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Slow, fast and in between: habitat distribution and behaviour of larvae in nine species of libellulid dragonfly

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SUMMARY

1. Activity and microhabitat use are important factors determining species performance in habitats that differ in permanence and species composition of top predators. This study examined the relationship between the distribution across a gradient of habitat permanence and an associated transition in the composition of top predators and the behaviour of species of larval dragonflies. It also assessed the relationship between larval behaviour, body size and the duration of the larval stage. In laboratory mesocosms the mobility of the different species was measured, as was the extent to which they associated with artificial vegetation.
2. Species mobility was positively related to their natural occurrence in habitats in which invertebrates or small-bodied fish were the top predators, and negatively related with the frequency with which species co-existed with large-bodied fish, the permanence of the habitat and the length of the larval stage.
3. Rather than falling into strict low and high mobility categories, habitat generalists that occurred across the habitat gradient, co-existing with different top predators, had variable mobility levels. In these generalists, mobility was positively related to how frequently they were found in natural habitats in which invertebrates were the top predators.
4. The extent to which species utilized the artificial vegetation in mesocosms was associated with the length of the larval period but was not associated with mobility or species habitat distribution in the field.

Keywords: activity, habitat generalists, habitat gradient, mobility, Odonata

Introduction

Activity can be an important behavioural trait determining the distribution of species across habitat gradients (amphibians: Woodward, 1983; Skelly, 1995; Relyea, 2001; Richardson, 2001; Odonates: McPeek, 1990; Johansson, 2000; Stoks & McPeek, 2003a; Johansson & Suhling, 2004; Trichopterans: Wissinger *et al.*, 1999). In freshwater systems, a general framework has been developed which predicts that species in temporary habitats will be more active and that the transition from fishless ponds with invertebrate predators to lakes where fish are the top predators is associated with a shift from more to less active prey (Wellborn, Skelly & Werner, 1996). Activity is part of a trade-off between growth rate and predation risk, because more active species potentially grow faster but are also more vulnerable to predators (Lima & Dill, 1990; Werner & Anholt, 1993).

In lentic systems, predation intensity and habitat permanence positively co-vary and species sorting along this gradient appears to be related with the degree of activity in many taxa. This results in species turnover along a gradient of habitat permanence and predator regime, with less active species predominating as permanence and predation intensity increase (Wellborn *et al.*, 1996; Stoks & McPeek, 2003a; Johansson & Suhling, 2004). Turnover across these

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gradients suggests that species fall into distinct categories distinguished by Sih (1987) as fast versus slow life-history strategies. These strategies are distinguished by differences in activity and developmental rate. 'Fast' species are more active and have more rapid development than 'slow' species, making it possible for them to complete development in temporary habitats but increasing their vulnerability to predators which excludes them from high-risk permanent habitats. In addition to activity, species differ in microhabitat use. Odonate larvae may also select different microhabitats within a pond and larvae that choose structurally complex microhabitats can decrease their vulnerability to fish predators (Wellborn & Robinson, 1987; Pierce, 1988). Sih (1987) suggested that microhabitat selection and activity may be correlated. He predicted that active species would also take greater risks in their habitat selection behaviour and utilize open microhabitats more than less active larvae which would be more frequently associated with vegetation or other elements in the habitat that provide refuges from predators.

In addition to habitat specialists, many freshwater communities also include generalist species with wide distributions across the permanence–predator gradient. The activity of generalist species has been explored less thoroughly than that of species which segregate across this gradient. Research on coenagrionid damselflies in permanent habitats has compared species of *Enallagma*, which segregate across top predator habitats, with *Ischnura* species which do not and are thus more widely distributed (McPeek, 1996, 2004). The habitat generalists (*Ischnura spp.*) were consistently more active than habitat specialists (*Enallagma spp.*) from both ends of the gradient, and this difference appeared to be important in facilitating their coexistence. The generality of this pattern, however, has not been widely explored. In particular, there is a lack of multi-species comparisons that explicitly relate species activity to their habitat distributions. One exception is Johansson's (2000) comparison of six species of larval odonates, including both dragonflies and damselflies. He related species activity and microhabitat use to their life-history, use of ephemeral habitats and vulnerability to fish. He found support for a slow–fast life-history dichotomy (Sih, 1987) but also suggested that this contrast was actually part of a continuum of activity.

