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Species and sex biases in ectoparasitism of dragonflies by mites

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An important problem in understanding the evolution of parasite host range is determining the extent to which parasite fitness varies among host species and the factors affecting that fitness variation. We present a detailed investigation on the patterns of host use and successful parasitism of two dragonfly species by the ectoparasitic water mite, *Limnochares americana* Lundblad. In our field surveys, we found both species biases and sex biases in parasitism by mites, which appear explained by differences in exposure. Differential habitat use by dragonflies helped explain male biases in parasitism in both host species, but was not useful in explaining species biases in parasitism. Species biases in parasitism may be explained by more subtle variation in habitat use not explored in this study, or perhaps by differences in timing of emergence, as we found for the two dragonfly species. Despite species differences in parasitism in nature, we found that mites attached equally successfully to both dragonfly species during experimental infestations. However, mites failed to engorge more often on the dragonfly species less often used as a host in nature. This host species also was more likely to have dead mites in natural infestations as compared to the other host species, which was more often and more heavily parasitized. Our results are consistent with previous research suggesting parasites are less successful on less often used hosts. Such research has implications for understanding determinants of host range for animal parasites.

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Many species of animal parasites make use of several host species during single stages in their life cycle (Bush et al. 2001, Lajeunesse and Forbes 2002). Yet, the dependence of parasite fitness on the host species being parasitized is an understudied problem, despite its implications for understanding the evolution of host range for animal parasites (Perlman and Jaenike 2003). Studies have found that ecological factors, such as spatial and temporal overlap with potential host species, are important in explaining patterns of differential host use by parasites (Smith and McIver 1984, Janz et al. 2001, Rothstein et al. 2002). Furthermore, researchers have demonstrated, for a few well studied host–parasite associations, that parasites are most successful on host species more commonly used in nature (Singer et al. 1989, Forbes et al. 1999, 2002, Perlman and Jaenike 2003). However, determining which host species are most commonly used is not straightforward, since variation in geographical distributions of host species can affect local or regional patterns of host use by parasites (Thompson 1994).

Surprisingly few studies have attempted to explain factors influencing differential host species use and success of parasites, while also accounting for determinants of within-species variation in parasitism. One form of within-species variation frequently observed, and of considerable interest, is the difference in parasitism between conspecific males and females. Sexual dimorph-

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ism in morphological and physiological traits and/or sex differences in behaviour is often associated with differential exposure or susceptibility to parasites (Zuk and McKean 1996, Schalk and Forbes 1997, Moore and Wilson 2002, but see Sheridan et al. 2000). Identifying factors that influence trends in mortality between sexes, such as parasitism, can help discern the trade-offs of sexually selected traits.

In this study, we present a detailed investigation of parasitism of two dragonfly species by the ectoparasitic water mite, *Limnochares americana* Lundblad. We begin with surveys of males and females of both dragonfly species, *Leucorrhinia frigida* Hagen and *Nannothemis bella* (Uhler), to examine whether species or sex biases in ectoparasitism by mites were evident, following from earlier work by Smith and Cook (1991) and Smith (1999). We also examined whether there were species or sex biases in phoresy of pre-infective mite larvae. Such data inform whether phoresy mirrors actual parasitism, which would occur if differences in exposure explain differences in actual parasitism. From the same survey, we also compared males and females, and both species, with respect to the proportion of infested hosts that carried one or more dead mites. We used these measures as indices of differential success of mites on hosts.

Following descriptions of these patterns of parasitism, we tested various hypotheses on the causes of patterns in parasitism and factors affecting success of mites. First, males of both dragonfly species are territorial and perch on emergent vegetation (Hilder and Colgan 1985, Lee and McGinn 1986, Smith and Cook 1991). This emergent vegetation also serves as perches for mite larvae (Smith and Cook 1991). It is possible that males maintaining territories in such locations are more exposed to mite larvae than are females (Smith 1999), which are generally on the wing and foraging (Corbet 1999). We specifically examined habitat use by adult males and females of both host species and emergence patterns of both host species, in relation to where mite eggs were laid and when mite larvae were hatching. Together, these data and natural history observations could address species and sex biases in exposure to mite larvae.

