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Parasitism of *Sympetrum* dragonflies by *Arrenurus planus* mites: maintenance of resistance particular to one species

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Abstract

Using field surveys and histological methods, we show that a dragonfly species (*Sympetrum internum*) has an effective resistance, not seen previously in other odonates, to a mite parasite (*Arrenurus planus*). This mite is a generalist parasite known to effectively engorge on several other odonate species. We argue that selection is likely weak, favouring counter adaptations of *Arrenurus planus* to *Sympetrum internum*, in part because other host species are available. We further argue that this pattern is possibly linked to the fact that the mode of resistance is relatively novel, and because *Sympetrum internum* is rare compared to another host species, *Sympetrum obtrusum*, at our study site. Although resistance of *Sympetrum internum* is quite effective against *Arrenurus planus*, *Arrenurus planus* larvae still attach to this species, but less often than they attach to *Sympetrum obtrusum*. Attachment to unsuitable hosts may reflect constraints operating on *Arrenurus planus* larvae during host discovery. Such factors influencing the evolution of resistance, when several potential host species exist, have not received much attention.

Keywords: Dragonflies; Host–parasite interactions; Mites; Parasite-mediated competition; Resistance; Susceptibility

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1. Introduction

A central tenet in parasitology is that parasite–host interactions represent co-evolutionary arms races whereby adaptations of parasites to exploit their hosts are countered by host adaptations to resist and defend against parasites [1]. Many parasites, including some ectoparasitic mites, are generalists [2–4]. The generalist parasite is confronted with a suite of host defenses that differ in their specificity and efficacy for the hosts that deploy them, and in the difficulty and cost in overcoming them from the viewpoint of the parasite. Even with their generally shorter generation times and higher evolutionary rates [5], many parasites may show instances where they attack, but are unable to effectively exploit some species in a suite of potential hosts.

Many models of parasite–host interactions include processes such as frequency-dependent selection, which are thought to account for polymorphism within both parasite and host species (e.g. [6, 7]). Such reasoning can also be applied

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when the interactions include several potential host species. Here, the parasite is expected to be well adapted to the most common host species. Parasites may be less selected to counter defenses of the rarer species, particularly if those defenses are different from those typically deployed. Thus, some host species may become freed from the co-evolutionary arms race in that their defenses are effective when deployed, and there is little selection on parasites to overcome those defenses. The degree to which parasites reduce fitness of alternative host species will likely affect this process, as highly virulent parasites could exhaust their supply of exploitable hosts. Such parasites could then come under strong selection to counter resistance of other species. Thus, at least three factors should affect maintenance of resistance: relative abundance of a host species, novelty of its defense, and impact of parasites on alternative host species.

We had several objectives aimed at either garnering support for this general argument, or refuting it. We studied two species of *Sympetrum* dragonflies (Odonata: Libelluidae) from a single temporary pond in Eastern Ontario, Canada. This pond also supports a population of *Arrenurus planus* (Marshall) mites (Acari: Arrenuridae) that attend both species of dragonflies as well as lestid damselflies ([8]; personal observations). We first determined which of the two dragonfly species was most abundant. We next tested whether either species was more susceptible to attachment by mites. Following this, we examined the degree to which mites engorged on both species, after attachment. We then examined preparations of the host's cuticle to determine whether any resistance could be observed at the gross microscopic level, and whether resistance was histologically similar to that typically observed for other odonate insects parasitised by *Arrenurus* mites. Finally, we examined whether mites could have an impact on fitness of dragonflies, using indirect measures of survivorship.

Several aspects of dragonfly and mite biology are relevant. *Sympetrum* is represented by more than 50 species worldwide; in the New World, 16 species are recognised [9]. Five of these species appear closely related to one another, and include *Sympetrum internum* and *Sympetrum obtrusum*: the two host species considered in this study. These two species are often syntopic, but differ somewhat in their flight seasons, with *S. obtrusum* generally emerging later in the summer in Eastern Ontario [9]. These species are both medium-sized (ca. 30–40 mm body length) and inhabit a variety of freshwater habitats, including ephemeral ponds.

