Attachment sites, phenology, and growth of larvae of Eylais sp. (Acari) on Dytiscus alaskanus J. Balfour-Browne (Coleoptera: Dytiscidae)

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Larvae of aquatic mites are common ectoparasites of aquatic beetles. A population of Dytiscus alaskanus (Coleoptera: Dytiscidae) studied in a central Alberta lake was parasitized by members of the genus Eylais (Acari: Hydrachnellae). Mites attached preferentially in the costal–subcostal region of the ventral surface of the hindwings. Afferent blood flow in the costa and subcosta and the numerous blood sinuses in this region provide an abundant food source. The smallest (=youngest) larvae were taken on the first beetles caught in early spring, indicating that some mite larvac overwinter on the host. Mites grow rapidly, reach maximum size in late June and July, and then enter the nonparasitic phase of the life cycle. Rates of parasitism (proportion of beetles with parasites) was highest in early spring, declined throughout the summer, and rose again in the fall. In this way, the parasitic phase of the mite life cycle occurs at the same time as the peak in the population of adult beetles. There was constant recruitment throughout the year into the population of larvac mites indicating asynchronous cohorts or more than one mite species.


Les larvac d’acariens aquatiques sont des ectoparasites communs chez les coléoptères aquatiques. L’étude d’une population lacustre de Dytiscus alaskanus (Coleoptera: Dytiscidae) du centre de l’Alberta a révélé la présence de parasites du genre Eylais (Acari: Hydrachnellae). Les acariens s’attachent de préférence à la région costale–sous-costale de la surface ventrale des ailes postérieures. La circulation afferente dans la costale et dans la sous-costale de même que les nombreux sinus veineux présents dans cette région constituent une source de nourriture abondante. Les larvac les plus petites (= les plus jeunes) ont été trouvées chez les premiers coléoptères capturés au début du printemps, ce qui indique que des larvac d’acariens peuvent survivre à l’hiver sur l’hôte. Les acariens se développent rapidement, atteignent leur taille maximale à la fin de juin et en juillet et entreprennent alors la phase non parasitaire de leur cycle. La fréquence du parasitisme (proportion de coléoptères qui sont parasités) atteint son maximum au début du printemps, diminue durant tout l’été et augmente de nouveau à l’automne. De cette façon, la phase parasitaire des acariens se produit au moment où la population de coléoptères adultes atteint son apogée. Il se fait du recrutement durant toute l’année chez la population de larvac d’acariens, ce qui indique qu’il existe des cohortes différentes asynchrones, ou qu’il y a plus d’une espèce d’acariens.

[Traduit par le journal]

Introduction

Aquatic insects are hosts to numerous ecto- and endoparasites and aquatic beetles are no exception. Ectoparasites from such widely divergent groups as fungi (Scheloske 1976; Sugiyama 1977), ancyloid snails (Johnson 1904; Rosewater 1970), and aquatic mites (Lanciani 1970a; Nielsen and Davids 1975) have been found with aquatic beetles. While some, such as ancyloid snails, are phoretic and their attachment to beetles facilitates dispersal (Rosewater 1970), others, such as mites, feed on the host (Lanciani 1970a). In some aquatic insects, the feeding of mite parasites has been shown to lower the reproductive capacity of the host (Crisp 1959; Davids 1973; Davids and Schoots 1975) and increase host mortality (Davids 1973).

This paper deals with parasitism of an aquatic beetle, Dytiscus alaskanus (Coleoptera: Dytiscidae) by mites of the genus Eylais. Eylais mites are type II aquatic mite parasites (Böttger 1976) that have larvac which hatch underwater, go to the water surface, and rest there. Larvac enter the subelytral air space of their host when the host surfaces to replenish its air store. When inside the subelytral space, the larva attaches to its host and proceeds to engorge. When the larva is fully engorged, a nymphocyrtisal forms inside the larval skin and the parasitic phase of the mite’s life cycle ends. Thus, the parasitic phase is passed entirely in air.

In this paper, I examine the mites preference for certain attachment sites, parasite loads, and the growth rates and phenology of larvac of D. alaskanus.

Materials and methods

All mites studied were parasites of D. alaskanus. The beetles were collected weekly in floating bottle traps (Aiken and Roughley 1985) from May through August in 1982 and May through October in 1983. Beetles were transported to the laboratory in plastic containers packed on ice in Styrofoam coolers. In the laboratory, between 25 and 50 beetles of each sex (fewer when populations of beetles were low) were placed in water-filled plastic containers and frozen at −20°C.

When the beetles were thawed for dissection and the elytra, hindwings, and dorsum of the abdomen were removed and placed in 70% ethanol with a catalogue number for that beetle. In this way, body parts could be associated with a particular beetle for whom sex, weight, and a series of body measurements (R. B. Aiken and C. W. Wilkinson, in preparation) were recorded.

