carbonate and sodium bicarbonate-type waters, but at higher salinities they are sodium sulphate and sodium carbonate (Topping and Scudder, 1977). The salinities and sizes of the lakes have been documented by Scudder (1969a, 1969b). Since the salinities can change over time, recordings of the studied lakes in 1990 and
Figure 2.

Study Site a.) British Columbia
    b.) Cariboo-Chilcotin Region
        1. Becher's Prairie
        2. Kamloops (Lake LB 2)

Inset of figure 1a. depicts *Cenocorixa expleta* (4X life size). Numbers on thin lines of figure 1b. indicate highway numbers.
Figure 3. The studied water bodies of Becher's Prairie

1. Box 27 (Pond)
2. Barkley Lake
3. Near Opposite Crescent (Pond)
4. Greer Lake
5. Near Pothole Lake (Pond)
6. Long Lake (Chilcotin)
7. Lake Lye
8. Barnes Lake
9. Round-up Lake

Lakes are listed in ascending salinity from 1 through 9. Barkley Lake and the pond Near Pothole Lake were studied by Smith (1977), but were not studied in depth in this study. Their relative salinities are assumed to be similar, (or slightly higher) than previous studies (784 to 942 μS cm⁻¹ and 3841 to 4987 μS cm⁻¹ respectively in 1976/77).
Figure 3.
1991 were taken and are presented along with dimensional data in Table 4. Generally, the salinities of all lakes have been gradually increasing to their highest levels on record. The biota of the lakes is also well studied. Reynolds (1979) gives a general account of the Crustacean zooplankton of the area and Scudder (1969b) catalogues some of the more common invertebrates (including Corixidae) with respect to salinity. Reynolds and Reynolds (1975) summarize the aquatic angiosperms. Submergent vegetation densely covers most of the fresher lakes, while those above 7 000 μS cm$^{-1}$ are devoid of such flora. More specific studies include those of Cannings and Scudder (1978) on the Chironomidae; Cannings and Cannings (1987) on the Odonata; Spence (1979) on the Gerridae; and Scudder and Mann (1968) on the Hirudinea. In general, the diversity of the lakes is inversely proportional to their salinity.
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<td>Round-up</td>
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<td>787.6</td>
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<td>7 179</td>
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<td>18 742</td>
<td>15 224</td>
<td>22 724</td>
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<td>(3 370-20 000)</td>
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<td>13 687</td>
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<td>1283.2</td>
<td>2.8</td>
<td>6 383</td>
<td>(4 000-12 000)</td>
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<td>9 807</td>
<td>12 072</td>
<td>12 427</td>
<td>13 493</td>
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<td>Long (Chilcotin)</td>
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<td></td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>9 232</td>
<td>13 848</td>
<td>12 215</td>
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<tr>
<td>Greer</td>
<td>15.17</td>
<td>156.8</td>
<td>1.0</td>
<td>1 848</td>
<td>(1 525-2 240)</td>
<td>6 329</td>
<td>3 923</td>
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<td>2 108</td>
<td>3 905</td>
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<td>(26 - 75)</td>
<td>39</td>
<td>49</td>
<td>203</td>
<td>128</td>
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B. GENERAL TECHNIQUES

1. Corixid Collection

Corixids for experiments were collected from Barnes Lake (high salinity) to ensure that they were unparasitized. Bugs were collected with an aquatic sweep net using a consistent sweeping technique for each collection. After a sweep was completed, the contents of the net were dispensed on to a white, dissecting tray to allow for easier identification. Adults were separated from nymphs and the adults that were required for an experiment were placed in insulated flasks with lake water and aquatic foliage for transportation to the laboratory. The remaining bugs were returned to the lake except some final instar nymphs that were kept and reared in wading pools at the lake edge to observe the last moult and subsequent sclerotization of teneral adults.

Identification of adult corixids was done mainly in the field, although closer scrutiny in the laboratory was necessary for some newly eclosed adult bugs. Extensive handling, especially of unsclerotized morphs, increases mortality. For this reason, handling was minimized. Identification of species was done according to the overall shape, size, and morph. If identification was still equivocal, then the number of hairs on the pala (distal leg segment) of the forelegs was examined as described in Jansson (1972).

Verification of morph and the corresponding wing muscle development was done by examining the darkening of the mesonotum.
according to Scudder (1971). For the pale, non-flying morphs, teneral specimens were used, up to early stage 2 of wing muscle development with only a slight beginning of darkening of the metathorax and abdominal segment 1. For the dark, flying morphs, only stage 6 individuals were used with entirely dark thoraces, and heavy darkening of at least abdominal segments 1 through 5. Non-flying individuals that appeared to have over-wintered were not used for experiments, nor were specimens that displayed full wing muscle development, but had yet to fully darken their anterior abdominal segments.

Over the summer, the two species’ abundances changed, as did the proportions of flying and non-flying morphs. Experiments were carried out as the numbers of each species and morph became large enough for easy collection. Experiments were started no more than 12 hours after collection.

Samples of corixids from the lake were taken to check for parasitism levels (see Methods Section D. 4 for dates). These corixids were kept alive at 5°C until examination because preservation in alcohol whitens the mites, causing them to be harder to see on light-coloured hosts. This makes determination of parasitism rates more time-consuming.

2. Mite Collection

Eggs of Eylais spp. were collected from Lakes Greer, Long, and Lye, and identified to species after rearing in the laboratory (See below). Oviposition occurred earlier in Lake
Greer than in Lake Lye or Long Lake which corresponded with general trends for the development of *Cenocorixa* spp. in these lakes. In Lake Greer, eggs of the genus *Eylais* were laid on unanchored strands of *Ruppia* sp. and *Zanichelia* sp. (water weeds) that collected on the surface around the lake edges. The eggs were found cemented to the long, tubular, grass-like strands in masses about 1 to 4 cm in length to a maximum diameter of 0.4 cm. The masses were orange and completely encircled the thin strands of vegetation. In contrast, the eggs of *E. discreta* were much brighter red when freshly laid and were found in masses up to 20 cm in length and 0.5 cm in diameter. In Long Lake and Lye Lake, eggs were found on the submerged stems of *Scirpus* spp. and *Juncus* spp.

Collection was facilitated by the fact that egg masses were always clumped on the reeds farthest from the shore, with many egg masses layered on top of each other on a relatively small number of reeds (5 to 20). The reeds were cut as far down the stem as possible, and then transported to the laboratory in lake water in insulated flasks. Egg masses were also found on submerged logs, rocks and other aquatic vegetation, but were not as easily located and collected.

The egg-laden vegetation was taken to a trailer at the Riske Creek Forestry Station that served as a laboratory. It was then transferred with the original lake water to transparent, plastic stacking dishes (diameter 25 cm by 10 cm depth). A close-fitting lid was placed on the stacking dishes and the water
level was kept so that the egg masses remained submerged. Through a hole in the lid, a small aeration tube was inserted and kept bubbling very gently throughout the incubation period. A 40 watt lightbulb, illuminated for 16 hours a day, was kept near the hatching eggs. Because larval mites are phototactic, the light was shone from below the stacking dishes so that on hatching, the larvae would not climb out of the dishes.

When hatching occurred, the mites could be seen as a red cloud at the bottom of the dish nearest to the light source. For identification purposes, mites were regularly examined under a compound microscope to ensure that only *E. euryhalina* was used for experiments. The length of the longitudinal furrows on the dorsal plate was used as the criterion for differentiating *E. euryhalina* from other species of the subgenus *Syneylais* following Smith (1986) (See Figure 4). The morphologically similar *Eylais (Syneylais) lancianii* Smith has been recorded in Lake Greer, but was not found in large numbers, and does not occur in Long Lake or Lake Lye where the majority of the mites were taken for experiments. Larval *Eylais (Eylais) discreta* are much larger than any of the species of the subgenus *Syneylais* and is easily differentiated from these with the naked eye.

To ensure that only live and active mites were used in all experiments, the light source was moved above the container just prior to host inoculation. A pipette was then used to withdraw only the mites that were gathering close to the water surface. This mite-infected water was placed in small drops on a waxed
Figure 4. Dorsal plates of larval mites of the genus Eylais found in British Columbia (adapted from Smith, 1986).

a. Eylais (Syneylais) euryhalina
b. Eylais (Syneylais) lancianii
c. Eylais (Syneylais) peutrilli (not recorded at Becher's Prairie)
d. Eylais (Eylais) discreta
dish facilitating counting of the mites under a dissecting microscope. The mites were transferred to the experimental water by submerging the dish.

3. Infection Experiments

Water for all experiments was gathered from the pond called Box 27 (< 300 μS cm⁻¹), Long Lake (10 000 to 15 000 μS cm⁻¹) or Barnes Lake (18 000 to 25 000 μS cm⁻¹). Water samples, taken periodically, were bottled and later tested for salinity with a Bach - Simpson™ conductivity meter. All experimental water was held in 10 gallon carbuoys for five or more days to kill any larval water mites that may have been present in the lake samples. In addition, water was strained just prior to the experiment using 44 μm Nitex™ netting. (Larval E. euryhalina are 50 μm wide.) Two litres of strained water were poured into a white plastic 4 litre ice cream bucket for each experiment. The experiments were run at 20 ± 2°C for 24 hours with 16 hours of light. A 12 cm by 12 cm piece of mosquito netting was placed in the bottom of the bucket on which the corixids could cling.

Once the appropriate number of E. euryhalina had been added to the water, the corixids were added. Care was taken that the various types of bugs were added to the water alternately so that there was no bias for one species, morph or sex of bug being exposed to the parasites for longer than any other. Equal numbers of males and females were used for all species and morphs in each experiment unless this was impossible because of an limited availability of one sex in collection. In these
cases, the nearest equal ratio of males and females was used and was never greater than a 60 percent bias towards one sex. After adding all corixids, a transparent lid was placed over the bucket to prevent exit of bugs or entry of other insects.

All experiments were run for 24 hours except the long-term experiments (See Methods, Section B.5). At the end of each experiment dead bugs were removed and placed in labelled, water-filled vials at 5°C. These bugs were not included in any analyses because they were not in contact with the mites in the same manner for the full 24 hours.

New, strained water was placed in a second bucket with netting in the bottom and the live post-experimental corixids were then moved to these containers by way of a wide-meshed net. Precautions were taken to prevent water from the experiment being transferred to the new water which ensured that only mites that were clinging to the corixids would be left in contact with their hosts past the experimental period. The corixids were then left at 20°C for a further 24 hours after which they were removed to 5°C and total darkness until analysis. Analysis was always done within 5 days of the conclusion of the experiment.

4. Analysis of Hosts from Infection Experiments

Infected corixids were examined with a dissecting microscope for attachment of mites and verification of sex, species, and degree of sclerotization. Those bugs that had died after the 24 hour exposure period, but prior to analysis were examined first.
The hemelytra and wings were lifted to allow examination of the wings, thoracic dorsum, and abdominal dorsum. The number and position of mites were recorded for each corixid. Terminology for corixid morphology was taken from the study of Parsons (1970) on *Hesperocorixa*. In addition to the position of mites on hosts, attachment of the mites was also determined.

Those mites that were walking around when the wings were moved, were recorded as unattached. Those that were not moving were examined more closely by lifting the abdomen of the mite to ensure that the mouthparts were inserted. If the abdomen could be lifted, while the cephalothorax remained in contact with the host, then the mite was considered attached. If the entire mite came free when the abdomen was moved, then the mite was considered unattached. In addition, mites that were obviously dessicated were considered unattached (for all practical purposes) as were ones in which the mouthparts could be seen as unattached.

For the 24 hour experiments, if there was any atypical degree of engorgement (i.e. more than a slight swelling), then the bug was discarded because of the suspicion that the attachment of the mite occurred in the field before collection. Additionally, if any *E. discreta* or *Hydrachna* spp. were present, then that particular bug was excluded from analyses. In Barnes Lake (where experimental bugs were collected), this occurred only on flying individuals that had flown in from lower salinity lakes and was very rare (less than 0.1 percent). Any time the
identification of a mite was at all uncertain, it was removed and examined under a compound microscope. Those corixids that were still alive at the time of analysis were killed prior to analysis. All bugs were then placed in vials of 95 percent alcohol, or for purposes of photography or mite identification, in Koenike’s solution (5 parts glycerine, 2 parts glacial acetic acid, 3 parts water).

5. Long-term Engorgement Experiments

To ensure that initial attachment of *E. euryhalina* led to the onset of engorgement, long-term experiments were conducted. Corixids were infected with *E. euryhalina* as in the 24 hour infection experiments. Immediately after 24 hour exposure, all bugs were taken out to small enclosures kept in Long Lake. It was decided to do all growth experiments in the lake instead of in the laboratory because the constant movement of water was better for corixid survival, and because lake experiments would be more indicative of actual growth in the field. In addition, all bugs were used, rather than only parasitized ones, because examination for parasites caused significant mortality of the corixids.

The enclosures were plastic basins of dimensions 30 cm by 35 cm and 12 cm deep. Lake water could pass into these basins through windows cut in opposite ends of the basins: 44 µm Nitex™ netting over these windows allowed water to enter, but kept mites and additional food out. A close-fitting lid of mosquito netting was kept over the enclosures to prohibit entry
or exit of bugs. Each enclosure was held in a wooden base weighted to the lake bottom and positioned at the lake edge so that the water level of the basin was half full.

On each day of the experiment, corixids were fed with copepods (Diaptomus spp.) from Barnes Lake. Individuals that had died in the previous 24 hours were removed and taken to the laboratory for analysis. After the allotted experimental period (6 or 8 days), all corixids were taken from the field and analysed immediately in the laboratory. The duration of the experiment was chosen because mortality proved to be too high if done for 10 or more days (based on preliminary experiments in 1990). Also, after 6 to 8 days, a measurable level of engorgement had already occurred. Experimental bugs were killed at two different times so that sample sizes of infected, engorging mites would be large enough to render average sizes of engorgement for both 6 and 8 days post-infection.

6. Lake Sampling for Parasitism

Samples of both flying and non-flying C. bifida and C. expleta were collected from Long Lake and Lye Lake (See Methods Section D.4 for dates). As well, collections from Round-up Lake and Barnes Lake were done to ensure that no parasites were present, while Lake Greer and Near Opposite Crescent Pond were sampled to determine if other parasites apart from E. euryhalina were present at lower salinities. All sampling was done in the same manner as described in Methods Section B.1 (General
Techniques: Corixid Collection) and whenever possible, collections were made at the same location every time. Analysis of parasitism was also similar to the infection experiments, so that lake sample data could be compared to the experiments.