To address potential explanations for differences in mite success on hosts, we infected individuals of both host species with newly hatched mites and scored attachment and engorgement success of these mites. This experiment enabled us to determine whether differential success of mites on different host species occurred in the lab. Since age of mites was controlled in our experiments, any differences in success of mites on different host species would have to be due to differences between host species in suitability or resistance (and not to differences among mites attending to different species of hosts). Although there is evidence that animal parasites are more successful on common host species, there is little information on how this differential success is achieved.

Material and methods

Study site and species

Our study site was Hebert's bog, located 10 km from the Queen's University Biological Station near Chaffey's Locks, Ontario Canada (44°35′ N; 76°19′ W). Both dragonflies in this study are common to bog ponds in northeastern North America, with *Nannothemis bella* almost exclusive to these bogs (Walker and Corbet 1975). *Limnochares americana* also occurs in bog ponds and is known to parasitise at least 25 dragonfly and damselfly species (Conroy and Kuhn 1977, Cook 1991). Female *L. americana* lay clutches on submerged stems of emergent vegetation (Smith and Oliver 1986). Newly hatched larvae swim to the water surface, crawl up emergent vegetation, and then may climb on to dragonflies alighting on this vegetation. These phoretic mites may be removed by grooming (Léonard et al. 1999); otherwise, mites will attach to dragonflies by inserting chelicerae through the host's cuticle. Attachment is followed by formation of a feeding tube (Smith 1988), and larvae will feed and engorge, if feeding tube formation is not countered by host melanotic encapsulation, as seen in other dragonflies (Yourth et al. 2002). Once engorged, mites drop off hosts and complete their life cycle as aquatic predators (Smith 1988).

Patterns of phoresy, parasitism, and engorgement success on field caught dragonflies

We compared prevalence and intensity of mite infestation (sensu stricto Bush et al. 1997) on 147 male and 23 female *L. frigida* and 66 male and 22 female *N. bella*, surveyed during 25 trips to Hebert's bog (between 21 June and 18 August, 2001). On each trip, sampling began at ca 10:30 EDST (ending after one hour), occurred in a ca 2500 m^2 of the bog's southern margin (following Smith and Cook 1991), and was restricted to ca 5 m from the bog's edge where the sphagnum mat met open water (hereafter edge habitat). All *L. frigida* and *N. bella* dragonflies were netted, sexed (following Walker 1953) and aged as either teneral (newly eclosed adults with pliant, lustrous wings, and soft exoskeletons with little pigmentation), or as sexually mature (with rigid, dull wings, and full body pigmentation). Acquisition of new *L. americana* larvae occurs throughout the life of adult dragonflies, such that larvae in several stages of engorgement could be present on a single host (Smith and Cook 1991). Using a 20 × loupe, we counted these engorging or engorged mites (legs partially or entirely obscured by their swollen bodies), and also counted dead mites (which are flat and silver in colour; Léonard et al. 1999). *Limnochares americana* larvae have a motile phoretic phase before attachment (Smith 1988); numbers of these mites could be used as an index of host contacts or exposure. We thus also recorded the number of phoretic mites on every individual. All dragonflies were marked (to prevent resampling) and released on site, after dotting wings with non-toxic Sharpie® pens (Sanford Corporation, Bellwood, U.S.A.).

Location and timing of mite egg laying and hatching and habitat use by dragonflies

The bog edge is where mite clutches were laid and where larval mites were active (Cook 1991). We inspected emergent vegetation for mite clutches in four 2 × 1 m quadrats at the bog's edge on 15 trips, every third day between June 23 and August 10, 2001. We recorded days on which clusters of *L. americana* clutches appeared on emergent stems, and labeled these stems with numbered flagging tape. On each visit, clutches were scored either as having hatched (semi-translucent/white in colour, no larvae visible inside eggs) or as not having hatched (red, larval mites still present within eggs). Hatching dates were approximated, as visits were made every third day; for example, if a visit found a clutch to have hatched, then the maximum date of hatch would be that day, and the minimum date of hatch for that clutch would be the day of the previous visit. We were unable to track the progress of six clutches, which were lost, through to completion (i.e. to time of hatching).

