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## Conflict between antipredator and antiparasite behaviour in larval damselflies

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**Abstract** Larval damselflies resist infestation by parasitic larval mites by exhibiting behaviours such as grooming, crawling, swimming, and striking at host-seeking mites. Larval damselflies are known to increase time spent in these behaviours in the presence of mites but reduce time spent in these behaviours in the presence of fish predators. The presence of both fish and larval mites presents an obvious conflict: a larval damselfly may actively avoid parasitism by mites, thus increasing its risk of predation, or it may reduce its activity when fish are present, thus increasing its risk of parasitism. We analysed the behaviour of larval *Ischnura verticalis* in an experiment where we crossed presence and absence of fish with presence and absence of larval mites. Presence of mites induced a large increase in activity of larval *I. verticalis* but fish had no effect and there were no interpretable interactions between effects of mites and fish. Subsequent experiments indicated that larval *I. verticalis* in the presence of both mites and fish were more likely to be attacked and killed by fish than those exposed only to fish. The high activity level of *I. verticalis* larvae in the presence of both fish and mites may suggest that costs of parasitism are high, or that under field conditions it is rare for larvae to be in the immediate presence of both fish predators and potentially parasitic mites.

**Key words** Antipredator behaviour · Antiparasite behaviour · Predation risk · Odonata · Water mites

### Introduction

It is well established that antipredator behaviour of aquatic prey insects can affect their foraging rate by changing their activity (Heads 1986; Dixon and Baker 1988; Macchiusi and Baker 1992) or choice of micro-

habitat (Soluk and Collins 1988; Kohler and McPeck 1989). There is also evidence that these changes in foraging can influence development (Ball and Baker 1995; Peckarsky et al. 1993; Feltnate and Williams 1991) although the extent of these changes under natural conditions in the field has rarely been studied (Macchiusi and Baker 1992).

Antipredator behaviour may also conflict with other behaviours that may have far-reaching effects on prey populations. One potentially important effect of predator-induced changes in behaviour of larval Zygoptera is increased risk of parasitism. Larval mites of the genus *Arrenurus* parasitize adult damselflies by first attending the larval odonate and then crawling onto the adult when it emerges (Smith 1988). Larval mites parasitize the adult damselfly by piercing its exoskeleton with their chelicerae and inserting a feeding tube (Smith 1988). Parasitism by mites reduces longevity and fecundity of damselflies (Åbro 1982; Robinson 1983; Forbes and Baker 1991) as well as mating success of males (Forbes 1991). Larval Zygoptera rid themselves of attendant mites by crawling more and by “grooming”: vigorously rubbing the body with the legs or tip of the abdomen (Forbes and Baker 1990). In contrast, when fish are near, larval damselflies reduce both crawling and grooming – the latter by at least an order of magnitude (Dixon and Baker 1988). Thus, when exposed to both predators and parasites, a larval zygopteran must deal with conflicting responses; by actively avoiding parasitic mites, a damselfly larva may increase its risk to predators that cue in on movement; however, by reducing its activity when fish are present, a larva may increase its risk of parasitism.

This paper reports results from experiments designed to test for conflicts between antipredator and antiparasite behaviour of the larval damselfly *Ischnura verticalis*. Our expectation was that, when confronted with both predators and parasites, larvae would respond more to the presence of the potentially lethal predators and thus expose themselves to parasites. We analysed the behaviour of *I. verticalis* larvae in an experiment where we crossed presence and absence of pumpkin-

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seed sunfish (*Lepomis gibbosus*) with presence and absence of larval mites of the genus *Arrenurus*. We used principal component analysis (PCA) to reduce the number of response variables and remove the correlation between response variables. Results of the behavioural analysis indicated that *I. verticalis* responded more to the presence of larval mites; subsequent experiments tested if larval *I. verticalis* exposed to water mites suffered increased rates of attack and predation by pumpkinseed sunfish.