C. Parasitism Parameters

1. Measures of quantity of mites.

The rates used to quantify differences in the numbers of mites between host types were chosen to correspond with previous studies of mites on water boatmen (Harris and Harrison, 1974; Smith, 1977; Reilly and McCarthy, 1991), and to follow the recommendations of Margolis et al. (1982) regarding usage of terms in parasitological studies. Prevalence is the proportion of hosts in any given population that are parasitized. Abundance is the average number of mites on each host. They were calculated as follows:

\[
\text{Prevalence} = \frac{\text{Bugs Parasitized}}{\text{Total Bugs}} \times 100
\]

\[
\text{Abundance} = \frac{\text{Total Mites}}{\text{Total Bugs}}
\]

In each experiment, replicates were performed and the average values of prevalence and abundance for the replicates were used for statistical analysis.

Prevalence and abundance are measures that include all of the mites found on the hosts, regardless of whether they are unattached, attached, or engorging. These two rates are, therefore, the measures of recruitment of mites to their hosts,
but do not take into account the potential effect that a mite may later have on its host. Nevertheless, I deemed it important to measure mite recruitment between host types, because I wanted to know if the cause of *C. expleta*'s exclusion was because it initially attracted more mites than *C. bifida*.

I also wished to measure initial mite attachment on each host type. By excluding mites that were obviously unattached, I calculated prevalence (attached only) and abundance (attached only). These parameters were calculated as follows:

\[
\text{Prevalence} = \frac{\text{Bugs with Attached Mites}}{\text{Total Bugs}} \times 100
\]

\[
\text{Abundance} = \frac{\text{Attached Mites}}{\text{Total Bugs}}
\]

By analyzing these parameters, I sought to determine whether *C. expleta*'s exclusion was a result of mites being able to attach to it more easily than to *C. bifida*.

Finally, one of my experiments allowed the mites to engorge over 6 days (see Material and Methods: Part D.3). For the engorgement data, additional rates were calculated: prevalence (engorging only) and abundance (engorging only) as follows:

\[
\text{Prevalence} = \frac{\text{Bugs with Engorging Mites}}{\text{Total Bugs alive after 3 days}} \times 100
\]

\[
\text{Abundance} = \frac{\text{Engorging Mites}}{\text{Total Bugs alive after 3 days}}
\]

* Because some bugs died before engorgement could commence (i.e. 3 days), it was not valid to include all hosts in calculations of prevalence (engorging only) and abundance (engorging only). (Inclusion of all hosts in calculations would class the hosts...
that died prior to 3 days as negative with respect to mite engorgement, despite not knowing if these mites would have engorged or not.)

Analysis of prevalence (engorged only) and abundance (engorged only) allowed me to determine whether *C. expleta*’s exclusion was related to the ability of mites to engorge more easily on it than on *C. bifida*.

2. Measures of Location of Mites

Recall from the Introduction (hypothesis 2b), that the quantity of mites is not the only factor involved in determining if mites are having a greater effect on one host type. Only in uncrowded situations will all mites be able to engorge, so that size of a host’s susceptible area is important. Comparing the location of mite attachment between host types allowed me to determine if one host type presented a larger area for attachment.

The areas of the hosts’ body where attachment occurred are shown in Figure 5. The susceptible areas were then subdivided into regions (see Figure 6). Numbering of abdominal segments followed Parsons (1970). Both the thoracico-abdominal membranes (T.A.M.) and the anterior edge of each abdominal tergum were apparently used for attachment more often than would have been randomly expected. For this reason, the T.A.M. (both right and left) was considered as a separate area for analysis, as were the anterior edges of each abdominal tergum. I named the anterior edges with respect to the two adjoining terga, thus
Figure 5. Recorded areas of attachment by *E. euryhalina* on *Cenocorixa* spp.
Figure 6. Divisions used to plot attachment of *E. euryhalina* on the terga of *Cenocorixa* spp.
A.S. 1-2 is the anterior edge of abdominal tergum 2, situated just posterior and partially underneath the posterior edge of abdominal tergum 1. To calculate which regions had the greatest attachment, I analyzed each bug separately and then summed all the attachment records in the replicate. I then knew the total number of mites that had attached to each host region for each replicate. To standardize these data, I then converted the numbers of mites in each region to a percentage of total mites in the replicate as follows:

\[
\text{Percent of Mites in Area} = \frac{\text{Mites Attached in Area}}{\text{Total Mites Attached}} \times 100
\]

The results of all replicates were then averaged.

To statistically test differences in mite attachment between host treatments, I decided to study attachment to the T.A.M. because it is the only morphologically conservative region in all 4 host types. (It is constant in terms of size and sclerotization.) Differences in attachment to the T.A.M. should, therefore, be a good indicator of differences in overall attachment patterns between host treatments. While comparing only one area does not account for differences in all regions, it approximates attachment differences overall because most of the variability in attachment between host types was found in the T.A.M. (See Results). A further \( \chi^2 \) analysis was performed on the 6 to 8 day attachment and engorgement data to determine if attachment of mites was more on the left, centre or right portions of the hosts' body.
3. Statistical Testing

All statistical tests were done using Systat™. For all data in percentage form, percentages were changed to proportions and arcsine transformed before analysis. Paired t-tests were used whenever comparing experiments in which two host types were inoculated with mites together (i.e. in the same bucket). Other tests used are as stated in the Results. For graphical and statistical analysis of the location of attachment, unnatached mites were not included.

D. EXPERIMENTS AND FIELD SAMPLES

1. Initial Mite Recruitment and Attachment (1 day)

Of the 5 questions asked in the Introduction, the first 3 pertained to the initial stages of the mite-corixid interaction. Questions 1 and 2 were answered by Experiment 1 (moderate salinity) while question 3, regarding the role of salinity in the exclusion of C. expleta, was answered by a similar experiment done at low salinity (Experiment 5), and another test at high salinity (Experiment 6).

In Experiment 1, larval E. euryhalina were offerered equal numbers of each of the four host types in moderate salinity water. It was then possible to study both the effects of host species (Question 1) and host sclerotization (Question 2) on initial mite attachment. By using lake water from Long Lake (10 000 to 15 000 μS cm⁻¹), I was able to test the attachment of mites at the highest salinity from which C. expleta is excluded.
This could then be compared with a similar experiment at low salinity to ensure that the effects of mites are the same throughout the regime of *C. expleta*’s exclusion (Question 3). Recall from the Introduction:

**Question 1.** Does *species* of host affect a.) quantity of initial mite attachment and b.) location of initial mite attachment?

**Question 2.** Does host *sclerotization* (wing morph) affect a.) quantity of initial mite attachment and b.) location of initial mite attachment?

The design of Experiment 1 was as follows:

**Experiment 1:** (2 replicates)

<table>
<thead>
<tr>
<th>Corixids</th>
<th>Mites</th>
<th>Salinity</th>
</tr>
</thead>
<tbody>
<tr>
<td>30 <em>C. bifida</em> teneral non-flying</td>
<td>600 mites</td>
<td>Moderate (10 000 to 15 000 μS cm⁻¹)</td>
</tr>
<tr>
<td>30 <em>C. bifida</em> flying</td>
<td></td>
<td></td>
</tr>
<tr>
<td>30 <em>C. expleta</em> teneral non-flying</td>
<td></td>
<td></td>
</tr>
<tr>
<td>30 <em>C. expleta</em> flying</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

From Experiment 1, six sets of data were collected to answer the various parts of question 1 and 2. The six questions were as follows:

**1a.** Does host *species* affect quantity of initial mite recruitment?

**1b.** Does host *species* affect location of initial mite attachment?
2a. Does host sclerotization affect quantity of initial mite recruitment?

Does host sclerotization affect quantity of initial mite attachment?

2b. Does host sclerotization affect location of initial mite attachment?

Note that questions 1a and 2a have two parts, firstly comparing mite recruitment and then mite attachment. (For simplicity, the hypotheses and questions in the Introduction were stated in terms of attachment only.)

For each of the questions above, a data set was collected and compared to the expected results (based on the hypotheses in the Introduction).

1a. Does host species affect quantity of initial mite recruitment?

Data collected:

Prevalence and abundance of mites were compared between C. bifida and C. expleta (regardless of host sclerotization).

Expected results:

Prevalence and abundance of E. euryhalina on C. expleta is greater than on C. bifida.

Analysis:

Greater initial recruitment of mites to C. expleta is at least partially responsible for C. expleta’s exclusion from low salinity.
Does host species affect quantity of initial mite attachment?

Data collected:
Prevalence (attached only) and abundance (attached only) were compared between *C. bifida* and *C. expleta* (regardless of host sclerotization).

Expected results:
Prevalence (attached only) and abundance (attached only) of *E. euryhalina* on *C. expleta* is greater than on *C. bifida*.

Analysis:
Greater initial attachment of mites on *C. expleta* is at least partially responsible for *C. expleta*’s exclusion from low salinity.

Question 1b: Does host species affect location of initial mite attachment?

Data collected:
Percentage of total mites collected that attach on the T.A.M. was compared between *C. bifida* and *C. expleta* (regardless of host sclerotization).

Expected result:
There is no significant difference in the percentages of attached mites on the T.A.M. between *C. expleta* and *C. bifida*.

Analysis:
Since there was no difference in the location of mite attachment between host species, this factor is not important in the exclusion of *C. expleta* from low salinity.
Question 2a: Does host sclerotization affect quantity of initial mite recruitment?

Data collected:

Prevalence and abundance were compared between non-flying (non-sclerotized) and flying (sclerotized) hosts (regardless of host species).

Expected result:

Prevalence and abundance of mites is greater on non-flying hosts than flying hosts.

Analysis:

Lack of sclerotization causes higher recruitment of mites compared to sclerotized hosts. Since C. expleta is predominantly unsclerotized in the field, this condition is important in C. expleta’s exclusion from low salinity.

Does host sclerotization affect quantity of initial mite attachment?

Data collected:

Prevalence (attached only) and abundance (attached only) were compared between non-flying hosts and flying hosts (regardless of host species).

Expected results:

As for the effect of sclerotization on initial mite recruitment.

Analysis:

As above.
Question 2b: Does host sclerotization affect location of mite attachment?

Data collected:
Percentage of total mites collected that attach on the T.A.M was compared between non-flying hosts and flying hosts (regardless of host species).

Expected results:
On flying (sclerotized) hosts, all mites attach to the T.A.M., whereas on non-flying (unsclerotized) hosts, attachment is possible over the entire area of the host dorsum.

Analysis:
Sclerotization of the host reduces the surface area available for mite attachment. Since *C. bifida* is predominantly sclerotized in the field, it is less susceptible to mite parasitism than *C. expleta* which is mainly unsclerotized.

To replicate the results of Experiment 1, three further experiments were run using only 2 of the potential hosts. While it would have been ideal to perform Experiments 2, 3, and 4 with a total of 120 corixids and 600 mites per replicate (as in Experiment 1), the numbers of *E. euryhalina* hatching at any one time constrained this. Each replicate was accordingly halved in size with 60 bugs total and only 300 mites.

Experiments 2 and 3 held host sclerotization constant, and were thus only concerned with testing for the effect of host species on quantity and location of mites (Question 1). The
designs were as follows:

Experiment 2: (2 replicates)

<table>
<thead>
<tr>
<th>Mites</th>
<th>30 C. bifida teneral non-flying</th>
<th>30 C. expleta teneral non-flying</th>
</tr>
</thead>
<tbody>
<tr>
<td>300 mites</td>
<td>300 mites</td>
<td></td>
</tr>
<tr>
<td>Moderate</td>
<td>(10,000 to 15,000 μS cm⁻¹)</td>
<td></td>
</tr>
</tbody>
</table>

Experiment 3: (2 replicates)

<table>
<thead>
<tr>
<th>Mites</th>
<th>30 C. bifida flying</th>
<th>30 C. expleta flying</th>
</tr>
</thead>
<tbody>
<tr>
<td>300 mites</td>
<td>300 mites</td>
<td></td>
</tr>
<tr>
<td>Moderate</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Experiment 4 held host species constant, and was only concerned with testing for the effect of host sclerotization (Question 2).

The design was as follows:

Experiment 4: (2 replicates)

<table>
<thead>
<tr>
<th>Mites</th>
<th>30 C. expleta teneral non-flying</th>
<th>30 C. expleta flying</th>
</tr>
</thead>
<tbody>
<tr>
<td>300 mites</td>
<td>300 mites</td>
<td></td>
</tr>
<tr>
<td>Moderate</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The data collected from these experiments were tested in exactly the same manner against the hypotheses of question 1 and 2.

2. Effect of Salinity

Question 3 of the Introduction dealt with the effect of salinity on the exclusion of C. expleta.

3.) Does salinity affect a.) quantity of mites initially attaching and b.) where mites initially attach?

The first part of hypothesis 3a. dealt exclusively with low salinity and this factor was studied in Experiment 5. The experiment was the same as Experiment 1 except for salinity.
Experiment 5: (2 replicates)

<table>
<thead>
<tr>
<th>Corixids</th>
<th>Mites</th>
<th>Salinity</th>
</tr>
</thead>
<tbody>
<tr>
<td>30 C. bifida teneral non-flying</td>
<td>600 mites</td>
<td>Low (&lt; 300 μS cm⁻¹)</td>
</tr>
<tr>
<td>30 C. bifida flying</td>
<td></td>
<td></td>
</tr>
<tr>
<td>30 C. expleta teneral non-flying</td>
<td></td>
<td></td>
</tr>
<tr>
<td>30 C. expleta flying</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The following data were collected to answer the various parts of question 3 at low salinity.

Question 3a (low salinity). Does low salinity affect quantity of initial mite recruitment?

Data collected:

Prevalence and abundance were compared between host types and between salinities (for similar host types).

Expected Result:

Prevalence and abundance show the same differences between host types at moderate and low salinity. From hypothesis 1a, C. expleta will have more mites recruiting to it than C. bifida at both moderate and low salinities. From hypothesis 2a, non-flying hosts will have more mites recruiting to them than flying hosts at both salinities.

Analysis:

Low salinity does not affect the quantity of mites recruiting to different hosts compared to moderate salinity.
Does low salinity affect quantity of initial mite attachment?  
Data collected:  
Prevalence (attached only) and abundance (attached only) were compared between hosts and between moderate and low salinities.  
Expected result:  
As above for initial mite recruitment.  
Analysis:  
Low salinity does not affect the quantity of mites attaching to different hosts compared to moderate salinity.  

