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ECTOPARASITISM OF DAMSELFLIES BY WATER MITES IN CENTRAL FLORIDA

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ABSTRACT

Little is known about the frequency of water mite ectoparasitism (Acari: Hydrachnida) within and among damselfly species of Central Florida. Here I present a field survey of the assemblage of damselflies and their water mite parasites at the Archbold Biological Station (Lake Placid, FL) during late Mar, 2006. During this period, 4 species of damselfly were abundant: *Ischnura hastata* (Say) and *Nehalennia gracilis* Morse captured only at pond sites; and *Argia fumipennis atra* Gloyd and *Ischnura ramburii* (Selys) captured at a lake site. Only pond damselflies had water mites, and 12.2% and 12.5% of *I. hastata* and *N. gracilis* were parasitized, respectively. These are 2 novel and unreported odonate-acari associations for this area. I also examined within-species differences in ectoparasitism by sex, body size, and wing-cell fluctuating asymmetry. However, these factors did not relate to the prevalence and intensity of parasitism in the field. My study indicates that brief surveys of odonates in Central Florida will likely generate novel, unreported associations with parasitic water mites—this information is important to address the gap in natural history for southeastern distributions of North American water mites.

Key Words: *Arrenurus*, Odonata, Hydrachnida, sex-bias, life-history trade-offs, body size, asymmetry, field surveys

RESUMEN

Poco es lo conocido sobre la frecuencia de ectoparasitismo por parte de los ácaros acuáticos (Acari: Hydrachnida) en cada especie y entre especies de pequeñas libelulas (Odonata: Zygoptera) en la región central de la Florida. Aquí se presenta un sondeo de campo del complejo de libelulas (conocidas también como caballitos del diablo o gallegos) y sus ácaros parásitos en la Estación Biológica de Archbold (Lake Placid, Florida) durante la última parte de marzo del 2006. Durante de este periodo, de las 4 especies de libelulas mas abundantes, *Ischnura hastata* (Say) y *Nehalennia gracilis* Morse fueron capturadas solamente en sitios de los lagitos; *Argia fumipennis atra* Gloyd y *Ischnura ramburii* (Selys) fueron capturadas en un sitio del lago. Solamente las libelulas capturadas en los lagitos tenían ácaros acuáticos, y 12.2% y 12.5% de los *I. hastata* y *N. gracilis* estaban parasitizadas, respectivamente. Estas son 2 asociaciones de odonata-ácaro claras y que no estaban reportadas para esta área. También, se examino las diferencias intra-específicas en el ectoparasitismo por el sexo, el tamaño de cuerpo, y la asimetría fluctuante de las células del ala. Sin embargo, estos factores no fueron relacionados con la prevalencia e intensidad del parasitismo en el campo. Mi estudio indica que la realización de sondeos breves de los Odonata en la región central de la Florida probablemente resultará en el descubrimiento de asociaciones nuevas y no reportadas con sus parásitos de ácaros acuáticos—esta información es importante para dirigirse a la brecha en la historia natural para la distribución de ácaros de agua en el sureste de América del Norte.

Basic information on the natural history of water mite parasitism (Acari: Hydrachnida) within and among odonate species is scarce (Smith 1988), and is urgently needed to assess the host range and geographic distribution of these parasites (Bush et al. 2001; Rolff 2001). Cook (1976) broadly surveyed adult water mites of Florida (mainly Hydrachnida: *Arrenurus*), and described many new species, adding 35 to the 14 previously described. However, nothing is known on the larval ecology of the mites, which are often parasitic on adult damselflies and dragonflies. Here I report field patterns of larval mite parasitism among the assemblage of damselflies species

found in the southernmost region of Lake Wales Ridge, Central Florida.