Wings, elytra, and abdomens were examined with a Wild M-5 microscope fitted with an ocular micrometer. For specimens taken in 1982, the total number of mite parasites on the host, the attachment site of each mite, and its life stage (larva or nymphocyrtisal) were noted. Similar data were taken for mites captured in 1983 and, in addition, the total length of each mite, measured from the anterior end of the gnathostome to the tip of the abdomen was taken.

Results

Attachment sites

Eylais larvac enter the subelytral space of aquatic beetles when the beetles come to the surface and attach to the elytra, abdominal tergites, and hindwings. In 2 years of collecting, only 1 larva in over 2000 mites examined was attached to the underside of an elytron. This larva will not be considered
TABLE 1. Summary of attachment sites of mite larvae and nymphochrysalids for 1982 and 1983

<table>
<thead>
<tr>
<th>Parasite stage</th>
<th>Year</th>
<th>Right</th>
<th>Left</th>
<th>Dorsal</th>
<th>Ventral</th>
<th>C/Sc</th>
<th>AxC</th>
<th>Abdomen</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Larva</td>
<td>1982</td>
<td>553</td>
<td>540</td>
<td>35</td>
<td>1058</td>
<td>1092</td>
<td>1</td>
<td>44</td>
<td>1137</td>
</tr>
<tr>
<td></td>
<td>1983</td>
<td>324</td>
<td>414</td>
<td>44</td>
<td>694</td>
<td>736</td>
<td>2</td>
<td>107</td>
<td>845</td>
</tr>
<tr>
<td>Nymphochrysalid</td>
<td>1982</td>
<td>58</td>
<td>37</td>
<td>0</td>
<td>95</td>
<td>95</td>
<td>0</td>
<td>5</td>
<td>100</td>
</tr>
<tr>
<td></td>
<td>1983</td>
<td>33</td>
<td>26</td>
<td>0</td>
<td>59</td>
<td>59</td>
<td>0</td>
<td>12</td>
<td>71</td>
</tr>
</tbody>
</table>

**Note:** See text for explanation of abbreviations. Values in parentheses are percentages of the total mites attached at any site.

In 1982 and 1983, 3.9 and 12.7% of mite larvae were attached to the abdominal tergites, respectively (Table 1). The larvae (and hence nymphochrysalids) occur most frequently on the third abdominal tergite. The differences in numbers of mites on each tergite were significant ($\chi^2 = 91.12; p << 0.001$).

**Abdominal tergites**

The vast majority of larvae (96.1% in 1982, 87.2% in 1983) and nymphochrysalids (95% in 1982, 83.1% in 1983) were attached to the hindwings of the beetles. Only two areas of attachment were noted: the leading edge of the wing (labelled C/Sc for the costal and subcostal veins) and the trailing proximal corner of the wing (labelled AxC for the axillary cord (see Ward 1979)). If only hindwing parasites are considered, 99.9% ($\chi^2 = 1089, p << 0.001$) and 99.7% ($\chi^2 = 730, << 0.001$) were attached to the C/Sc region in 1982 and 1983, respectively.

Parasites attached to the hindwing also show a strong preference for the ventral surface of the wing (Table 1) ($\chi^2 = 838.4, p << 0.001$ for 1982; $\chi^2 = 630.7, p << 0.001$ for 1983). A G-test of heterogeneity (Sokal and Rohlf 1969) revealed no homogeneity between years ($G = 1503.04, p << 0.001$), indicating that while the ventral preference is the same between years, its magnitude is different.

Preference of right versus left wing was less clear. In 1982, no significant preference for either wing was found ($\chi^2 = 0.973; p > 0.1$). In 1983, a significant preference for the left wing occurred ($\chi^2 = 27.86, p << 0.001$). Pooled data for both years, however, showed no significant ($\chi^2 = 1.21, p > 0.2$) difference in attachment to the right or left wing.

**Rates of parasitism and parasite load**

The proportion of the beetle population parasitized showed similar trends in both years and for both sexes (Fig. 1). In 1982 and 1983, parasitism rates began relatively high in the late spring and then gradually declined in mid- to late-August. Similarly, both sexes had high rates of parasitism at the beginning of the season, a decline in late summer, and another increase in early fall (Figs. 1A and 1B).

In both years, most parasitized beetles had one to two larvae attached to them (Fig. 2). Thereafter, there were fewer beetles...
with larger numbers of larvae. In 1983, there was a more marked preponderance of beetles with only one parasite than in 1982. When both distributions are compared with an expected Poisson distribution (including beetles with no parasites, 198 in 1982 and 351 in 1983), both are significantly different ($\chi^2 = 534.12, p << 0.001$ for 1982 and $\chi^2 = 920.01, p << 0.001$ for 1983).

