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THE RELATIONSHIP BETWEEN COMPETITION AND MORPHOLOGY. II. EXPERIMENTS ON CO-OCCURRING DYTISCID BEETLES

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SUMMARY

(1) We performed field experiments at two sites to test for interspecific competition and whether morphologically similar species compete more intensely in assemblages of dytiscid beetles.

(2) In a small acidic ditch where co-occurring species showed patterns of morphology consistent with random assembly of species, feeding rate was unaffected by manipulation of density of adults, and was unrelated to the presence of potential competitors, regardless of body size. Field data indicated that adult *Hydroporus* at this site were not food limited.

(3) Competition for food or cannibalism imposed density-dependent survival on larvae of *Hydroporus* across the natural range of densities. Density-dependent survival among larvae probably kept populations of adults sufficiently low for competition among adults to be minimal.

(4) In a large well-buffered canal where co-occurring dytiscids are more widely and regularly dispersed in morphological space than expected from random assembly of species, increasing density of adults reduced feeding rate; however, there was no effect of differences in body size on intensity of competition. Adults at this site did not appear to be food-limited at natural densities. The observed non-random pattern of morphologies does not seem to be a result of interspecific competition.

INTRODUCTION

Community ecologists have long assumed that there is a strong relationship between morphological similarity and ecological similarity (Hutchinson 1959; Hespenheide 1973; Ricklefs & Travis 1980; James & Boecklen 1984; Moulton & Pimm 1986). Often this assumption has centered on the relationship between body size and prey size (Hutchinson 1959; Pearson 1980; Pacala & Roughgarden 1982, 1985; Greene 1987), but more generally, it is assumed that morphological similarity should lead species to use the same resource in similar ways (e.g. Ricklefs & Travis 1980; James & Boecklen 1984; Findley & Findley 1985; Schiebe 1987). This implies that within a community, morphologically similar species should compete most intensely, and that there may be some critical value of morphological similarity that is just small enough to enable two species to coexist (Horn & May 1977).

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The presumed relationship between resource partitioning and competition has spawned several lines of research. First, it has led ecologists to look for patterns in morphologies of co-occurring species (i.e. over-dispersion of species in morphological space; Ricklefs & Travis 1980; Ricklefs, Cochran & Pianka 1981; Findley & Findley 1985; Moulton & Pimm 1986; Schiebe 1987; Juliano & Lawton 1990), often using null models (Harvey *et al.* 1983; Strong *et al.* 1984) to test for such patterns. Second, it has helped to stimulate experimental tests for food limitation and competition (see Schoener 1983; Connell 1983 for reviews). However, surprisingly few investigators have done both types of studies, and rarely have both types of studies been done on the same system (for one example see Munger & Brown 1981; Bowers & Brown 1982). It is therefore largely unknown whether the two approaches to the issue produce congruent results. It is also uncommon for experimenters to go beyond studies of whether competition occurs, and test whether morphological similarity is related to the intensity of competition (Schoener 1983). Pacala & Roughgarden (1982, 1985) showed that competition was less intense between two species of *Anolis* of different sizes than between two species of *Anolis* of the same size. Moulton & Pimm (1986) found that probability of extinction declined as morphological similarity declined for introduced birds in Hawaii. Although these studies with vertebrates have supported the supposition that morphology and competition are related, the generality of this conclusion remains unknown (Schoener 1986).

In this paper we test for interspecific competition among co-occurring water beetles in the family Dytiscidae at two sites in short-term field experiments. We ask whether competition is less intense between adults of species that differ in size, and compare results from two sites, one where co-occurring dytiscid adults show widely and regularly spaced morphologies consistent with limiting morphological similarity, and one where no such morphological pattern is present.

STUDY SITES AND ORGANISMS

We used two study sites (Juliano & Lawton 1990). Pocklington Canal (Humberside, England) is an unused navigation canal connected to the River Derwent. It is approximately 10 m wide, with steep sides, and is slightly basic. Emergent vegetation at the margins includes *Carex*, *Juncus*, *Sparganium*, and *Glyceria*. All work was done at a site near Bielby, Humberside, where the canal is unshaded by trees.

Skipwith Ditch (North Yorkshire, England) is a small body of water, only 2 m wide, with mosses, grasses, and *Potamogeton* the dominant plants. The ditch flows from a World War II-era runway, where it is buffered by the limestone base of the runway, out onto the Skipwith Common, where soil buffering capacity is low. The site at which these experiments were done (site 3, Juliano & Lawton 1990) is just beyond the runway edge (pH = 4·5). The site is partially shaded by birch.

The two sites have very different dytiscid assemblages. Pocklington Canal has ten species of small dytiscids, of which *Hyphydrus ovatus* (L.), *Hygrotus versicolor* (Schall.), *Hydroporus planus* (Fab.), *H. palustris* (L.), and *Laccophilius hyalinus* (Deg.) are abundant. Ditch site 3 has eleven species, all but one in the genus *Hydroporus*. *Hydroporus gyllenhalii* Sch., *H. erythrocephalus* (L.), *H. palustris* (L.), *H. striola* (Gyll.), and *H. umbrosus* (Gyll.) are common (Juliano & Lawton 1990). Larger dytiscids in the genera *Agabus*, *Ilybius*, and *Dytiscus* occur at both sites.

The small dytiscids studied form both a taxonomic and ecological unit. Many species are often taken together in the same pass of a pond net. All experiments were done with

members of the subfamily Hydroporinae, which consists of small (< 5·5 mm in length) species. Adults are active year-round. Larvae are present and sometimes abundant in summer, and are primarily benthic.