I also examine whether sex, body size, and fluctuating asymmetry relate to patterns of parasitism in the field. Life-history theory predicts an interaction between the reproductive effort among sexes and susceptibility to parasitism (Poulin 1996; Johnsen & Zuk 1999). This interaction can result in the characteristic male-bias of parasitism found in mammals and dioecious plants (Schalk & Forbes 1997; Moore & Wilson 2002; Cornelissen & Stiling 2005). However, the direction of this bias (either female or male) is dependent on the group of parasites under study (i.e.,

for birds there is a female bias in blood parasites, see McCurdy et al. 1998). Among invertebrate hosts, odonates are among the very few to show sex-biases in parasitism (Hecker et al. 2002; Lajeunesse et al. 2004; cf. Sheridan et al. 2002; Kelly 2005); although studies finding no bias are also common (Sheridan et al. 2002). Specifically for damselfies parasitized by water mites, the factors known to mediate sex-biases in parasitism include sex differences in immunity, adult behavior and/or phenology (Yourth et al. 2001; Lajeunesse et al. 2004; Robb & Forbes 2006). Sex-biases in parasitism can also be generated as an effect of body size dimorphism between sexes. Here the larger sex (or larger individual, more generally) may harbor a greater intensity of parasitism (i.e., number of parasites per host) because a larger size may represent a greater resource for more individual parasites (Bush et al. 2001).

In addition to sex and body size, fluctuating asymmetry has also been linked to parasitism for many animals including damselfies (c.f. Bonn et al. 1996). Field variation in ectoparasitism may be associated with damselfly symmetry, should the stressful conditions during larval growth (e.g., competition, predation, and/or parasitism) that influence the symmetric development of wings, also affect the susceptibility to, or recruitment of parasites (Leung & Forbes 1996). However, wing-cell asymmetry of adult damselfies is only a coarse surrogate of physical condition during larval-to-adult emergence and not adult condition (which is difficult to assess for insects). However despite this shortcoming, wing cell asymmetry may explain some variation of field parasitism given that many species of water mite are first phoretic on damselfly larvae and then parasitize hosts shortly after adult emergence (Smith 1988).

MATERIALS AND METHODS

I surveyed all damselfies (Odonata: Zygoptera) at 3 sites near the Archbold Biological Station (ABS; Lake Placid, FL) for 10 days (18-III-2006 to 30-III-2006). Two of these sites were ephemeral ponds located near ABS, and a third was located on the shore of Lake Annie. These sites have distinct vegetation types (see below), differ in size, but were primarily fields dominated by grasses or shrubby hypericum (*Hypericum* spp.). The edges of these fields were mostly dominated by palmettos (*Serenoa* spp.). The vegetation of the field surrounding my larger seasonal pond (ca. 1500 m²; hereafter large pond, N 27°10'50.7", W 81° 21'10.8") was mostly hypericum with small patches of redroot (*Lachnanthes caroliniana*), gallberry (*Ilex glabra*), fetterbush (*Lyonia lucida*) and several pine snags (*Pinus* spp.). The edge habitat surrounding this field had scrubby oak species (*Quercus inopia* and *Q. germinata*). The second seasonal pond (ca. 200 m²; N 27°11'14.1",

W 81°21'27.1") had mostly hypericum plants, and had an edge habitat composed of palmettos and maidencane (*Panicum hemitomon*), but did not have any pine snags. Finally, the lake site (N 27°12'39.3", W 81°20'58.7") had mostly southern ridge saw-hill flora (see description in Abrahamson et al. 1984).

At the two ponds, I sampled damselfies in the morning (ca. 10:30 am) and afternoon (ca. 4:00 pm), and rotated these sampling times daily (from afternoon to morning) to control for differences in activity between damselfly species. My survey at Lake Annie occurred daily at 1:00 pm. During surveys, I collected all possible damselfies with a sweep-net for 1 h. Rigorous sampling for a narrow time-frame can provide information on the relative frequency and abundance of damselfly species at a particular site. Captured damselfies were processed at ABS.

Damselfly species were identified following Westfall and May (1998) and were verified with specimens from the ABS invertebrate museum collected by M.J. Westfall. Individuals were sexed and divided into two age classes: teneral (e.g., newly emerged with soft, translucent wings) or adult (e.g., full coloration and rigid, dull wings). Westfall and May (1996) found an age related color-polymorphism of adult females in *I. hastata*, with young females having an orange coloration and older females with a darker brown to black coloration. This distinction was used to separate age classes for this species.

Symmetry of damselfies was estimated as the absolute difference in the number of cells (c) between the nodus and pterostigma on left (L) and right (R) wings. The total asymmetry (a) was the sum of the wing cell asymmetry between fore- and hind-wings (f and h , respectively). Specifically, asymmetry was calculated as follows:

$$a = |c_L^f - c_R^f| + |c_L^h - c_R^h|$$

When $a \neq 0$, damselfies were treated as asymmetric in analyses.