Some ephemeral ponds also support populations of *A. planus*. These mites show genetic differentiation across regions based on allozyme data (Bohonak AJ, 1998, Dispersal and gene flow in freshwater invertebrates, PhD dissertation, Cornell University, Ithaca, NY), which suggests limited gene flow. Limited gene flow may favour local adaptation in these parasites. It is important to note that *Arrenurus* mites spend only part of their lives as parasites. Adult *Arrenurus* mites are aquatic predators; however, their eggs hatch into free-swimming larvae that are phoretic on dragonfly larvae [10, 11]. When a dragonfly larva emerges and moults into an imago, attending mites chew through its exoskeleton, secrete a mucopolysaccaride feeding tube (stylostome) and feed on either haemolymph or digested tissue [12–14]. Because these mites attach at host emergence, engorgement is more or less synchronous, unlike limnocharid mites that attach to adult dragonflies [4].

Many odonate species respond to attached mites by aggregating their haemocytes at the sites of puncture and by producing melanotic encapsulation of feeding tubes [12–14]. Melanotic encapsulation is a widespread defense in other insect hosts; it can be costly [15] and, perhaps for this reason, is linked to a recognition system for some insect–parasite associations [16]. Without a recognition system, hosts could respond to inappropriate cues with costly immune defenses, e.g. cues from other mite species which attach but which are relatively harmless.

2. Methods

Our study was done near the Queen's University Biological Station (QUBS) ca. 2 km west of Chaffeys Lock, Canada (44°34′ N, 79°15′ W). Collections were made at Yzerinac Pond, ca. 6 km southwest of QUBS in The Hilda and John Pangman Conservation Reserve. Sampling began June 8, 1998 (when the first adult *Sympetrum* dragonfly was seen, following daily observations from 1 June) and continued until 1 August, 1998.

Dragonflies were either netted and released ($n = 570$) or collected ($n = 75$) for viewing mite stylostomes. We processed dragonflies that were caught and released in two ways. At first, they were netted and brought back to QUBS. There, they were housed overnight in plastic 250-mL cups with 10–20 mL of water (under fiberglass screening), which helped prevent desiccation (while allowing dragonflies to perch). Dragonflies were then identified to species and their numbers of attending *A. planus* mites were counted, using a dissecting microscope. Dragonflies were marked with a spot(s) of blue, red, or yellow acrylic paint on either their left (or right) hind or forewings. Marks were unique for capture dates, so that relative ages of hosts and engorgement stages of mites could be assigned for any recaptures. We first brought dragonflies back to the lab to become comfortable with their identification and various techniques used in measuring and marking them, and with enumerating mites and scoring their engorgement. Later, we processed dragonflies in the field. Most field sampling was based on initially unmarked individuals, although we also processed some recaptures. In the field, we identified dragonflies and examined them for mites using 10× and 20× loupes, and marked and released them, as described above.

We scored engorgement of mites using this scale: 0 = body flat, no separation between ventral sclerites and dorsal plate; 1 = slight separation between sclerites and dorsal plate; 2 = mites ca. twice the length of their dorsal plate; 3 = mites three times the length of their dorsal plate; 4 = mites four times the length of their dorsal plate; 5 = mites fully engorged, or 5 times the length of their dorsal plate. A score of 1 represents an engorgement size from 0.15–0.22 mm ($n = 7$), whereas a fully engorged mite was 0.88–0.91 mm ($n = 7$). We measured wing lengths of dragonflies by holding the right forewing onto a piece of paper and marking positions of the tip and nodus and then measuring this distance using digital calipers (±0.1 mm). Wing length is an estimate of body size in odonates ([17], and references cited therein).