We also were interested in whether males and females of both species differed in how frequently they perched on edge habitat (where mite larvae were active) versus non-edge habitat. Surveys and marking of dragonflies were done on two sampling days two days apart, during the peak of mite emergence (Results). We first conducted a two-hour survey on July 14, 2001 in the morning ca 5 m from the bog edge, followed by a second survey ca 18 m from the edge in the afternoon. On July 16, we reversed this sampling order (sampling 18 m from the edge in the morning and near edge in the afternoon). The sampling perimeter was established by placing flagging rods 18 m from corresponding rods set along the bog edge (distances were measured using a Bushnell Pro 400 laser rangefinder). This distance represented the greatest contrast between edge and non-edge habitat that could be made while still sampling on the bog. All dragonflies were netted, sexed, aged and marked (as above) and included in samples only once.

Timing of emergence of dragonfly host species

We examined whether *N. bella* and *L. frigida* differed in timing of emergence by collecting dragonfly exuviae from emergent vegetation as they appeared, during 17 trips to Hebert's Bog between 21 June and 14 August, 2001. Exuviae were collected in the same four quadrats used for surveying mite clutches. Exuviae were stored in vials with bog water and kept at ca 5°C until they were sorted and identified to species using larval keys (Walker and Corbet 1975). Exuviae without heads, thoraxes or appendages were included in analyses if lateral spines on the last four abdominal segments were not missing or damaged. Only exuviae arising from larval to adult moults, where wing sheaths reached at least the fourth abdominal segment, were included in counts.

Experimental infestations of mites on different dragonfly sexes and species

Our surveys would address whether measures of parasitism varied depending on host species or sex, and whether any differences in infestation mirrored differences in phoresy by mites. Data on emergence and frequency of habitat use by hosts, both in relation to where and when mite larvae were hatching, would allow us to determine whether particular categories of dragonflies should be more exposed to mites. The survey data also addressed whether there were differences in likelihood of finding dead mites on particular categories of dragonflies. However, these data would not allow us to address possible causes of differences in successful parasitism. We thus performed experimental exposures of dragonflies to mites, with specific interest in determining whether species or sex affected likelihood of mites attaching to, and/or engorging on, hosts. During these experiments, we controlled for numbers of mites challenging hosts and for how recently those mites hatched (i.e. approximate age; below).

To obtain mite larvae, 62 adult female mites were collected between 4–6 July 2001 at Herbert's bog, and were each kept in water-filled vials containing short wooden dowels serving as an oviposition site. Females were maintained at 24.5 ± 1°C in an incubator (Blue M, Electric Company, Blue Island, U.S.A.) until 12 laid clutches (after 9.2 ± 0.8 days; mean ± SE). Ten of these clutches hatched after 5.4 ± 0.9 days, and averaged 61.8 ± 10.9 mite larvae per clutch. These larvae were used in transfers to experimental hosts.

For experimental transfers, *L. frigida* and *N. bella* adults were collected from Hebert's bog on 10 trips from 15–27 July, 2001. We collected individuals with few or no mites, as Smith (1999) found that number of larval mites was indicative of age of male *L. frigida* (older males have more mites). We collected relatively young adults, but did not use teneral dragonflies. In total, 22 male and 8 female *L. frigida*, and 20 male and 13 female *N. bella* were collected (63 dragonflies in total). We first counted naturally occurring mites that were attached to hosts, to verify that initial numbers of attached mites did not differ. Any attached mites prior to experimentation were controlled in subsequent analyses. The effect of these mites may not have been substantial, since most dragonflies (52 of 63) had no mites prior to tests, ten had one attached mite, and only one dragonfly had two attached mite larvae. Any phoretic mites that were naturally acquired were removed with a fine paintbrush prior to use of the host in the experiment. Test dragonflies were kept individually in plastic cups containing 2 ml of water beneath a fiberglass mesh screen, with a wooden dowel (ca 4 mm in diameter), serving as a perch (following Leung and Forbes 1997). Each cup was covered with aluminum foil and placed in the incubator for a minimum of two hours before mite exposure.

