

Condition and fecundity of the damselfly, *Enallagma ebrium* (Hagen): the importance of ectoparasites

Mark R.L. Forbes and Robert L. Baker

Department Zoology, Erindale College, University of Toronto, Mississauga, Ontario, L5L 1C6, Canada

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Summary. The extent, magnitude, and cause of natural covariation between degree of parasitism and other variables known or suspected of influencing host fitness (such as host age or body size) has been understudied. We demonstrate that degree of parasitism by larval water mites (*Arrenurus* spp.) was associated with reduced condition of males and with lowered fecundity of young females of the damselfly, *Enallagma ebrium* (Hagen) (Odonata: Coenagrionidae). We also demonstrate that degree of parasitism can covary with both age and size of host damselflies. We explain the putative causes of such natural covariation, and we suggest that degree of parasitism, host age, and host size can all interact to determine damselfly fitness. We expect that natural covariation between the host's phenotype and degree of parasitism will be frequently observed. Studies of such natural covariation will help researchers to assess better the importance of several variables on host reproductive success and to understand better the dynamics of host-parasite interactions.

Key words: *Arrenurus* – *Enallagma* – Mite – Damselfly – Host-parasite interactions

Evolutionary ecologists often investigate the effects of age and body size on reproductive success of animals in order to formulate and test predictions about life-history tradeoffs (Smith et al. 1987; Pianka 1988). Several studies on insects have shown that both body size and adult age can affect survivorship (Thornhill and Alcock 1983; Banks and Thompson 1985), current and lifetime fecundity of females (Juliano 1985; Banks and Thompson 1987), territoriality and mating success of males (Thornhill and Alcock 1983; Hyashi 1985), and use of alternative reproductive tactics (Forsyth and Montgomerie 1987; McLachlan and Neems 1989).

Parasites have often been related to condition, survival, and reproduction of their hosts (Price 1980; but see Gill and Mock 1985). Several recent studies have shown that degree of parasitism of individuals within host populations can depend on host size (Blower and Roughgarden 1988; Forbes and Baker 1990), host sex (Schall 1983; Zuk 1987) and age of hosts (Folstad et al. 1989; Borgia and Collis 1989). The extent, magnitude, and cause of such natural covariation has been understudied. Many researchers examine the direct effects of parasites on particular age or size classes of hosts, while others have simply neglected parasites and pathogens (and covariation between parasitism and other variables) in their studies on reproductive success of animals. In a recent book devoted entirely to the topic of reproductive success of animals (Clutton-Brock 1988), very little attention was paid to the importance of parasites.

Understanding the dynamics of host-parasite interactions may well depend on the nature and magnitude of covariation between degree of parasitism and other variables known or suspected of influencing host fitness. If such covariation is recurring and strong in nature then size- or age-dependent effects of parasites should be considered in more realistic models of host-parasite interactions. Moreover, by knowing the causes of such covariation, researchers may design more meaningful experiments.

Our objective in this study is to determine whether ectoparasitic larval water mites are harmful to their damselfly host, *Enallagma ebrium* (Hagen) and to examine the extent and cause of natural covariation between size and age of damselflies and degree of parasitism. Our specific objectives are three-fold. First, we describe the patterns of site attachment by larval *Arrenurus* on imaginal *E. ebrium* to determine whether mites directly interfere with spiracles, legs, wings, or particular organs. Second, we examine whether degree of parasitism by larval water mites is related to i) condition of adult *E. ebrium* males, and ii) age-specific fecundity of adult *E. ebrium* females. Third, we examine whether there is i) seasonal variation in the numbers of *Arrenurus* mites parasitizing adult

E. ebrium or ii) seasonal declines in size of adult *E. ebrium* as found for other insects (Crespi 1989), including odonates (Tsubaki and Ono 1987; Baker 1989). Seasonal variation in numbers of mites and sizes of hosts could produce covariation between both host size and age, and degree of parasitism.