As indicated, most dragonflies were marked and released; 75 were prepared for viewing mite stylostomes. For preparations, the head and first pair of legs were removed using forceps. Next, we separated the rest of the legs, wings and abdomen from the thorax. The thorax was placed in a small, glass vial (4.5 cm×1.5 cm) and covered with Andre's solution (1:1:1, chloral hydrate:acetic acid:water, by weight). Vials were labelled and stored at room temperature for up to 1 month before further dissections were done. We next separated the cuticle of the dragonfly from the underlying tissue, using fine forceps and syringe needles (2.5 cm, 22 gauge needles). The cuticle (usually the undersurface of the thorax) was placed outer surface down on a microscope slide and covered with glycerin and a coverslip. Slides were examined at 100× (phase-contrast) and scanned for mites and stylostomes. If present, images of stylostomes were captured using Snappy® software (available from Play Inc., 1996), and their widths were measured.

3. Results

In total, 76 *S. internum* and 569 *S. obtrusum* were collected that either emerged from the pond or were caught as young or mature dragonflies within 15 m the pond. *Sympetrum obtrusum* accounted for ca. 88% of all captures. Following Ref. [9], different ages were recognised for both dragonfly species. Teneral dragonflies were weak flyers with a vitreous sheen to their wings, whereas young, pre-reproductive dragonflies had hard bodies and partially dried wings, but no mature colouration. Reproductive adults had dried wings, hard bodies, and mature colouration [9].

For *S. internum*, 32 and 12 teneral, zero and three young, and five and 24 mature, females and males were collected, respectively. For *S. obtru-*

sum, 220 and 93 teneral, 54 and 78 young, and 46 and 78 mature, females and males were collected, respectively. No teneral *S. internum* were collected after day 11 (day 1 = June 9, 1998), whereas collections of newly-emerged *S. obtrusum* started on day 6 and continued until day 40.

We found that distributions of mite numbers (based on data for tenerals collected soon after mites attached), were significantly different from normal distributions for *S. internum* females, but not males (females: maximum difference = 0.16, $P < 0.05$, $n = 32$; males: maximum difference = 0.14, $P > 0.50$ $n = 12$, Kolmogorov–Smirnov test), and for both female and male *S. obtrusum* (females: maximum difference = 0.16, $P < 0.001$, $n = 220$; males: maximum difference = 0.15, $P < 0.001$, $n = 93$). For this reason, we transformed mite numbers on hosts (sqrt $(x + 0.5)$) before proceeding with analyses. This transformation had the desired effect of producing normal distributions for seven of eight species-by-sex or sex-by-age categories used in subsequent comparisons.

To examine whether either species was more susceptible to colonisation by mites, we first controlled for days 6–11 when both species were emerging together from the pond. We controlled for time of season because mite numbers declined seasonally for both teneral females and males of *S. obtrusum* (females: $r = -0.56$, $P < 0.001$; males: $r = -0.51$, $P < 0.001$) both of which emerged from days 6–40. Mite numbers did not show significant seasonal declines for either teneral females or males of *S. internum* (females: $r = -0.19$, $P > 0.25$; males: $r = 0.34$, $P > 0.2$); however, their emergence period was greatly abbreviated (days 1–11). For days 6–11, we found that prevalence of *A. planus* was 100% for both sexes of both species. Sample sizes were 20 and 4, and 123 and 42, for *S. internum* females and males, and *S. obtrusum* females and males, respectively. Using a 2-way ANOVA on transformed data [18], we found that species of host accounted for significant variation in mean numbers of mites ($F_{1,186} = 10.2$, $P < 0.005$), whereas sex of host and the interaction term were not significant (sex: $F_{1,186} = 0.08$, $P > 0.65$; interaction: $F_{1,185} = 0.80$, $P > 0.35$). Although sample sizes for teneral male *S. internum* were low and thus the variation in the estimate of the mean number of mites correspondingly high, we found more mites on both male and female *S. obtrusum* than on either male or female *S. internum*; this result was significant for female *obtrusum* compared to female *internum*. (Table 1).