Four estimates of body size were measured: (1) wing-length (the distance between the nodus to the pterostigma for the right forewing; ± 0.01 mm Spi 31-44 caliper), (2) femur- and (3) tarsus-length (the first right leg of each individual was immersed in oil and had the femur and tarsus measured with use of a compound microscope at 10 \times ; ± 0.01 mm Olympus BX60F5). When the first right leg was missing, I used the first left leg for measurements. Finally, (4) wet weight was measured for each damselfly immediately following surveys (± 0.0001 g; Mettler Toledo digital scale, model AB104-5). These measures of body size were collapsed into a single size estimate with Principle Component Analyses (PCA; Zar 1984), but were $\log_{10}(x + 1)$ transformed prior to PCA analyses.

Water mites are parasitic only during a single stage in their life cycle, but Smith (1988) provides more details on this stage or the stages outlined below. After hatching from eggs, mite larvae are motile, and in many water mite species (i.e., *Arrenurus* mites) larvae are phoretic on damselfly larvae. When larval damselflies eclose from the water, phoretic mites abandon the exuviae and crawl back onto the newly emerged (teneral) damselfly. At this stage, phoretic mites locate suitable areas on the damselfly to attach and insert their feeding tubes (i.e., ventral side of the thorax or abdomen). Several mite larvae can attach to a single damselfly host, and at this stage they are parasitic and feed on the host. Once engorged, mites drop off their hosts when hosts return to water to reproduce. Finally, these water mites cycle through additional larval stages until they reach adulthood as aquatic predators.

In this study, larval water mites on each damselfly were counted and grouped as either phoretic (i.e., not attached with legs) or attached (e.g., with feeding tube inserted, engorged and without visible legs). Larval mites also were grouped by their attachment-site on the damselfly, either on the ventral side of the thorax or abdomen.

RESULTS

Richness of Species Assemblages and Abundances and Age Classes of Species

The most abundant pond species of damselfly in late Mar was *Ischnura hastata*, followed by *Nehalennia gracilis* (Table 1), whereas *Argia fumipennis atra* Gloyd was more common than *Ischnura ramburii* (Selys) at the lake site. However, abundance estimates were biased against *I. ramburii* captures because this species occupied more offshore areas (i.e., among emergent vegetation at the lake's edge) than the field area surveyed (ca. 2-20 m from the lake's edge). Of the 2 ponds, the larger had greater richness and abundance of both damselfly species than compared to the smaller pond—assuming an equal probability of capture at both ponds (Table 1; *I. hastata*: $\chi^2 = 10.3$, $df = 1$, $P = 0.0013$; *N. gracilis*: $\chi^2 = 6.7$, $df = 1$, $P = 0.0094$). However, only a single teneral of *A. fumipennis atra* and *I. ramburii* were captured at the large pond site. These 2 species are more common to permanent sources of water (Westfall and May 1998), and it is unknown whether they had emerged from this site or dispersed from a more permanent site (e.g., Lake Annie).

Damselfly species captured at pond sites differed in number of adult captures: 75% of 16 *N. gracilis* and 37% of 114 *I. hastata* were adults (species contrast: $\chi^2 = 8.4$, $df = [1, 128]$, $P = 0.0037$). However, the frequency of adult capture did not differ among the smaller and larger ponds for

both damselfly species (*I. hastata*: $\chi^2 = 0.1$, $df = [1, 112]$, $P = 0.76$; *N. gracilis*: $\chi^2 = 0.1$, $df = [1, 14]$, $P = 0.72$). For the 2 lake species, 12% of 53 *A. fumipennis atra* and all *I. ramburii* were adult ($n = 7$).

Water Mite Groups

In total, 92 larval mites were found (24 phoretic and 68 attached), and those attached could be divided into 3 groups: orange and spotted thoracic mites (e.g., common on the ventral side of the mesepimeron, metepimeron and tergites 1 and 2), dark-red abdominal mites (e.g., generally on 4th to 7th sternites), and a bright-red mite on the upper posterior of thoracic mesepimeron. By far the most abundant were the orange thoracic mites, with 61 attached individuals found on 15 damselflies. There also was over dispersion of thoracic mites, where 49% of attached mite larvae were found on 3 damselfly individuals (Table 1). The other 2 mite groups were uncommon and found only on single individuals: 6 abdominal mites on *I. hastata* from the small pond and a single bright-red mite on *N. gracilis* from the large pond.