## Methods

### Effects of larval mites and fish on behaviour of larval *I. verticalis*

In early June 1993 we collected final instar larvae of *I. verticalis* from a shallow pond in an abandoned quarry in the city of Burlington Ontario (43°21'N, 79°52'W). Larvae were returned to the laboratory and housed in 75-ml plastic vials supplied with a dowel for a perch. They were kept at approximately 21°C with a photoperiod of 14:10 L:D and were fed approximately five *Daphnia* sp. per day.

During late May and early June 1993 we collected adult female *Arrenurus* spp. of the *superior* group (*A. pseudosuperior*, *A. magnicaudata* and an undescribed species near *A. pseudosuperior*) from several sites near the Queen's University Biological Station (44°34'N, 79°15'W). Adult females were housed individually in shell vials (17 mm internal diameter×48 mm high) and kept at room temperature with no food. Vials were supplied with a small piece of paper for the females to oviposit upon; larvae that hatched from eggs were used in the experiment. Mites were transported to the laboratory at Erindale College and kept at the same temperature and photoperiod as the larval Zygoptera.

Approximately 30 pumpkinseed sunfish (*L. gibbosus*) were collected from the pond on the Erindale College Campus of the University of Toronto (43°33'N, 79°15'W) in summer 1992 and were housed in 100-l aquaria at the same temperature and photoperiod as described above. Fish were fed commercial fish foods plus an assortment of live aquatic insects including chironomids and larval damselflies. By the time fish were used in experiments they ranged from 8 to 10 cm in length.

The experiment involved four experimental conditions (presence or absence of larval mites crossed with presence or absence of a pumpkinseed sunfish) with each condition replicated ten times. Experiments were run in four glass aquaria (35×21×21 cm) filled with dechlorinated water. Temperature was approximately 21°C and the photoperiod was 14:10 L:D.

We started each replicate by placing a final instar larvae of *I. verticalis* into a clean 75-ml plastic vial (36 mm internal diameter×60 mm high) filled with dechlorinated water and supplied with a wooden dowel that reached from the bottom of one side of the vial to the top on the opposite side. For replicates with mites present we added approximately 15 larval mites to the vial, and for replicates with fish we provided possible olfactory cues of fish presence by adding a few drops of water from an aquarium holding several pumpkinseed sunfish. Vials were then capped, inverted, and placed on the bottom of the aquarium, one vial per aquarium. We inverted vials because the opaque caps on top of vials hindered our view of larvae. In replicates involving fish, a single pumpkinseed sunfish was added to the aquarium when vials were added.

We ran one replicate of each of four treatments in both the morning and afternoon of each day; all observations were completed within a 5-day period. We randomized the order of observations of the treatments within each morning or afternoon. No damselfly or mite larva was used more than once. Fish were returned to the holding aquarium after each treatment; they were never used twice in the same day but may have been used on sub-

sequent days. Aquaria were emptied, rinsed and refilled after every treatment.

Each damselfly larva was observed for a total of 10 min. Observations began 15 min after vials were added to the tanks; occurrences of all behaviours were recorded on an NEC event recorder. We observed and recorded eight different behaviours. For six of the behaviours (Crawl Forward, Strike, Lateral Bend, Abdomen Wave, Swim, 180° Turn) we chose to use the names and descriptions published in Richardson and Anholt (1995). Our description of Groom differs from that of Richardson and Anholt (1995) and they did not observe the behaviour Wiggle.