Host-parasite association: general biology

Larval *Arrenurus* (*Arrenurus*) spp. contact and colonize odonate larvae, but are only parasitic on adult odonates. Larval mites are carried on the larval odonate until emergence of the host. Upon emergence of the host, larval mites abandon the exuvia of the larval odonate and move on to the newly-emerging adult (Åbro 1982). Larval mites then pierce the adult host's exoskeleton and start to engorge. Notes on the general biology of *Arrenurus* mites parasitizing adult odonates can be found in Mitchell (1959, 1968); Smith (1988), and Forbes and Baker (1990).

Materials and Methods

Study site

Our study site was Two-island Lake or TL. TL is a large freshwater marsh (approximately 50 ha) located within 10 km of the Queen's University Biological Station, near Chaffeys Lock, Ontario, Canada (44° 34' N; 79° 15' W).

Patterns of parasitism

On 25 June 1990, we netted 60 newly-emerged *E. ebrium* (30 males and 30 females) at TL. For each adult, we recorded the number of newly-attached larval mites in specific regions of the host's thorax and abdomen. Thoracic mites were probably all *Arrenurus mucronatus* (Lavers), whereas abdominal mites were likely *Arrenurus magnicaudatus* Marshall. Species identifications for mites were made on adult males which were reared from larvae collected off of *E. ebrium* adults netted at TL in 1989 (Forbes and Baker 1990).

Male condition

To examine condition of males in relation to degree of parasitism by mites, we collected sexually-mature males carrying engorged *Arrenurus* mites on 6 and 9 July 1990 at TL. Males were all approximately the same age because their *Arrenurus* mites were engorged, but had not yet detached (Smith and Cook 1990). Condition of males was defined in two ways. First, we calculated dry mass corrected for head width (size) as one estimate of odonate condition (see Johnson et al. 1984; Baker 1989). We also brought one sample of males into the lab, and recorded their longevity under situations of no food as a second index of male condition. Fasting leading to death through starvation may occur regularly in nature as *Enallagma* damselflies do not fly or forage on rainy or cool days (personal observations).

We then counted numbers of mites on males collected for condition estimates based on dry mass. All males had one or more *Arrenurus* mites; four males had 1 engorging *Limnochares americana* Lundblad mite which was also counted. Thus, no unparasitized males were found and none were included in the analysis. We killed each male by thoracic compression and placed them individually

into vials. After approximately 1 h of collection, we transported males back to the lab and stored them in a refrigerator at 0° C overnight (for roughly 16 h). The following morning, we removed any mites that were still attached to hosts by gently scraping them away with an insect pin. We then measured head width of each male to the nearest 0.1 mm using a binocular microscope provided with an ocular micrometer. Because wings of some males were torn or missing, we carefully cut all wings at their junction with the pterothorax to ensure that each male had the same amount of wing "damage". Males were then dried at 50° C for 3 days, before we weighed them using an electronic microbalance.

For males collected for condition estimates based on fasting duration, we counted engorged mites and then immediately placed males individually into large vials (75 mL). As before, all males had at least one or more mites; unparasitized individuals were not included in this experiment. Vials were provided with a dowel for a perch and capped with perforated plastic. Vials also had a 2 × 2 cm piece of paper towel which was soaked in water to keep conditions moist. We defined lightly-parasitized animals as those carrying ≤ 14 *Arrenurus* mites (n = 14), and heavily-parasitized animals as those with ≥ 19 mites (n = 14) which allowed for equal numbers of males in each parasitism category.

Vials containing lightly- and heavily-parasitized males were alternately placed (on their side) in two large plastic tubs (30 × 18 × 12 cm). Because vials were placed end to end and because the plastic caps were opaque, a male could not see the male directly in front of, or directly behind, him. Paper towel barriers soaked with water were placed between rows of vials to prevent desiccation of males (desiccation is a major source of mortality for damselflies housed in the laboratory, Hinnekint 1987) and to prevent males from seeing males beside them. Vials were checked for dead animals every 2–3 h (between 0800 and 2400 h each day). From approximately 0600–2100 h, the lab was naturally illuminated. The lab was temporarily illuminated by artificial fluorescent lights for no more than 10 minutes during checks at 2200 h and 2400 h. Mean lab temperature was 25 ± 1.9° C.