We tested whether this greater attachment was possibly due to *S. obtrusum* representing a larger ‘target’ for encounter by mites. Again, we included only tenerals emerging from days 6–11 because we found seasonal declines in wing lengths (an estimate of body size), for both sexes in *S. obtrusum* (females: $r = -0.16$, $P < 0.001$, $n = 220$; males: $r = -0.19$, $0.05 < P < 0.10$, $n = 93$), although not for either sex of *S. internum* (females: $r = 0.20$, $p > 0.25$, $n = 32$; males: $r = -0.078$, $p > 0.80$, $n = 12$). For days 6–11, we found that species accounted for significant variation in wing lengths ($F_{1,186} = 27.3$,

Table 1
Mean numbers of *Arrenurus planus* mites and mean wing lengths (±2 SEM) for teneral female and male *Sympetrum internum* and *Sympetrum obtrusum* collected from days 6–11

Species	Sex	N	Mite numbers	Wing length
S. internum	F	20	30.1 (20.2–41.8)^{a}	13.4 ± 0.20^{c}
	M	4	41.4 (13.3–85.1)^{a,b}	13.4 ± 0.22^{c}
S. obtrusum	F	123	59.4 (51.7–67.7)^{b}	12.8 ± 0.078^{d}
	M	42	52.4 (40.0–65.6)^{a,b}	12.8 ± 0.14^{d}

Species-by-sex groups with the same letter designation have statistically indistinguishable mite numbers or wing lengths, each of two comparisons based on Tukey’s post hoc test (Wilkinson L. SYSTAT: the System for Statistics, Evanston, IL: Systat, 1991). Mean numbers of mites refer to back-transformed means. As such, errors are asymmetrical about the mean and are represented as a range.

Table 2
Numbers of mature dragonflies of both *Sympetrum internum* and *Sympetrum obtrusum* that had mites

Species	Sex	Engorgement score					
		0	1	2	3	4	5
S. internum	F	5	0	0	0	0	0
	M	21	0	0	0	1	1
S. obtrusum	F	2	0	0	3	9	14
	M	3	0	1	0	14	29

The categories of mite engorgement refer to the number of times that the mite is larger than its dorsal plate, with fully engorged mites (engorgement score 5) nearing 1 mm in length (see text for actual measurements).

$P < 0.001$), whereas both sex and the interaction term were non-significant (sex: $F_{1,186} = 0.85$, $P > 0.30$; interaction: $F_{1,185} = 0.25$, $P > 0.60$). However, *S. internum* females and males were significantly larger than *S. obtrusum* females and males (Table 1), contrary to what was expected if size of adults, which relates to size of final-instar larvae, affects likelihood of colonisation by mites.

To score engorgement of mites, we used all 28 mature *S. internum* caught and 75 of 124 mature *S. obtrusum* that were caught (other *S. obtrusum* were released in the field without returning them to the lab for accurate scoring of engorgement). For *S. internum* matures, only 2 of 23 males had mites that made it past engorgement stage 2, and 26 of 28 mature dragonflies had mites that failed to start engorging. In contrast, few *S. obtrusum* matures had mites that failed to start engorging, or that engorged only to stage 2 by the time hosts were captured (six of 73 dragonflies). Rather, most mature *S. obtrusum* had mites engorged to at least stage 3 and often to stages 4 or 5 (Table 2). When engorgement categories were collapsed into two categories (0–2: little or no engorgement; 3–5: becoming or fully engorged), we found that *S. internum* and *S. obtrusum* differed significantly in the proportion of individuals carrying mites that were becoming engorged or that were fully engorged (males: 0.7 versus 93.6%, respectively, $P < 0.001$, Fisher's exact test; females: 0 versus 92.8%, $P < 0.001$, Fisher's exact test).

Examination of cuticular preparations allowed us to determine the gross histological nature of host resistance. We were successful in obtaining 61 (of 75 attempted) preparations where 1–14 mites were still attached to a portion of the host's 'cleared' cuticle. Of the 42 preparations for *S. obtrusum*, only one showed slight brown discolouration near the mite's mouthparts; the remaining 41 were typified by bubble-like stylostomes for all mites observed (Fig. 1A). Of the 19 preparations for *S. internum*, 18 were typified by golden-brown blotches partially or wholly obscuring the mouthparts of the mite and by a collapsed or missing stylostome of the mite (Fig. 1B). One teneral *S. internum* female had mites with bubble-like stylostomes. Thus, *S. internum* appears to mount an immune response that is quite effective in collapsing stylostomes and killing mites, whereas *S. obtrusum* does not mount this response, or rarely mounts a less intense response.