1. Crawl Forward. Any forward movement in which the animal maintains continuous limb contact with the substrate.
2. Strike. Rapid extension of labium, generally in the direction of prey or debris on the floor of the container. (In the current study Strike was always directed at mites but we have seen larvae strike at inanimate objects).
3. Lateral Bend. A transverse bend occurs in the abdomen so that the lamellae and last 6–7 abdominal segments are at an angle greater than 60° from the rest of the body. Lamellae were sometimes apposed, sometimes divergent. This bend could be held for several seconds. On some occasions, only a single bend occurred, on other occasions the abdomen was straightened and the bend repeated, either to the same or to the opposite side.
4. Abdomen Wave. The animal repeatedly performs a low-amplitude (at an angle of approximately 10° from the rest of the body) transverse motion of the last 6–7 abdominal segments and lamellae. Although similar to Lateral Bend, this behaviour is easily distinguished from that behaviour by a difference in amplitude and greater rhythmicity.
5. Swim. Any movement through water, in which the animal does not maintain contact with the substrate. This movement was accomplished by a transverse undulation of the abdomen and lamellae.
6. 180° Turn. Keeping in the same place on the perch, the animal turns so that it is facing the opposite direction. This could be either a fast or a slow movement in which the head starts turning and lamellae follow.
7. Groom. All movements in which either the tarsal claws or distal segments of a leg or pair of legs were rubbed against any part of the body; Groom also includes the lateral bending of the abdomen to the point where the distal tip of the abdomen is brought over the head and rubbed against the dorsum of the head and prothorax.
8. Wiggle. A very rapid lateral undulation of the entire abdomen resulting in a series of waves passing down the body; each occurrence lasted only a second or two.

The statistical difficulty with the data is that various behaviours exhibited by an animal are not independent. Therefore, following the suggestion by McPeck (1990), we first used PCA to collapse the original  $\log(x+1)$ -transformed variables into fewer, statistically uncorrelated, variables. We used the correlation matrix option on the Principal Components program of Systat, version 5. We chose the correlation matrix option rather than the covariance matrix because it codes the variables to have means of 0 and variances of 1; this was important because our behavioural variables varied widely in values and ranges and we did not want behaviours with large values to have "an undue influence on the principal components" (Manly 1986).

### Effects of larval mites on susceptibility of larval *I. verticalis* to attack by *L. gibbosus*

To test if the presence of mites increased the frequency of attack by fish on Zygoptera we used opaque polypropylene tanks (35×30×15 cm) filled with dechlorinated water. On the day before a trial we placed a pumpkinseed sunfish (same lengths as above) in each tank. On the day of a trial we added three of the same 75-ml vials used previously, each capped and filled with dechlorinated water, to each tank. The three vials were fixed to a white opaque plexiglass plate (23×5 cm). Four (7×5 cm) pieces of the

same plexiglass material were mounted vertically at the two ends of the plate and at a distance one-third the distance from each end so that each vial had an upright plate on each side. The upright plates prevented larvae from seeing larvae in adjacent vials and afforded fish the same perspective of each vial. The plate (with vials attached) was placed against the midpoint, and parallel to, one of the long walls of the tank.

Approximately 5 min before inserting the vials in the tanks, we placed a final-instar larvae of *I. verticalis* in one of the vials, 10–15 larval mites in another, and a final instar larvae of *I. verticalis* with 10–15 larval mites in the third vial. Each vial contained a wooden dowel that extended from the bottom of one side of the vial to the top on the opposite side. Relative position of the three types of vials was randomized within each replicate. Vial caps were coded as to treatment; when vials were viewed from above the observer was blind as to what was in each vial.

After inserting vials into each of two tanks, we arranged the tanks side by side and videotaped them with a television camera suspended directly over the tanks and connected to a time-lapse video recorder. Tanks were video-taped for 2 h. Twenty-two tanks were video-taped over a 4-day period. Trials were run between 9:00 a.m. and 5:00 p.m.; temperature and photoperiod were the same as in the previous experiment.

We replayed tapes and recorded fish-strikes against the coded vials. A strike was defined as a rapid swimming motion aimed directly at the vial with clear contact between the fish's mouth and the vial. Fish occasionally "nudged" the vials (and walls of the tanks) as they swam slowly around, but these nudges were not counted as strikes as they were distinctly different from the rapid strikes used to attack live prey added to holding tanks. In a few cases a fish swam quickly towards a vial but stopped a few centimeters away and did not contact the vials; these occurrences were not considered strikes.