Female fecundity

From 23–28 June 1990, 30 adult females were collected in copulo or in tandem with males. Only females which were captured ≥ 5 m from the water's edge were included in the analysis described below. We were sure that these females had just arrived at TL and were on their way to oviposit. Females collected in tandem with males over water were found to have partially empty abdomens strongly suggesting that they had already oviposited some eggs. Females were immediately placed individually into small plastic vials filled with 95% ethanol. We later measured their head widths as described above, and counted their engorged mites. We also measured length of the right forewing from the nodus to the tip of the wing for each female. We again controlled for age by including only females that had engorged mites. Females were dissected and their numbers of eggs (see below) were counted. As with males, all females were found to carry one or more mites; thus, unparasitized individuals were not included in the analysis.

Seasonal variation in mite numbers

To examine whether there was seasonal variation in numbers of *Arrenurus* spp. mites parasitizing *E. ebrium*, we netted newly-emerged adults at TL at approximately one-week intervals from the first week of June to the end of the first week of July in both 1989 and 1990. This five-week period covered most of the emergence period of *E. ebrium*. In both years, we marked newly-emerged adults with a single black dot at the nodus of the right forewing (using a permanent marker), counted their numbers of larval mites, and released them. Animals which were recaptured were released without reassessment of mite numbers. In 1989, but not in 1990, un-

parasitized animals were found and were included in analyses. In 1990, we collected a minimum of 10 males and 10 females each sampling day to examine whether size of damselfly adults changed seasonally. For each individual, we measured its head width and length of its right forewing as described above.

Results

Patterns of parasitism

Mites were not found occluding any spiracles nor were they found on or near damselfly wings. Mites attached only to the venter of the thorax and abdomen of host damselflies. Thoracic mites attached on the ventral sternites between the meso- and meta-thoracic legs (site I), on the coxae of the pro-, meso- or metathoracic legs, or on the metinfraepisternum or mesepimeron near the coxae (site II), and on the sternite behind the metathoracic legs (site III). Thoracic mites showed similar patterns of site use on male and female hosts (Table 1).

Abdominal mites attached to segments VI, VII, and VIII in the pleural folds between the tergum and sternum. For females, 2 mites (6.1% of all abdominal mites on females) were found on abdominal segment VI, 29 (87.8%) on segment VII, and 2 (6.1%) on segment VIII. For males, 0 mites were found on abdominal segment VI, 27 (71.1%) on segment VII, and 11 (28.9%) on segment VIII. Of the 11 mites found on segment VIII of males, 7 were found on a single male. Thus, abdominal mites also showed similar patterns of site use on male and female hosts. No mites were found attached at the second abdominal segment near the male's intromittent organ.

Male condition

We found no significant relationship between numbers of mites and dry mass of males, after statistically controlling for male head widths using partial correlations (Snedecor and Cochran 1980) (partial $r = -0.18$, $df = 28$, $p = 0.15$). Neither of the bivariate correlations between dry mass and numbers of mites (Pearson $r = 0.042$, $p = 0.82$) or head width and numbers of mites (Pearson $r = 0.227$, $p = 0.13$) were statistically significant. Longevity of males housed in vials, however, was dependent on whether males were lightly- or heavily-parasitized. Longevity of these males was recorded in half days. Males found dead

Table 1. Numbers of mites found attached to various sites on male and female *Enallagma ebrium* and number of males and females with one or more mites found attached at each site. Percentages of mites and percentages of individuals are in parentheses. See text for specific descriptions of site locations