Individual dragonflies were exposed with experimental larvae on the day of their collection and the day of mite hatching (depending on the experimental subjects and the mite larvae used in experiments). To expose dragonflies, we held each dragonfly by its wings, positioned the venter of its thorax near the tip of the wooden dowel (within the vial), and waited until larvae climbed onto the host (Léonard et al. 1999). We controlled for numbers of experimental larvae on each host, removing or adding mites using a fine paintbrush. Newly infested dragonflies were returned to their containers, and removed at daily intervals for feeding. Feeding was necessary because Léonard et al. (1999) found that *L. americana* larvae may delay engorgement if hosts are deprived of food. Dragonflies were manually fed with chironomids (midges) and/or trichopterans (caddisflies) collected from UV-lights at night. After three days, attachment and engorgement success of mites was scored on each dragonfly.

Analyses

Prevalence of attached and phoretic mites were compared using nominal logistic regressions with species and sex as factors, and presence or absence of mites as the response variable. Wilcoxon median tests were used to compare parasitism intensities on males and females of each species; since intensity data were distributed similarly, but not normally. Due to the scarcity of females in both species, we tested for species effects on the likelihood of finding individuals with dead mites, using χ^2 tests based on males only. Similar data are presented for females of both species for comparison, but were not included in tests because statistical assumptions concerning expected frequencies would have been violated. We compared median dates of emergence between dragonfly species using Wilcoxon tests (again t-test assumptions were violated; Zar 1984); these data are presented as median dates and ranges. For tests of frequency of habitat use, we performed a multifactorial logistic regression with species and sex as factors, and the habitat location where a dragonfly was captured (edge vs non-edge) as the response variable.

Data from lab experiments were amenable to parametric analyses. For experimental infestations, we compared mean numbers of mites successfully attaching to hosts, by treating species and sex as factors in two-way ANOVA. We preceded these tests with a comparison of mean numbers of experimental larvae successfully placed on males and females of both species, to verify our experimental approach did not introduce bias. We then compared the proportion of individuals with dead mites for each dragonfly species, using χ^2 tests separately for males and females. Here, we were interested in species comparisons because our survey suggested that the likelihood of mites engorging successfully differed between host species. All tests were performed using Jmp (SAS Institute Inc. 1999).

Results

Patterns of phoresy, parasitism, and engorgement success on field caught dragonflies

We found both species and sex biases in prevalence of infestation by *L. americana* mites (Fig. 1), where 85.3% of *L. frigida* and 23.9% of *N. bella* had one or more attached mites. Of those infested, 93.4% *L. frigida* and 90.5% *N. bella* were males. These species and sex biases also occurred with prevalence of phoretic mites (Fig. 2), where 43.5% of *L. frigida* (94.6% of which were male) and 15.9% of *N. bella* (92.9% male) had at least one phoretic larvae.