Question 3b (low salinity). Does low salinity affect location of initial mite attachment?  
Data collected:  
Percentage of total mites attaching on the T.A.M. was compared between host species and between moderate and low salinity.  
Expected Result:  
Percentage of total mites attaching on the T.A.M. shows the same differences between host types at moderate and low salinity. From hypothesis 1b, there is no difference in location of mite attachment between C. bifida and C. expleta at both moderate and low salinity. From hypothesis 2b, significantly more mites attach to the T.A.M. of the flying hosts than the non-flying at both salinities.  
Analysis:  
Low salinity does not affect the location of mite attachment, with respect to moderate salinity.
High salinity:

The same questions were asked of high salinity, but because the expected result from hypothesis 3 was that no mites would attach, this experiment was done with only 2 hosts and half the number of mites. (It was much harder to set up an experiment with 4 hosts.) The results were then compared to the similar experiment performed at moderate salinity (Experiment 2).

The design was as follows:

Experiment 6: (2 replicates)

<table>
<thead>
<tr>
<th>Corixids</th>
<th>Mites</th>
<th>Salinity</th>
</tr>
</thead>
<tbody>
<tr>
<td>30 C. bifida non-flying</td>
<td>300 mites</td>
<td>18 000 to 25 000 µS cm⁻¹</td>
</tr>
<tr>
<td>30 C. expleta non-flying</td>
<td></td>
<td>High</td>
</tr>
</tbody>
</table>

Question 3a (high salinity). Does high salinity affect quantity of initial mite recruitment?

Expected Result:

Prevalence and abundance are significantly lower (approaching 0 %) at high salinity compared to moderate.

Analysis:

High salinity decreases the quantity of initial mite recruitment (compared to moderate salinity).
Does high salinity affect quantity of initial mite attachment?

Expected Result:

Prevalence (attached only) and abundance (attached only) are significantly lower (approaching 0 %) at high salinity compared to moderate.

Analysis:

High salinity decreases the quantity of initial mite attachment (compared to moderate salinity).

Question 3b (high salinity). Does high salinity affect location of initial mite attachment?

Since it is predicted that prevalence of mites at high salinity approaches 0 %, a comparison of location of mite attachment is not necessary.

3. Mite Engorgement Study (6 to 8 days)

Question 4 of the Introduction was concerned with mite engorgement.

4.) When does the effect of mites occur, or more specifically does the effect occur initially and/or during mite engorgement for a.) quantity of mites and b.) location of mites?

Experiments 1 through 4 dealt with the initial effect of mites on different host types at moderate salinity. Experiment 7 studied the effects of mite engorgement at moderate salinity over 6 to 8 days. While it would have been ideal to do Experiment 7 with all four host types, time constraints did not
allow this. In addition, teneral, non-flying C. bifida harden very quickly creating problems in the analysis of engorgement of mites on flying versus non-flying morphs. I chose, therefore, to use flying C. bifida, and non-flying C. expleta, because these two morphs were most abundant in their natural populations and consequently, most important to study for the effects of mite parasitism on the exclusion of C. expleta. The design was as follows:

Experiment 7: (4 replicates)

<table>
<thead>
<tr>
<th>Corixids</th>
<th>Mites</th>
<th>Salinity</th>
</tr>
</thead>
<tbody>
<tr>
<td>60 C. bifida flying</td>
<td>600 mites</td>
<td>Moderate</td>
</tr>
<tr>
<td>60 C. expleta non-flying</td>
<td></td>
<td>(10 000 to 15 000 μS cm⁻¹)</td>
</tr>
</tbody>
</table>

Two of the replicates were kept in Long Lake for 6 days after the initial 24 hours, while the other two replicates were kept for 8 days so that size of engorged mites could be compared at these times.

The following data were collected to answer the various parts of question 4.

Question 4a: Does host affect the quantity of mite attachment over 6 to 8 days?

Data collected:

Prevalence (attached only) and abundance (attached only) of mites were compared between flying (sclerotized) C. bifida and non-flying (non-sclerotized) C. expleta.
Expected results:
More mites are able to attach on non-flying *C. expleta* than on flying *C. bifida* over 6 to 8 days.

Analysis:
The predominant morph of *C. expleta* is more susceptible to mite attachment than the predominant morph of *C. bifida* over 6 to 8 days.

Does host affect **quantity** of mite **engorgement** over 6 to 8 days?

Data collected:
Prevalence (engorged only) and abundance (engorged only) were compared between flying *C. bifida* and non-flying *C. expleta*.

Expected results:
As for the effect of host on quantity of mite attachment.

Analysis:
As above.

Question 4b: Does host affect **location** of mite **attachment** over 6 to 8 days?

Data collected:
Percentage of total mites collected that attach on the T.A.M. was compared between flying *C. bifida* and non-flying *C. expleta* over 6 to 8 days.

Expected results:
On flying *C. bifida* all mites attach on the T.A.M., whereas on non-flying *C. expleta*, mites attach over the entire dorsum.
Analysis:

Sclerotization of the host reduces the surface area available for mite attachment. Since *C. bifida* is predominantly sclerotized in the field, it is less susceptible to mite parasitism over 6 to 8 days than *C. expleta* which is mainly unsclerotized.

Does host affect location of mite engorgement over 6 to 8 days?

Data collected:

Percentage of total mites collected that engorge on the T.A.M. was compared between flying *C. bifida* and non-flying *C. expleta*.

Expected results:

As for the effect of host on the location of mite attachment.

Analysis:

As above.

4. Field Studies.

Corixids were sampled throughout the summer at lakes of varying salinity. Lakes to be sampled were chosen based on the parasitological data of Smith (1977) to give an overview of the mite-corixid interaction over a wide salinity range.

Corixids were collected for 3 reasons:

1.) To ensure that laboratory experiments were representative of field infections with respect to the quantity and location of *E. euryhalina* on its hosts (question 5).
2.) To determine the relative proportions of *C. bifida* and *C. expleta* in lakes (demonstrating that mites are excluding *C. expleta* where they are present).

3.) To determine the relative proportions of flying and non-flying *Cenocorixa* spp. (demonstrating that the sclerotization of the host is related to the presence of mites).

Samples were made in the following lakes and on the following dates:

<table>
<thead>
<tr>
<th>Water body</th>
<th>Date</th>
<th>Salinity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Near Opposite Crescent Pond</td>
<td>September 14, 1991</td>
<td>Low moderate</td>
</tr>
<tr>
<td></td>
<td></td>
<td>4 261 µS cm⁻¹</td>
</tr>
<tr>
<td>Long Lake</td>
<td>June 2, 1991</td>
<td>Moderate</td>
</tr>
<tr>
<td></td>
<td>July 17, 1991</td>
<td>11 220 to 13 848 µS cm⁻¹*</td>
</tr>
<tr>
<td></td>
<td>September 13, 1991</td>
<td>12 215 µS cm⁻¹</td>
</tr>
<tr>
<td>Lake Lye</td>
<td>October 21, 1990</td>
<td>Moderate</td>
</tr>
<tr>
<td></td>
<td>June 2, 1991</td>
<td>11 788 to 13 493 µS cm⁻¹*</td>
</tr>
<tr>
<td></td>
<td>August 17, 1991</td>
<td>11 788 µS cm⁻¹</td>
</tr>
<tr>
<td></td>
<td>September 13, 1991</td>
<td>13 493 µS cm⁻¹</td>
</tr>
<tr>
<td></td>
<td></td>
<td>High</td>
</tr>
<tr>
<td>Barnes Lake</td>
<td>August 14, 1991</td>
<td>18 464 to 19 528 µS cm⁻¹*</td>
</tr>
<tr>
<td>Round-up Lake</td>
<td>August 14, 1991</td>
<td>18 820 to 21 304 µS cm⁻¹*</td>
</tr>
</tbody>
</table>

* Water samples were not taken on these days of corixid sampling, so the ranges found in that year are given instead.
1.) Comparison of field parasitism and laboratory parasitism.

Question 5.) Are the data collected from one- and six-day laboratory experiments representative of mite parasitism in populations of field collected corixids for a.) quantity of mites and b.) location of mites?

Of all the field samples, only July 17 (Long Lake), October 21 (Lake Lye), August 17 (Lake Lye), and September 13 (Lake Lye), yielded enough parasitological data for analysis. Smith (1977) gives a much more thorough account of the overall parasitism rates for *C. bifida* and *C. expleta* in a number of lakes.

The following data were collected to answer the various parts of question 5.

Question 5a: Are laboratory experiments representative of the quantity of mites attaching on field collected corixids?

Data collected:

Prevalence (attached only) and abundance (attached only) were compared between field collected host types and then compared to similar values for initial (1 day) and long-term (6 day) laboratory experiments.

Expected results:

Relative quantities of mites attaching on hosts are the same in the field and the laboratory.

Analysis:

One- and 6-day mite attachment studies in the laboratory are
representative of mite attachment occurring in the field with respect to quantities of mites.

Question 5b: Are laboratory experiments representative of the location of mites attaching on field collected corixids?

Data collected:

Percentage of total mites attached on the T.A.M. was compared between field collected host types and then compared to similar values for initial (1-day) and long-term (6-day) laboratory experiments.

Expected results:

In field collections, location of mite attachment is the same as in laboratory experiments on non-sclerotized C. bifida and non-sclerotized C. expleta (mites attach all over the dorsum). Location of mite attachment on sclerotized C. bifida and C. expleta differs between field collections and laboratory experiments. In the laboratory experiments, these hosts are predicted to have attachment only on the T.A.M. In the field, they are predicted to have attachment all over the dorsum.

Analysis:

Location of mite attachment on the non-sclerotized C. bifida and C. expleta is the same in the field and laboratory because these hosts offer an entire unsclerotized dorsum to the mites whether they are in a laboratory experiment or collected from the field. The sclerotized field-collected hosts exhibit different mite attachment from laboratory experiments because in the laboratory, the attachment of mites occurs after
sclerotization (by design) causing all mites to attach on the T.A.M. In the field, however, attachment may occur prior, during or after sclerotization. Mite attachment prior to sclerotization could occur anywhere on the host's dorsum causing the difference in predicted attachment patterns between field and laboratory infected sclerotized hosts. Laboratory experiments are not always representative of location of mite attachment in the field.

2.) Proportions of *C. bifida* compared to *C. expleta*.

Since the salinities of the lakes have changed since the study of Smith (1977), the relationship between salinity, mites, and corixids was re-examined. This was done by noting the salinities at which mites are present (See Appendix 1), and the relative percentages of *C. bifida* and *C. expleta* in the studied lakes (see Results). *C. bifida* should be predominant where mites are present, whereas *C. expleta* should predominate above the salinity at which mites exist.

3.) Proportions of flying and non-flying *Cenocorixa* spp.

Since the proportions of flying and non-flying morphs of *Cenocorixa* spp. change over time (Scudder, 1975), it was necessary to determine what forms were predominant in 1990 and 1991 (See Results). Based on previous collections, it was predicted that *C. bifida* should be predominantly flying, whereas *C. expleta* should be predominantly non-flying.
RESULTS

A. Initial Mite Recruitment and Attachment (Moderate Salinity).

1. Effect of Host Species.

Question 1a. Does host species affect quantity of initial mite recruitment?

Data collected:

In Experiment 1 (Table 5) with all four host types, prevalence of *E. euryhalina* was not significantly different between *C. bifida* and *C. expleta* (Two-way ANOVA, grouped by host species: $F = 0.200, P = 0.678$). In Experiment 2 with non-flying hosts only (Table 6) there was also no significant difference, $t = -1.230$, $(P = 0.435)$, and neither was there in Experiment 3 with flying hosts only (Table 7) ($t = -1.849$, $P = 0.316$). Abundance was also not significantly different between host species in Experiments 1, 2, and 3.

Summary:

In 24 hour laboratory experiments, host species did not affect quantity of mite recruitment.

Does host species affect quantity of initial mite attachment?

Data collected:

For Experiment 1 (Table 5), prevalence (attached only) of *E. euryhalina* was not significantly different between *C. bifida* and *C. expleta* (Two-way ANOVA, grouped by host species: $F = 0.001, P = 0.976$). Experiment 2 (non-flying hosts only) followed the same trend ($t = -1.760$, $P = 0.329$) (Table 6), as did experiment 3 with flying hosts only ($t = 0.909$, $P = 0.530$) (Table 7).
Abundance (attached only) followed the same trend.

Summary:

In 24 hour laboratory experiments, host species did not affect the quantity of mites attachment.

Question 1b: Does host species affect location of initial mite attachment?

Data collected:

In experiment 1, the percentage of total mites that attached on the T.A.M. was not significantly different between C. expleta and C. bifida (Two-way ANOVA, grouped by host species: F = 0.174, P = 0.698) (see Figure 7). Neither was Experiment 3 for flying hosts only (t = -5.798, P = 0.109) (see Figure 9). Experiment 2, however, had a significantly higher percentage of the collected mites attached on the T.A.M. of non-flying C. bifida compared to non-flying C. expleta (t = 145.4, P = 0.004) (see Figure 8). An overview of the host types shows that flying C. bifida and flying C. expleta had a consistently high proportion of mites initially attaching on the T.A.M., whereas C. expleta non-flying had a consistently low proportion. C. bifida non-flying had attachment proportions on the T.A.M. that were variable and intermediate between the flying hosts and non-flying C. expleta. This variance in the attachment patterns of mites on non-flying C. bifida was consistent throughout all experiments.

Summary:
On the flying hosts, species of host did not appear to affect the location of attachment of mites (Experiments 1 and 3). On the non-flying hosts, the variance in the attachment patterns of mites on non-flying C. bifida precluded a definite answer of this question (Experiments 1 and 2).

2. Effect of Host Sclerotization.

Question 2a: Does host sclerotization affect quantity of initial mite recruitment?

Data collected:

In Experiment 1 (Table 5), prevalence of E. euryhalina was not significantly different between non-flying (non-sclerotized) and flying (sclerotized) hosts (Two-way ANOVA, grouped by host sclerotization, $F = 0.010$, $P = 0.925$). The same was true for Experiment 4 (Table 8) with only C. expleta (t = 0.326, $P = 0.799$). Abundance was also not significantly different between non-flying and flying hosts in Experiments 1 and 4.

Summary:

In 24 hour laboratory experiments, host sclerotization did not affect quantity of mite recruitment.

Does host sclerotization affect quantity of initial mite attachment?

Data collected:

In Experiment 1 (Table 5), prevalence (attached only) of E. euryhalina was not significantly different between non-flying and flying hosts (Two-way ANOVA, grouped by host sclerotization,
F = 0.617, P = 0.476). The same trend was found in Experiment 4 with only C. expleta (t = 1.049, P = 0.485) (Table 8). Abundance (attached only) was also not significantly different between host species in Experiments 1 and 4.

Summary:

In 24 hour laboratory experiments, host sclerotization did not affect quantity of mite attachment.