Site	Number of mites		Number of individuals	
	female	male	female	male
I	567 (86.4%)	492 (83.4%)	30 (100%)	30 (100%)
II	65 (9.9%)	77 (13.1%)	19 (63.3%)	20 (66.7%)
III	24 (3.6%)	21 (3.5%)	16 (53.3%)	13 (43.3%)

between 0000 h and 1200 h on the first day were recorded as dead on day 1, males found dead between 1200 h and 2400 h on the first day were recorded as dead on day 1.5, etc. We used a t-test (preceded by an F-test for homogeneity of variances: $F_{14,14} = 1.19$ $p > 0.5$) and found that mean survival of lightly- (4.9 days) and heavily-parasitized males (3.9 days) differed ($t = -1.971$, $df = 25$, $0.025 < p < 0.05$). For comparisons between lightly- and heavily-parasitized adults with respect to condition or fecundity, statistical tests were one-tailed because we expected *a priori* that mites would have a negative impact on host damselflies. In contrast, because there was no reason to expect that mites would have an effect on adult size (which was fixed at emergence before the onset of parasitism), statistical comparisons between lightly- and heavily-parasitized individuals with respect to size are two-tailed. We found no differences in mean head widths between lightly- (3.78 mm) and heavily-parasitized males (3.76 mm) ($t = -0.81$, $df = 26$, $p = 0.42$).

Fecundity of females

Three types of follicles were found in females. Developed eggs were translucent and elongate (Walker 1953), their cuticles were easily distinguishable and their widths were roughly $\frac{1}{4}$ – $\frac{1}{5}$ of their lengths. Undeveloped follicles were approximately half the lengths of developed eggs and were more elongate (their widths were $\frac{1}{6}$ – $\frac{1}{8}$ their lengths). Undeveloped follicles were less translucent and were off-white, but not milk-white, in colour. The third type of follicle was found in low numbers; these were opaque and milk-white, and shorter and squatter than undeveloped follicles. We suspect that these short follicles were resorbing.

Only developed eggs were counted. The mean number of developed eggs (276.8 eggs, $n = 15$) carried by heavily-parasitized females (females with 19–32 mites) was lower than that (323.4 eggs, $n = 15$) carried by lightly-parasitized females (females with ≤ 15 mites) ($t = 1.94$, $df = 28$, $0.025 < p < 0.05$). We defined lightly-parasitized females as carrying ≤ 15 mites to have equal numbers of females in each parasitism category. We found no differences in mean head widths between heavily- (3.71 mm) and lightly- (3.71 mm) parasitized females ($t = 0.76$, $df = 28$, $p = 0.94$) and no significant correlation between head widths and the number of eggs females carried (Pearson $r = 0.040$ $df = 28$, $p = 0.83$). However, wing length and egg number were positively correlated (Pearson $r = 0.365$, $df = 28$, $p = 0.047$).

Seasonal variation in mite parasitism

To examine whether mean mite loads differed between sexes of *E. ebrium* across 5 sampling dates, we used two-way parametric analyses of variance (Wilkinson 1989) and analyzed data from each year separately. Two distributions of untransformed mite numbers on newly-emerged *E. ebrium* (one each year) were non-normal

(Kolmogorov-Smirnov test, maximum differences ranged from 0.104–0.205; all $p > 0.05$) (Wilkinson 1989). Log_{10} -transformation did not normalize the non-normal samples. Because analyses of variance are robust to departures of samples from normality (Zar 1984), and because we found that all 10 distributions for each year had equal variances using a Bartlett's test (Wilkinson 1989) (1989: $X^2 = 16.7$, $df = 9$, $p > 0.05$; 1990: $X^2 = 16.5$, $df = 9$, $p > 0.05$), we decided to include the non-normal samples in the first of two analyses for each year. In the second analysis for each year, the date on which non-normal sample was collected was omitted.