Mite intensity also differed between species (Wilcoxon $Z = -6.04$, $P < 0.001$), were *L. frigida* had more attached mites than *N. bella.* Specifically for *L. frigida*,

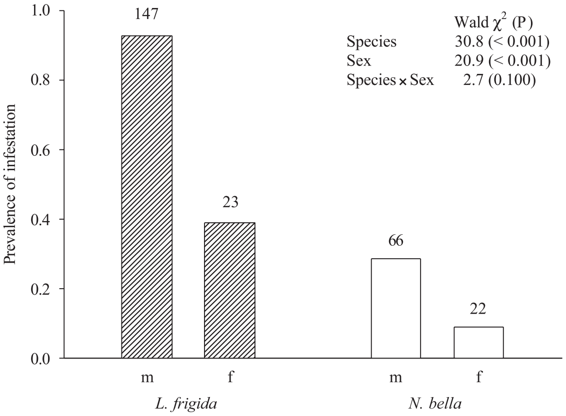

Fig. 1. Prevalence of *L. americana* parasitizing males and females of two species of dragonfly hosts. Numbers above bars refer to the total sample size for that category of dragonflies. Results of logistic regression examining the influence of sex and species on likelihood of having parasitic mites are also presented.

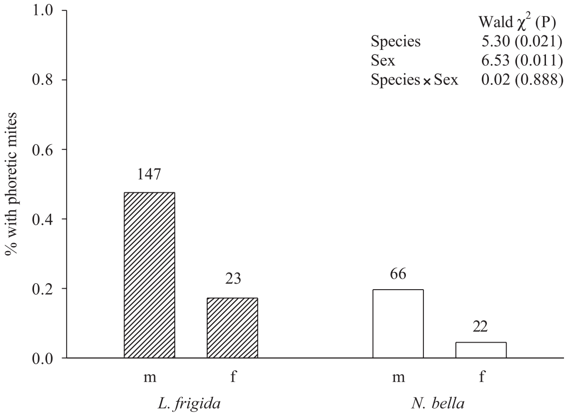

Fig. 2. Percentage of males and females of two species of dragonfly hosts caught with one or more phoretic *L. americana* mites. Numbers above bars refer to the total sample size for that category of dragonflies. Results of logistic regression examining the influence of sex and species on likelihood of having phoretic mites are also presented.

the median intensity was 8 mites with an inter-quartile range (or IQR) of 4–14 mites (the full range or R was 1–47 mites), whereas *N. bella* had a median intensity of 1 mite (IQR = 1–3 and R = 1–4 mites). Sex biases in mite intensity existed for *L. frigida* dragonflies (Wilcoxon Z = −4.07, $P < 0.001$). Males had a median of 9 mites (IQR = 5–14 and R = 1–47 mites) compared to a median of 2 mites for females (IQR = 1–3.5 and R = 1–5 mites). However, *N. bella* sexes did not differ in mite intensity (Wilcoxon Z = −1.14, P = 0.26), where each sex had a median intensity of 1 mite; for males, IQR = 1–3 and R = 1–4 mites, whereas for females, only 2 were infested, each with 1 mite.

In comparing frequencies of individuals with one or more dead mites, we found that most individuals with dead mites were *N. bella* dragonflies. Only 3.7% of 136 infested male *L. frigida* had one or more dead mites, whereas none of the 9 infested females had dead mites. For *N. bella*, 47.4% of 19 males had one or more dead mites, as did one of the two infested females. These two host species differed in numbers of individuals with dead mites ($\chi^2 = 38.7$, df = 1, $P < 0.001$; analysed with only males). Over all categories of individuals, numbers of dead mites ranged from zero to four.

Location of dragonflies in relation to timing and location of mite egg laying and hatching

Mites were observed to lay eggs at the edge of the bog, similar to another study (Cook 1991). The median date for appearance of clutches was day 15 (day 1 of the field season refers to June 21, 2001; Table 1). The minimum and maximum estimates of hatching were median dates 22.5 and 30.5, respectively. Surveys of habitat use by dragonflies were done on 14th and 16th July 2001, corresponding to dates 26 and 28, which lie between the minimum and maximum estimates of median dates of hatching. Thus, surveys were done when mite larvae were active at the bog edge.