Adults and larvae are predators feeding on microcrustacea and small insects (Leech & Chandler 1956; Pajunen 1983; Nilsson 1986a; Jeffries 1988; personal observations). Size of adults is positively associated with prey size (Lawton & Hassell 1984; Juliano & Lawton 1990), though this relationship is variable. Community studies of dytiscids have primarily involved documenting correlations between assemblage composition and physical variables (e.g. Ranta 1982, 1985; Cuppen 1983, 1986; Nilsson 1984; Larson 1985; Eyre, Ball & Foster 1986). A few investigators have tested for morphological patterns consistent with competition (e.g. Ranta 1982; Lawton & Hassell 1984; Nilsson 1986a) and there has been one laboratory study on feeding ecology of larvae and assemblage composition (Nilsson & Soderstrom 1988). Our study is the first to use field experiments on dytiscid assemblages.

Dytiscid assemblages at the two sites show very different patterns of adult morphology (Juliano & Lawton 1990). Pocklington Canal has seven genera, and species are significantly more widely and regularly dispersed in a multivariate morphological space than randomly formed assemblages (Juliano & Lawton 1990). Ditch site 3 is dominated by one genus (*Hydroporus*), and has species that are not significantly more widely and regularly dispersed in morphological space than randomly formed assemblages (Juliano & Lawton 1990). In fact, species at Ditch site 3 have convergent morphologies, and are closer together in morphological space than random assemblages. These results lead to the following predictions that we test in this paper.

Ditch assemblage

(a) Interspecific competition for food among adults is absent, or if competition is present, it is unaffected by the morphology (specifically, body size) of the competitors.

(b) Other ecological processes limit populations of dytiscids, and reduce the likelihood of competition among adults. We focus on density-dependent interactions among larvae (resource competition or cannibalism) as the most likely alternative process, and predict that density dependence will be strong at this site.

Canal assemblage

(a) Interspecific competition for food among adults is present.

(b) Body size of competing adults influences the intensity of competition; less similar species compete less intensely.

We test these predictions using some of the abundant species at each site. Although we cannot test these predictions for every species in each assemblage, we will determine whether these predictions are accurate for these abundant species. This is necessary, but not sufficient, to establish that competition influences morphology of all species in these assemblages.

METHODS

Ditch assemblage

Laboratory. A preliminary experiment was conducted to determine if mass gain was a reliable indicator of recent feeding rate of adults. Individuals of *H. erythrocephalus*, *H. obscurus* Sturm, and *H. gyllenhalii* were collected at Skipwith Ditch, brought to the

laboratory, blotted dry (they survive well in air), and weighed to the nearest 0·005 mg. Individuals were maintained in 20 ml of dechlorinated tap water containing a wooden cocktail stick as a perch, at 15 °C and 14 h light: 10 h dark. Four feeding regimes were randomly assigned to these beetles: 0, 1, 4 and 10 *Daphnia magna* Straus (> 1·5 mm long, from a laboratory culture) per 2 days. Water was changed every second day, and *Daphnia* replenished. After 14 days, beetles were reweighed.

Field. Because mass change in response to feeding was most dependable in *H. erythrocephalus* (see below), we used it as the target species in a field experiment designed to test for competition for food and the influence of body size on competitive interactions. The experiment was conducted in November 1987. Enclosures were constructed of plastic drain pipe with an internal diameter of 0·20 m (area = 0·03 m^2). Each enclosure was approximately 34 cm tall and had three 2·5 cm holes covered with 0·5 mm nylon net to allow some exchange of water between the enclosure and surroundings. Most invertebrates, including the microcrustacea that are the primary prey of these dytiscids, were unable to pass through this mesh. Thirty-nine enclosures were inserted into the substrate along the margins of the ditch in four spatial blocks (11, 10, 9 and 9 enclosures per block). They extended 4–6 cm above the water.

Immediately after placing the enclosures, the contents of each were collected with a pond net, and all dytiscids were removed. The contents plus all other organisms were returned and allowed to settle for at least 2 days prior to starting the experiment. The number of *Hydroporus* trapped within each enclosure when it was placed provided an estimate of the natural density.

Nine enclosures in each block were randomly assigned one of nine treatments that were combinations of three densities of *H. erythrocephalus* (1, 2 or 4 individuals) and three competitor treatments (alone, *H. gyllenhalii*, or *H. obscurus*). The two competitors differ in size, with *H. gyllenhalii* (mean ± S.E. – mass 3·79 ± 0·02 mg, length 3·6–4·0 mm, $N = 24$) similar in length to *H. erythrocephalus* (mean ± S.E. – mass 5·57 ± 0·18 mg, length 3·7–4·3 mm, $N = 24$), and *H. obscurus* much smaller (mean ± S.E. – mass 2·06 ± 0·05 mg, length 2·8–3·1 mm, $N = 20$). The number of *H. gyllenhalii* added to an enclosure was equal to the number of *H. erythrocephalus* present. The number of *H. obscurus* added was twice the number of *H. erythrocephalus* present, resulting in an approximately equal biomass of competitor species in the two treatments with added competitors. The nine treatments therefore consisted of 1, 2 and 4 *H. erythrocephalus* alone, 1, 2 and 4 *H. erythrocephalus* with 1, 2 and 4 *H. gyllenhalii*, and 1, 2 and 4 *H. erythrocephalus* with 2, 4 and 8 *H. obscurus*, respectively. The extra three enclosures in blocks 1 and 2 were used as closed controls to check for the completeness of removal of beetles prior to the experiment, or for the ability of beetles to enter the enclosures once the experiments had started. No *Hydroporus* were added to these enclosures.