Based on (a) the coloration of mites, (b) the body sites to which they attached to hosts, (c) that all phoretic mites were found on newly emerged tenerals, and (d) that all mites were found on coenagrionid damselflies, it is likely that these larvae are 2 species of *Arrenurus* water mite (B.P. Smith, Biol. Dept., Ithaca College, personal communication 2006). Unfortunately, it is impossible to assess the species of these mite larvae without prior knowledge of the adult water mites that occupy this area (this information is unknown for ABS), or without rearing larval mites on hosts until they detach and reach adulthood (Botman et al. 2002). Generally, only adult males are useful for identifying species.

Finally, the single brightly colored mite found on *N. gracilis* had attached to an atypical region for odonates (see above); suggesting that this mite is likely more often parasitic on a completely different insect order.

Water Mite Parasitism

The majority of mites were found on *I. hastata*, where 12.2% of individuals had 82 mites (19 phoretic and 63 attached; Table 1). However, despite the overall difference in abundance between *I. hastata* and *N. gracilis*, both had similar prevalence ($\chi^2 = 0.1$, $df = [1, 128]$, $P = 0.98$) and intensity of parasitism (Kruskal-Wallis $\chi^2 = 0.05$, $df = 1$, $P = 0.81$). All phoretic mites were found on newly emerged tenerals: 2 ♀ *I. hastata* with 2 and 17 phoretic mites, respectively, and 1 ♀ *N. gracilis* with 5 phoretic mites. These 2 damselfly-mite associations are novel and unreported for Central Florida.

TABLE 1. FREQUENCY OF DAMSELFLY SPECIES AND PARASITISM BY WATER MITES OF 3 SITES NEAR THE ARCHBOLD BIOLOGICAL STATION. NUMBER OF DAMSELFLIES CAPTURED (n) AND THEIR RELATIVE FREQUENCY (F) ARE PRESENTED, AS WELL AS THE PREVALENCE OF PARASITISM (P) WITH LOWER (LCI) AND UPPER (UCI) 95% CONFIDENCE INTERVALS, AND MEDIAN INTENSITY (I) OF PARASITISM WITH INTER-QUARTILE (IQR) AND FULL RANGE (FR). LCI AND UCI WERE CALCULATED FOLLOWING JAYNES' (1976) BAYESIAN METHOD. THIS METHOD ESTIMATES UCI WHEN PREVALENCE IS ZERO, AND INDICATES THE LIKELIHOOD OF CAPTURING PARASITIZED INDIVIDUALS GIVEN THE CAPTURE FREQUENCY (E.G., SURVEY SAMPLE SIZE).

Damsel fly assemblage	n	F	Parasitism estimates					
			P	Prevalence		Intensity		
				LCI	UCI	I	IQR	FR
All sites								
<i>Argia fumipennis atra</i>	53	0.28	0.000	0.000	0.054	—	—	—
<i>Ischnura hastata</i>	114	0.60	0.122	0.071	0.191	3.5	1.75-6.25	1-22
<i>Ischnura ramburii</i>	7	0.04	0.000	0.000	0.312	—	—	—
<i>Nehalennia gracilis</i>	16	0.08	0.125	0.038	0.364	5.0	1-9	1-9
Lake Annie								
<i>Argia fumipennis atra</i>	52	0.90	0.000	0.000	0.055	—	—	—
<i>Ischnura ramburii</i>	6	0.10	0.000	0.000	0.348	—	—	—
Small pond								
<i>Ischnura hastata</i>	40	0.93	0.100	0.041	0.231	4.0	1.75-16.75	1-21
<i>Nehalennia gracilis</i>	3	0.07	0.000	0.000	0.602	—	—	—
Large pond								
<i>Argia fumipennis atra</i>	1	0.01	0.000	0.000	0.776	—	—	—
<i>Ischnura hastata</i>	74	0.83	0.135	0.075	0.232	2.5	1.75-6.25	1-22
<i>Ischnura ramburii</i>	1	0.01	0.000	0.000	0.776	—	—	—
<i>Nehalennia gracilis</i>	13	0.15	0.154	0.046	0.428	5.0	1-9	1-9