Table 1. Median dates of appearance of mite clutches and minimum and maximum estimates of median dates of hatching (Methods). N refers to the total number of clutches found or the number of clutches that could be scored for hatching. Day 1 refers to June 21, 2001. Surveys of dragonflies were done on 14 and 16 July, 2001, which corresponds to dates 26 and 28. These dates are between the minimum and maximum estimates of median dates of hatching. Dragonflies were scored for their use of edge habitats where mite eggs were laid, at a time when mite larvae were active. IQR and R are the inter-quartile and full ranges of dates, respectively.

Limnochares americana clutches	N	M	IQR	R
Appearance day	36	15.0	3–25	3–51
minimum day of hatching	30	22.5	15–39	6–7
maximum day of hatching	30	30.5	21–49	12–55

Males of both species were more likely to be caught at the edge of the bog than were females (Fig. 3). In fact, only sex and not species, nor the interaction between these two factors, accounted for significant variation in frequency of habitat use by dragonflies (Fig. 3). For *L. frigida*, 66% of 71 males were caught at the bog's edge compared to 19% of 21 females, and for *N. bella*, 69% of 42 males, and none of the 13 females, were caught at the bog's edge (Fig. 3).

Timing of emergence and abundance of both host species

Median emergence time differed between *N. bella* and *L. frigida* dragonflies based on our 50 day survey of

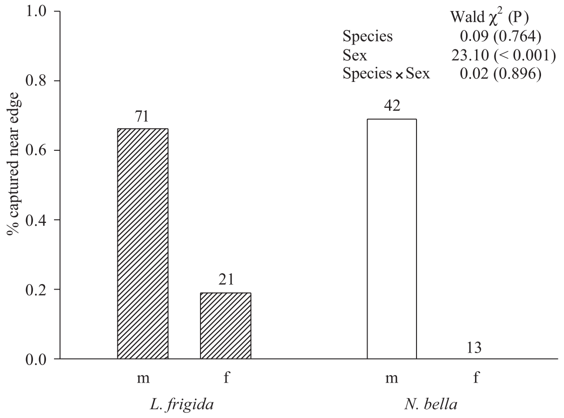

Fig. 3. Percentage of males and females of both dragonfly species that were caught near the edge of the bog where mite eggs were laid, at a time when mite larvae were active. Results from logistic regression, examining the influence of sex and species on location where dragonflies were caught, are also presented. Numbers above bars refer to the total sample size for that category of dragonflies (none of 13 female *N. bella* was caught near the edge of the bog).

exuviae (Wilcoxon $Z = -8.29$, $P < 0.001$). Proportionately more *N. bella* final-instar exuviae ($N = 182$) were found earlier in the season than *L. frigida* exuviae ($N = 201$). Specifically, *L. frigida* had a median emergence date of 28, or midway between estimates of median hatching times of mites (Table 1; $IQR = 10-34$ and $R = 1-51$). In comparison, *N. bella* had a median emergence date of 4.5 ($IQR = 1-20$ and $R = 1-47$). A similar number of exuviae were found for each species at the bog edge throughout the season ($\chi^2 = 0.943$, $df = 1$, $P = 0.33$; assuming a null expectation of 1:1). However, these data do not reflect relative numbers of the two host species, but rather only relative numbers where emerging dragonflies were surveyed (from our observations, *L. frigida* was less restricted than *N. bella* in where it emerges). In our field surveys, adult *L. frigida* and *N. bella* did differ in total representation at this site with the former dragonfly being by far the most numerous (170 *L. frigida* were captured versus 88 *N. bella*; $\chi^2 = 26.5$, $df = 1$, $P < 0.0001$).

Experimental infestations of mites on different dragonfly species and sexes

The numbers of mites transferring to dragonflies during experiments was not dependent on host species, host sex, or their interaction (ANOVA species: $F_{1,63} = 0.38$, $P = 0.54$; sex: $F_{1,63} = 0.04$, $P = 0.85$; species × sex: $F_{1,63} = 0.41$, $P = 0.52$). For *L. frigida*, mean numbers ±SE of test mites transferred were 6.6 ± 0.27 for males and 6.8 ± 0.45 for females, whereas for *N. bella*, mean numbers were 6.6 ± 0.29 and 6.3 ± 0.35 for males and females, respectively. Thus, any subsequent differences in numbers of mites that were successful (across sexes or species of hosts) could not be explained by challenging particular hosts with fewer or more mites.