In 1989, there was no significant interaction, no effect of date, and no effect of sex, on mean numbers of mites carried by newly-emerged *E. ebrium* (sex X date interaction $F_{4,233} = 0.259$ $p = 0.90$; date: $F_{4,233} = 0.200$, $p = 0.65$; sex: $F_{1,233} = 0.313$ $p = 0.87$). Similar results were obtained if the date on which the non-normal sample was collected in 1989 was omitted from the analysis.

In 1990, there was no significant sex X date interaction ($F_{4,307} = 0.588$, $p = 0.67$) or independent effect of sex ($F_{1,307} = 2.74$ $p = 0.099$) on mean numbers of mites carried by newly-emerged *E. ebrium*. However, date had a significant effect ($F_{4,307} = 5.49$ $p = 0.0001$) on mean numbers of mites carried by adults that year. Similar results were obtained if the date on which the non-normal sample was collected was omitted from the analysis.

For males collected in 1990, abundances of larval mites were low beginning early in the season and increased throughout the remainder of the season until the second-last sampling date (Fig. 1). On the last sampling date, mite numbers declined but were still higher than abundances recorded at the beginning of the season. For females in 1990, mite numbers were lowest early in the season, but reached their highest levels on the second sampling date (Fig. 1). For the remaining three dates, numbers of mites were somewhat lower than the second sampling date, but were still quite higher than those at the beginning of the season. Although there was no significant effect of sex in 1990, males carried more mites into adulthood than did females on 4 of 5 sampling dates. In general, mite numbers were higher in 1990 than in 1989 for both sexes (Fig. 1).

Size

We found no significant interaction ($F_{4,120} = 2.32$, $p = 0.060$) between date of sampling and host sex on head widths of newly-emerged *E. ebrium*. However, both date of sampling ($F_{4,120} = 21.37$ $p = 0.0001$) and sex ($F_{1,120} = 42.15$, $p = 0.0001$) were independently and significantly associated with head widths of newly-emerged adults. *E. ebrium* adults were sexually dimorphic over all but one date with males having wider heads than females; both sexes showed seasonal declines in head capsule widths (Fig. 2). In contrast, females had longer forewings than males over all dates. Although forewing length also declined during the season for both sexes (Fig. 2), the decline was more abrupt than that shown by head capsule widths.

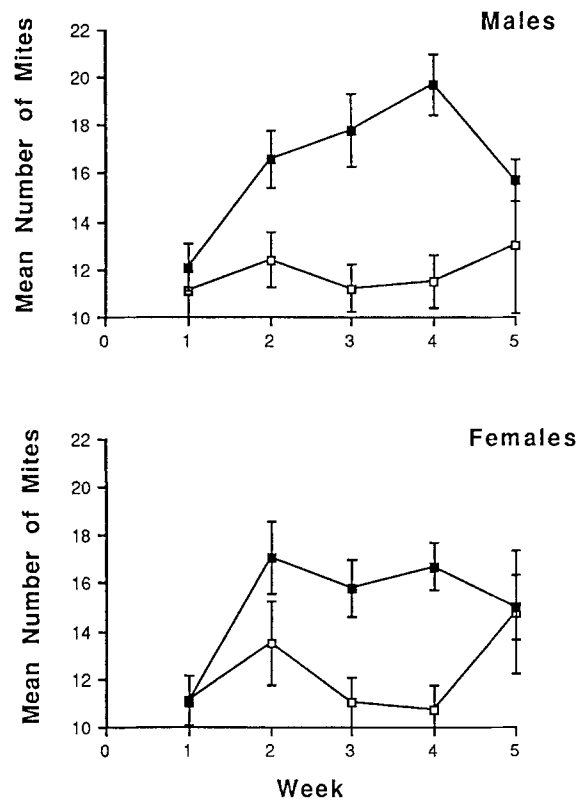


Fig. 1. Mean numbers of mites for males and females in relation to year (open squares represent 1989; filled squares represent 1990) and week of emergence period. Error bars represent ± 1 standard error. Sample sizes for each mean ranged from 14–34 damselflies