Damsel flies from the large or small pond were not more likely to have parasites ($\chi^2 = 0.56$, $df = [1, 128]$, $P = 0.45$), and there was no site-by-species interaction in likelihood of being parasitized (Wald $\chi^2 = 0.01$, $df = [1, 128]$, $P = 0.93$). Thus, parasitism frequency was not dependent on the site from which damselflies emerged in whole, or individually by species (*I. hastata*: $\chi^2 = 0.3$, $df = [1, 112]$, $P = 0.58$; *N. gracilis*: $\chi^2 = 0.89$, $df = [1, 14]$, $P = 0.34$).

I did not find any larval mites on *A. fumipennis atra* or *I. ramburii* at my lake site (Table 1). Thus, all following analyses are limited to *I. hastata* and *N. gracilis* because these were the only species parasitized by my water mites. I also combine data from the adult and teneral damselflies in all following analyses, because (a) *Arrenurus* mites are only recruited by damselflies during larval emergence (thus the prevalence and intensity of parasitism does not accumulate among age classes), and (b) the frequency of parasitism among age classes did not differ (*I. hastata*: $\chi^2 = 0.2$, $df = [1, 112]$, $P = 0.62$; *N. gracilis*: $\chi^2 = 0.67$, $df = [1, 14]$, $P = 0.41$).

Sex and Parasitism

Males were as common as females in both species of damselfly: *I. hastata* had 59 ♀ and 55 ♂ (assuming equal sex ratio: $\chi^2 = 0.14$, $df = 1$, $P =$

0.17) and *N. gracilis* had 7 ♀ and 9 ♂ ($\chi^2 = 0.25$, $df = 1$, $P = 0.62$). However, no one sex was more likely to be parasitized (Fig. 1a; *I. hastata* had 7 ♀ and 7 ♂ parasitized: $\chi^2 = 0.02$, $df = 1$, $P = 0.888$; *N. gracilis* had 1 ♀ and 1 ♂ parasitized: $\chi^2 = 0.04$, $df = 1$, $P = 0.85$), or have a greater intensity of larval water mites (*I. hastata*: Kruskal-Wallis $\chi^2 = 1.51$, $df = 1$, $P = 0.22$). Too few individuals of *N. gracilis* were parasitized to test whether intensity of water mites differed between sexes.

The large and small pond also did not have different sex ratios of both species (*I. hastata*: $\chi^2 = 0.45$, $df = [1, 111]$, $P = 0.5$; *N. gracilis*: $\chi^2 = 0.17$, $df = [1, 14]$, $P = 0.68$), and did not contribute to frequencies of parasitism among sexes (site-by-sex interaction for *I. hastata*: Wald $\chi^2 = 0.06$, $df = 1$, $P = 0.81$; and *N. gracilis*: Wald $\chi^2 < 0.01$, $df = 1$, $P = 0.99$).

Body Size and Parasitism

Body size measures (i.e., wing-, femur-, and tarsus-length, and weight) were collapsed into a single estimate of size (hereafter PC1) with PCA, and calculated separately for each species. The PC1 for *I. hastata* explained 59.3% of the variation among body size traits (eigenvalue = 2.37), and 41% for *N. gracilis* (eigenvalue = 1.64). Both damselfly species were overall similar in PC1 ($t <$

0.01, $df = 94$, $P = 1.0$), however only *I. hastata* was sexually dimorphic with females being larger than males (Fig. 1b; *I. hastata*: $t = 9.01$, $df = 83$, $P < 0.001$; *N. gracilis*: $t = 0.25$, $df = 9$, $P = 0.81$).

Body size did not relate with prevalence of parasitism in *I. hastata* (log-likelihood test, $\chi^2 = 0.08$, $df = 1$, $P = 0.77$), intensity of infection ($r^2 = 0.07$, $F = 0.79$, $df = 10$, $P = 0.39$), or relate to size differences between sexes (e.g., no sex-by-size interaction: Wald $\chi^2 = 0.31$, $df = 1$, $P = 0.58$). Again, too few parasitized individuals were available to assess whether water mite parasitism related to body size or sex for *N. gracilis*.