Similar trends were noted for the number of nymphochrysalids on a beetle. Although far fewer beetles were found with nymphochrysalids, most still carried one and the maximum was three in 1982 and five in 1983 (Fig. 2).

**Growth rates and phenology**

Larval mites were found on the first beetles to be taken in early spring and mites taken at this time had among the lowest mean lengths found (Fig. 3). Mites grew rapidly and reached a maximum larval size in late June and July. Those attached to females reach their maximum size (1.72 mm) earlier than those attached to males (Fig. 3), although mites on male beetles attain a larger mean length (2.29 mm) than those on females. The differences in maximum size, however, are not significant ($t = 1.68, 0.1 > p > 0.05$). There is a marked drop in the mean length of larvae in early August. This drop corresponds exactly to the times when larval mites form nymphochrysalids (Fig. 4). Nymphochrysalids were found on the beetles until October when the lake froze.

A frequency distribution of size classes of mites throughout 1983 is presented in Fig. 5. As might be expected, there is,
throughout the season, a steady increase in the number of animals in the larger size classes. There is also, for most weeks, a steady recruitment of very young animals in the larger size classes. There is also, for most weeks, the smallest mites into the population, so that for most weeks, the smallest mites are the most numerous.

A regression of mean length of mite larvae on the number of mites per beetle ($r^2 = 0.637$, $t = 2.166$, $0.05 > p > 0.02$) showed a significant decrease in the mean length of mites in more heavily parasitized beetles (Table 2). There was also a significant difference in the mean length attained by mites on the wings (1.29 mm) compared with mites on the abdomen (1.47 mm) ($t = 8.47$, $p << 0.001$).

### Discussion

A preference for a particular attachment site on a host has been noted for mites parasitizing several species of aquatic insects. Davids (1973) and Harris and Harrison (1974) indicate that mites of the genus *Hydrachna* preferentially attached to the corium of the hemelytra of their corixid hosts. Davids et al. (1976) noted a preference by *Eylais* mites for the anterior abdominal tergites of their hosts and Lanciani (1980) described a preference by *Hydrachra virella* for the thoraces of their notonectid hosts.

Lanciani (1970a) enumerated the attachment sites on several genera in the families Dytiscidae and Hydrophilidae. Of 19 mite species he examined, only 3 were recorded as attaching to the wings, indicating that attachment to the underwings is a rather uncommon phenomenon. Instead, most preferred the tergites or elytra. Lanciani (1970b) did note that larvae of *E. harmsani* attached to the subcostal–median trunk of dytiscids; an observation confirmed in this study.

Why does the strong preference for the ventral leading edge (coastal–subcostal) of the hindwing exist? Lanciani (1970b, 1971) proposed that the limiting resources of the host were the volume of the subelytral space and the amount of nutrient to be derived from the host. The attachment preference of mite larvae seen in this study represents an attempt to maximize both these resources.

The volume available for growth beneath the elytra is limited dorsally by the rigidity of the elytra and limited ventrally, to a lesser extent, by the tergal sclerites. The most pliable area of the dorsum is the pleural membrane containing the spiracles. When the hindwing is folded at rest, the ventral costal–subcostal portion of each wing lies directly over this pleural membrane. Any mite growing in this area can displace the membrane as it grows and not be restricted by the rigidity of the elytra.

### Table 2. Relationship between the number of larvae carried by a beetle and the mean length attained by each larva

<table>
<thead>
<tr>
<th>No. of mite larvae per host</th>
<th>Mean length (±SD)</th>
<th>N (parasites)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>of each larva (mm)</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>1.16±1.11</td>
<td>180</td>
</tr>
<tr>
<td>2</td>
<td>1.19±0.929</td>
<td>90</td>
</tr>
<tr>
<td>3</td>
<td>0.83±0.698</td>
<td>45</td>
</tr>
<tr>
<td>4</td>
<td>0.77±0.638</td>
<td>37</td>
</tr>
<tr>
<td>5</td>
<td>0.86±0.617</td>
<td>15</td>
</tr>
<tr>
<td>6</td>
<td>0.81±0.695</td>
<td>5</td>
</tr>
</tbody>
</table>

also exploit one of the more blood-rich vein areas in the wing. Arnold (1964) noted that there is a strong afferent flow of blood through both the costa and subcosta and that the blood sinuses of the adephagan wing are concentrated in the leading edge. Consequently, any mite larva attaching in this area has a high probability of encountering a dependable and plentiful source of food whether that source be a vein or sinus.