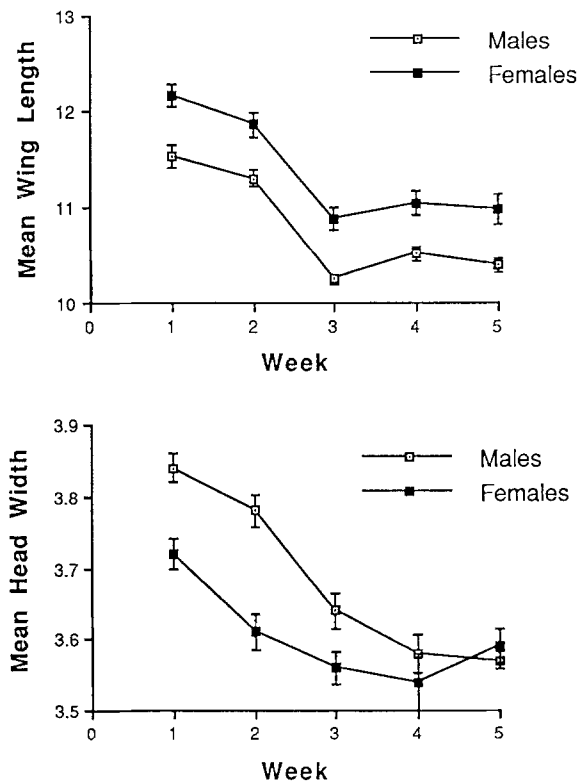


Fig. 2. Mean head widths and wing lengths of males (open squares) and females (filled squares) in relation to week of emergence period in 1990. Error bars represent ± 1 standard error. Sample sizes for each mean ranged from 11–15 damselflies

Discussion

Water mites have been shown to reduce survivorship and fecundity of several aquatic insects (Lanciani 1983; Smith 1983, 1988). However, the importance of water mites to odonate reproduction and survival has received little attention. Åbro (1982) argued that *Arrenurus* mites enfeeble damselflies by piercing through the host's exoskeleton and feeding on host tissues and haemolymph. However, Åbro did not provide data on longevity of damselflies in relation to degree of parasitism. Robinson (1983) showed that "old" female *Ischnura posita* parasitized by one or more water mites (identified as *Hydrachna* spp.) were less likely to be recaptured than "old" unparasitized females. Robinson (1983) was unable to detect an effect of water mites on survivorship of other age and sex classes of *I. posita*. Although Robinson's results are suggestive of a negative impact of water mites on odonate survival, he did not record evidence of past parasitism such as mite scars left on damselflies (see Åbro 1982). Thus in Robinson's study, old unparasitized damselflies could have been individuals who had been parasitized, but whose mites had already detached.

Whether or not larval mites are more debilitating to either sex of host damselflies will have to await more detailed observations. However, because patterns of site attachment by larval mites were independent of host sex, male and female hosts would have had similar patterns of exoskeletal damage (i.e. around the venter of the thorax and certain abdominal segments). Mitchell (1968) and Åbro (1982) showed that damage to the host's exoskeleton can cause leakage of haemolymph; and such leakage may result in problems of water balance for host damselflies. Whether either sex is more affected by water imbalance is unknown.

In this study, larval water mites were not found on the wings of damselflies (as reported for one species of dragonfly, Münchberg 1982) nor were they found occluding spiracles. Thus, these species of *Arrenurus* would not directly interfere with damselfly flight. However, in some regions of Eastern Ontario, Canada, numbers of mites on single *E. ebrium* damselflies can exceed 100. These mite loads can account for up to 15% of a damselfly's wet mass (unpublished data) which may interfere indirectly with damselfly flight. Usually insect nets are required to catch damselflies, but such heavily-parasitized damselflies have been caught by hand (Åbro 1982, personal observations). In addition, the legs of such heavily-parasitized damselflies were laterally displaced. Such displacement may interfere with perching, or may prevent damselflies from holding their legs up during flight. Because no mites were found attached at the second abdominal segment near the male's intromittent organ, mites would not directly interfere with the male's ability to copulate.