While males and females of both species were equally likely to have mites initially transferred to them during experiments, there was a significant interaction effect between species and sex in explaining mites that successfully attached following transfer (ANOVA species: $F_{1,62} = 0.02$, $P = 0.887$; sex: $F_{1,62} = 1.03$, $P = 0.315$; species × sex: $F_{1,62} = 8.52$, $P = 0.006$). Controlling for host species, we found that *L. frigida* males had fewer mites attaching successfully (3.4 ± 0.46; mean ±SE) than did conspecific females (5.6 ± 0.77; $t = 2.51$, $P < 0.025$). For *N. bella*, numbers of mites that attached successfully were similar for males (4.4 ± 0.32) and females (3.7 ± 0.40; $t = -1.27$, $P = 0.21$).

We also were interested in whether mites had different engorgement success on each dragonfly species because *N. bella* was more likely to have dead mites in our survey. The number of individuals with one or more dead test mites varied between species (Yates $\chi^2 = 8.7$, $P = 0.003$), but not appreciably between males and females of a given species. For *L. frigida*, none of the 8 females and one of the 22 males had dead test mites. For *N. bella*, 46% of 13 females and 55% of 20 *N. bella* males had one or more dead test mites. Treating these data separately by sex revealed a greater propensity for male *N. bella* to have dead test mites than *L. frigida* males (Yates $\chi^2 = 5.7$, $P = 0.017$). Although a similar trend existed between females, we could not detect differences between species in the number of females with dead mites (probably reflecting low sample size; Yates $\chi^2 = 1.7$, $P = 0.20$).

Discussion

Many parasite species make use of several host species, yet little has been written on the determinants of host range for animal parasites, and on the implication of broad host ranges (but see Lajeunesse and Forbes 2002, Perlman and Jaenike 2003). One lacuna in the literature is how fitness of the parasite relates to host abundance, assessed locally or regionally. To address this question, we first describe the potential determinants of differences in host use within and between our study species, before exploring possible reasons why differences in mite success occur for different host species.

We found that the more numerous host species is more often parasitized by the water mite, *L. americana* (Fig. 1), similar to results from another mite species that is phylogenetically distant to *L. americana* and which parasitizes different dragonfly species (Forbes et al. 2002). This differential parasitism was further reflected in mite phoresy, which should be related to exposure (Fig. 2). In both species, males were more often parasitized than females, but sex differences in intensity of parasitism could be detected only for the commonly parasitized *L. frigida* dragonfly. Habitat use by males and females of both species, relative to where mite larvae were located, may explain some degree of sex biases in parasitism (although perching behaviour of territorial males also appears important; Smith and Cook 1991, Smith 1999). Based on the phoresy counts, species differences in exposure existed, but this difference could not be explained by differences in habitat use by each species. Perhaps differences in timing of emergence of dragonfly species may explain some of this among species variation in parasitism (recently emerged individuals of a given species such as *L. frigida* may be more available to mites). Alternatively, more subtle species differences in habitat use may account for some variation in exposure. Male *N. bella* generally establish territories over small pools inside the bog mat (Hilder and Colgan 1985). Cook (1991) suggested that abundance of larval mites was higher along the main edge of the bog than in pools inside the bog mat.

In both dragonfly species, parasitism is likely a cost of reproduction or at least a cost of territorial behaviour for males, and avoidance of high-exposure habitats would be adaptive if it were not for the relative value of these areas for other important functions. Male dragonflies will commonly defend territories that females briefly visit to mate and oviposit (Corbet 1999). Males of both male *L. frigida* and *N. bella* defend potential oviposition sites; albeit generally in different areas. Males of the former species typically defend shoreline areas whereas *N. bella* males defend sites along near-shore pools. Apparently, males of both species suffer the trade-off of increased exposure to parasitism.