Here, I compared activity within a single family of dragonflies (Libellulidae) within, as well as across, genera. I also used data from extensive regional surveys to relate the distribution of species across the permanence–predator gradient to their activity and use of artificial vegetation in the laboratory. Finally, I included the length of the larval period and body size in analyses to assess whether these species traits were also related with activity. These data were used to address two questions. First, what is the relationship between species activity (specifically movement behaviour), association with structurally complex or simple microhabitats, habitat distribution across the permanence–predator gradient, body size and duration of the larval period? Secondly, are there distinct sets of species that correspond to the proposed slow–fast dichotomy (e.g. Sih, 1987), or is there a set of more active generalists (e.g. McPeek, 1996, 2004)? I addressed these questions by quantifying behaviour in a group of nine species including those whose distribution reflects a segregation across the presence or absence of fish as well as generalists that coexist with a wide variety of top predators.

Methods

This paper presents data on behaviour in the absence of predators for nine species of libellulid dragonfly larvae (Odonata: Anisoptera: Libellulidae) (Table 1). Because of differences in their developmental phenology, species were observed independently in identical experimental set-ups but at different times during the summer and autumn so that all observations were made on late instar larvae. Experiments were conducted in the laboratory at water temperatures ranging from 18 to 23 °C (exact control of temperature was not possible). To test for temperature effects, Pearson's correlation was used to assess the relationship between the three behaviours measured (movement rate, movement distance, and association with artificial vegetation) and water temperature during the observation period. No correlation was found between water temperature and any measure of behaviour. Therefore, temperature was not used as a variable in further analyses.

Larvae were collected from the field and therefore had been exposed to a natural set of predators (e.g. McPeek, 1990). One species (*Libellula pulchella*, Drury) is difficult to collect in adequate numbers from natural ponds and, therefore, larvae for this study were collected from cattle drinking tanks filled with

Table 1 Species used in behavioural trials, codes used to identify species in figures, habitat distributions, and species characteristics

Species	Species code	INV	SBF	LBF	Mean hydroperiod	Development time (months)	Head-width (mm)
Celithemis fasciata, Kirby	cefa	0.00	0.00	1.00	1.00	12	5.25
Erythemis simplicollis, Say	ersi	0.11	0.24	0.65	0.96	18	5.00
Leucorrhinia intacta, Hagen	lein	0.25	0.44	0.31	0.87	12	5.00
Libellula incesta, Hagen	liin	0.00	0.00	1.00	1.00	12	5.05
Libellula luctuosa, Burmeister	lilu	0.06	0.13	0.81	0.99	12	5.50
Libellula pulchella, Drury	lipu	0.47	0.47	0.07	0.95	12	6.20
Pachydiplax longipennis, Burmeister	palo	0.06	0.36	0.58	0.93	12	5.50
*Sympetrum obtrusum/S. rubicundulum**, Hagen/Say	syor	0.73	0.27	0.00	0.77	4.5	4.50
Sympetrum vicinum, Hagen	syvi	0.19	0.33	0.48	0.88	5.5	4.50

Species habitat distributions are characterized by the mean hydroperiod of habitats in which they occurred and by the proportion of habitats with one of three top predator communities (INV, predatory invertebrate; SBF, small-bodied fish; LBF, large-bodied fish) which they occupied.

*These two species were lumped because rearing larvae to the adult stage suggests that current keys do not reliably distinguish them and that they share a common habitat distribution (C.J. Davis unpubl. data).

well-water which they had naturally colonized. All larvae were held in well water in the laboratory for a minimum of 2 days before use in trials, so that their behaviour did not reflect recent reactions to predator cues. Each larva was housed individually in a glass aquarium (21 × 40.5 cm and 27 cm deep) filled to *c.* 3 cm from the top with well water. To create artificial vegetation, two pieces of yellow polypropylene rope 60 cm in length, frayed into 15–20 strands, and weighted at their centre point were placed into each aquarium. The 'vegetation' extended from top to bottom of the water column and then spread out over the surface creating an *c.* 6 cm floating mat.

To facilitate comparison of the data presented here with equivalent experiments in which larvae were exposed to cues of risk from various top predators, empty 'predator' cages were present in each aquarium. These cages were 1 L clear plastic bottles the tops of which were below the water surface. These were weighted to the bottom with gravel, capped with window screening, and an air–stone diffused air into bottles throughout the experiment. These materials, cleaned and bleached between trials, were used in all nine behaviour trials.