The experiment ended after 2 weeks, when *Hydroporus* were collected, weighed, and measured to the nearest 0·1 mm, together with a sample of free-ranging *H. erythrocephalus* from the vicinity of the enclosures.

We determined mass changes by taking the difference between the summed masses of *H. erythrocephalus* within each enclosure at the beginning and end of the experiment. Mass change per individual was obtained by dividing by the number of individuals present. Because of our method, we could only analyse enclosures in which all the original *H. erythrocephalus* were recovered (see p. 838).

Field samples of free-ranging *H. erythrocephalus* were collected at this site on five dates throughout the autumn and winter of 1987–88, and individuals weighed and measured.

We used these data as an indication of whether free-ranging *H. erythrocephalus* were relatively well fed or relatively poorly fed.

Larvae. An experimental manipulation of density of *Hydroporus* larvae was conducted at Skipwith Ditch in spring of 1988. In order to estimate natural density of larvae we took six samples using a 0·18 × 0·18 m aluminium box sampler. In the experiment we used two sizes of enclosures: the same 0·20-m diameter enclosures used with adults, and smaller 0·11-m diameter enclosures of similar design. These were placed into the substrate in three spatial blocks of thirteen (seven large alternating with six small) along the edges of the site. All adults and larvae of dytiscids were removed by netting, and remaining contents were returned to the enclosures. Counts of larvae removed gave us a second estimate of their natural density. After a minimum of 2 days settling, larval *Hydroporus* were added to the enclosures.

Larvae of *Hydroporus* are very difficult to identify to species (Nilsson 1986b). We therefore did not attempt to identify the experimental animals, except to exclude larvae of *H. erythrocephalus*, which are easily separated by head colour and morphology (Nilsson 1986b). The majority of larvae collected at this site were more 'typical' *Hydroporus*, and probably included *H. gyllenhalii*, *H. palustris*, *H. striola*, and *H. umbrosus*. Larvae fell into two size-classes, large larvae (third instars of the larger species), and small larvae (younger instars and third instars of the smaller species).

Within blocks, large enclosures received five (three enclosures), ten (two enclosures), or twenty (one enclosure) larvae, corresponding to densities of 159, 318, and 637 larvae m^{-2}; small enclosures received five (three enclosures), ten (two enclosures), or fifty (one enclosure) larvae, corresponding to densities of 577, 1155, and 5774 larvae m^{-2}. One small enclosure assigned to receive five larvae inadvertently had eight larvae stocked. Because we used actual density of larvae as a continuous variable in our analysis, we did not delete this mis-stocked replicate. In each enclosure we used equal numbers of large and small larvae (when five larvae were used, we used three small and two large). Within each block, one large enclosure received 0 larvae and served as a closed control to check for incomplete removal, immigration, or hatching of eggs.

After 2 weeks, we collected the contents of the enclosures, and took four samples of the same area as the large enclosures to determine whether natural density of larvae changed greatly over the course of the experiment.

Canal assemblage

Laboratory. A preliminary laboratory experiment with adult *Hygrotus versicolor* was conducted to determine whether body fat content was a better indicator of recent feeding rate than total body mass. Adults were collected in mid-June and housed individually in 50 ml of dechlorinated tap water, with nylon net as a perch, at 15 °C and 14 h light: 10 h dark. Three feeding treatments were given: high food = at least ten *Daphnia magna* per day; low food = one *Daphnia* every 4 days; and no food. Beetles in the high food treatment never ate all ten of the *Daphnia*, and we therefore assumed that this constituted *ad libitum* feeding. Containers were checked daily. Dead beetles were weighed to the nearest 0·0005 mg, measured to the nearest 0·05 mm, and frozen for later fat analysis. The experiment lasted 25 days. At the end of the experiment, all survivors were weighed, measured, and frozen.

Fat was extracted using chloroform: methanol (Herbes & Allen 1983), modified by Juliano (1986). Three blanks (solvent only) were extracted, and the average mass of the blanks was subtracted from each experimental mass. Because *H. versicolor* weigh only

about 4·1 mg, and relative error is greater for smaller masses (Herbes & Allen 1983), we pooled beetles receiving the same treatments into groups of four (in one case five) for fat extraction. Percentage fat was determined based on fresh mass of the beetles.

Field. A field experiment was conducted at the canal in June (the reproductive season) 1988 in order to test for competition for food and for any effects of size differences on the intensity of competition. Enclosures were similar to those used in the ditch, but were larger (large enclosures 0·49 m in diameter; small enclosures 0·15 m in diameter; both approximately 1 m tall). These enclosures were inserted into the soft substrate along the edge of the canal in three spatial blocks, each consisting of four large and four small enclosures. All dytiscids and large predatory insects (e.g. *Notonecta glauca* L.) were removed by netting, and remaining animals and substrate returned to each enclosure. After at least 2 days of settling, experimental animals were added.

The experiment was designed as a randomized complete block, with eight levels consisting of the combination of density (low = large enclosures, high = small enclosures) and the species of beetles added (treatments). The species used in this experiment were *H. versicolor*, the target species (mean ± S.E. mass 4·150 ± 0·026 mg, length 3·31 ± 0·01 mm, $N = 189$), and two competitor species, *Hyphydrus ovatus* (mean ± S.E. mass 14·445 ± 0·659 mg, length 4·60 ± 0·06 mm, $N = 11$), and *Hygrotus inaequalis* (mean ± S.E. mass 3·070 ± 0·057 mg, length 2·89 ± 0·02 mm, $N = 36$). These three species share a similar morphology, all being relatively round-bodied (Juliano & Lawton 1990). The two species used as competitors of *H. versicolor* differ primarily in body size, and we used them to test the hypothesis that size differences affect competition.