Question 2b: Does host sclerotization affect location of initial mite attachment?

Data collected:

In experiment 1, the percentage of total mites that attached on the T.A.M. was significantly different between non-flying and flying hosts (Two-way ANOVA, grouped by host sclerotization: F = 34.001, P = 0.004) (see Figure 7). So was Experiment 4 with only C. expleta (t = -57.079, P = 0.011) (see Figure 10). Flying hosts had a high percentage of mites attached on the T.A.M., whereas non-flying hosts had a low percentage, with most mites attaching on the centres (laterally) of abdominal terga 2, 2-3, and 3.

Summary:

Host sclerotization affected the location of initial mite attachment. Mites on sclerotized hosts attached almost exclusively on the T.A.M., whereas mites on unsclerotized hosts were all over the dorsum.
Table 5. Experiment 1. Parasitism rates for quantity of mites associated with all 4 host types over 24 hours at moderate salinity (10 000 to 15 000 $\mu$S cm$^{-1}$). All parasitism rates show no significant difference between hosts. For statistical analyses, see text.
Figure 7. Experiment 1. Location of mite attachment on all host types at moderate salinity (10,000 to 15,000 μS cm⁻¹), plotted as a percent of total mites collected on each host type. Numbers of mites in boxes are attached mites only (per replicate) associated with number of bugs directly below. Error bars are standard error.

LOCATION OF ATTACHMENT as measured by percent of total mites on T.A.M.

Two-way ANOVA, grouped by host species: F = 0.174, P = 0.698

Two-way ANOVA, grouped by host sclerotization: F = 34.001, P = 0.004
Figure 8. Experiment 2. Location of mite attachment on non-flying hosts at moderate salinity (10 000 to 15 000 μS cm\(^{-1}\)) plotted as a percent of total mites collected on each host type. Numbers of mites in boxes are attached mites only (per replicate) associated with number of bugs directly below. Error bars are standard error.

Table 6. Experiment 2. Parasitism rates and statistical analyses for quantity and location of mites associated with non-flying hosts over 24 hours.
Figure 9. Experiment 3. Location of mite attachment on flying host types at moderate salinity (10 000 to 15 000 μS cm⁻¹), plotted as a percent of total mites collected on each host type. Numbers of mites in boxes are attached mites only (per replicate) associated with number of bugs directly below. Error bars are standard error.

Table 7. Experiment 3. Parasitism rates and statistical analyses for quantity and location of mites associated with flying hosts over 24 hours.
Figure 10. Experiment 4. Location of mite attachment on C. expleta (non-flying and flying) at moderate salinity (10 000 to 15 000 μS cm⁻¹), plotted as a percent of total mites collected on each host type. Numbers of mites in boxes are attached mites only (per replicate) associated with number of bugs shown directly below. Error bars are standard error.

Table 8. Experiment 4. Parasitism rates and statistical analyses for quantity and location of mites associated with C. expleta (non-flying and flying) over 24 hours.
B. Initial Mite Recruitment and Attachment: Low and High Salinity

1. Low salinity.

Question 3a (low salinity). Does low salinity affect quantity of initial mite recruitment?

Data collected:

High mortality of flying C. expleta in Experiment 5 did not permit analysis of this host type, but prevalence of mites at low salinity did not differ between the remaining three host types (F = 5.704, P = 0.095) (Table 9). Abundance followed the same trend. Comparing prevalences of these hosts at low salinity with the same hosts at moderate salinity (Experiment 1) revealed no effect attributable to salinity (Two-way ANOVA, grouped by salinity: F = 1.177, P = 0.320).

Summary:

Low salinity does not affect the quantity of initial mite recruitment (compared to moderate salinity).

Does low salinity affect quantity of initial mite attachment?

Data collected:

Prevalence (attached only) in Experiment 5 (Table 9) was not significantly different between host types at low salinity (F = 1.706, P = 0.320). Comparing the same host types at moderate salinity showed that there was no effect because of low salinity on prevalence (attached only) (Two-way ANOVA, grouped by salinity: F = 1.320, P = 0.294).
Summary:

Low salinity does not affect quantity of initial mite attachment (relative to moderate salinity).

Question 3b (low salinity). Does low salinity affect location of initial mite attachment?

Data collected:

Percentage of total mites attaching on the T.A.M. was greater on flying *C. bifida* compared to non-flying *C. bifida* and non-flying *C. expleta* ($F = 110.65$, $P < 0.001$) (Figure 11).¹ An analysis of the location of mite attachment on the three host types at moderate and low salinity showed no salinity effect (Two-way ANOVA, grouped by salinity: $F = 3.701$, $P = 0.103$).

Summary:

Low salinity did not affect the location of initial mite attachment (relative to moderate salinity).

2. High salinity:

Question 3a (high salinity). Does high salinity affect quantity of initial mite recruitment?

Data collected:

Prevalence was significantly lower on non-flying *C. bifida* and non-flying *C. expleta* at high salinity (Experiment 6, Table

¹The attachment of mites on one replicate of flying *C. expleta* is shown in Figure 11 for graphical comparison only. These data were not used for any statistical analysis.
10) compared to moderate salinity (Experiment 2, Table 6) (Two-way ANOVA, grouped by salinity: F = 94.794, P = 0.001). Although mite recruitment was minimal at high salinity, it did occur. Abundance was also significantly lower at high salinity compared to moderate salinity.

Summary:
High salinity decreased the quantity of initial mite recruitment (with respect to moderate salinity).

Does high salinity affect the quantity of initial mite attachment?

Prevalence (attached only) was significantly less on hosts at high salinity (Table 10) than at low salinity (Table 6) (Two-way ANOVA, grouped by salinity: F = 87.199, P = 0.001). Abundance (attached only) followed the same trend.

Summary:
High salinity decreased the quantity of initial mite attachment (with respect to moderate salinity).

Question 3b (high salinity). Does high salinity affect location of initial mite attachment?

Very low attachment of mites at high salinity made this question unanswerable.
Table 9. Experiment 5. Parasitism rates for quantity of mites associated with all 4 host types over 24 hours at low salinity (< 300 µS cm⁻¹). All parasitism rates show no significant difference between hosts. For statistical analyses with moderate salinity (Experiment 1), see text.

<table>
<thead>
<tr>
<th></th>
<th>C. bifida</th>
<th>C. bifida</th>
<th>C. expleta</th>
<th>C. expleta</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>non-flying</td>
<td>flying</td>
<td>non-flying</td>
<td>flying</td>
</tr>
<tr>
<td>PREVALENCE (+/−S.E.)</td>
<td>73.3 (+/−3.55)</td>
<td>37.1 (+/−0.38)</td>
<td>78.0 (+/−2.33)</td>
<td># of bugs</td>
</tr>
<tr>
<td>PREVALENCE (ATTACHED ONLY) (+/−S.E.)</td>
<td>67.8 (+/−5.4)</td>
<td>37.1 (+/−0.38)</td>
<td>59.6 (+/−3.38)</td>
<td>alive</td>
</tr>
<tr>
<td>ABUNDANCE (+/−S.E.)</td>
<td>2.00 (+/−0.16)</td>
<td>1.50 (+/−0.18)</td>
<td>2.30 (+/−0.28)</td>
<td>is too</td>
</tr>
<tr>
<td>ABUNDANCE (ATTACHED ONLY) (+/−S.E.)</td>
<td>1.45 (+/−0.12)</td>
<td>0.84 (+/−0.12)</td>
<td>1.76 (+/−0.21)</td>
<td>low</td>
</tr>
</tbody>
</table>
Experiment 5. (Low salinity).

Figure 11. Experiment 5. Location of mite attachment on all host types at low salinity (< 300 μS cm$^{-1}$), plotted as a percent of total mites collected on each host type. Numbers of mites in boxes are attached mites only (per replicate) associated with number of bugs shown directly below. Error bars are standard error.

LOCATION OF ATTACHMENT as measured by percent of total mites on T.A.M.

One-way ANOVA: $F = 110.65$, $P = 0.001$

Analysis of location of mite attachment between moderate salinity (Experiment 1) and low salinity (Experiment 5).

Two-way ANOVA, grouped by salinity: $F = 3.701$, $P = 0.103$. 
<table>
<thead>
<tr>
<th>PARASITISM RATES (AVG. OF 2 REPS)</th>
<th>HOST</th>
<th>Statistical Analysis between Hosts</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>C. bifida non-flying</td>
<td>C. expleta non-flying</td>
</tr>
<tr>
<td>PREVALENCE (%) (+/−S.E.)</td>
<td>13.9 (+/−0.25)</td>
<td>10.9 (+/−2.72)</td>
</tr>
<tr>
<td>PREVALENCE (ATTACHED ONLY) (+/−S.E.)</td>
<td>9.4 (+/−3.50)</td>
<td>10.9 (+/−2.72)</td>
</tr>
<tr>
<td>ABUNDANCE (+/−S.E.)</td>
<td>0.14 (+/−0.01)</td>
<td>0.14 (+/−0.05)</td>
</tr>
<tr>
<td>ABUNDANCE (ATTACHED ONLY) (+/−S.E.)</td>
<td>0.10 (+/−0.03)</td>
<td>0.13 (+/−0.04)</td>
</tr>
</tbody>
</table>

Table 10. Experiment 6. Parasitism rates and statistical analyses for quantity of mites associated with non-flying hosts over 24 hours at high salinity (> 18 000 μS cm⁻²). For statistical comparison with moderate salinity (Experiment 2), see text.
C. Long-term Attachment and Engorgement.

1. Attachment

Data for this section were collected from Experiment 7 and were the summation of 8 days of data. The mortality data for the two host types, while not of direct importance to the questions asked below, are displayed in Table 11. This shows the dynamics of the mite-corixid interaction over 6 to 8 days on the predominant morphs of both host species. It was found in this study and in a similar study in 1990, that the mortality rate of non-flying C. expleta was higher in the first 3 days than flying C. bifida, but that this was true of unparasitized controls as well. Non-flying C. expleta was dying more quickly than flying C. bifida even without parasitism by E. euryhalina.

As with questions 1, 2, and 3, recruitment followed the same trends as attachment. For brevity’s sake, I do not mention recruitment in the Results of Questions 4 and 5, but consider it fully in the Discussion.

Question 4a: Does host affect the quantity of mite attachment over 8 days?

Data collected:

In Experiment 7 (Table 12), prevalence (attached only) of E. euryhalina was significantly greater on non-flying (non-sclerotized) C. expleta than flying (sclerotized) C. bifida (t = -3.996, P = 0.028). Abundance (attached only) was also significantly different.
Summary:
Over 6 to 8 days, non-flying *C. expleta* had significantly more mites attaching to it than flying *C. bifida*. Host type affected mite attachment.

Question 4b: Does host affect **location** of mite **attachment** over 8 days?

Data collected:
The percentage of total mites attached on the T.A.M. in Experiment 7 was significantly greater on flying *C. bifida* than non-flying *C. expleta* (t = 6.319, P = 0.008) (See Figure 12). Mites on flying *C. bifida* were exclusively attached to the T.A.M. and wings, whereas mites on non-flying *C. expleta* were attached all over the dorsum, especially terga 2, 2-3, and 3. A $X^2$ analysis supported these data. Mites on flying *C. bifida* were attached more than would be randomly expected to the left and right thirds of the host dorsum, compared to the centre third ($X^2 = 58.3, P < 0.001$). Mites on non-flying *C. expleta* were attached more on the centre of the dorsum, compared to the left and right thirds ($X^2 = 80.6, P < 0.001$).

Summary:
Host type affected location of mite attachment over 8 days.

2. Mite Engorgement.

Question 4a. Does host affect **quantity** of mite **engorgement** over 6 to 8 days?

Data collected:
Prevalence (engorged only) in Experiment 7 was significantly greater on non-flying C. expleta compared to flying C. bifida in Experiment 7 ($t = -3.83$, $P = 0.031$) (see Table 13). Abundance (engorged only) was also significantly different.

Summary:
Host type affected the quantity of mites able to engorge over 6 to 8 days.

Does host type affect location of mite engorgement over 6 to 8 days?

Data collected:
In Experiment 7, percentage of total mites collected that engorged on the T.A.M. was significantly greater on flying C. bifida compared to non-flying C. expleta ($t = 64.2$, $P < 0.001$) (Figure 13). All mites that commenced engorgement on flying C. bifida were found on the T.A.M., whereas most of the mites engorging on non-flying C. expleta were found on the centres of abdominal segments 2, 2-3, 3, and 3-4. A $X^2$ analysis of the mites on the left, right, and centre thirds of the host showed the same pattern as for mite attachment ($X^2_{C. bifida} = 37.2$, $P < 0.001$, $X^2_{C. expleta} = 80.6$, $P < 0.005$). In general, location of mite engorgement was very similar to mite attachment over 8 days.

Summary:
Host type affected the location of mite engorgement over 6 to 8 days.
<table>
<thead>
<tr>
<th>Time (days) after initial infection</th>
<th>1 - 2.5</th>
<th>2.5 - 4.5</th>
<th>4.5 - 6</th>
<th>0 - 6</th>
<th>0 - 8'</th>
</tr>
</thead>
<tbody>
<tr>
<td>Percentage of <em>C. bifida</em> dead (+/- S.E.)</td>
<td>3.96 (+/- 1.04)</td>
<td>7.76 (+/- 0.75)</td>
<td>5.50 (+/- 1.52)</td>
<td>17.2 (+/- 1.55)</td>
<td>23.3 (+/- 3.92)</td>
</tr>
<tr>
<td>Percentage of total mites collected (+/- S.E.)</td>
<td>4.49 (+/- 2.50)</td>
<td>26.1 (+/- 11.8)</td>
<td>8.92 (+/- 3.30)</td>
<td>39.6 (+/- 8.13)</td>
<td>59.8 (+/- 4.87)</td>
</tr>
<tr>
<td>Percentage of <em>C. expleta</em> dead (+/- S.E.)</td>
<td>42.2 (+/- 2.74)</td>
<td>26.9 (+/- 4.12)</td>
<td>16.8 (+/- 3.84)</td>
<td>86.0 (+/- 4.52)</td>
<td>91.8 (+/- 5.76)</td>
</tr>
<tr>
<td>Percentage of total mites collected (+/- S.E.)</td>
<td>56.3 (+/- 4.57)</td>
<td>23.8 (+/- 3.37)</td>
<td>10.4 (+/- 3.66)</td>
<td>90.5 (+/- 6.82)</td>
<td>89.6 (+/- 7.33)</td>
</tr>
</tbody>
</table>

*Only 2 replicates were allowed to run for 8 days.*

Table 11. Experiment 7. Mortality data for flying *C. bifida* and non-flying *C. expleta* over 6 to 8 days of mite growth in Long Lake.
Figure 12. Experiment 7. Location of mite attachment on flying *C. bifida* and non-flying *C. expleta* over 6 to 8 days at moderate salinity (10 000 to 15 000 μS cm\(^{-1}\)). Data are plotted as a percent of total mites collected on each host type. Numbers of mites in boxes are attached mites only (per replicate) associated with number of bugs shown directly below. Error bars are standard error.