For each trial, one larva was placed into each aquarium on the previous afternoon (18–20 h before the first observation). Sample sizes for each species varied from 16 to 25 because of three factors; occasional mortality, individuals excluded because they moulted during the trial, and pre-trial misidentifications in the genus *Libellula*. Twenty *Daphnia* were added to each tank after the larva was introduced. Throughout the trial, 5–10 additional *Daphnia* were added to each tank every day to keep larvae feeding *ad libitum*. Aquaria were randomly placed on five shelves in the laboratory on a 14 : 10 (day : night) cycle. Two observation periods were conducted a day, with the first starting at *c.* 10:00 hours and the second at noon. During observations a researcher went to each tank in sequence and recorded larval position. With the exception of one species (*Celithemis fasciata*, Kirby), behavioural observations were conducted at 5-min intervals during each session. This species was the first to be observed and observations of this species were made every 3 min. In observations of subsequent species this time period was found to be too short to guarantee all observations could be completed within 3 min. To address this issue, data were standardized by comparing the number of moves per hour observed. This has the potential to introduce a bias, overestimating the movement frequency of this species. However, this potential bias does not appear important in estimates of movement rate, as this species had the fewest number of moves observed per hour of all the species in these trials.

Larval activity was measured by quantifying movement frequency and movement distance. The methodology used was based on that of Johansson (2000). Movement was detected by comparing larval position on each observation to its position in the previous observation. Larval position was based on dividing the tank into 16 cells of equal size. An eight-block (four top, four bottom) grid of 8.75 × 12 cm squares drawn on white paper was attached to the back of

each tank, and a line on the side of the aquaria divided the width of the tank in two equal halves. This grid provided 16 possible positions (blocks 1–8 and front or back) in which a larva could be recorded, each a cell with a volume of $8.75 \times 12 \times 10.5$ cm^3. A larva was scored as having moved if it was found in different cells in subsequent observations. Movement distance was measured as the minimum distance a larva travelled between observations (i.e. the shortest path between two cells was assumed). Movement distance was scored based on the minimum number of cell divisions that must be crossed to complete the move (i.e. movement between adjacent cells constituted a movement of one unit while a movement between two cell separated by another cell would be scored as two movement units). Comparisons of species were also made in a third behavioural attribute, their level of association with habitat structure. This was quantified by recording whether individuals were in contact with the artificial vegetation present in the aquarium.

The number of observations differed between years. In 2002, each observation period was 1.5-h long and larvae were observed for two observation periods on 1 day for a total of 3 h of observation (36 observations were made) per replicate. In 2003, observations were made on two sets of congeners, three species in *Libellula* and two species in *Sympetrum*. Because congeners were expected to be more similar than the species from different genera that were compared in 2002, longer observation periods and more sessions were used. In 2003, each observation period was 2-h long (25 observations were made per period) and observations were made for 2 days (two observation periods per day). Larvae were observed for a total of four observation periods for a total of 8 h (100 observations) made on each replicate. To compare all species across these different protocols, behavioural measures were corrected as moves per hour and as the proportion of observations in which individuals were in contact with the artificial vegetation.

Data analysis

Species were characterized based on larval developmental period, body size, presence in habitats with differing top predators, and distribution across the hydroperiod gradient (Table 1). Developmental period in *Sympetrum* was estimated from experiments on hatching time (S. J. McCauley, unpubl. data) and, for other taxa, from a literature review (Walker & Corbet, 1978; Corbet, 1999). Developmental period was entered as the approximate number of months spent as a larva. For species that have either uni- and multivoltine life-histories, this was estimated as the mean of these developmental periods. A measure of species body size (final instar larval head width) was taken from the literature (Walker & Corbet, 1978). Head width is an integrative measure of body size for odonate larvae (Benke, 1970). Species habitat associations were based on surveys over several years that quantified their distributions in 57 lakes and ponds in southeast Michigan (McCauley, 2005). Habitats included waterbodies with three alternative top predator types; predatory invertebrates (INV), small-bodied fish (SBF) and large-bodied fish (LBF). Dragonfly species distributions across these predator environments were characterized as the proportion of their total pond occupancy in each habitat type (the number of ponds with a given top predator type inhabited/total number of ponds inhabited). Species were also characterized based on the mean hydroperiod (proportion of the year a waterbody holds water) of the ponds in which they occurred (Table 1).

Although the species in this study included both congeners and species from different genera, each species was treated as independent in analyses. If activity level, life-history characters and habitat distribution are constrained by shared evolutionary history this could potentially inflate the degrees of freedom of these contrasts. However, the congeners within *Sympetrum* and *Libellula* were chosen for this study in part because they differed from each other in their habitat distributions and could therefore provide insight into the relationship between habitat distribution and activity within a lineage. The effects of phylogenetic relationships between species and their relationship to movement behaviour are considered in the Discussion.