Four treatments were used at both low and high densities: (i) eight *H. versicolor* per enclosure (abbreviated V8); (ii) double the density, with sixteen *H. versicolor* (V8/V8); (iii) double the density (by biomass), using eight *H. versicolor* and ten *H. inaequalis* (V8/I10); and (iv) double the density (by biomass) using eight *H. versicolor* and two *H. ovatus* (V8/O2). Within a block, large and small enclosures were arranged alternatively, with combinations assigned at random to enclosures of a given size.

After 25 days, all surviving beetles were weighed, measured, and frozen for fat analysis, together with a sample of free-ranging *H. versicolor* collected near each block. All *H. versicolor* from a given replicate were extracted as a group, and proportion of fat determined based on combined fresh mass.

Fat content was analysed using analysis of variance and a priori orthogonal contrasts (Rosenthal & Rosnow 1985) on arcsin–square root transformed proportions. First, if experimental manipulation affected feeding rate, we predicted that the free-ranging control group should differ from the combined mean for all enclosed replicates (natural vs. experimental, two-tailed). Second, if increased density led to competition for food, we predicted that fat content in low density replicates should be greater than that in high density replicates (low vs. high density, one-tailed). Within a density group, if doubling the density led to competition for food, we predicted that fat content for treatment V8 should be greater than the average for treatments V8/V8, V8/I10, and V8/O2 (competition, one-tailed). Within a density group, if the intensity of interspecific competition differed from the intensity of intraspecific competition, we predicted that fat content for treatment V8/V8 should differ from the average for treatments V8/I10 and V8/O2 (intra- vs. interspecific, two-tailed). Finally, within a density group, if a competitor of a different size has a lower competitive effect than a competitor of the same size, we predicted that fat content for treatment V8/O2 should be greater than that for treatment V8/I10 (size of competitor, one-tailed).

TABLE 1. Analysis of variance for weight gain of *Hydroporus* under different laboratory feeding regimes: (a) analysis of variance, $r^2 = 0{\cdot}399$; (b) Multiple comparisons of main effect means. Means within each main effect followed by the same letter are not significantly different (Tukey's HSD, experiment-wise alpha = 0·05)

(a) Effect	d.f.	*F*	*P*
Feeding	3	5·20	0·0031
Species	2	5·64	0·0059
Feeding × Species	6	1·49	0·1969
Error	56		

(b) Main effect	Group	Mean ± S.E.	(*N*)	
Feeding	0 *Daphnia*/2 days	−0·007 ± 0·030	(17)	a
	1 *Daphnia*/2 days	0·114 ± 0·036	(17)	ab
	4 *Daphnia*/2 days	0·162 ± 0·048	(17)	b
	10 *Daphnia*/2 days	0·176 ± 0·036	(17)	b
Species	*H. erythrocephalus*	0·190 ± 0·043	(24)	a
	H. obscurus	0·071 ± 0·021	(20)	b
	H. gyllenhalii	0·066 ± 0·030	(24)	b

RESULTS

Ditch assemblage

Laboratory. Feeding regimes significantly affected mass gain in the *Hydroporus* species tested (Table 1). The species differed in the amount gained (Table 1), but there was no significant interaction between species and feeding regime, indicating that all species were affected in approximately the same way. *Hydroporus* gained mass even when given but one *Daphnia* per 2 days (Fig. 1). *H. erythrocephalus* showed the strongest and most consistent response to feeding regime (Fig. 1). These results indicate that mass change is a good indicator of recent feeding history.

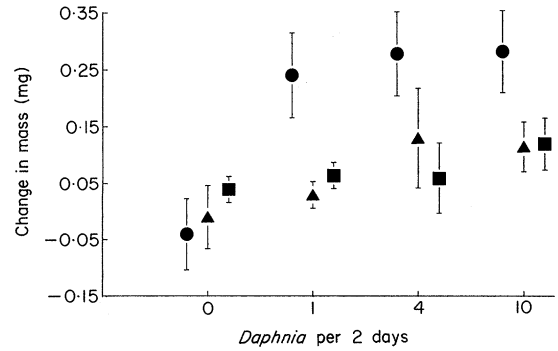

FIG. 1. Change in mass (mean ± S.E.) as a function of feeding regime for *Hydroporus* species in the laboratory experiment: for *H. erythrocephalus* (●) and *H. gyllenhalii* (▲), $N = 6$; for *H. obscurus* (■) $N = 5$.

TABLE 2. Analysis of variance for the effects of density and competitor on weight gain of *H. erythrocephalus* in the Skipwith Ditch field experiment; $r^2 = 0{\cdot}414$

Effect	d.f.	*F*	*P*
Block	3	3·05	0·0555
Density	2	0·03	0·9683
Competitor	2	0·64	0·5374
Density × Competitor	4	0·79	0·5438
Error	18		

Field. The natural density of *Hydroporus* was (mean ± S.E.) 1·82 ± 0·37 per enclosure ($N = 39$). This estimate indicates that densities used in the experiment ranged from about half natural density to about six times natural density (based on number of individuals). Thus, the densities used in the experiment span natural densities.