#### Effects of larval mites on susceptibility of larval *I. verticalis* to predation by *L. gibbosus*

These experiments were designed to test if presence of mites increased predation rates of fish on Zygoptera. On the day before the experiment we filled 18 of the same tanks used in the previous experiment with dechlorinated water. We added artificial vegetation in the form of nine 10-cm lengths of plastic *Elodea*-like stems which were fixed in a regular pattern to a 18×11 cm mat of plastic meshing (mesh opening 8 ×8 mm) in one end of each tank. We then added four final instar larvae of *I. verticalis* to each tank; larvae had been collected 1 week earlier from the site in Burlington, Ontario, and had been kept individually in 75-ml vials supplied with a dowel and fed ad lib with *Daphnia* sp. No food was added to tanks; temperature and photoperiod were as in the previous experiment.

At 9:30a.m. on the day of the experiment we divided each tank into two halves by inserting white, opaque, plastic dividers at the midpoint of each tank. Fifteen minutes later we put a single pumpkinseed sunfish (same lengths as above) in each tank on the side opposite the artificial *Elodea* sp. Fish were fed the day before, but not on, the day of the experiment. Because damselfly larvae remained on the artificial vegetation, fish and larvae were on opposite sides of the tanks. One hour after adding the fish we added approximately 3,600 larval mites to each of nine tanks. Mites (*A. pseudosuperior* or an undescribed species near *A. pseudosuperior*) were hatched from egg masses collected at Charleston Lake near the Queens University Biological Station. Tanks with and without mites were arranged in an alternating pattern on the laboratory bench to control for any effect of location. Five minutes after we added mites we removed the dividers to allow fish access to the Zygoptera. Tanks were left for a further 4 h after which we removed the fish with a net and counted the Zygoptera larvae that remained. We assumed all missing Zygoptera were killed by fish; cannibalism is rare in *I. verticalis* (Richardson 1994) and we never found partly consumed individuals.

Results of the experiment described above indicated relatively few larvae were killed during the 4-h period. We repeated the experiment in 1996 using the same basic setup except that both fish and dividers were put in place on the day before the experiment and six larval *I. verticalis* were added to the vegetation side of each of the 18 tanks at 9:30 a.m. on the day of the experiment. Larvae were left to settle for 1 h after which we added approximately 440 larval mites (same species as above) to each of nine tanks and lifted the dividers in all tanks. Tanks were left for 24 h (photoperiod 15L:9D) after which we removed the fish and counted remaining larvae.

## Results

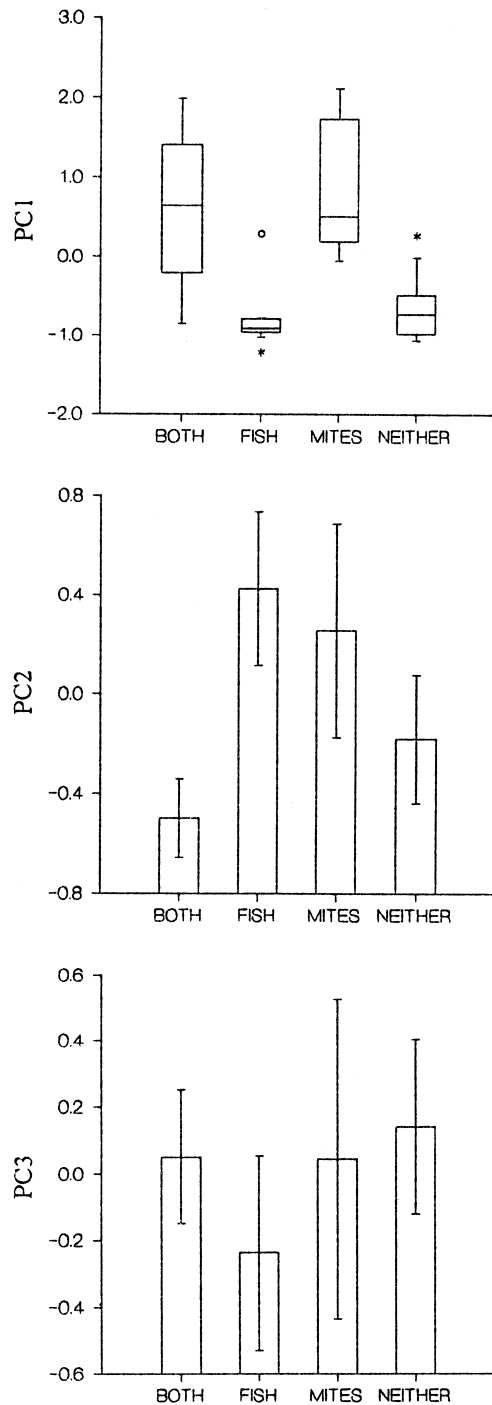
### Effects of larval mites and fish on behaviour of larval *I. verticalis*