To prevent movement rate and movement distance from being confounded, I calculated the mean movement distance of each larva as the sum of the total distance moved during an observation period divided by the number of moves made in that period. For individuals that moved at least once per trial this made distance travelled independent of movement frequency, so that these two aspects of activity can be evaluated independently. Nonetheless, movement

rate and movement distance were positively associated (individuals that moved often also made longer moves than more sedentary individuals) and so these two measures were combined into a integrative measure of movement rate and distance using a pricipal component analysis (PCA) analysis on all individuals in these trials. Movement rate and movement distance loaded strongly and positively on a single principal component (both loadings were 0.89 using an unrotated loading). Scores for this component were used in further analyses as a composite measure of activity. This composite variable is hereafter referred to as mobility.

A MANOVA was used to determine whether species differed in their behaviour. Both behavioural variables, individual mobility and the number of observations per hour for which an individual was in contact with artificial vegetation (square-root transformed: $\sqrt{\text{observationsperhour} + 0.5}$), were included as dependent variables and species as the predictor variable in this analysis. This analysis uses individual larva as the replicate. *Post hoc* ANOVA analyses assessed whether there were differences between species for each behavioural variable (mobility and association with artificial vegetation). Tukey's HSD *post hoc* tests were used to determine differences between species for each behavioural variable.

A PCA analysis was used to examine the relationship between species mobility, use of artificial vegetation, body size, developmental time, mean hydroperiod of habitat distribution and proportional occupancy of habitat types with alternative top predators. In this analysis species was the replicate unit. To address one of the central questions of this study, how mobility is related to species distribution across alternative top predator habitats, partial correlation was used to examine the relationship between mobility and species distribution across the three top predator habitats (as proportion of each type occupied) while controlling for variables that loaded strongly on the same axes as mobility and habitat distribution in the PCA analysis. All analyses were conducted in SPSS 11.5 (SPSS Inc., Chicago, IL, U.S.A.).

Results

There were significant behavioural differences between species in mobility and association with artificial vegetation (Wilks' $\lambda = 0.348$, $F_{16,398} = 17.27$, $P < 0.001$). ANOVAs found differences between species for both behavioural variables compared, mobility ($F_{8,200} = 28.26$, $P < 0.001$) and association with artificial vegetation ($F_{8,200} = 7.92$, $P < 0.001$) but there was broad overlap between species in both measures (Fig. 1).

Mobility and the use of habitats with insectivorous invertebrates or SBF as top predators were positively correlated with the first principal component axis, while mean hydroperiod inhabited, the length of the larval development period, and the use of habitats with LBF were negatively correlated with this axis (Fig. 2). Principal component one explained 53.7% of the variation in these data. Mean hydroperiod inhabited, duration of the larval developmental period and larval body size (head width) were all positively correlated with the second principal component (PC2), which explained 23.1% of the variation in the data (Fig. 2). Association with artificial vegetation and the length of the developmental period were both positively loaded on the third principal component (PC3), which explained 16.7% of the variation in the data (Table 2).

There was a significant positive correlation between mobility and the proportion of habitats with invertebrates as the top predators occupied by species, when controlling for mean hydroperiod of habitat occupied and larval developmental period ($r = 0.96$, d.f. $= 5$, $P = 0.001$, Fig. 3a). There was also a trend towards a negative correlation between mobility and the frequency with which species occupied habitats where LBF are present ($r = -0.74$, d.f. $= 5$, $P = 0.058$). There was no correlation between mobility and the use of habitats with SBF ($r = 0.16$, d.f. $= 5$, $P = 0.73$). One taxon (*Sympetrum obtrusum*, Hagen *S. rubicundulum* Say), whose larvae are highly active and never occur with LBF, was an extreme point in this correlation. To evaluate whether this correlation remains when this habitat specialist is excluded, I performed the same partial correlation without this species. With the remaining eight species, which all occur in lakes with LBF, there was a positive relationship between mobility and how frequently a species occurs in habitats with INV ($r = 0.95$, d.f. $= 4$, $P = 0.004$), a negative relationship between activity and occurrence in sites with LBF ($r = -0.92$, d.f. $= 4$, $P = 0.009$, Fig. 3b), and narrowly insignificant positive correlation between mobility and how often a species occurs in habitats where SBF are the top predators ($r = 0.80$, d.f. $= 4$, $P = 0.058$).