<table>
<thead>
<tr>
<th>PARASITISM RATES (AVG. OF 4 REPS)</th>
<th>HOST</th>
<th>Statistical Analysis between Hosts</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>C. bifida</td>
<td>C. expleta</td>
</tr>
<tr>
<td>PREVALENCE (+/-S.E.)</td>
<td>25.1 (+/-2.45)</td>
<td>64.6 (+/-5.0)</td>
</tr>
<tr>
<td>PREVALENCE (ATTACHED ONLY) (+/-S.E.)</td>
<td>22.8 (+/-2.45)</td>
<td>63.7 (+/-5.0)</td>
</tr>
<tr>
<td>ABUNDANCE (+/-S.E.)</td>
<td>0.71 (+/-0.21)</td>
<td>2.72 (+/-0.31)</td>
</tr>
<tr>
<td>ABUNDANCE (ATTACHED ONLY) (+/-S.E.)</td>
<td>0.51 (+/-0.11)</td>
<td>2.49 (+/-0.29)</td>
</tr>
<tr>
<td>% OF MITES ATTACHED ON T.A.M. (+/-S.E.)</td>
<td>87.9 (+/-3.15)</td>
<td>7.2 (+/-0.32)</td>
</tr>
</tbody>
</table>

Table 12. Experiment 7. Parasitism rates and statistical analyses for quantity and location of attached mites associated with flying *C. bifida* and non-flying *C. expleta* over 6 to 8 days mite growth in Long Lake.
Figure 13. Experiment 7. Location of mites engorging on flying *C. bifida* and non-flying *C. expleta* over 6 to 8 days at moderate salinity (10 000 to 15 000 μS cm$^{-1}$). Data are plotted as a percent of total mites collected on each host type. Numbers of mites in boxes are attached mites only (per replicate) associated with number of bugs shown directly below. Data are plotted as a percent of total mites collected on each host type. Error bars are standard error.

Table 13. Experiment 7. Parasitism rates and statistical analyses for quantity and location of engorging mites associated with flying *C. bifida* and non-flying *C. expleta* over 6 to 8 days mite growth in Long Lake.
Unfortunately, low sample sizes prohibited a statistical analysis of size of engorgement between host types over 6 and 8 days. Some qualitative data however, are given in Appendix 1 on the engorgement process of *E. euryhalina*.

**D. Field Studies.**

Recall from the Materials and Methods that corixids were collected for 3 reasons:

1) To ensure that the quantity and location of *E. euryhalina* in laboratory experiments is representative of field infections (question 5).

2) To determine the relative proportions of *C. bifida* and *C. expleta* in lakes (i.e. that mites are still excluding *C. expleta* at low salinity).

3) To determine the relative proportions of flying and non-flying *Cenocorixa* spp. (i.e. that flying hosts predominate where mites are present).

1) Comparison of field parasitism and laboratory parasitism.

Question 5a: Are laboratory experiments representative of the **quantity** of mites attaching on field collected corixids?

Data collected:

The September 13, 1991 collection had prevalence (attached only) on flying *C. bifida* of 29.4 % (Table 14b), on non-flying *C. expleta* of 46.8 % (Table 15b), and on *C. expleta* flying of 37.8 % (Table 16b), but these values were not significantly
different ($F = 1.226, P = 0.297$). In the collections of August 17, 1991 (Table 15a, 16a) and October 21, 1990 (Tables 14c, 15c, 16c), prevalence (attached only) was also not significantly different between host types. Abundance (attached only) followed the same trend. Collections of non-flying *C. bifida* were too low for statistical comparison.

Summary:

Prevalence of attached mites was not significantly different between host types in field collections. This result was the same as initial laboratory experiments, but different than the 8 day study between flying *C. bifida* and non-flying *C. expleta* which found a significant difference.

Question 5b: Are laboratory experiments representative of the location of mites attaching on field collected corixids?

Data collected:

In the September 13, 1991 collection, there was no significant difference in the percentage of mites attaching on the T.A.M. between flying *C. bifida* (Figure 14), non-flying *C. expleta* (Figure 15) and flying *C. expleta* (Figure 16) ($F = 0.112, P = 0.894$). This result was different than lab experiments which showed significantly more mites on the T.A.M. of flying hosts compared to non-flying. Other field collections also found no significance in the location of mite attachment between hosts.

Comparing individual host types collected in the field to
laboratory experiments, the attachment of mites on non-flying *C. expleta* was similar in that mites were mainly attached to abdominal segments 2, 2-3 and 3 (Figure 15). Attachment of mites to flying *C. expleta* was different in that a much lower proportion of mites was attaching to the T.A.M. in the field (Figure 16). Attachment in the field occurred through the hardened terga of abdominal segments 2, 2-3 and 3.

Attachment of mites on flying *C. bifida* was similar to laboratory data in the July 17, 1991 collection with over 70 % attachment to the T.A.M., but different on September 13, 1991 and October 21, 1990 with less than 10 % of mites on the T.A.M. in each collection (Figure 14).

Summary:

Location of attachment was similar in the laboratory and the field on non-flying *C. expleta*, but different on flying *C. expleta*. On flying *C. bifida*, location of attachment was similar in one collection, but different in two others.
### Table 14a.

<table>
<thead>
<tr>
<th>DATE</th>
<th>PREVALENCE (%)</th>
<th>PREVALENCE (%) (ATTACHED ONLY)</th>
<th>ABUNDANCE</th>
<th>ABUNDANCE (ATTACHED ONLY)</th>
</tr>
</thead>
<tbody>
<tr>
<td>July 17, 1991</td>
<td>57.1</td>
<td>57.1</td>
<td>3.07</td>
<td>1.86</td>
</tr>
</tbody>
</table>

### Table 14b.

<table>
<thead>
<tr>
<th>DATE</th>
<th>PREVALENCE (%)</th>
<th>PREVALENCE (%) (ATTACHED ONLY)</th>
<th>ABUNDANCE</th>
<th>ABUNDANCE (ATTACHED ONLY)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sept. 13, 1991</td>
<td>32.3</td>
<td>29.4</td>
<td>0.32</td>
<td>0.29</td>
</tr>
</tbody>
</table>

### Table 14c.

<table>
<thead>
<tr>
<th>DATE</th>
<th>PREVALENCE (%)</th>
<th>PREVALENCE (%) (ATTACHED ONLY)</th>
<th>ABUNDANCE</th>
<th>ABUNDANCE (ATTACHED ONLY)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oct. 21, 1990</td>
<td>25.0</td>
<td>25.0</td>
<td>0.25</td>
<td>0.25</td>
</tr>
</tbody>
</table>

Figure 14. Field studies. Location of mite attachment on flying C. bifida by collection date, plotted as a percent of total mites collected.

Field Samples

Table 15a.

<table>
<thead>
<tr>
<th>PARASITISM RATES</th>
<th>DATE</th>
<th></th>
<th>PREVALENCE (%)</th>
<th>(ATTACHED ONLY)</th>
<th>ABUNDANCE</th>
<th>(ATTACHED ONLY)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aug. 17, 1991</td>
<td></td>
<td></td>
<td>38.9</td>
<td>38.9</td>
<td>0.77</td>
<td>0.77</td>
</tr>
</tbody>
</table>

Table 15b.

<table>
<thead>
<tr>
<th>PARASITISM RATES</th>
<th>DATE</th>
<th></th>
<th>PREVALENCE (%)</th>
<th>(ATTACHED ONLY)</th>
<th>ABUNDANCE</th>
<th>(ATTACHED seulement)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sept. 13, 1991</td>
<td></td>
<td></td>
<td>48.9</td>
<td>46.8</td>
<td>0.66</td>
<td>0.64</td>
</tr>
</tbody>
</table>

Table 15c.

<table>
<thead>
<tr>
<th>PARASITISM RATES</th>
<th>DATE</th>
<th></th>
<th>PREVALENCE (%)</th>
<th>(ATTACHED ONLY)</th>
<th>ABUNDANCE</th>
<th>(ATTACHED ONLY)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oct. 21, 1990</td>
<td></td>
<td></td>
<td>29.3</td>
<td>29.3</td>
<td>0.34</td>
<td>0.34</td>
</tr>
</tbody>
</table>

Figure 15. Field studies. Location of mite attachment on non-flying C. expleta by collection date, plotted as a percent of total mites collected.

Field Samples

<table>
<thead>
<tr>
<th>Time</th>
<th>Host Region</th>
<th>Mites</th>
<th>Bugs</th>
</tr>
</thead>
<tbody>
<tr>
<td>T.A.M.</td>
<td>NOTU-AS 1</td>
<td>24</td>
<td>45</td>
</tr>
<tr>
<td>7.A.M.</td>
<td>NOTU-AS 2</td>
<td>20</td>
<td>22</td>
</tr>
<tr>
<td></td>
<td>AS 3-4</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>AS 4-6</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>AS 8-6</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Wing (vein)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Wing (memb.)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

August 17, 1991
Lye Lake

Figure 16. Field studies. Location of mite attachment on flying C. expleta by collection date, plotted as a percent of total mites collected.

Table 16a.

<table>
<thead>
<tr>
<th>Parasitism Rates</th>
<th>Date</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prevalence (%)</td>
<td>Aug. 17, 1991</td>
</tr>
<tr>
<td>(Attached only)</td>
<td></td>
</tr>
<tr>
<td>Abundance</td>
<td>Aug. 17, 1991</td>
</tr>
<tr>
<td>(Attached only)</td>
<td></td>
</tr>
</tbody>
</table>

| Mites Attached Per Region (Percent of Total) |

August 17, 1991
Lye Lake

<table>
<thead>
<tr>
<th>PARASITISM RATES</th>
<th>DATE</th>
</tr>
</thead>
<tbody>
<tr>
<td>PREVALENCE (%)</td>
<td>Aug. 17, 1991</td>
</tr>
<tr>
<td>(ATTACHED ONLY)</td>
<td></td>
</tr>
<tr>
<td>ABUNDANCE</td>
<td>Aug. 17, 1991</td>
</tr>
<tr>
<td>(ATTACHED ONLY)</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>PARASITISM RATES</th>
<th>DATE</th>
</tr>
</thead>
<tbody>
<tr>
<td>PREVALENCE (%)</td>
<td>Sept. 13, 1991</td>
</tr>
<tr>
<td>(ATTACHED ONLY)</td>
<td></td>
</tr>
<tr>
<td>ABUNDANCE</td>
<td>Sept. 13, 1991</td>
</tr>
<tr>
<td>(ATTACHED ONLY)</td>
<td></td>
</tr>
</tbody>
</table>

Table 16b.

2) Proportions of *C. bifida* compared to *C. expleta*.

Percentages of *C. bifida* versus *C. expleta* in the various lakes over time are given in Table 17. *C. bifida* comprised over 90% of *Cenocorixa* spp. in all collections in Long Lake (9 232 to 13 484 μS cm⁻¹). Collections below this salinity in Near Opposite Crescent Pond, Greer Lake, and Box 27 never recorded *C. expleta* during 1990 or 1991, whereas *C. bifida* was present in all 3 bodies of water. In Lake Lye (9 807 to 13 493 μS cm⁻¹), the percentage of *C. expleta* fluctuated from 57.2% to 66.9%. In the 2 high salinity lakes (Round-up and Barnes) (> 13 000 μS cm⁻¹), *C. expleta* dominated comprising over 90% of the total *Cenocorixa* spp.
<table>
<thead>
<tr>
<th></th>
<th>July 20/90</th>
<th>June 2/91</th>
<th>August 12/91</th>
<th>Sept. 14/91</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Body of Water</strong> (salinity)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Long (Chilcotin)</td>
<td>bif 94.6 %</td>
<td>bif 100 %</td>
<td>bif 100 %</td>
<td>bif 96.2 %</td>
</tr>
<tr>
<td>(9 232 to 13 484 μS cm⁻¹)</td>
<td>exp 5.4 %</td>
<td>(n = 56)</td>
<td>(n = 32)</td>
<td>(n = 26)</td>
</tr>
<tr>
<td>Lye</td>
<td>n/a</td>
<td>exp 42.8 %</td>
<td>bif 33.8 %</td>
<td>bif 33.1 %</td>
</tr>
<tr>
<td>(9 807 to 13 493 μS cm⁻¹)</td>
<td></td>
<td>(n = 28)</td>
<td>(n = 68)</td>
<td>(n = 148)</td>
</tr>
<tr>
<td>Barnes</td>
<td>n/a</td>
<td>bif 4.2 %</td>
<td>n/a</td>
<td>n/a</td>
</tr>
<tr>
<td>(13 687 to 19 528 μS cm⁻¹)</td>
<td></td>
<td>exp 95.8 %</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Round-up</td>
<td>n/a</td>
<td>bif 9.3 %</td>
<td>n/a</td>
<td>n/a</td>
</tr>
<tr>
<td>(15 224 to 22 724 μS cm⁻¹)</td>
<td></td>
<td>exp 90.7 %</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**bif = C. bifida exp = C. expleta**

Table 17. Field data. Percent composition of *Cenocorixa* spp. water boatmen collected in lakes by date. n/a = not available.
3) Proportions of flying and non-flying *Cenocorixa* spp.

Percentages of non-flying (sclerotized and non-sclerotized) and flying morphs are presented in Table 18. In Long Lake, the over-wintering population of *C. bifida* for 1990 was 100 % flying (based on June 2, 1991 sample: n = 32). The following over-wintering generation (based on September 14th sample of 25) was 80 % flying.

Lake Lye followed a similar trend with a June 2nd collection revealing 100 % flying (n = 12) and a September 14th collection of 77.3 % flying (n = 44). The few *C. bifida* that were found over-wintering at higher salinities (Barnes and Round-up) were also predominantly of the flying morph.