We analysed duration of all behaviours except Strike where we analysed frequency. PCA was run on all eight behavioural variables. The first three factors explained 35.1, 19.8 and 16.2% of the total variance respectively (Table 1) and had eigenvalues greater than 1. The next three factors explained only 8.4, 7.1 and 6.1% of the variation and had eigenvalues less than 1, indicating that each explained less of the variance than the original variables (variance is standardized to 1 for correlation matrices: Manly 1986). Because the fourth factor, and all subsequent factors, explained such a small proportion of the variance they were dropped from further analysis. PC1 was readily interpretable in that Wiggle, Lateral Bend, Strike, Crawl Forward all loaded higher than 0.6 and Groom loaded at 0.59; most of these behaviours can be interpreted as functioning to rid the zygopteran of attendant mites (see Discussion). Abdomen Wave and 180° Turn loaded higher than 0.6 on PC2 while Swim loaded at 0.47 and 180° Turn at 0.59 on PC3. Lilliefors tests (Marascuilo and McSweeney 1977) indicated that the distributions of scores for PC1 were significantly different from normal so we analysed the data with a two-way extension of the Kruskal Wallis test. Distributions of scores for PC2 and PC3 were not significantly different from normal and were analysed with two-way ANOVA.

PC1 clearly increased when mites were present ( $H=21.4$ ,  $df=1$ ,  $P<0.001$ ; Fig. 1) but was not affected by

**Table 1** Correlation between the original  $\log(x+1)$  transformed variables and the first three principal components

	PC1	PC2	PC3
Wiggle	0.85	0.01	0.10
Bend	0.79	0.09	-0.33
Strike	0.70	-0.17	0.24
Crawl	0.68	0.01	-0.49
Groom	0.59	-0.46	0.35
Swim	0.39	0.56	0.47
Turn	0.10	0.63	-0.59
Wave	0.02	0.79	0.43
% Variance explained	35.1	19.8	16.6



**Fig. 1** Top Box and whisker plots (central horizontal line is the median and the upper and lower sections of the box are the upper and lower quartiles; see Wilkinson 1990 for remaining symbols) of PC1 values under the four experimental conditions (BOTH fish and mites present, FISH fish present, mites absent, MITES fish absent, mites present, NEITHER neither fish or mites present). Middle and bottom, means  $\pm$  1 SE of PC2 and PC3 under the same four experimental conditions described above;  $n=10$  for each treatment

fish presence ( $H=0.42$ ,  $df=1$ ,  $P>0.5$ ); there was no statistical interaction between the effects of mites and fish ( $H=0.006$ ,  $df=1$ ,  $P>0.9$ ). For PC2 there was a statistical interaction between effects of fish and mites ( $F=4.94$ ,  $df=1$ ,  $P=0.033$ ) with scores tending to be lower when both mites and fish were present or both were absent (Fig. 1). There were no independent effects of fish ( $F=0.05$ ,  $df=1$ ,  $P>0.81$ ) or mites ( $F=0.62$ ,  $df=1$ ,  $P>0.43$ ). There were no effects of fish ( $F=0.32$ ,  $df=1$ ,  $P>0.57$ ), or mites ( $F=0.087$ ,  $df=1$ ,  $P>0.76$ ), or statistical interaction between mites and fish ( $F=0.34$ ,  $df=1$ ,  $P>0.56$ ) on PC3 (Fig. 1).