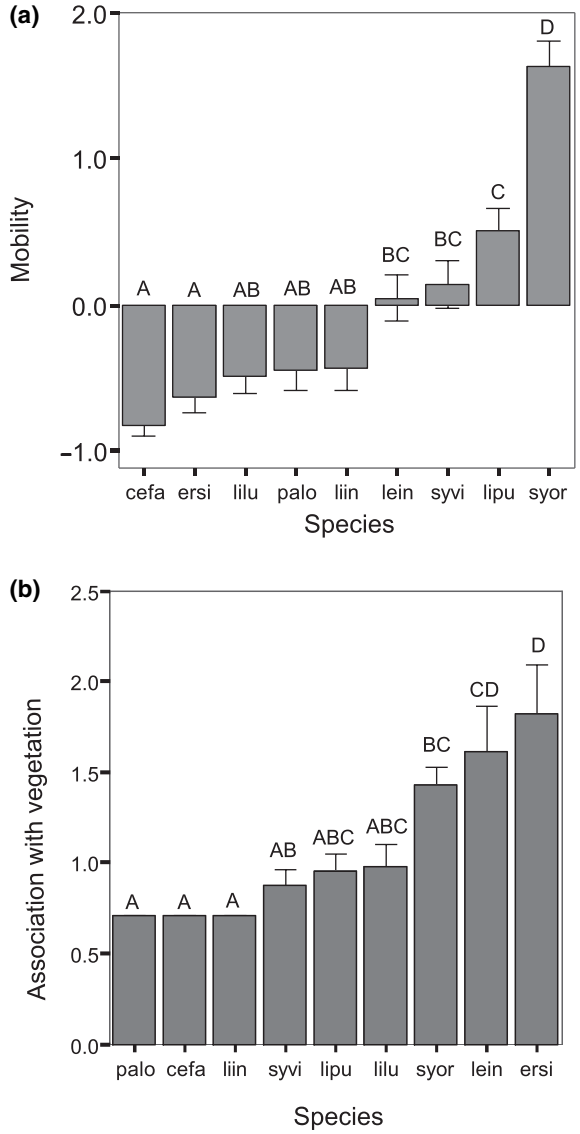

Fig. 1 Results for behavioural observations of nine species of larval libellulid dragonfly. Results presented are (a) species mobility, composite mobility PC-scores based on movement rate and movement distance, and (b) the proportion of observations species associated with artificial vegetation, untransformed data are presented. Species are identified by species codes (Table 1). Bars represent mean ± 1 SE. Bars identified with the same letter do not differ significantly ($P > 0.05$, Tukey's HSD). Note that the order of species differs in parts (a) and (b).

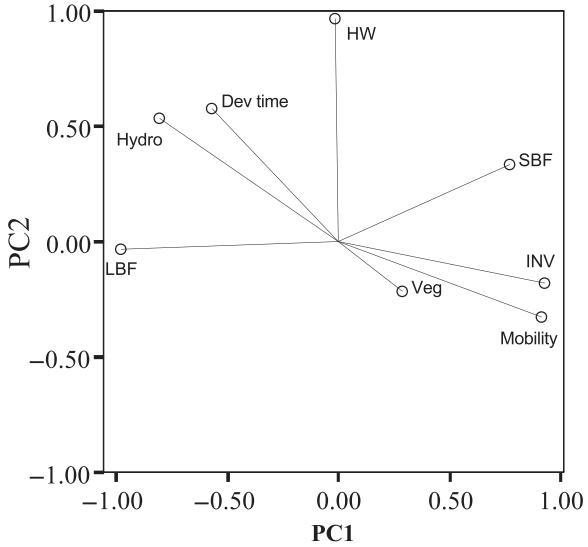

Fig. 2 Loadings of species means of behaviour, habitat distribution, developmental period and body size characteristics on PC1 and PC2 in principal components analysis. Mobility, mean mobility score; Dev time, approximate length of the larval stage in months; HW, larval head-width; Hydro, mean hydroperiod of habitats occupied; INV, proportion of habitats with predatory invertebrates as top predators occupied; LBF, proportion of habitats with large-bodied fish as top predators occupied; SBF, proportion of habitats with small-bodied fish as top predators occupied; Veg, mean number of observations per hour larva was in contact with artificial vegetation (square-root transformed).