We also examined whether mites may be costly to *S. obtrusum* by examining differences in mite numbers between tenerals that emerged from the pond and young dragonflies caught near the pond's edge. We assumed that young dragonflies with *A. planus* mites had emerged from the pond, because ephemeral ponds were widespread. We only compared young dragonflies with tenerals because mature dragonflies were often found 'scarred', indicating that they had lost mites (fully engorged *A. planus* mites detach when dragonflies are at edges of temporary ponds, [19]). Young dragonflies were not old enough for mites to fully engorge and were rarely scarred (only one of 132 individuals showed a single scar). Using a 2-way ANOVA on transformed mite numbers, we found that age did account for sig-

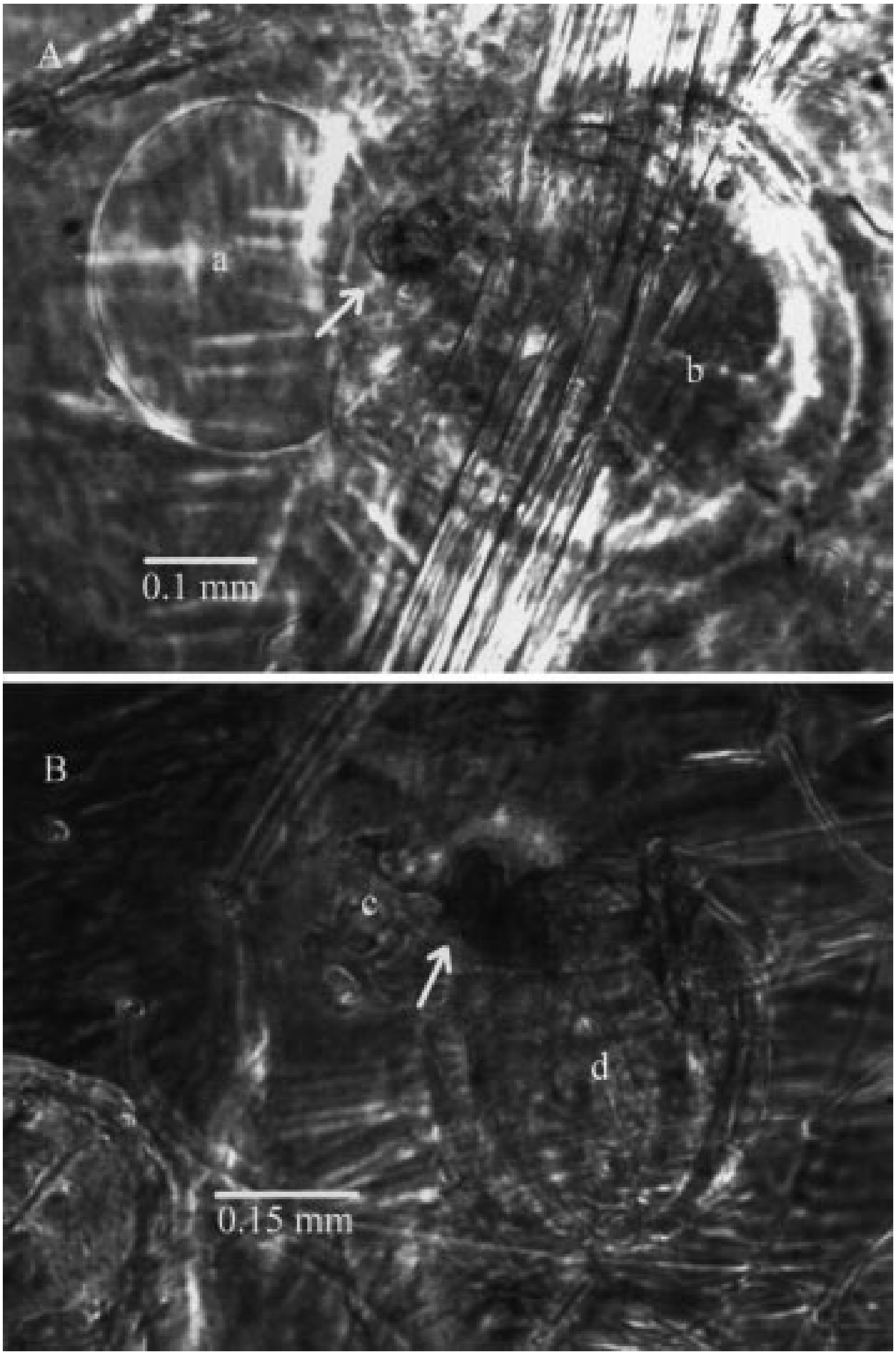

Fig. 1. (A) Light micrograph of *Arrenurus planus* attached to *Sympetrum obtrusum* photographed through the host's cleared cuticle. Note the bubble-like stylostome (a) of the mite (b) emanating from near the mite's mouthparts or gnathostome (white arrow). Note also that this area is not typified by dark material obscuring a view of the mouthparts or by a missing or collapsed stylostome (see B); (B) Light micrograph of *Arrenurus planus* attached to *Sympetrum internum*. Note the collapsed stylostome (c, wrinkled mass) of the mite (d) and dark material obscuring the mite's mouthparts (white arrow). Scale bars indicated.

nificant variation in mite numbers ($F_{1,445} = 5.14$, $P < 0.05$), whereas both sex of host and the interaction term were non-significant (sex: $F_{1,445} = 2.30$, $P > 0.10$; interaction: $F_{1,444} = 0.26$, $P > 0.60$). Young *S. obtrusum* carried fewer mites than tenerals. Teneral females averaged 40.9 mites (backtransformed mean; range of 2 S.E. was 35.7–46.4). In comparison, young females averaged 29.8 mites (range: 20.8–40.4). Teneral males averaged 32.6 mites (range: 25.5–40.6), whereas young males averaged 26.6 mites (range 19.5– 33.9). Thus, the age effect is largely attributable to the comparison between teneral females and young males: the latter carrying significantly fewer mites than the former, based on Tukey post hoc comparisons. We also examined whether unparasitised individuals represented a larger proportion of young dragonflies than tenerals. For females, we found that unparasitised individuals represented 2.3% of all tenerals ($n = 220$) and 7.5% of all young individuals ($n = 54$), consistent with a prediction of mite-induced mortality. However, this result was only nearly significant ($X^2 = 3.59$, $0.05 < P < 0.06$). For males, unparasitised individuals accounted for 5.4% of teneral males ($n = 93$) and ca. 9.0% of young males ($n = 78$) ($X^2 = 0.84$, $P > 0.35$). Overall, these results are suggestive of mite-induced mortality, but the effect is relatively weak to moderate.

Finally, three of seven recaptures could be identified individually, based on a combination of sex, position and colour of marks, mite numbers, and cell counts of leading edges of right and left forewings to the nodus. We found that aging from teneral to young took ca. 7 days, at which time, mites were only half engorged. By 17 days, tenerals aged to matures and mites became fully engorged. The last recapture was caught 37 days after marking; it was mature and only had scars.

4. Discussion

Biologists interested in the evolutionary maintenance of host resistance should consider interactions where several potential host species exist. Selection to overcome resistance should be strongest when parasites are involved in interactions with single host species, or with an abundant species in a suite of potential hosts. A parasite that does not overcome resistance of its main (or only) host species may face extinction, a trajectory that is especially relevant for insect macroparasites that can have evolutionary rates on par with their hosts [2]. Several factors, taken together, might help maintain resistance in some host species, including: relative frequency of a host species; nature of the resistance relative to what is commonly deployed; degree of impact of parasites on alternative host species; and the physiological cost of resistance.