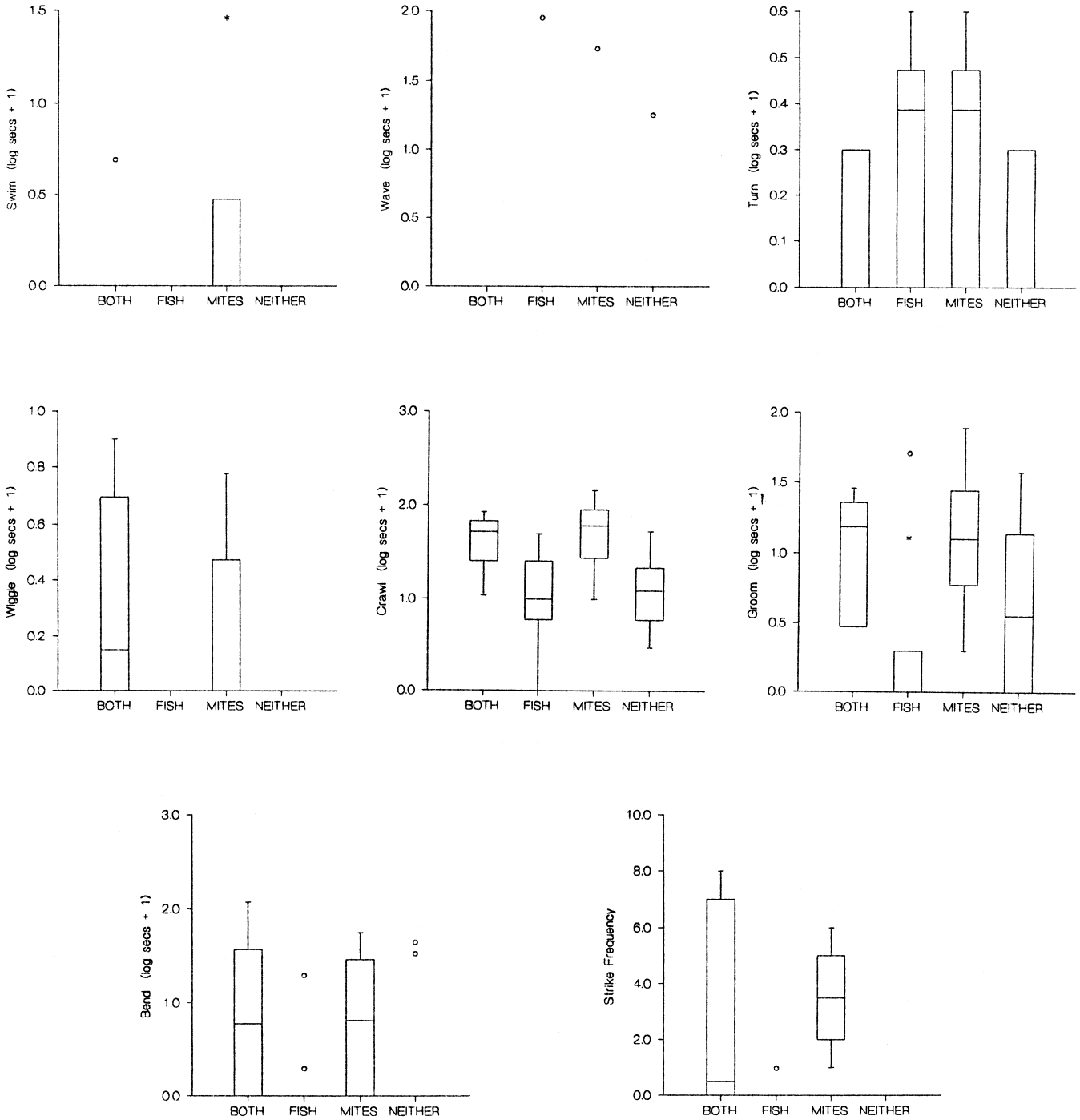
Results of the Kruskal Wallis analysis on PC1, and the fact that Crawl Forward, Groom, Wiggle, Strike, and Lateral Bend loaded heavily on PC1, are reflected in the trend for each of these behaviours to be increased in the presence of mites and mites plus fish (Fig. 2). Swim also tended to increase with mite presence. 180° Turn and especially Abdomen Wave were rare and did not show any clear pattern with respect to the treatments (Fig 2).