Table 2 Factor loadings for varimax rotated PCA

Variable	PC1	PC2	PC3
Mobility	**0.910**	−0.325	−0.074
Associated with artificial vegetation	0.283	−0.210	**0.923**
Development time (months)	**−0.568**	**0.578**	**0.561**
LBF	**−0.982**	−0.033	−0.180
SBF	**0.769**	0.335	0.292
INV	**0.929**	−0.179	0.060
Mean hydroperiod	**−0.805**	**0.537**	−0.142
Larval head-width	−0.013	**0.967**	−0.159

PCA, principal component analysis; INV, predatory invertebrate; SBF, small-bodied fish; LBF, large-bodied fish.
PCA of species behaviour, habitat distribution, life history and body size are the three principal components explained 93.6% of the variation in the data. Variables with factor loadings >0.4 are considered to be strongly correlated with the PC-components (PC1, PC2 and PC3) and are indicated in bold.

Discussion

Species differed in mobility and in their choice of microhabitat. However, only one taxon (*S. obtrusum*/*S. rubicundulum*) differed in its mobility (incorporating both movement frequency and distance) from all other species. The other eight species, rather than forming discrete clusters of active and inactive species, exhibited a gradient of mobility. Similar results were observed in species microhabitat choices, specifically the frequency with which they were in contact with artificial vegetation. In this behaviour, no

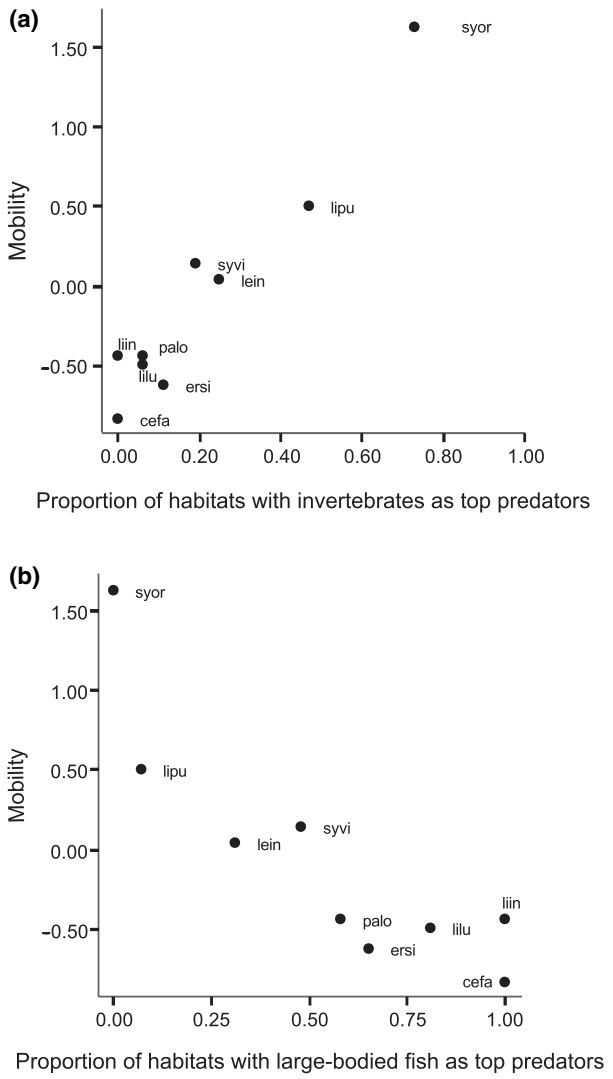

Fig. 3 Relationship between species mobility (PCA scores for the combination of movement frequency and distance) and their distributions across habitats with different top predators. (a) Species mobility and the proportion of habitats with invertebrate top predators that species occupy. (b) The relationship between mobility and frequency of occurrence in habitats with large-bodied fish as top predators. Species are identified using species codes given in Table 1.

species differed from all other species. Species behaviours ranged from those which were never in contact with artificial vegetation (*Pachydiplax longipennis* Bumeister, *C. fasciata*, *Libellula incesta* Hagen) to species that were frequently associated with artificial vegetation (*Leucorrhinia intacta* Hagen, *Erythemis simplicollis* Say), but there were also species whose choice of microhabitat was intermediate and no sharp dichotomy in this behaviour was apparent.

Results from the PCA indicate that species mobility was related with distribution across the permanence–top predator gradient and the duration of the larval stage. Mobility was negatively correlated with how frequently species occurred with LBF, the length of the larval period and mean hydroperiod inhabited, and was positively correlated with how frequently species co-existed with INV and SBF. The partial correlations found that, controlling for hydroperiod and length of the larval stage, the relationship between species distribution across habitats with different top predators and mobility remained. Results from both analyses supported the conclusion that species mobility is related with habitat distribution. The more frequently a species occurred in permanent habitats with LBF, which impose a high predation risk (McCauley, 2007), the less mobile they were. In contrast, species found in ponds with invertebrate top predators and in non-permanent sites were more active. Johansson *et al.* (2006) found similar patterns in 17 species of European odonates, in which there was a negative relationship between activity and their abundance in lakes with fish. I also found that body size (final instar head-width) was not correlated with mobility but was positively associated with the mean hydroperiod occupied and the length of the developmental period. A longer larval period provides more time to grow to a large body size but also requires that the pond retains water throughout the larval lifespan.