*C. expleta* on the other hand was more often found as the non-flying morph. Lake Lye had 75.0 % non-flying (n = 16) on June 2nd and 69.6 % non-flying on September 13th (n = 92). The September collection had 18.5 % of the total *C. expleta* with entirely darkened dorsa, but only stage 2 wing muscle development (non-flying). (In June, 37.5 % of the *C. expleta* were non-flying, but completely dark.) Higher salinities had mostly non-flying *C. expleta*. Round-up had 77.6 % non-flying on June 2, 1991.
<table>
<thead>
<tr>
<th>Body of Water (salinity)</th>
<th>Corixid Type</th>
<th>June 2/91</th>
<th>August 12/91</th>
<th>Sept. 14/91</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Long (Chilcotin)</strong> 94232 to 13 484 μS cm⁻¹</td>
<td>bif nf</td>
<td>0 %</td>
<td>0 %</td>
<td>20.0 %</td>
</tr>
<tr>
<td></td>
<td>bif fly</td>
<td>100 %</td>
<td>100 %</td>
<td>80.0 %</td>
</tr>
<tr>
<td></td>
<td>exp nf (light)</td>
<td>n/a</td>
<td>n/a</td>
<td>0 %</td>
</tr>
<tr>
<td></td>
<td>exp nf (dark)</td>
<td>0 %</td>
<td>0 %</td>
<td>100 %</td>
</tr>
<tr>
<td></td>
<td>exp fly</td>
<td>(n = 32)</td>
<td>(n = 26)</td>
<td>(n = 25)</td>
</tr>
<tr>
<td><strong>Lye</strong> (9 807 to 13 493 μS cm⁻¹)</td>
<td>bif nf</td>
<td>0 %</td>
<td>13 %</td>
<td>22.7 %</td>
</tr>
<tr>
<td></td>
<td>bif fly</td>
<td>100 %</td>
<td>87 %</td>
<td>77.3 %</td>
</tr>
<tr>
<td></td>
<td>exp nf (light)</td>
<td>37.5 %</td>
<td>51.1 %</td>
<td>51.1 %</td>
</tr>
<tr>
<td></td>
<td>exp nf (dark)</td>
<td>37.5 %</td>
<td>24.5 %</td>
<td>18.5 %</td>
</tr>
<tr>
<td></td>
<td>exp fly</td>
<td>25.0 %</td>
<td>24.4 %</td>
<td>30.4 %</td>
</tr>
<tr>
<td></td>
<td>exp nf (light)</td>
<td>(n = 16)</td>
<td>(n = 45)</td>
<td>(n = 44)</td>
</tr>
<tr>
<td><strong>Barnes</strong> (13 687 to 19 528 μS cm⁻¹)</td>
<td>bif nf</td>
<td>0 %</td>
<td>n/a</td>
<td>n/a</td>
</tr>
<tr>
<td></td>
<td>bif fly</td>
<td>100 %</td>
<td>(n = 3)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>exp nf (light)</td>
<td>62.9 %</td>
<td>17.1 %</td>
<td></td>
</tr>
<tr>
<td></td>
<td>exp nf (dark)</td>
<td>20.0 %</td>
<td>(n = 70)</td>
<td></td>
</tr>
<tr>
<td><strong>Round-up</strong> (15 224 to 22 724 μS cm⁻¹)</td>
<td>bif nf</td>
<td>0 %</td>
<td>n/a</td>
<td>n/a</td>
</tr>
<tr>
<td></td>
<td>bif fly</td>
<td>100 %</td>
<td>(n = 5)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>exp nf (light)</td>
<td>38.8 %</td>
<td>38.8 %</td>
<td></td>
</tr>
<tr>
<td></td>
<td>exp nf (dark)</td>
<td>22.4 %</td>
<td>(n = 49)</td>
<td></td>
</tr>
</tbody>
</table>

bif nf = *C. bifida* non-flying  
bif fly = *C. bifida* flying  
exp nf = *C. expleta* non-flying  
exp fly = *C. expleta* flying

Table 18. Field data. Percentages of flying and non-flying *Cenocorixa* spp. in lakes at given times. n/a = not available.
DISCUSSION

A. Initial Mite Recruitment and Attachment (Moderate Salinity).

1. Effect of Host Species.

Question 1a. Does host species affect quantity of initial mite recruitment?

Host species does not affect quantity of initial mite recruitment. Recruitment, as measured by prevalence and abundance, was not significantly different between host species (Tables 5, 6, and 7). This contradicts Hypothesis 1a. It was expected that there would be a difference in recruitment based on the studies of Smith (1977). The lack of a significant difference means that the exclusion of C. expleta is not because more mites are initially finding C. expleta compared to C. bifida.

Does host species affect quantity of initial mite attachment?

Host species does not affect the quantity of initial mite attachment. Attachment, as measured by prevalence (attached only) and abundance (attached only) did not differ significantly between host species (Tables 5, 6, and 7). This also contradicts Hypothesis 1a. The exclusion of C. expleta is not because more mites are initially able to attach to C. expleta compared to C. bifida.
Question 1b. Does host species affect location of initial mite attachment?

Host species does not affect the location of initial mite attachment. Experiments with all hosts (Figure 7) and flying hosts (Figure 9) showed no significant difference in attachment between species when sclerotization was held constant. This supports Hypothesis 1b. In Experiment 2 (Figure 8) with non-flying hosts only, there appeared to be a species effect, as significantly more mites attached to the T.A.M. of non-flying C. bifida compared to non-flying C. expleta. Post-experimental examination determined however, that some of these non-flying C. bifida had become partially sclerotized, resulting in inability of the mites to attach to the abdominal segments. Since the location of mites does not differ between C. bifida and C. expleta (when sclerotization remains constant), a species-specific effect on mite location is not the cause of C. expleta's exclusion.

Overview of Initial Host Species Differences.

I predicted Hypothesis 1a on mite recruitment and attachment because of the results of Smith (1977), who found significantly more mites attaching to C. expleta compared to C. bifida. Discrepancies between my results and his must have arisen because his experiments may have used both sclerotized and unsclerotized hosts, and were of variable time. Also, his low sample sizes and lack of replicates did not allow for the fact
that the attachment of E. euryhalina is largely dependent on chance, and variability within replicates and between host types is bound to occur.

Acceptance of Hypothesis 1b implies that there is no morphological or behavioural difference between C. bifida and C. expleta that would cause mites to attach in different locations between species. Since the location of attachment is similar between species, energy loss because of parasitism should be the same. (Differences in energy loss are possible when mites become crowded on one host type: see Discussion, Question 2b.)

The implication that morphological differences between species are not great enough to cause differences in mite parasitism is confirmed by Jansson (1972). His descriptions show that morphological differences between Cenocorixa bifida and C. expleta are primarily restricted to the hairs on the distal segment of the forelegs (Jansson, 1972). Since this area is not used for attachment by water mites, the lack of host differences in mite location and quantity is understandable. The only noticeable morphological difference that could cause differences in the initial mite attachment and/or recruitment is the predominance of the sclerotized morph of C. bifida compared to the normally unsclerotized C. expleta (see Question 2).

Behavioural differences between species were similarly not great enough to cause differences in mite attachment. Davids (1973) speculated that differences in the grooming behaviour of corixids may account for differences in the quantity and
location of the mite *Hydrachna conjecta*. I saw both *C. bifida* and *C. expleta* groom against mites but could discern no difference between species. Another behaviour that might have caused higher quantity of mites on *C. expleta*, is if *C. expleta* spent more time near the water surface where mites collect. I observed that both species spent approximately the same amount of time near the water surface, and Reynolds (1974) concluded that habitat utilization in the field was not significantly different between species.

2. Effect of Host Sclerotization.

Question 2a. Does host **sclerotization** affect quantity of initial mite **recruitment**?

Host sclerotization does not affect quantity of initial mite recruitment. *C. expleta*'s predominant unsclerotized morph did not have more mites recruiting to it than the predominant flying morph of *C. bifida* (Tables 5 and 8). This contradicts Hypothesis 2a. Greater recruitment to the predominant unsclerotized morph of *C. expleta*, compared to the predominant sclerotized morph of *C. bifida*, is not the cause of *C. expleta*'s exclusion.

Does host **sclerotization** affect quantity of initial mite **attachment**?

Host sclerotization does not affect quantity of initial mite attachment. Initial attachment of *E. euryhalina* was not significantly different between sclerotized and unsclerotized
hosts (Tables 5 and 8). This also contradicted Hypothesis 2a. The exclusion of *C. expleta* is not because more mites are initially attaching to the predominant unsclerotized morph of *C. expleta* compared to the predominant sclerotized morph of *C. bifida*.

Question 2b. Does host sclerotization affect location of initial mite attachment?

Host sclerotization does affect location of initial mite attachment (Figures 7 and 10). Most mites on sclerotized morphs attached to the T.A.M., whereas mites on non-sclerotized morphs were attached mostly on abdominal segments 2 and 3. This supported Hypothesis 2b. The crowding of mites on the T.A.M. of sclerotized *C. bifida* should offer partial protection from the effects of mite parasitism compared to non-sclerotized *C. expleta*. This is part of the cause of the exclusion of *C. expleta* (see below).

Overview of Initial Host Sclerotization Differences.

I predicted Hypothesis 2a on the recruitment and attachment of mites because I believed that differences in host sclerotization would cause differences in the quantity of mite attachment between host types, even after only 24 hours. I reject Hypothesis 2a because I conclude that these differences are not evident in the early stages of parasitism (but see Question 4).

Acceptance of Hypothesis 2b on the location of mites implies
that differences in the location of mite attachment between sclerotized and non-sclerotized hosts could be part of the cause of *C. expleta*’s exclusion. In the first 24 hours of the mite-corixid interaction, it is the only factor that is important to the exclusion of *C. expleta*. The cause is that mites are more crowded on the T.A.M. of sclerotized hosts, compared to the abdominal segments of non-sclerotized hosts.

There are many examples in which mites that are crowded together do not affect their hosts as much as non-crowded mites. Reilly and McCarthy (1991) found that *Hydrachna conjecta* were significantly smaller when 2 mites attached to the same hemielytron of their corixid hosts compared to when 1 mite attached to each hemielytra. (Smaller mite size is an indication of less host energy loss because of mite parasitism; Davids, 1973). Blockage of a mite’s feeding tube or stylostome may be one cause of the lessening of energy drain from a host. This can occur through host defenses or through competition by the stylostomes of other mites (Abro, 1982).

In interactions with relatively small hosts and proportionately large mites, impedance of mite growth can occur with even 2 mites per host. Aiken (1985) found significantly smaller *Eylais* sp. on the beetle *Dytiscus alaskanus* J. Balfour-Browne when 2 mites were present compared to single infections. Similar results were found by Lanciani (1971b) on beetles and corixids, and Davies (1959) on black flies.

In cases of extreme crowding, mite mortality can occur, which
must cause less energy loss to the host than if evenly spaced mites are engorging. Mitchell (1968) found up to 50% mortality of the mite *Arrenurus mitoensis* Imamura and Mitchell when mite density approached 30 mites per segment of the host damselfly *Cercion hieroglyphicum*. Observations of mites attached to the T.A.M. of *Cenocorixa* spp. indicate that in the later stages of engorgement, mite mortality occurs such that only one mite per T.A.M. can proceed past the initial stages of engorgement.

Lanciani (1971b) suggested that the size of mites on aquatic insects is limited by the size of the subelytral space and demonstrated this through a study of the mite *Hydrachna stipata* Lundblad on a backswimmer of the genus *Notonecta*. When attached on the outside of the hemielytra, *H. stipata* was significantly larger than when attached on the underside of the hemielytra. Based on the size of a fully engorged *E. euryhalina* (less than 2 mm dorsal diameter = 6.28 mm²), full engorgement of even one mite could not occur if attached on one of the T.A.M (a triangular area of 0.5 mm by 0.25 mm = 0.06 mm²). I have witnessed the effects of attempted engorgement on the T.A.M. from mites collected in the field on non-flying *C. expleta*. The mites become very elongated, with the anterior portion of their abdomens stretched, while engorgement proceeds only in the posterior of the abdomen, where the depth of the subelytral space is greater. Such deformity would most probably slow mite growth and certainly preclude metamorphosis to a nymphochrysalid. Thus the maximum energy drain on flying *C.*
bifida would be less than the equivalent of 2 fully engorged mites (1 per side), and energy may even be drained at a slower rate than from a normally engorging mite. Fully sclerotized hosts would, therefore, have an advantage over their non-sclerotized conspecifics if the abundance of mites in the population was over 2.

The parasitism rates in the field often exceed this level as seen in my study and the more extensive field studies of Smith (1977). For example, my July 17th collection in Long Lake, taken at peak time for larval E. euryhalina, showed an abundance of 3.07 mites per host on flying C. bifida, but an abundance (engorged only) of only 0.5 mites per host. The sclerotization appeared to be providing the flying hosts with some protection from super-parasitism by limiting the number of mites that could commence engorgement to 2 or less. This number is within the range that flying C. bifida can withstand, as shown by the presence of 2 nymphochrysalid shells on some sclerotized hosts in the spring.

B. Initial Mite Recruitment and Attachment: Low and High Salinity

1. Low salinity.

Question 3a (low salinity). Does low salinity affect quantity of initial mite recruitment? 

Low salinity does not affect quantity of initial mite recruitment compared to moderate salinity. Mite recruitment was
the same at low salinity (Table 9) and moderate salinity (Table 5) for three of the host types. (High mortality of flying C. expleta at low salinity precluded an analysis of this host type.) This supports Hypothesis 3a. Based on this conclusion, Experiments 1, 2, 3, and 4 should be indicative of mite recruitment throughout the salinity at which C. expleta is excluded.

Does low salinity affect quantity of initial mite attachment? Similarly, low salinity does not affect quantity of initial mite attachment compared to moderate salinity. Mite attachment was the same at low salinity (Table 9) compared to moderate salinity (Table 5) for three host types. This also supports Hypothesis 3a. Experiments 1 through 4 are indicative of mite attachment at the salinity at which C. expleta is excluded.

Question 3b (low salinity). Does low salinity affect location of initial mite attachment? Low salinity does not affect location of initial mite attachment (Figure 11) relative to moderate salinity (Figure 7). Location of mite attachment on three host types was not significantly different between moderate and low salinity. This supports Hypothesis 3b. Experiments 1 through 4 are indicative of the location of mite attachment throughout the salinity at which C. expleta is excluded.
Overview on the Effects of Low Salinity on Mite Parasitism.

Hypothesis 3a and 3b were predicted because I believed that the effects of mites would be the same from low salinity all the way through to the highest salinity from which C. expleta is excluded. Evidence for this is provided by Scudder et al. (1972). They found no difference between C. bifida and C. expleta in the long-term ability to osmoregulate in lake water from 730 to 12 200 μS cm⁻¹. From this, they concluded that both were physiologically freshwater insects. In terms of the exclusion of C. expleta, the verification of Hypothesis 3 shows that low salinity causes no change in C. expleta (i.e. in behaviour) that would cause more mites to attach to it compared to C. bifida. The increased mortality of flying C. expleta may indicate however, that this host type is more susceptible to initial osmoregulatory shock than other host types.