Our results do indicate that naturally-occurring levels of parasitism by larval water mites are harmful to both male and female damselflies. Degree of parasitism by water mites was associated with reduced longevity of young males in the laboratory, although degree of parasitism was not correlated with dry mass of males, after

correcting for their size. Corrected dry mass may not accurately reflect condition of animals as measured by the animal's ability to withstand starvation or other stresses. In addition, degree of parasitism was associated with lowered fecundity of young females, although we realize that fecundity at any single bout of oviposition may not be an accurate index of lifetime fecundity of females (see Banks and Thompson 1987).

We believe that degree of parasitism (which can show an extreme range) will be an important determinant of reproductive success for both sexes of many insects. By including parasites in their studies, researchers might clear up some discrepancies between studies as to the importance of body size and age to male and female reproductive success. For example, McVey (1988), who did not measure condition of animals or their degree of parasitism, was unable to find any phenotypic variables that covaried with male mating success in her study of the territorial dragonfly, *Erythemis simplicollis*. That McVey's work contrasts with other studies on male mating success in territorial odonates (Tsubaki and Ono 1987, one of two species described by Fincke 1988) could be due to several factors, one of them being the role of parasites. In addition, researchers reporting effects of body size on insect reproductive success may have confounded body size effects with effects attributable to parasites that were not assessed.

As noted by other researchers (Borgia and Collis 1989), ectoparasites probably do not act alone in determining their effects on hosts. Ectoparasites can be vectors of endoparasites (Bartlett and Anderson 1987) and ectoparasites can be correlated with other variables (such as host size (Forbes and Baker 1990) or host age (Borgia and Collis 1989)) that are known or expected to influence host reproductive success. We suspect that developmental time for late instars of odonates and other aquatic insects will greatly affect their susceptibility to colonization by water-borne parasites and pathogens (Forbes and Baker 1990). Recently, McLachlan (1989) has shown that aquatic midges which develop faster attain a larger adult size than do slower-developing larvae, under extreme densities. If large size means faster development through immature stages, then we might expect negative covariation between adult size and degree of parasitism.

Forbes (unpubl. data) found negative correlations between body size of sexually-mature male *E. ebrium* and their mite numbers for 6 samples taken in 1 of 2 years of study. This study provides one explanation for such covariation because we found seasonal increases in abundances of larval mites, and seasonal declines in body size (as measured by head widths and wing lengths), for both sexes in 1 of 2 years of study. Seasonal declines in body size have also been found in studies of other insects (Crespi 1989), yet the significance of such declines is largely unknown. Regardless, males and females which emerged at the beginning of the 1990 season were both larger and parasitized by fewer water mites than males and females which emerged later that season.

Mitchell (1967) also noted extreme seasonal increases in abundances of larval water mites parasitic on two species of dragonflies. In both Mitchell's study and this

study, covariation between host age and degree of past or present parasitism can be expected (i.e. samples of mature adults collected late in the season will be comprised of both old lightly-parasitized individuals and young more heavily-parasitized individuals). Researchers often test hypotheses on age-related variation in reproductive effort (Pianka and Parker 1975). Obviously, calculations of reproductive effort will be greatly influenced by the amount of energy that individuals could potentially devote to reproduction which will, in turn, be affected by age-related variation in degree of parasitism. Such age-related variation has been found for insects (this study) and other animals (Folstad et al. 1989).

In conclusion, we have demonstrated that parasitic mites can have negative effects on host damselflies. We also demonstrate that parasite numbers on hosts can covary with both body size and age of hosts. We expect that such natural covariation between the host's phenotype and degree of parasitism will be frequently observed and we suggest that degree of parasitism, age, and size of hosts likely all interact to determine fitness of damselflies. Studies on the extent, magnitude, and cause of such natural covariation will help us to assess better the importance of several variables on host reproductive success and to understand better the dynamics of host-parasite interactions.

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