Contrasting species that segregate across the hydroperiod–top predator gradient, there are species that correspond to Sih's (1987) slow–fast dichotomy and these species are associated with opposite ends of the habitat gradient. For example, *C. fasciata*, is a 'slow' species which is extremely sedentary and restricted to permanent habitats with LBF. In contrast, the high mobility and rapid development of *S. obtrusum*/*S. rubicundulum*, which frequently occur in temporary habitats and never co-exist with LBF, indicate that these species have a 'fast' life-history and behavioural strategy. However, the mobility of habitat generalists was variable and did not clearly divide into either slow or fast categories.

One of the few studies that compared mobility in habitat specialists and generalists found that generalist *Ischnura* species were consistently more active than larvae of *Enallagma*, a genus containing both species

that co-exist with fish and species restricted to habitats with invertebrate top predators (McPeek, 1996, 2004). Mobility differences between these generalist and specialist coenagrionid larvae determine their vulnerability to predation and are correlated with growth rate differences that together facilitate the co-existence of these generalist and specialist strategies (McPeek, 1996, 2004). In contrast, the mobility of the habitat generalists examined here fell between that of habitat specialists that segregate across the gradient. This continuum of mobility is analogous to patterns observed by Johansson (2000) in six species of odonates, where slow, fast, and also intermediate activity levels were found. In the species of libellulid larvae I observed, this continuum of mobility appears to be strongly related to how frequently species co-exist with either INV or LBF.

If contrasting levels of mobility are favoured at either end of the habitat gradient, what factors might generate the intermediate mobility observed in this study? Plasticity in mobility was expected to be an important part of a habitat generalist's behaviour, allowing it to respond to the presence of different predators. However, in other work I have found little evidence of plasticity in mobility as measured in this experiment. With the exception of *L. pulchella* in the presence of a predatory invertebrate, there was no significant predator-induced change in mobility found in these species (McCauley, 2005). Behavioural plasticity in odonate larvae can take multiple forms and species may show idiosyncratic response patterns. In five species of odonates, Wohlfahrt *et al.* (2006) found that the larvae of only two species exhibited changes in their activity and these changes included one species that decreased activity in response to exposure to three different species of fish and one odonate species which became more active in the presence of one of the three species of fish. However, four of the five odonate species they examined exhibited spatial avoidance of predators (Wohlfahrt *et al.*, 2006), a factor not explored in this study that could be an important part of the behavioural repertoire of habitat generalists. Nonetheless, the baseline mobility of generalists I examined appear to represent the mobility exhibited by these species in the presence of both fish and INV. The mobility of these generalists was intermediate to that of habitat specialists from different ends of the habitat gradient and was correlated with how commonly they occurred in habitats with INV or LBF (Fig. 3). Brodin & Johansson (2004) found differences in larval activity in different families (kin groups) of larval *Coenagrion hastulatum* (Charpentier 1825) and hypothesized that maintenance of genetic variation in activity could be an important mechanism facilitating the use by this species of habitats both with and without fish. Because larvae in my study were drawn from natural habitats, or from artificial ponds colonized by free-ranging adults (*L. pulchella*), the relatedness of individuals in this study cannot be evaluated. However, the correlation between mobility and the extent to which species co-existed with these different predators suggests that intermediate mobility facilitates the use of a broad range of habitats and provides some support for this hypothesis but is not a conclusive test.

Species mobility was strongly related with the current habitat distribution and this was true in intra-and inter-generic comparisons. Species used in this study were from six different genera, with most genera being represented by a single species, and we lack a phylogeny that includes the relationship between all the genera used in this study. Consequently, the role of common evolutionary history in determining the expression of these behaviours can be only partially evaluated and phylogenetic inertia may act as a constraint on the expression of mobility (e.g. Suhling *et al.*, 2005). However, in this system, the contrasts between congeners that were used in these trials did not suggest that phylogeny was a strong determinate of mobility. *Libellula* and *Sympetrum* both had species of differing mobility which were more similar to species in other genera with similar habitat distributions than to their congeners (Figs 1a & 3). This supports the conclusion that mobility is principally related with current habitat distribution. However, one factor negatively related with mobility was the length of the larval period, and in *Sympetrum* this reflects an adaptation to temporary environments: a desiccation resistant over-wintering egg stage. *Sympetrum* must complete larval development more rapidly than species that over-winter as larvae and this is associated with higher mobility. However, the mobility of *Sympetrum vicinum* (Hagen) is more similar to that of *L. intacta*, which has a similar habitat distribution, than to its congeners (*S. obtrusum*/*S. rubicundulum*) suggesting that mobility is strongly moderated by the current habitat distribution.