In general, it does not appear that body size related to patterns of parasitism by larval mites. Finally, there were no differences in body sizes among damselflies emerging from the small or large pond (all damselflies: $t = 0.74$, $df = 94$, $P = 0.74$; *I. hastata*: $t = -0.45$, $df = 83$, $P = 0.63$; *N. gracilis*: $t = 0.56$, $df = 9$, $P = 0.59$).

Symmetry and Parasitism

Symmetry of damselflies did not relate to frequencies of parasitism observed in the field. Asymmetric damselflies were not more likely to be parasitized than symmetric individuals for all damselflies ($\chi^2 = 3.09$, $df = [1, 129]$, $P = 0.08$) or individually by species (*I. hastata*: $\chi^2 = 1.83$, $df = [1, 111]$, $P = 0.17$; *N. gracilis*: $\chi^2 = 2.52$, $df = [1, 14]$, $P = 0.11$). Asymmetric damselflies also did not have a greater intensity of parasitism than symmetric individuals (all damselflies: Kruskal-Wallis $\chi^2 = 2.89$, $df = 1$, $P = 0.09$; *I. hastata*: Kruskal-Wallis $\chi^2 = 0.01$, $df = 1$, $P = 1.0$; *N. gracilis*: Kruskal-Wallis $\chi^2 = 1.65$, $df = 1$, $P = 0.2$), and there was no site-by-symmetry interaction in predicting patterns of parasitism (Wald $\chi^2 = 0.01$, $df = 1$, $P = 0.94$). In addition, there was no variation in symmetry among the damselflies captured at the 2 ponds ($\chi^2 = 1.83$, $df = [1, 111]$, $P = 0.175$). Finally, the sexes of each damselfly species were equally symmetric (Fig. 1c; *I. hastata*: $\chi^2 = 0.02$, $df = [1, 111]$, $P = 0.89$; *N. gracilis*: $\chi^2 = 0.01$, $df = [1, 14]$, $P = 0.95$), and there was no relationship between symmetry and body size (*I. hastata*: Kruskal-Wallis $\chi^2 = 0.21$, $df = 1$, $P = 0.65$; *N. gracilis*: Kruskal-Wallis $\chi^2 = 1.2$, $df = 1$, $P = 0.27$).

DISCUSSION

Patterns of field parasitism have been reported for several odonate-water mite associations in northeastern North America (e.g., Forbes et al. 2002), but very few studies exist for southern North America. My survey found 2 novel host associations for *Arrenurus* water mites in Central Florida, where 12.2% of *I. hastata* and 12.5% of *N. gracilis* damselflies had larval mites. Should my survey have been seasonal, I likely would have found other novel hosts—given that many