2. High salinity:

Question 3a (high salinity). Does high salinity affect quantity of initial mite recruitment?

High salinity does affect the quantity of initial mite recruitment compared to moderate salinity. Initial mite recruitment was significantly lower at high salinity (Table 10) than at moderate salinity (Table 6). My result contradicts Hypothesis 3a, which predicted no mites would recruit, but since there is a significant decrease in recruitment, I conclude that high salinity does affect recruitment of E. euryhalina.
Does high salinity affect quantity of initial mite attachment?

See conclusions above for mite recruitment.

Question 3b (high salinity). Does high salinity affect location of initial mite attachment?

Owing to very low attachment of mites at high salinity, a comparison of the location of mite attachment at moderate salinity was not possible.

Overview on the Effects of High Salinity on Mite Parasitism.

Hypothesis 3a regarding high salinity was predicted because I believed that the factor that limited mites at high salinity was their inability to recruit and/or attach. With respect to the exclusion of C. expleta, the significant difference in attachment between moderate salinity and high salinity experiments shows that there is a salinity between 10 000 and 18 000 μS cm⁻¹ that mites lose their ability to attach at the same rate. At this salinity, mites cease to have a substantial effect on C. expleta, and consequently, C. expleta ceases to be excluded.
C. Long-term Attachment and Engorgement.

1. Attachment

Question 4a: Does host type affect the **quantity** of mite attachment over 6 to 8 days?

Host type affected the quantity of mite attachment over 6 to 8 days. Attachment was significantly greater on the predominant non-sclerotized morph of *C. expleta* compared to the predominant sclerotized morph of *C. bifida* (Table 12). This supported Hypothesis 4a. The exclusion of *C. expleta* from low salinity is caused, at least partially, by the higher number of mites that are able to attach to the predominant morph of *C. expleta* over 6 to 8 days of mite exposure.

Question 4b: Does host type affect **location** of mite attachment over 6 to 8 days?

Host type affected the location of mite attachment over 6 to 8 days. Mites attached more on the T.A.M. of sclerotized *C. bifida* than the T.A.M. of non-sclerotized *C. expleta* (Figure 12). This supported Hypothesis 2b. The decreased area of susceptibility of sclerotized *C. bifida* gives them a competitive advantage over non-sclerotized *C. expleta*, when in the presence of mites.
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2. Mite Engorgement.

Question 4a. Does host type affect quantity of mite engorgement over 6 to 8 days?

Host type affected the quantity of mite engorgement over 6 to 8 days. Significantly more mites were able to engorge on non-sclerotized C. expleta than on sclerotized C. bifida (Table 13). This supported Hypothesis 4a. After 6 to 8 days, the greater number of engorging mites on the predominant non-sclerotized morph of C. expleta is at least partially the cause of C. expleta’s exclusion.

Question 4b. Does host type affect location of mite engorgement over 6 to 8 days?

Host type affected the location of mite engorgement over 6 to 8 days. Significantly more mites engorged on the T.A.M. of flying C. bifida than on the T.A.M. of non-flying C. expleta (Figure 13). This supported Hypothesis 4b. After 6 to 8 days, the crowded nature of the engorging mites on flying C. bifida impedes some of the mites’ growth. This effect gives partial protection to flying C. bifida, whereas non-flying C. expleta is fully affected by mites, and is excluded from areas where mites are prevalent.
Overview of Long-term Mite Attachment and Engorgement.

Acceptance of Hypotheses 4a on mite attachment and engorgement is the first evidence I found that more mites are associated with C. expleta than C. bifida. Since I used the predominant field morphs in my long-term experiment, the attachment differences witnessed should be most representative of what is occurring to the two host species in the field. Higher prevalence on one host type has been shown to correlate with lower host fecundity (Davids and Schoots, 1975; Smith, 1977) and higher host mortality (Lanciani 1975, 1986). This could be the most important factor in the exclusion of C. expleta from lakes of low and moderate salinity.

The question of whether there is a long-term species effect or an effect of sclerotization was not fully determined because of the use of only the predominant morphs of each species. As already stated (pp. 60-61), I would have liked to have used all 4 host types as I did for Questions 1, 2, and 3, but use of teneral non-flying C. bifida over 6 to 8 days would have presented problems in analysis because some of them harden in this time. Nevertheless, the use of the predominant morphs of each species assured that the results in my experiments are representative of what is occurring in the field. From my finding that species has no effect initially, whereas sclerotization affects the location of initial mite attachment, I would speculate that the effects of sclerotization are more responsible for the results of Experiment 7.
I found that over 6 to 8 days, recruitment of mites (as measured by prevalence and abundance) differed between hosts. Since 24 hour studies (Experiments 1 through 4) indicated that mites recruit to hosts equally, differences in recruitment over 6 to 8 days must be because mites are leaving the hosts after 24 hours, or they are being removed by the hosts. I observed that disturbed *E. euryhalina* are capable of disattaching within three days of initial infection. These mites, perhaps failing to locate the T.A.M. or finding this location unacceptable, might leave the host and could conceivably even find and attach to a non-flying *C. expleta*. Mites were observed under laboratory conditions entering and exiting the air space of hosts after a few minutes of exposure.

With respect to mites being removed, Harris and Harrison (1974) stated that *Hydrachna* sp. (*H. barri* by Smith, 1987) may be knocked off the legs of their corixid hosts, and Davids (1973) speculated that *H. conjecta* may be brushed off the underside of the hemielytra. Mites could be dislodged during flight and since the lake temperature during Experiment 7 was above the temperature at which flight is initiated (15°C according to Scudder, 1969a), flight in the covered enclosures was possible. Whatever the cause, over 6 to 8 days, more mites were found on non-flying *C. expleta* compared to flying *C. bifida*, despite similar initial recruitment. Mite attachment, as measured by prevalence (attached only) was also significantly lower on flying *C. bifida* (Table 12). Mite engorgement, as
measured by prevalence (engorging only), followed the same trend (Table 13). The process by which C. bifida lowers the number of potential attaching and engorging mites is an important factor in its ability to withstand mite parasitism. Non-flying C. expleta, failing to lower mite engorgement is excluded from areas with mites.

Acceptance of Hypothesis 4b, regarding location of mites over 6 to 8 days, causes me to reach the same conclusions as for the effects of sclerotization on initial mite attachment (Hypothesis 2b). Since I was using only two host types, I cannot, with certainty, attribute the difference in location of mite attachment to a host sclerotization effect rather than a species effect. It does, however, seem most plausible that sclerotization is causing the effect, because of the initial differences caused by sclerotization. The fact that 100 % of the mites engorging on flying C. bifida are on the T.A.M. shows that this is truly the only susceptible area on this host type. Based on previous arguments (see Discussion, Hypothesis 2), flying C. bifida is protected from mite parasitism significantly more than non-flying C. expleta.
D. Field Studies.

1) Comparison of field parasitism and laboratory parasitism.

Question 5a: Are laboratory experiments representative of the quantity of mites attaching on field collected corixids?

Initial laboratory experiments were representative of the quantity of mites attaching on field collected corixids, but laboratory experiments over 6 to 8 days differed from field collections. In both initial laboratory experiments and field collections, I found no significant difference between host types. In 6 to 8 day laboratory experiments I did find a significant difference between non-flying *C. expleta* and flying *C. bifida*. Since it was found that attachment of mites in the field did not differ between host types, there is no evidence from these field collections that mites are affecting *C. expleta* more than *C. bifida* (but see Overview).

Question 5b: Are laboratory experiments representative of the location of mites attaching on field collected corixids?

Laboratory experiments were representative of location of mite attachment on non-flying *C. expleta*, but not representative on either flying host. This supported Hypothesis 5b. Field-collected non-flying hosts are always non-sclerotized, providing mites with their preferred attachment sites on abdominal segments 2 and 3. Field-collected flying hosts however, may have had mite attachment prior, during, or after sclerotization,
creating high variability in the location of mite attachment. Considering this in relation to how sclerotization protects flying hosts (Question 2b), mites will have a much longer period of time to find, attach and engorge on non-flying *C. expleta* compared to flying *C. bifida*. Location of mite attachment in the field supports the theory that water mites have a greater effect on *C. expleta* than on *C. bifida*.

**Overview of Field Collections**

From field collections, there was not a significantly greater quantity of mites attaching to *C. expleta* compared to *C. bifida*. My 6 to 8 day laboratory experiment would indicate, however, that more mites do attach to non-flying *C. expleta* compared to flying *C. bifida* over 6 to 8 days. This contradiction requires an explanation.

The field collections of Smith (1977), Reilly and McCarthy (1991), and Aiken (1985) show great variability in the quantity of *Eylais* spp. mites attaching to their hosts over time. They all show a relatively low overwintering prevalence, a higher peak in early summer when the summer generation of larval mites is present, and a decrease in prevalence shortly after; accounted for by completion of larval mite development, and/or death of infected hosts.

My collections showed no difference in prevalence, but this does not preclude the fact that *E. euryhalina* is excluding *C. expleta*. If mites are recruiting to their hosts at the same
rate (Experiment 1 through 4), then no difference would be seen in field collections at this time. Also, if *C. expleta* are dying more quickly because of the later stages of engorgement, then a collection at this time might actually show lower parasitism on *C. expleta*, because only uninfected hosts are left in the population. My collections must have been at times in the mite-corixid interaction when prevalences did not differ between hosts.

Both Smith (1977) and I found no nymphochrysalids on *C. expleta*. This would suggest that *C. expleta* has a higher long-term mite-induced mortality which is supported by my findings of Experiment 7. This finding may be because of an effect of host species and/or host sclerotization.

Acceptance of Hypothesis 2b on the location of mites in the field supports the theory that mites are excluding *C. expleta* because of the predominance of its non-flying morph. From my findings in the laboratory and the field, the sequence of events that creates a differential effect of parasitism on *C. expleta* is as follows:

Larval *E. euryhalina* recruit to all hosts at the same rate (Table 5). If the potential host is non-sclerotized (non-flying), mites attach to the preferred sites in the middle of the abdominal dorsum (Figures 7, 13: non-flying hosts). Presumably, as sclerotization continues, there becomes a point at which the integument of the abdomen is too hard or thick for the mite’s mouthparts to pierce, at which time attachment to the
T.A.M. becomes the mites’ only option apart from leaving the host (Figures 7, 10, and 13: flying hosts). This exodus of mites from sclerotized hosts is reflected in significantly less attached and engorging mites on flying C. bifida compared to non-flying C. expleta over 6 to 8 days (Tables 12 and 13). As postulated in the discussion of question 2b, attachment to the T.A.M. probably does not cause as much energy loss to the host. Therefore, in terms of parasitism, it is in the host’s best interest to become sclerotized as quickly as possible.

Support for the hypothesis that host sclerotization controls mite location is derived from a comparison of studies of mites that commence engorgement on teneral hosts during eclosion, with studies of mites that begin engorging on sexually mature (sclerotized) insects. Mites on teneral hosts are found engorging directly through the sclerites. Examples are *Hydrachna virella* Lanciani on the dorsal pronotum of the backswimmer *Buenoa scimitra* Bare (Lanciani, 1980); *Arrenurus agrionicolus* Uchida on the ventrum of the 7th abdominal segment of the damselfly *Cercion hieroglyphicum* (Mitchell, 1968); and *Hydryphantes tenuabilis* Marshall on the marsh treader *Hydrometra australis* (= myrae) Drake and Hottes that attaches through the abdominal segments directly after host eclosion (Lanciani, 1971a).

In contrast, the studies of mites that attach to hardened hosts show these hosts engorging exclusively through membranous regions. *Limnochares americana* Lundblad attaches to various
damselflies, but always at the bases of the legs (Conroy and Kuhn, 1977; life cycle from Smith and Cook, 1991). Partuniella thermalis usually attaches to the alary membranes at the base of the wings of the brine fly Paracoenia sp. (Wiegert and Mitchell, 1973). Thyas barbigera Viets attaches to the posterior face of the thorax of Aedes spp. mosquitoes 72.3 % of the time, and 9.3 % of the time on the cervical membrane between the head and thorax (Mullen, 1977). Arrenurus spp. attach at the base of the legs of the damselfly Lestes sponsa (Hansemann) (Abro, 1982).

2. Proportions of C. bifida compared to C. expleta.

Based on the field data from the summers of 1990 and 1991 (Table 17), it would appear that mite parasitism is still affecting C. expleta in the same way it did in the study of Smith (1977). In the summers of 1990 and 1991, E. euryhalina was breeding in all lakes up to and including the salinity of Lake Lye (9 807 to 13 493 μS cm⁻¹). Below this salinity, C. bifida comprised over 90 % of the Cenocorixa fauna in all lakes, while above this salinity, C. expleta comprised over 90 % of the Cenocorixa fauna (Table 17). In Lake Lye, where mite prevalance was moderate (not as high as in Long Lake), C. expleta comprised 57.2 % to 66.7 % of the Cenocorixa spp. This lake is at the upper limit of E. euryhalina's salinity tolerance, and from my findings on the effects of high salinity on E. euryhalina (Table

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7The posterior face of the thorax of mosquitoes is one of the softer parts of the body (Corbet, 1963).
6 compared to Table 10), the salinity may be lessening the effects of mite parasitism. This would allow C. expleta to establish itself. The field data of 1990 and 1991 on the occurrence of C. expleta, C. bifida and E. euryhalina support the hypothesis of Smith (1977) that parasitic water mites exclude C. expleta from lakes of low salinity.

3. Proportions of flying and non-flying Cenocorixa spp.

The proportions of flying and non-flying Cenocorixa spp. during the summers of 1990 and 1991 were similar to those reported in previous studies (Table 3). C. bifida was predominantly flying, whereas C. expleta was predominantly non-flying (Table 18). Smith (1977) reports that in the overwintering populations of 1976 and 1977, the non-flying morph accounted for no more than 1% of the population. In summary, the overwintering populations of C. bifida were predominantly flying in 1962, 1963, 1967, 1976, 1977, 1990, and 1991, or 7 out of 10 years studied. Only in 1968 and 1969 did the non-flying morph predominate, while in 1966, the flying and non-flying morphs were in equal proportions. In contrast, C. expleta was predominantly non-flying in the two years of my investigation, and all previous studies have found that C. expleta is mostly non-flying (Scudder, 1975).