A result that also emerges from this study is that categorizing habitats as with or without fish may be too simplistic, at least in some contexts. The two major groups of fish present locally are LBF (principally Centrarchidae) and SBF (principally Umbridae but also Cyprinidae), and have different associations with the distribution and mobility of Libellulidae. In the PCA analysis, the extent to which libellulids were associated with habitats where SBF were the top predators was positively correlated with larval mobility, while mobility and coexistence with LBF were negatively correlated. The extent to which species co-existed with either large or SBF was also related to how commonly they were found in habitats where invertebrates are the top predators. Species commonly co-existing with SBF were also often found in habitats with INV as the top predators while species that frequently co-existed with LBF were rarely found in habitats where carnivorous invertebrates are the top predators. Therefore, it appears that for libellulid larvae the critical transition is between habitats with LBF and SBF rather than between habitats with and without fish.

Umbra limi (Kirtland) is the most common SBF found locally in ponds without large fish, and this species will readily consume dragonfly larvae (McCauley, 2007; McCauley, pers. obs.). Consequently, both habitats have fish that will prey on larval dragonflies but the two categories of fish appear to have different functional effects on the dragonfly assemblage. More active species were found in habitats with SBF more frequently than less active species, which were more commonly found in lakes with LBF. Whether ponds with SBF or LBF represent distinct habitat types for other aquatic taxa is not known. However, it is probably that for many aquatic taxa the relevant divisions between habitat types along the permanence–predation gradient will be more complex than fish or no fish, and permanent or temporary. For example, Stoks & McPeek (2003b, 2006) found that species of *Lestes* (Odonata: Zygoptera: Lestidae) segregate along a permanence–predator gradient that can be subdivided into four distinct habitat types, that include habitats with and without fish but also distinguishes temporary habitats based on late or early drying regimes (and their consequences for the INV assemblage). More research incorporating finer scale differences along this gradient, and the relationship of these differences to species distribution, life-history and behaviour, will provide new insights into mechanisms structuring aquatic communities.

While clear patterns emerged in the relationship between species distributions and their mobility, the use of structural complexity in the environment was not clearly related with habitat distribution. No congeners differed significantly in the frequency with which they were associated with artificial vegetation, making it possible that contrasts in this behaviour are strongly constrained by common evolutionary history rather than reflecting adaptation to species' current habitat distributions. Association with vegetation was related only to the length of the larval period, although this pattern was not especially strong. Species that spend approximately 1 year in the larval stage spanned almost the entire spectrum in the frequency with which they associated with artificial vegetation. The use of artificial vegetation was not associated with species distribution across macrohabitat characteristics including the top predator type or hydroperiod. They did not appear to alter their use of artificial vegetation in the face of predation risk (McCauley, unpubl. data). These results suggest that association with structural elements in the habitats are not an important behaviour affecting species sorting across habitats that differ in hydroperiod or top predator type. These results do not support the hypothesis that lower mobility is also associated with increased use of complex microhabitats (Sih, 1987). Results from this study are similar to Johansson's (2000), who found that species differed in microhabitat use but that this was not related with activity.

There was clear evidence that species mobility, but not their use of habitat structure, is related with their distribution in predictable ways. Further, any dichotomy between fast and slow lifestyles (Sih, 1987) is only a part of what generates these different levels of mobility. Many habitat generalist species had intermediate levels of mobility that fell between those of the habitat specialists which segregate with respect to the different top predators. Additionally, habitat generalists appear to resolve the trade-offs between activity, growth rate and predator vulnerability differently than the damselfly habitat generalists that have been studied (e.g. *Ischnura*, McPeek, 1996, 2004). However, future work should explore the digestive physiology of libellulid habitat generalists and specialists which is also important in determining the relationship between activity, growth and predation risk in

damselfly larvae (McPeek, Grace & Richardson, 2001; Stoks & McPeek, 2003a; McPeek, 2004).

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