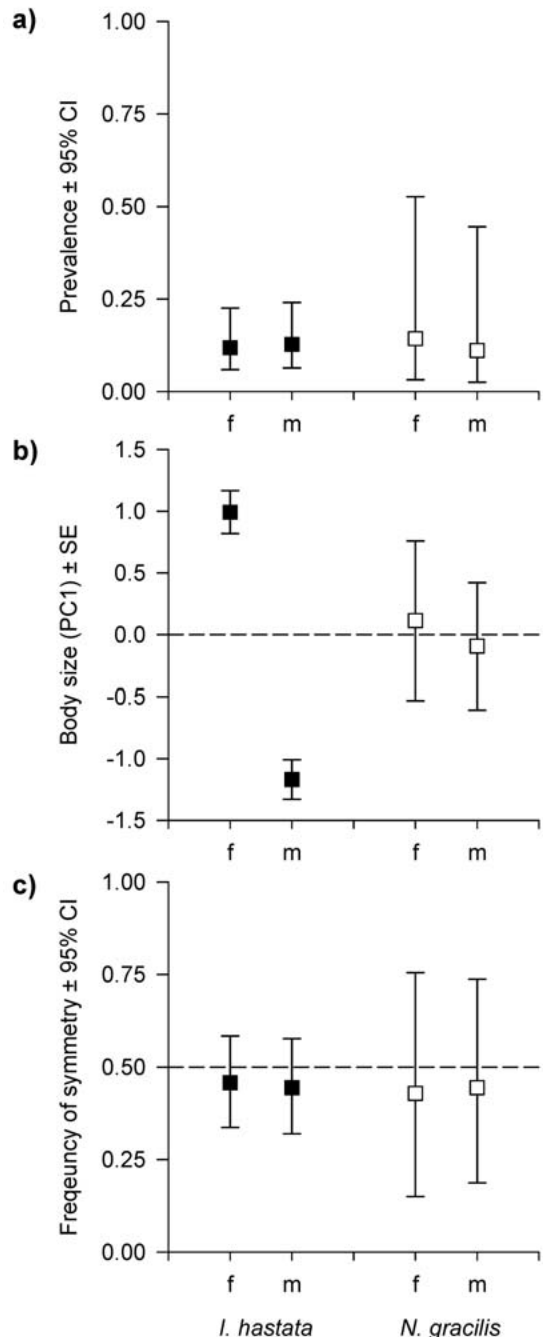


Fig. 1. Contrasts between females (f) and males (m) of pond species of damselfly in prevalence of water mite parasitism (a), body size (b) and the frequency of symmetry (c) defined as the ratio of symmetric vs. asymmetric individuals in wing cell number. Females and males are symmetric if 95% CI overlap with 0.5 (dashed bar). Sample sizes are as follows: *Ischnura hastata* 59 ♀/55 ♂ and for *Nehalennia gracilis* 7 ♀/9 ♂. Asymmetric 95% confidence intervals (CI) around proportions (e.g., prevalence and frequency of symmetry) were calculated following Jaynes (1976).

additional species of damselfly (and dragonfly) emerge at different periods throughout the year (Westfall & May 1996).

Field variation in parasitism by water mites can occur because of differences in host exposure, immunity, phenology, and spatial constraints. However, I could not detect differences in prevalence and intensity of parasitism between the two infected species of damselfly—despite being distantly related and differing significantly in abundance. Nor could I detect the contribution of sex, body size and asymmetry of hosts on observed field patterns in water mite parasitism. At this time of season, it appears that larval water mites are distributed randomly among species and classes (e.g., sex) of damselfly hosts.

These findings corroborate other studies that find no trend in parasitism among sexes for other insects (Sheridan et al. 2002), or more generally, no effect due to body size and asymmetry (Møller & Thornhill 1998; Forbes et al. 2004). However, my ability to detect such patterns, should they have existed, was poor due to the low prevalence of parasitism and overdispersion of mites on few individual hosts—a common problem to field surveys of parasites (Bush et al. 2001). A large number of parasitized individuals, with high representation among various host classes (e.g., sex, symmetry, etc.), would be required to confidently assess whether such mediating effects exist. This is perhaps best achieved through the experimental manipulation of mite infestations (Lajeunesse et al. 2004). However in the field, large sample sizes of parasitized individuals may not be attainable for damselfly species that are not abundant locally, or uncommon at certain times of the season, as seen for *N. gracilis* damselflies, where few were captured, and even fewer were parasitized.

I also did not find any dead larval mites and was unable to assess whether damselflies had lost mite larvae prior to surveys. Attached dead mites can indicate a successful immune response by damselflies (Yourth et al. 2001). However, a significant portion of the surveyed damselflies were general (63% of *I. hastata* and 25% of *N. gracilis*) and were perhaps too young to yet resist larval mite parasitism. In addition, there is the possibility that many of the surveyed damselflies had already lost mites before sampling. However, no mite scars were found on any individual (scars are left when mite larvae detach from hosts; Smith 1988), nor were there any large, fully engorged mite larvae found on any host. These observations indicate that the surveyed damselflies could not have lost mite larvae because mites had fully matured and detached from hosts to complete their life cycle (Smith 1988). To avoid these issues, future surveys should examine immunity to mite larvae feeding tubes (Yourth et al. 2001) or conduct a seasonal mark-recapture study to determine mite mortality (Lajeunesse et al. 2004).

Odonate-water mite associations are a model system to test key hypotheses on life-history trade-offs (Mitchell 1967), but the lack of field data on patterns of host use has hampered progress on understanding the ecology and evolution of these mites and their hosts (Bohonak 1999; Rolf 2002; Forbes et al. 2002; Lajeunesse et al. 2004). Additional field surveys, broadly sampling a diversity of habitats, can help address these issues and will likely generate novel, unreported host associations for parasitic water mites.

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