As previously stated, the difference in the percentage of flying morphs between C. bifida and C. expleta must affect the survivorship of the two species when field abundance levels are
Although both species begin their adult lives unsclerotized, *C. bifida* usually becomes flying and sclerotized, making it vulnerable only directly after eclosion to adult, a period which takes no more than 8 days at 20 °C (Scudder, 1971). *C. expleta*, however, will usually remain non-flying for its entire adult life, meaning that it must avoid the gauntlet of parasites for its entire adult life. This difference in the temporal "window of opportunity" for water mites, is the basis of the exclusion of *C. expleta* at low salinity.

**E. General Discussion**

My study of *E. euryhalina* has shown a greater effect of parasitism on *C. expleta* compared to *C. bifida*. The question remains, however, does a study of only *E. euryhalina* adequately account for the effects of all mites on *Cenocorixa* spp.?

Other mites are present at Becher’s Prairie, especially *E. discreta* and *H. davidsi* Smith, which are sometimes more prevalent than *E. euryhalina* especially at low salinity. With respect to *E. discreta*, there appears to be no reason why sclerotization of the host dorsum would not affect attachment in the same manner as for *E. euryhalina*. Davids et al. (1977) described the preferred attachment sites in the field for *E. discreta* on some corixids of the genera *Sigara* and *Cymatia*. They found that larval *E. discreta* preferred abdominal segments 2, 3 and 4 on all hosts and my observations on *E. discreta*
concur with these findings. Lanciani (1969) claims that *E. discreta* prefers the tergum of abdominal segment 3, followed by 2 and 4, with attachment to abdominal terga 1 and 5 only on heavily parasitized hosts. It appears that at low salinity, *E. discreta* and *E. euryhalina* occupy a similar niche, sometimes compete for the same attachment sites, and must be affected in the same way by host sclerotization.

I expect that a fully sclerotized host would prevent attachment of *E. discreta* in its preferred site because of field observations of *E. discreta* attaching to the T.A.M. of flying hosts as well as dead, dessicated *E. discreta* on the hardened terga of flying hosts. Preliminary measurements of the thickness of a sclerotized abdominal tergum show that it remains very thin, even when sclerotized, indicating that it is not the thickness of the sclerite that protects the host from mite engorgement. Longer chelicerae, therefore, would not help *E. discreta* to engorge because the host defense is more likely based on the hardness of the integument rather than its thickness.

*Hydrachna davidsi* poses another challenge to the exclusion theory based on sclerotization. Their attachment is to the underside of the hemelytra. As with *Eylais* spp. larvae, the parasitism only occurs on adult (winged) hosts, so in this respect, the effects of parasitism are acting on the same members of the population. I am not sure, however, that the degree of sclerotization of the hemelytra differs between flying
and non-flying hosts. If this were true, attachment of *H. davidisi* should be possible on both *C. bifida* and *C. expleta* for the entirety of their adult lives, irrespective of the degree of sclerotization. From this assumption, *H. davidisi* could not be limiting *C. expleta* by the same mechanisms as *Eylais* spp., if at all.

Attachment of *H. davidisi* on *C. expleta* and *C. bifida* was studied by Smith (1977). He found that mites attached significantly more often (*P < 0.05*) on *C. expleta* than on *C. bifida*. The mechanism responsible is not known, and a full study on *H. davidisi* and the sclerotization of the hemelytra of *Cenocorixa* spp. would be required to determine this. Nevertheless, the absence of *C. expleta* in low salinity lakes can be explained without an understanding of the effects of *H. davidisi*. The high prevalence of *E. discreta* and presence of *E. euryhalina* at low salinity means that there is no water body below the salinity of Barnes Lake (13 687 to 19 528 µS cm⁻¹ from my study), in which parasitism will not occur on *C. expleta*.

Combining the mite parasitism data from the lab and field with the historical percentages of flying and non-flying *Cenocorixa* spp., one can make speculate on the co-evolution of mites and water boatmen.

The long-term fluctuations in flying morphs of *C. bifida* are explained by differences in the temperature of the lake during development of the last larval instar (Scudder and Meredith, 1972). Above 15 °C, development to the flying morph occurs in
both species in the laboratory and interspecific differences in
the percentage of flying morphs are thought to arise from slight
differences in the timing of their life cycles (Jansson and
Scudder, 1974). It is possible, however, that abiotic factors
are not the only forces that control the proportions of flying
morphs found in the field. The hypothesis is forwarded here,
that parasitism by water mites is one factor accounting for
differences in the composition of corixid populations.

The findings of this work show a greater effect of parasitism
on non-flying individuals compared to flying forms. Increased
mortality of non-flying individuals in regions of parasitism
(low to moderate salinities) would cause the percentage of non-
flying individuals to be lower than in areas with no parasites
(high salinity). This helps explain the finding of Scudder
(1975) that at the lower salinity range of each species, there
are greater percentages of flying morphs than at the higher
limits of the salinity range.

In addition, parasitism may act as a selection agent favouring
flying morphs. One would expect that in areas of high
parasitism, both species would favour the production of the
flying morph at lower and lower temperatures towards a
physiological minimum. This minimum may be 15 °C as reported by
Scudder and Meredith (1972). In contrast, in permanent lakes
where there are no parasites, there may be selection pressure
against production of the flying morph (with its associated
ovarian diapause), because it is associated with reduced
reproductive fitness (Young, 1965b). There would be no reason for an individual in a permanent, productive lake to forego reproduction so that it could disperse. In these lakes, the percentage of flying morphs should be lower, as reported in Scudder (1975), and the temperature of inducement of wing muscle development should be higher.

From this reasoning, it can be further hypothesized that mite parasitism could have played a role in the speciation process of C. expleta and C. bifida. The ancestor of C. bifida and C. expleta would have had two different selection forces on it when mite parasitism evolved. At low salinities, where mites were present, the population would have evolved into a sclerotized, migratory form. At high salinity, where mites were not present, the population would have evolved into a non-flying, non-sclerotized, but more fecund form. Then through reproductive isolation, these two subpopulations may have speciated into the present-day C. bifida and C. expleta.
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Appendix 1.

A. Life History Study of Eylais euryhalina Smith

1. Life cycle

Figure 17 shows the life cycle of E. euryhalina throughout the summer at Becher’s Prairie based on field collections and observations in 1990 and 1991. Dates are only approximations and some information is not known because the study was only carried out from May to September. Letters below correspond to points on the life cycle diagram.

A. (May 4th) Mites were almost entirely in parasitic stages (larva or nymphochrysalis) although rare free-living nymphs were collected (1990). Larvae were either completely unengorged (and looked dessicated) or were approaching full engorgement. Nymphochrysalids displayed a wide range of development from freshly eclosed to showing full leg segmentation and ocelli development.

B. (June 2nd) Many free-living nymphs of E. euryhalina were present in Long Lake and Lake Lye. Eggs of E. euryhalina were found on Scirpus spp. in Lake Lye (1991) (12 427 μS cm⁻¹), but did not hatch after several weeks in the lab (I suspect that they may have been from the previous summer).

C. (June 9th) First E. euryhalina adult (female) was collected (1991) from Long Lake (13 848 μS cm⁻¹), and
Figure 17. Life cycle of *E. euryhalina* at Becher's Prairie compared to the life cycle of *Cenocorixa* spp. Letters correspond to approximate dates as described in text pp. 133 - 136.
identified as such by the presence of an ovipositor (not visible in nymphs).

D. (June 19th) Many adult *E. euryhalina* were seen in lakes. More eggs from Long Lake were collected, but they again do not hatch in the lab (1991). I was unable to find teleiochrysalids in field.

E. (June 27th) The first presence of *Eylais* spp. free-living larvae on the surface of Lake Greer (5 823 µS cm⁻¹) was observed (1991). In the laboratory, they were identified as both *E. euryhalina* and *E. discreta*. Egg masses of both species were found on *Ruppia* sp. and *Zanischella* sp. floating vegetation and successfully incubated in the lab.

F. (July 6th) Free-living *E. euryhalina* larvae were seen on Long Lake (1991).

G. (August 1st - 5th) Freshly laid *E. euryhalina* egg masses were no longer found in Lake Greer (*E. discreta* persisted for a week or two later), suggesting death of *E. euryhalina* adults that had over-wintered as parasitic larvae. Free-living larvae were relatively scarce in Long Lake compared to mid-July. A sentinel study (putting unparasitized hosts in a lake with parasites) in Long Lake showed only 10.3 % parasitism on *C. expleta* non-flying (N = 29) and 0 % on *C. bifida* non-flying (N = 11) (August 5th to 12th, 1991).
H. (September 13) Second summer generation adult and free-living *E. euryhalina* were present in Near Opposite Crescent Pond (4 261 μS cm\(^{-1}\)) as well as Lake Lye.

I. (October 21) Eggs collected from Lake Lye still hatch after incubation at 20 °C for 24 hours. Adults cannot be found in Lake Lye or Long Lake.

2. Salinity range

The presence of free-living larvae was used to determine whether *E. euryhalina* was breeding in a certain body of water. As shown in Table 1 (p. 13), *E. euryhalina* was found breeding from low salinity (Box 27: < 300 μS cm\(^{-1}\)), through moderate salinity (Near Opposite Crescent Pond, Lake Greer, Near Pothole Lake, Long lake (Chilcotin), and Lake Lye (9 807 to 13 493 μS\(^{-1}\)). Free-living larvae were not found in Barkley Lake (784 to 942 μS cm\(^{-1}\)), but extensive collections were not taken.

Field collections and observations of other life stages of *E. euryhalina* were also recorded. Engorging larvae and nymphochrysalids were found on flying hosts in all lakes including high salinity lakes such as Barnes, Round-up, and even LB2 (20 639 to 22 724 μS cm\(^{-1}\)). Free-living nymphs were also recorded in small numbers from these lakes, but adults and egg masses were never found.
3. Mite engorgement process

Following Lanciani (1971) and Reilly and McCarthy (1991), increase in area of the dorsal region was used to measure mite engorgement by the formula for area of an ellipse = 1/2 \( \pi \times \text{base} \times \text{height} \). The unengorged mites were 0.024 mm\(^2\) (0.15 mm long by 0.1 mm wide). Measurable engorgement was first witnessed 3.5 days after initial infection (2.5 days after hosts were removed from mite-infected water) with a slight increase in width. This was followed by an increase in length as the intersegmental membranes swelled beyond the posterior end of the dorsal shield. After engorgement began at 3.5 days, the mites' legs were entirely immobile, and by 8 days some of the mites had already attained a roughly spherical shape, unless in a site where full engorgement was inhibited. Some mites, however, remained unengorged after 6 to 8 days and closer examination revealed that they were dry and almost certainly dead. Under some of the unengorged mites were black, necrotic spots similar to that described for Hydrachna conjecta on Sigara falleni (Davids, 1973). The necrotic spot usually, but not always correlated with the unengorged state of the associated mite. Necrotic spots were not found on laboratory infected flying hosts as the reaction did not occur on the T.A.M. which was the only place where mites were able to commence engorgement. After 6 days, the
average size of mites for 2 replicates was 0.037 mm\(^2\) (n = 49) and 0.038 mm\(^2\) (n = 14) on C. bifida flying compared to 0.037 mm\(^2\) (n = 4) and 0.025 mm\(^2\) (n = 7) on C. expleta non-flying. After 8 days, C. bifida flying had mites of an average size of 0.031 mm\(^2\) (n=2) and 0.045 mm\(^2\) (n= 12) and C. expleta non-flying had mites of 0.047 mm\(^2\) (n = 7) and 0.033 mm\(^2\) (n = 4). Once again, these data were not statistically tested and are presented only to show that while engorgement was occurring, after 8 days the percentage of the total engorgement was very small. (A fully engorged E. euryhalina is nearly 2mm in diameter which equals 6.28 mm\(^2\).)

**B. Discussion of E. euryhalina Life History**

1. Life cycle

From observations in the field and laboratory, some important facts about *E. euryhalina* have been discovered. Eggs are present all year, but do not remain viable throughout the winter as evidenced by early collections of eggs which appeared unembryonated and failed to hatch in the laboratory. I found degradation of overwintered eggs and prelarvae, such that larval features evident in the fall (i.e. eyespots and vitelline) were not apparent in the spring. Lanciani (1970a) states that only 3 of 20 *Eylais* *spp.* studied in North America overwinter exclusively in egg
stage, and *E. euryhalina* does not appear to be in this category. From early spring observations, *E. euryhalina* overwinters exclusively as a parasitic larvae.

The potential infection period by *E. euryhalina* is established at 4 months: from late June until the lakes freeze in October with a decrease (or absence) of free-living larvae in August and September; the period of non-infectivity being dependent on the lake. It appeared that the less saline, usually smaller lakes (Near Opposite Crescent and Lake Greer) had earlier appearance of free-living larvae than the larger, moderate salinity lakes (Long Lake and Lake Lye). Shallow surface temperatures in these lakes are similar and show a small degree of variation between years (Scudder, 1975), so differences in mite life cycles may have been related to salinity, with lower salinity being quicker. (Free-living larvae were witnessed on June 27th in Lake Greer compared to July 6th for Long Lake.) Correspondingly, the absence of first generation free-living larvae in summer also occurred earlier in the smaller, less saline lakes as well. The actual dates of the appearance of the second generation free-living larval mites was not determined. By September 13, 1991, second generation free-living larvae were present on both Near Opposite Crescent Pond and Lake Lye.
From the presence of new, viable eggs in the field, it can be estimated that *E. euryhalina* laid eggs for about 35 days in the summer of 1991. With respect to the duration of the parasitic stage, an approximation of the period of overwintering for *E. euryhalina* can be judged by determining the parasitic duration of the latest possible attaching mite in the fall. Ice formed on the lakes at the end of October 1990, and assuming that the last attaching mite is the last one to leave the host in the spring (the end of May), the maximum possible time of the parasitic interaction (larvae and nymphochrysalis) is 7 months at this latitude (52 °N). Lanciani (1969) states that larvae of the genus *Eylais* may be parasitic for a maximum of 11 months. The duration of the parasitic phase in the summer was not definitively determined, as laboratory rearing of mites on corixids in this study and others (Davids, 1973) has proven difficult.

2. Salinity range

It was found that the upper salinity limit of *E. euryhalina* was not based on failure of the larval form to be able to recruit or attach at high salinities. Experiment 6 demonstrated ability of the larvae to attach at salinities above the natural range of the species (albeit at low rates). Collections of nymphs in high salinity lakes suggests that inability to engorge is not the limiting factor, although
perhaps commencement of engorgement must occur at lower salinities before migration of the host to high salinity. The absence of adult mites in collections at these same high salinities implicates the development from nymph to teleiochrysalis, or teleiochrysalis to adult as the limiting life stage for *E. euryhalina* at high salinity.

3. Mite engorgement

Because of the short duration of laboratory induced mite engorgement, no conclusions are drawn regarding the effects of host type on mite growth rate.