Although three closed control enclosures yielded no beetles at the end of the experiment, a total of seventeen contaminant beetles (71% of which were *H. umbrosus*, *H. tristis* (Pay.), and *H. neglectus* Sch., three small species) were recovered from eleven enclosures, indicating that either preliminary removals were incomplete or that enclosures were leaky. All of the introduced *H. erythrocephalus* were recovered from thirty-one of the thirty-six enclosures. In one enclosure an extra *H. erythrocephalus* was recovered. Mass gain for *H. erythrocephalus* in the enclosures was analysed in two ways, either using enclosures in which all *H. erythrocephalus* were recovered and omitting the enclosure with the extra *H. erythrocephalus* ($N = 30$ enclosures) or using only those enclosures in which all *H. erythrocephalus* were recovered and no extra beetles of any species were recovered ($N = 20$ enclosures). Conclusions were identical for both analyses, and we report only the results from the former.

There were no significant effects of density, competitor, or interaction in this experiment (Table 2), indicating no evidence of competition for food among adults. *H. erythrocephalus* in these enclosures tended to gain mass (Fig. 2), with an average gain across all enclosures of 0·33 mg. There is no apparent pattern in the treatment means (Fig. 2). In the absence of competitive interactions, the question of the effect of similarity of the added species becomes irrelevant. Least squares mean mass (adjusted for length) of free-ranging *H. erythrocephalus* collected outside the enclosures at the termination of the experiment was not significantly different from that of the beetles in the enclosures (Table 3), indicating comparable feeding rates for experimental vs. free-ranging beetles. Weight gains for *H. erythrocephalus* in the field experiment were similar to those observed in the laboratory at high food levels (compare Figs 1 and 2).

Data from field-collected *H. erythrocephalus* provide further support for the high feeding rate of natural populations (Fig. 3). Analysis of covariance, with log(length) as the covariate, shows that field-collected beetles taken at five times through autumn and early winter differ significantly in log(mass) (Date effect, $F_{4,99} = 6{\cdot}84$, $P = 0{\cdot}0001$). Weight increased rapidly in October and November, with stable body masses thereafter. The change in least squares mean mass from October to November is again 0·3–0·4 mg, consistent with weight gains for well-fed laboratory animals.

Experiments on adult *Hydroporus* at Skipwith Ditch consistently indicate that adults are well fed and that competition for food among adults does not occur, at least over the time-scale examined. This suggests that the population of adults is not greatly influenced

TABLE 3. Analysis of covariance comparing log (mass) of *H. erythrocephalus* from Skipwith Ditch enclosures to that for free-ranging *H. erythrocephalus* collected at the same time. $r^2 = 0{\cdot}758$. *F*-test for homogeneity of slopes for the two groups was not significant ($P \gg 0{\cdot}10$). Least squares means, adjusted for log (length), represent back-transformed values

Effect	d.f.	*F*	*P*
Log (length)	1	290·64	0·0001
Enclosed vs. free-ranging	1	0·22	0·6424
Error	93		
	Least square mean (mg)	±S.E.	*N*
Enclosed	5·61	5·56–5·66	77
Free-ranging	5·66	5·56–5·76	19

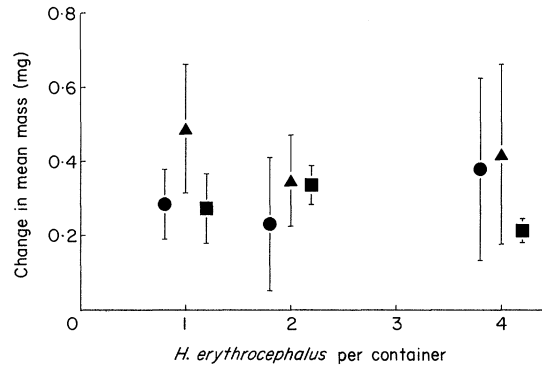

FIG. 2. Change in mean mass (mean ± S.E. among replicate enclosures) for *Hydroporus erythrocephalus* alone (●) and with *H. gyllenhalii* (▲) and *H. obscurus* (■) in the Skipwith Ditch experiment.

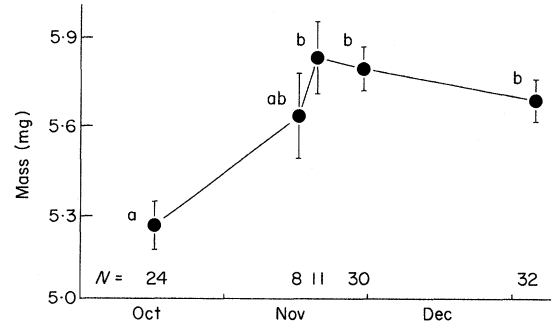

FIG. 3. Mass (least squares mean ± S.E.) of field-collected *Hydroporus erythrocephalus* at Skipwith Ditch during autumn and winter 1987–88. Least squares means are back transformed from analysis of covariance on log (mass) with log (length) as a covariate. Least squares means associated with the same letter are not significantly different (Bonferroni multiple comparisons, experiment-wise alpha = 0·55).

TABLE 4. Mean ± S.E. densities of *Hydroporus* larvae (m^{-2}) estimated during clearing of Skipwith Ditch enclosures prior to experimental manipulation of density of larvae. Combined block means followed by the same letter are not significantly different (Tukey's HSD, family alpha = 0·05)

	Enclosure size		
	Large ($N=7$)	Small ($N=6$)	Combined block mean
Block			
1	123 ± 24	173 ± 71	147 ± 34 a
2	556 ± 62	385 ± 83	477 ± 55 b
3	636 ± 138	289 ± 98	476 ± 97 b
Combined size mean	438 ± 70 a	282 ± 50 b	

by food supply, but leaves unanswered the question of what does determine the population size of adult *Hydroporus* species at this site. The experimental study of interactions among larvae provides an answer to this question.