*Eylais* mites inhabit standing water (Young 1969) and their attachment to the wings underscores Lanciani’s (1970b) assertion that wing parasitism should be a feature of hosts that inhabit such water bodies. Such hosts are presumably less likely to fly and thereby displace the larvae. In Lanciani’s (1970b) list of hosts and attachment sites of several species of *Eylais*, those beetles primarily associated with permanent water carry wing parasites while residents of temporary ponds have mites attached on the ventral surface of the elytra or on the tergites. Such is true here. The *D. alaskanus* of George Lake are not prone to dispersal as indicated by catches of marked animals in successive years (Aiken and Roughley 1985).

Parasite load of an individual beetle indicates that mites may be actively choosing previously unparasitized hosts or hosts with only a few parasites. Comparisons of the frequency distribution of the number of mites per beetle (Fig. 2) to a Poisson distribution revealed that attachment was not random. Work done by Nielsen and Davids (1975) indicates that mites actively select sites on a host. Data in Table 2 offer one explanation for such selectivity. Mites attaching to already parasitized hosts are smaller than those on hosts that are previously unparasitized (see Lanciani 1976).

Rates of parasitism found in this study are generally higher than those reported elsewhere (Lanciani 1970a; Nielsen and Davids 1975). Martin (1975) indicated that differences in infestation rates could be due to either host attractiveness or the host’s particular habitat preference. Mark–recapture experiments (R. B. Aiken, unpublished data) suggest that *D. alaskanus* is a highly mobile animal that would encounter several habitat types in a short time. *A priori*, one might expect that infestation occurs when the water is calm but, beyond this, microhabitat differences would not seem to be important.

In both years, the general decline in rates of parasitism throughout the summer and increase again in the fall (Fig. 1) are due to life cycles of both the mites and beetles. The summer decline in rates of parasitism can be first attributed to the completion of the parasitic phase of the mite’s life cycle (the larva). The appearance of nymphochrysalids signals a change to a free-living nonparasitic nymph. The decline in rates of parasitism was also due to the appearance of a new cohort of teneral beetles (R. B. Aiken and C. W. Wilkinson, in preparation) that are only rarely parasitized.

These facts taken together reflect the coordination of the life cycle of the mite with that of the host. Greatest parasitism rates are found in the spring and early summer and fall (Fig. 1), when beetle populations are high or increasing (R. B. Aiken and C. W. Wilkinson, in preparation), affording the mite higher numbers of potential hosts. When beetles are scarce (July and August), most mites have completed their larval growth and are in nonparasitic stages.

The phenology of larval mites (Fig. 5) shows both expected and unexpected trends. The high numbers in small size classes and the gradual increase of numbers in larger size classes through June is expected for a species of mite overwintering as an egg or larva. The nymphochrysalids appearing in August would then be the products of this overwintering generation.
The number of nymphochrysalids vis a vis the number of small larvae and the lack of any distinct bulge in the frequency distribution as one cohort grows from week to week (Fig. 5) indicate that in the early larval period, there is a very high mortality.

The consistently high numbers in the small size classes indicate steady recruitment of young larvae throughout the year. Such recruitment in the early and late portions of the season indicate that nymphochrysalids emerging in August would, according to Lanciani's (1969) data, have time to complete the life cycle and produce a new larval cohort that attaches to the host in late summer or early fall. Those nymphochrysalids appearing in September or October would probably not have time to complete the life cycle in the fall and would either finish it slowly over the winter or in the early spring when the ice left the lake. This would explain the recruitment in May.

The large numbers of small larvae throughout June and July and the lack of any bulge in the frequency distribution as one cohort grows from week to week (Fig. 5) indicate that nymphochrysalids emerging in August would, according to Lanciani's (1969) data, have time to complete the life cycle and produce a new larval cohort that attaches to the host in late summer or early fall. Those nymphochrysalids appearing in September or October would probably not have time to complete the life cycle in the fall and would either finish it slowly over the winter or in the early spring when the ice left the lake. This would explain the recruitment in May.

The large numbers of small larvae throughout June and July are confusing. There may be two asynchronous cohorts of the same species. The end of the parasitic phase of the first cohort is represented by the few nymphochrysalids appearing in late June. This cohort then completes its free-living phase quickly in the lake and reinvests the hosts in July, accounting for the large numbers of small animals. The second cohort, represented by the few nymphochrysalids in August, September, and October would then be the majority of the mite population. This cohort is less cohesive than the first and individuals of a particular stage can be found for a long period of time. Consequently, overwintering may occur at any stage. This would account for the consistent preponderance of small animals in the following spring and early summer. Cook (1974) and Lanciani (1969) noted that some species of Eylais have two generations per year but did not consider the possibility of asynchronous cohorts.

A final possibility is that there is more than one species of mite involved. These mites, however, are difficult to determine to species and the taxonomy of the group is uncertain (Cook 1974). Unfortunately, little is known about the nonparasitic stages of this mite in George Lake. The phylogeny of free-living stages would help verify or reject some of the hypotheses mentioned here.

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