Results from our study relate to the first three factors. First, *S. internum* was relatively rare, whereas *S. obtrusum* was abundant at our study site. Second, *S. internum* are almost entirely resistant to *A. planus* following attachment, whereas this mite most often engorges and successfully detaches from *S. obtrusum*. Related to this point, *S. internum* uses a defense mechanism that has not been reported from other odonate insects and which is quite different from melanotic encapsulation of the feeding tube (cf. [12–14]). Rather, 'clots' appear in the region of the mite's mouthparts (cf. [20]). Third, *A. planus* attach to both species, although *S. internum* are less often used as hosts. Finally, higher mite loads were found on newly-emerged *S. obtrusum* than on young individuals patrolling the pond. This result is consistent with mite-induced mortality.

A generalist parasite, such as *A. planus*, faces constraints. Perhaps one of the strongest constraints for *Arrenurus* mites parasitising odonate insects is host discovery. In comparison with arrenurids that are dipteran parasites, whose hosts often number in the thousands per m^2, *arrenurus* parasitising odonates have to contend with low host density [10]. As such, there is strong selection on females to produce relatively large clutches with young that may have limited resources for persistence [10]. These larval mites may lose viability rapidly over time and opt to attach to inappropriate hosts (with a small chance of being successful), rather than continue searching and fail to attach to any host. From days 6–11, some 881 mites attached to 24 teneral *S. internum* (compared with 10 841 mites on 165 teneral *S. obtrusum* at that time). Although 881 represents ca. 7.5% of all mites observed at that time, almost all of those mites are expected to have zero fitness.

As mentioned, *A. planus* appear to depress fitness of *S. obtrusum* hosts. Mite-associated reductions in lifespan, dispersal and mating success have been reported for other odonates [21–23] and many other aquatic insects [12]. However, effects shown here are not as drastic as seen in other insect–mite associations, where host survivorship is greatly compromised by even a few mites [12]. Because *A. planus* appears only to have moderate effects on its main host, *S. obtrusum*, selection to exploit other hosts may not be extreme. *Arrenurus planus* is not expected to have any effects on *S. internum*, other than indirectly through the costs of *S. internum* mounting an immune response. These mites are only phoretic on *S. internum* and numbers do not get high enough for them to affect sense organs, as shown in other insect–phoretic mite associations [24].

These factors, taken together, probably mean that there is little selection on *A. planus* to overcome defenses of *S. internum*. *Sympetrum internum* is rare, at least at our study site. This might not present a problem for a generalist parasite, unless adaptations to the common species carry with them costs or constraints in exploiting other species (analogous to different parasite genotypes exploiting different host genotypes within species) [6]. When a rare species employs a novel or specific resistance, then this species may remain resistant, unlike the common species to which the parasite should be most adapted, and unlike other rare species that deploy common forms of resistance. Recently, Imhoof and Schmid-Hempel [25] showed how difficult it can be to predict parasitic impacts within allopatric versus sympatric populations of their hosts. By analogy, it should be difficult to predict the impact of generalist parasites on commonly encountered versus newly encountered host species. However, this paper suggests that we may be able to identify host species that can maintain resistance.

Our results are important for other reasons. Other examples exist where single parasite species exploit several host species [3]. There are also other instances where one host species shows resistance and the other is susceptible [20, 26]. These situations are similar to that shown by *A. planus* and its dragonfly hosts. The water mite, *Limnochares americana*, provides a supporting case because it fails to engorge on *Nannothemis bella* (a rare dragonfly), but is able to exploit several other common species (BPS, unpubl. data). We do not yet know the nature of resistance of *N. bella* compared with other species.

Although empirical data are scant, other researchers have shown that common insect species harbour more parasites than rarer species [27]. If parasites are easily transmitted across species, then common species that disperse may, by invading other localities, displace rare species that are not well adapted to novel parasites and pathogens. Of course, such occurrences depend on resistance not being well developed in the rarer species. If such resistance develops, it may be maintained if the rarer species is a small agent of selection for the parasite. There are also examples of potential parasite-mediated competition between host species [28, 29]. Researchers may now want to address why one competitor appears more susceptible to parasites. Does this imbalance relate to its greater abundance and its greater likelihood of becoming an agent of selection for parasites? Our study suggests that one outcome of interactions between generalist parasites and host species is that one host species remains relatively rare and resistant, while another is more abundant but susceptible to parasites with moderate effects on fitness.

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