Larvae. Based on preliminary samples, estimated natural density of *Hydroporus* larvae (mean ± S.E.) was 641 ± 85 m^{-2} ($N=6$); clearing the enclosures provided additional estimates (Tables 4). Analysis of variance of these density estimates revealed significant effects of enclosure size ($F_{1,33}=4·77$, $P=0·0361$) and block ($F_{2,33}=8·80$, $P=0·0009$). Interaction was not significant ($F_{2,33}=2·58$, $P=0·0912$). The block effect indicates that there is considerable spatial variation in density of larvae. The size effect indicates that the area of the sample influences estimated density. Estimates from large enclosures in blocks 2 and 3 were comparable to the preliminary estimates of 641 m^{-2} obtained using the box sampler, which sampled nearly the same area as the large enclosures (0·032 m^{-2} and 0·031 m^{-2}, respectively). At the end of the experiment, estimated natural density of larvae was 462 ± 118 m^{-2} ($N=4$). Experimental densities ranged from 159 m^{-2} to 5774 m^{-2}, and therefore extend from the lowest naturally observed mean density to aproximately 10 × the highest naturally observed mean density.

The three closed control enclosures yielded 0, 1 and 0 *Hydroporus* larvae at the end of the experiment. These same enclosures yielded 3, 18 and 45 larvae, respectively, when the enclosures were cleared of larvae; i.e. 98% of larvae in these enclosures (65 out of 66) were removed. This indicates that the enclosures were effective at keeping larvae out, that there was no hatching of *Hydroporus* eggs within the enclosures, and that the initial clearing of the enclosures removed virtually all larvae.

Logistic regression (see Trexler, McCulloch & Travis 1988) of proportion surviving vs. log(density) of larvae indicates a significant effect of density on probability of surviving ($\chi^2=26·59$, d.f. = 1, $P<0·0001$). Block × log(density) interaction was not significant ($\chi^2=0·04$, d.f. = 2, $P \gg 0·10$). A significant block effect ($\chi^2=14·88$, d.f. = 2, $P<0·0001$) indicates that baseline survival probabilities vary among the blocks. Although the logistic regression fits a sigmoid curve to the data, the relationship of survival to density appears to be nearly linear across the densities used in this experiment (Fig. 4), which themselves span the range of natural densities. In other words, there is good evidence that some sort of density-dependent effect typically influences survival of these larvae.

The simplest logistic model (block, log(density)) resulted in a significant likelihood ratio ($\chi^2=108·22$, d.f. = 32, $P<0·0001$), implying significant lack of fit. We attempted to

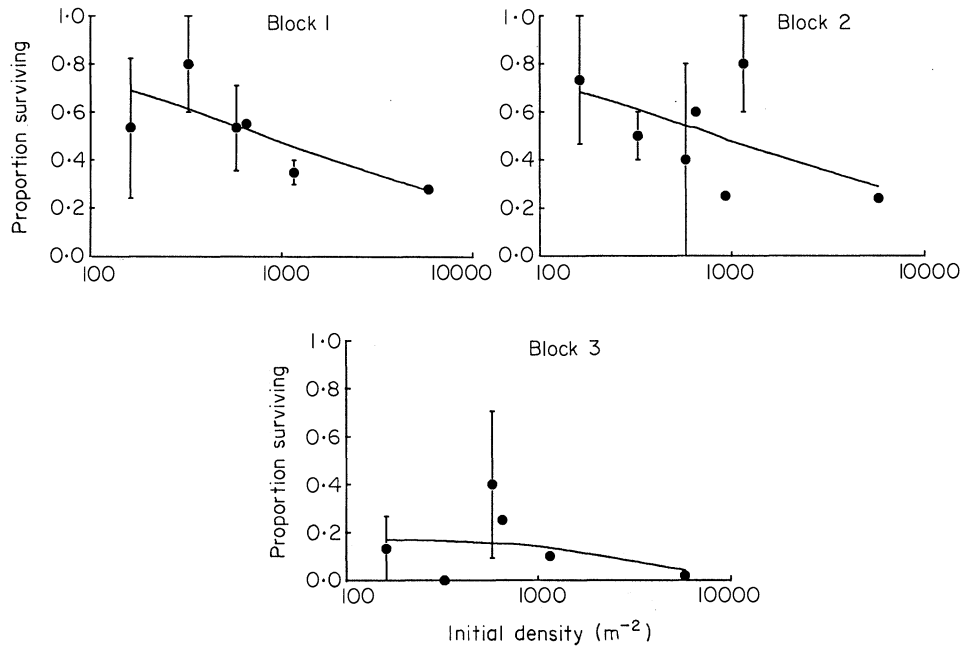

FIG. 4. Proportion of *Hydroporus* larvae surviving (mean ± S.E.) after 2 weeks in experimental enclosures at Skipwith Ditch as a function of density. Curves estimated by logistic regression (SAS Institute Inc. (1987), procedure CATMOD).

improve the fit of the model by including the pre-experiment density of larvae (i.e. the density estimated during clearing of the enclosures). High pre-experiment densities of larvae may, for example, indicate high local food availability. Log of pre-experiment density had no significant effect on proportion surviving ($\geqslant 0{\cdot}10$), and addition of this factor did not improve lack of fit. Size of enclosures was also not significant ($P \geqslant 0{\cdot}10$). Figure 4 indicates that the data were widely scattered about the predicted logistic regression, but does not indicate a systematic departure of the data from the regression. Whatever additional factors may influence probability of survival for larvae of *Hydroporus*, it seems clear that increasing density reduces probability of survival.

The conclusions from these data on *Hydroporus* at the Skipwith Ditch site are that competition among adults is unlikely and that adults in nature seem to be very well fed. Some type of density-dependent interaction influences survival of larvae, and the effect is demonstrable within the range of densities occurring naturally at this site.