As indicated, the most numerous host species was more often parasitized and had a higher intensity of mite parasitism. Furthermore, in surveys of naturally occurring populations, *L. frigida* was least likely to have dead mites. Although sex differences in attachment of test mites were apparent in *L. frigida* (Léonard 1999) found male *L. frigida* to be more likely than females to show grooming behaviours following contact by mites), species differences in attachment by mites was not evident. However, there were obvious differences between host species in successful engorgement of mites. *Nanothemis bella* dragonflies were more likely to have dead test mites, whereas few *L. frigida* dragonflies had dead test mites. These findings corroborated our results from field caught dragonflies.

We do not yet know why many mites fail to engorge on *N. bella*. We initially thought that the *N. bella* individuals included in our samples were likely to be older than many of the *L. frigida* hosts surveyed over the same time period. We believed that this age difference would be associated with differences in hardness of the cuticle and would help explain failure of more mites to engorge on *N. bella*. Another possible explanation was that early-emerging *N. bella* were more often encountering mites that had searched for longer (and were less 'vigorous') than mites typically attending *L. frigida*. Such mites may be easier to defend against. These explanations were inadequate, however, since age of hosts, and mite 'vigour', was controlled in our experimental infestations.

Our results, therefore, indicate that similarly aged hosts of both species, subject to mites of the same age, differ in their likelihood of having mites engorge successfully. Further, the magnitude of this difference is similar to that seen in field surveys. One reasonable explanation for this difference is that *N. bella* actually mounts resistance to the small multi-branched feeding tubes of *L. americana*. Unfortunately, this mite–dragonfly association has not proved amenable to exploring the nature of resistance, as compared to other mite–dragonfly associations (Forbes et al. 1999, Yourth et al. 2001). It is also possible that *N. bella* dragonflies are simply less able to support large numbers of engorging mites because they are smaller than *L. frigida* hosts. However, this mite species appears to engorge quite easily on much smaller sized damselflies, such as *Enallagma ebrium* (Hagen; M.R. Forbes, pers. obs.).

When addressing questions about differential host use and resistance, it is important to consider selection acting on parasites. At our particular site, *L. frigida* is found in much greater numbers than *N. bella* dragonflies, and thus is likely a greater agent of selection for *L. americana* mites at least locally, but probably also regionally. Frequency of interactions between parasites and hosts is thought to affect both parasite infectivity (e.g. success on hosts) and host resistance (May and Anderson 1983, Nowak and May 1994). Selection may have favored mites to optimally infest *L. frigida*, if even at the expense of not doing well on *N. bella* dragonflies. Although both species are equally likely to have mites attach in experiments, mites on *N. bella* do less well. It is also interesting that timing of egg laying by mites is not synchronized with the bulk of emergence of *N. bella* dragonflies. It is likely that differences between dragonfly species in phenology may account for some of the differential host use seen in nature, as has been found in studies of aquatic mites parasitizing mosquitoes (Smith and McIver 1984).

Our study has several important implications for directing future research. Resistance is presumably important for some odonates, as water mite parasitism has been associated with costs to hosts (reviewed by Corbet 1999). If selection imposed by *L. frigida* dragonflies on mites is strong, then it may be possible that *N. bella* dragonflies can maintain some degree of effective resistance without it being countered by mite adaptations to evade resistance. In fact, *N. bella* may 'hide' in the background of the major interaction between *L. frigida* and *L. americana* mites (Nee et al. 1991). It would be interesting to explore the relative fitness costs of parasitism by *L. americana* for both species in situations in which *N. bella* is the more numerous dragonfly locally (i.e. sites where strong selection is imposed on mites by *N. bella*). Research into similar questions for other parasite–host associations, including those where parasites exhibit higher fitness on rarer hosts (Singer 1983), is desperately needed. Such findings will have implications for understanding the determinants of parasite host range.

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