#### Effects of larval mites on susceptibility of larval *I. verticalis* to attack by *L. gibbosus*

Vials containing mites but no damselfly larvae were never struck by fish and were dropped from analysis. Data were analysed with a Wilcoxon paired-sample test since a Lilliefors test indicated that data were not normally distributed. Fish struck more ( $T=9$ ,  $P<0.025$ , one-tailed test) at vials containing both mites and larval damselflies (median=0.5, range 0–4) than at vials containing only larval damselflies (median=0.0, range 0–3). Within tanks the mean difference in number of strikes at vials with both Zygoptera and mites versus Zygoptera alone was 0.55 for all 22 cases, and 0.92 for cases where fish struck at least once ( $n=13$ ).

#### Effects of larval mites on susceptibility of larval *I. verticalis* to predation by *L. gibbosus*

Data were analysed with a Mann-Whitney  $U$ -test since a Lilliefors test indicated that they were not normally distributed. In the first run of the experiment a median of 1 zygopteran larva was killed when mites were present (range 0–2) and a median of 0 zygopteran larvae were killed (range 0–1) when no mites were present, ( $U=55.5$ ,  $P=0.068$ , one-tailed). In the second run a median of 6 zygopteran larvae were killed when mites were present (range 4–6) and a median of 5 zygopteran larvae were killed (range 4–6) when no mites were present, ( $U=54.5$ ,  $P=0.093$ , one-tailed). Because both runs of this experiment tested the same hypothesis: “Does presence of mites increase predation rate?”, we combined the probabilities from the two analyses using the technique described in Sokal and Rohlf (1995). Analysis indicated there was a significant effect ( $P<0.05$ ); larvae were more likely to be killed by fish when mites were present.



**Fig. 2** Box and whisker plots of the eight behavioural variables under the four experimental conditions. See Fig. 1 for abbreviations

**Discussion**

Overall, larval damselflies in the presence of mites or mites and fish were far more active than larvae in the absence of mites, and the analysis of PC1 suggests it can be interpreted as a suite of antiparasite behaviours. PC2 and PC3 each explained a smaller proportion of the vari-

ance than did PC1 and did not show any clear or readily interpretable pattern with respect to treatments. Crawl Forward, Groom, Wiggle, and Labial Strike all increased in the presence of mites and it is relatively easy to envision these behaviours reducing the number of potentially parasitic mites that attach to a larval zygopteran. Groom clearly acted to force a mite from the larva's body; mites were large enough to see during the observations and on several cases we saw a larval mite land on a larval Zygoptera and the zygopteran immediately responding by grooming the body in the immediate vicinity of the mite. In one case the grooming dislodged the mite from the

zygoteran's abdomen. Wiggle reminded us of horses and cattle shuddering to rid themselves of flies; mites landing on a zygopteran were dislodged by the vigorous shaking action. Wiggle may function exclusively as an antiparasite behaviour; R. L. B. has never seen the behaviour except in the presence of mites. Crawling or swimming may also help reduce the likelihood of parasitism by reducing the time larval damselflies spend near areas with high concentrations of parasites. Abdomen Bend also increased with the presence of mites but it is hard to visualize how this behaviour could act to reduce parasitism. This behaviour has been shown to occur more often when other larval zygopterans are near (Baker 1981) and may indicate that the larva is agitated. Turn and Wave showed no relationship to mite presence and are probably not involved in avoiding parasites.

Labial Strike led to several mites being killed by the Zygoptera and this will reduce the probability of a parasite infesting a host simply by reducing the number of parasites. Given our experimental setup it is difficult to determine whether Labial Strike was functioning as an antiparasite or foraging behaviour and this raises the possibility that some of the other behavioural responses may represent behaviours associated with foraging and not the avoidance of parasites. However, comparing our results with those of Richardson and Anholt (1995), this is highly unlikely. Richardson and Anholt (1995) found presence of food increased the frequency of Strike in *I. verticalis* but decreased duration of Crawl, Swim, Bend and Turn whereas we found presence of mites increased duration of Crawl, Swim, and Bend, and had no apparent effect on Turn. In addition, as described above, mites clearly increased Groom and Wiggle while Richardson and Anholt, who did not experiment with mite presence, found no effect of food on Groom and never observed Wiggle in a total of 454 h of observation. We conclude that responses of larval *I. verticalis* to presence of mites is distinctly different from responses to food and leaves open the possibility that Strike functions as an antiparasite behaviour as well as in foraging.