Canal assemblage

Laboratory. Feeding regime significantly affected survival of *Hygrotus versicolor* in the laboratory (survival analysis, $\chi^2 = 9{\cdot}71$, d.f. $= 2$, $P = 0{\cdot}0078$). Beetles receiving the high food regime had nearly 100% survival, whereas beetles receiving the low or no food regimes suffered high mortality (Fig. 5).

Feeding also affected fat content ($F_{2,9} = 14{\cdot}95$, $P = 0{\cdot}0014$). *H. versicolor* receiving high food had a significantly greater fat content than those receiving either low or no food, although those receiving low and no food did not differ (Tukey's HSD, experiment-wise alpha $= 0{\cdot}05$; Fig. 6).

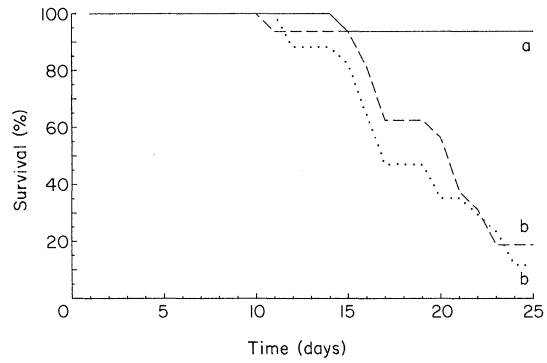

FIG. 5. Survivorship of *Hygrotus versicolor* on three feeding regimes in the laboratory: (——) high ($N=16$); (– – –) low ($N=16$); (· · · · ·) none ($N=17$). Survivorship curves associated with the same letter are not significantly different (experiment-wise alpha = 0·05).

Comparison of these experimental animals with free-ranging animals from the canal indicated that free-ranging animals did not differ from the high food group, but did have significantly greater fat content than the low or no food groups (Dunnett's test, experiment-wise alpha = 0·05; Fig. 6). It thus appears that *H. versicolor* at the canal site should be sufficiently well fed to have high survival, and are probably not food-limited, at least during the summer breeding season.

Field. Twelve large enclosures yielded a total of twenty-six small dytiscids (five species). Mean ± S.E. total fresh mass of beetles removed from the large enclosures was 13·59 ± 4·94 mg (range 0–58·97 mg). By comparison, the lowest density of beetles used in the experiment (treatment V8 at low density) had an estimated fresh mass of 33·20 mg per large enclosure. Thus, by biomass, even the lowest density used in the experiment may be over twice the apparent natural density.

Recovery of *H. versicolor* from the field experiment was high in most cases (Table 5). Analysis of variance indicated no significant effect of density ($F_{1,14}=0·07$, $P=0·7900$),

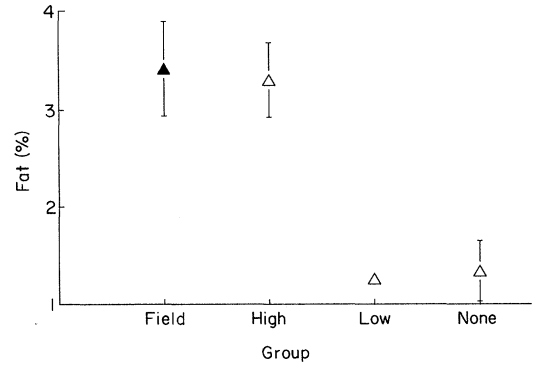

FIG. 6. Fat content (mean ± S.E. % fresh mass) for *Hygrotus versicolor* on three laboratory feeding regimes (△, $N=4$ replicate groups), and field-collected from Pocklington Canal (▲, $N=3$ replicate groups).

TABLE 5. Recovery of *H. versicolor* from the field experiment enclosures at Pocklington Canal. Reported are the number and percentage of beetles recovered from each enclosure, and means by treatment. Of 240 beetles placed into enclosures, 165 (69%) were recovered

Density	Treatment (see text)	Block I N	Block I %	Block II N	Block II %	Block III N	Block III %	Mean (S.E.)	Overall percentage
Low	V8	8	100	6	75	3	38	5·7 (1·5)	71
	V8/V8	15	94	10	63	9	57	11·3 (1·9)	71
	V8/I10	8	100	0	0	3	38	3·7 (2·4)	46
	V8/O2	8	100	5	63	6	75	6·3 (1·0)	79
High	V8	6	75	6	75	7	88	6·3 (0·3)	79
	V8/V8	10	63	9	57	10	63	9·7 (0·6)	60
	V8/I10	7	88	5	63	8	100	6·7 (1·0)	83
	V8/O2	6	75	5	63	5	63	5·3 (0·6)	67

treatment ($F_{3,14}=0{\cdot}25$, $P=0{\cdot}8586$), or interaction ($F_{3,14}=1{\cdot}48$, $P=0{\cdot}2641$). Thus, there is no evidence that density of conspecifics or interspecific competition influenced survival of *H. versicolor*.

In contrast to survival, analysis of variance for fat content of *H. versicolor* from the enclosures and of free-ranging *H. versicolor* indicated that density had a significant effect on fat content (Table 6, Fig. 7), and hence, feeding rate. There was no significant difference between free-ranging *H. versicolor* and the *H. versicolor* from the enclosures (Table 6, Fig. 7), suggesting that feeding rates in the enclosures were, on average, roughly comparable to natural feeding rates. *H. versicolor* from the low density enclosures had higher fat contents than did *H. versicolor* from the high density enclosures (Table 6, Fig. 7), suggesting lower feeding rates at higher densities. However, the actual percentage fat for high-density treatments (means between 3·16% and 3·95%, Fig. 7) is similar to well fed beetles in the laboratory (compare Figs 7 and 6). The difference due to density is rather small compared to the differences associated with very low vs. very high feeding rates.