In his study on the effects of ticks on grooming by impala, Mooring (1995) suggested that natural selection should favour individuals with efficient defences against ectoparasites and that the frequency of grooming may depend, not only on the abundance of parasites, but also "upon the cost/benefit ratio of competing feeding or vigilance activities". For example, Mooring and Hart (1995a) found that during the breeding season territorial male impalas "need to remain vigilant in herding females and repulsing challenging males", and, possibly as a result, groomed less and suffered much higher tick loads than females. The implication of this is that, for males, the costs of being parasitized are less than the costs of increased grooming and the consequent reduction in time spent herding females and repulsing other males. In our study, presence of fish did not reduce the antiparasite behaviour of *I. verticalis* and thus there is no reason to suggest that antipredator behaviour reduces antiparasite behaviour; i.e. increased parasitism does not appear to be a

cost of antipredator behaviour. That *I. verticalis* larvae responded strongly to potentially parasitic mites, despite the presence of fish, may indicate that the fitness costs of being parasitized are high compared to the probability of being eaten by fish.

Our results demonstrate that increased predation is a potential cost of antiparasite behaviour. Presence of mites increased the activity of larval *I. verticalis* even when fish were present and, likely as a result of the mite-induced increase in activity, there was a significant increase in the attack rate by fish and a significantly higher predation rate for larval Zygoptera exposed to mites. There is also evidence that the behaviour avoidance of parasites can lead to increased predation in completely different systems. Mooring and Hart (1995b) reported that reciprocal allogrooming may be important in controlling the number of ticks on the heads and necks of impala but that it leads to significantly reduced vigilance to predators.

It has been recognized for some time now that, despite the huge number of parasitic species and numbers of parasitic individuals, parasitism has received far less attention among ecologists than interactions like competition and predation (Price 1980), and in recent years there has been a lot of work on mathematical modelling of parasite-host systems (Begon et al. 1990). However much of the modelling has focused solely on the parasites and hosts, and Begon et al. (1990) suggest that "it is dangerous to consider (and to model) the interaction between parasites and hosts as though there are only these two components to the interaction". Price et al. (1986) suggest that "Parasite-mediated interactions are due much more attention in ecological and evolutionary studies". Our work on damselflies and mites, and Mooring and Hart's work on impalas and ticks, clearly indicate that, by altering its susceptibility to predators, a host's antiparasite behaviour may have important implications for population dynamics.

However, while our study suggests the possibility that parasites may influence population dynamics of Zygoptera by altering the behaviour and consequently the predation rate of larvae, we have no data on how important the interaction is in the field. It may be that the probability of a zygopteran larvae exhibiting antiparasite behaviours at the same time that a predator is near is relatively low and thus the actual impact of parasitism on predation risk may also be low. Such a scenario may account for our finding that *I. verticalis* larvae did not alter their response to potentially parasitic mites when fish were present; there may be little selection pressure to reduce the response to mites. However, the fact that zygopterans are often heavily parasitized in nature (Smith 1988) indicates they must have frequent contact with potentially parasitic larval mites. This, in combination with the high density of benthivorous fish like sunfish in eutrophic lakes and ponds (Scott and Crossman 1973), and the readiness of fish like sunfish to eat Zygoptera larvae, suggest that the avoidance of parasitism may result in substantially higher mortality. During the past

10–15 years work there has been a great deal of work on the implications of aggressive interactions and antipredator behaviour to the population dynamics and community ecology of larval Odonata (Johnson 1991); results from this study suggests research on interactions between larval odonates and their potential parasites may lead to new insights.

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