Within the low-density enclosures, there was no significant differences due to the doubling of density, due to adding *H. versicolor* vs. adding other species, and due to adding different sized species (Table 6). Thus, for low-density enclosures, there is no evidence for competitive interactions. Among the high-density enclosures the pattern was similar, indicating that despite the fact that higher densities appear to lead to reduced feeding rates, whether the higher density is due to more conspecifics, more similarly sized congenerics, or more individuals of a distantly related, larger species is unimportant. In other words, there is no evidence for a difference in the strength of inter- vs. intraspecific competition, and no evidence for differential competitive effects based on morphological similarity.

DISCUSSION

It is clear from this study that the absence of a statistically significant pattern of overdispersed morphologies does not necessarily indicate that competition is absent, and

TABLE 6. Analysis of fat content for *H. versicolor* in the Pocklington Canal experiment: (a) analysis of variance on arcsin-square root transformed data; (b) orthogonal linear contrasts. 'Natural' indicates free-ranging *H. versicolor* collected at the end of the experiment near each of the spatial blocks. Other abbreviations as in Fig. 7. One-tailed contrasts were used whenever appropriate (see text)

(a) Effect	d.f.	*F*	*P*
Block	2	1·49	0·2569
Group	8	1·34	0·2955
Error	15		

(b) Contrast	*t*	*P*	
Natural–experimental	−0·95	0·3576	2-tailed
Low–high density	2·27	0·0191	1-tailed
Low density			
V8–V8/V8, V8/I10, V8/O2 (competition)	0·87	0·2000	1-tailed
V8/V8–V8/I10, V8/02 (intra- vs. inter-)	−0·68	0·5092	2-tailed
V8/O2–V8/I10 (size of competitor)	0·17	0·4335	1-tailed
High density			
V8–V8/V8, V8/I10, V8/O2 (competition)	1·39	0·0919	1-tailed
V8/V8–V8/I10, V8/O2 (intra- vs. inter-)	1·14	0·2710	2-tailed
V8/O2–V8/I10 (size of competitor)	−0·10	0·5438	1-tailed

that the presence of a statistically significant pattern of overdispersed morphologies does not necessarily indicate that present-day interspecific competition has caused the pattern. In the ditch assemblage, there is no evidence for limiting similarity among adult *Hydroporus* (Juliano & Lawton 1990) and, as expected, there is no evidence for

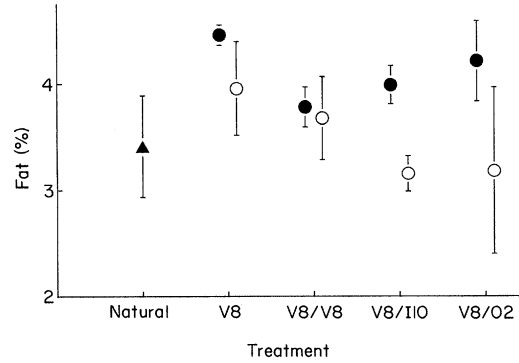

FIG. 7. Fat content (means ± S.E.% fresh mass) for *Hygrotus versicolor* at low (●) and high (○) densities in the Pocklington Canal experiment. Natural = free-ranging *H. versicolor*, V8 = 8 *H. versicolor*/enclosure, V8/V8 = 16 *H. versicolor*/enclosure, V8/I10 = 8 *H. versicolor* + 10 *Hygrotus inaequalis*/enclosure, V8/O2 = 8 *H. versicolor* + 2 *Hyphydrus ovatus*/enclosure. $N = 3$ replicates, except for low density V8/I10, where $N = 2$.

competitive effects acting on adults of one common member of this assemblage, *H. erythrocephalus*. However, there is good evidence for competition or density-dependent cannibalism among *Hydroporus* larvae. Although it is unknown whether interactions among *Hydroporus* larvae have any community-level effects (e.g. certain species are excluded from sites occupied by other species), it is clear that competitive interactions may have major effects on *Hydroporus* populations. Between the lowest and highest naturally observed densities of larvae, survivorship over a 2-week period declined from nearly 70% to about 45%. Density-dependent survival may provide a potent regulatory mechanism for *Hydroporus* populations, and appears to result in adult populations too low for competition among adults to be important.

Experiments with *H. versicolor* in the canal show that food limitation among adults is unlikely at natural densities, although it is possible at higher densities. Although we detected no effects on survival, we found small differences in the fat content of adults between density treatments. It is clearly advantageous to use some index of feeding rate in competition experiments: feeding rate of individuals responds sooner than population dynamics (survival, reproduction). However, even when we created an experimental situation where competition could be detected as a reduction in body-fat levels in high density treatments, there was no effect of body size of a competitor on the results. This result is not consistent with the argument that competition among adults underlies the overdispersion of adult morphologies at this site (Juliano & Lawton 1990). Many authors have noted that most natural community patterns are consistent with more than one explanation (e.g. Simberloff & Boecklen 1981). Our study suggests that the most obvious (or popular) explanation may not be the correct one.

Our results raise at least two questions about dytiscid assemblages. First, what if anything, does cause overdispersion of morphologies at Pocklington Canal? Predation has been proposed as another ecological process that can produce such patterns (Ricklefs & O'Rourke 1975; Jeffries & Lawton 1984; Juliano & Lawton 1990). Dytiscid adults are preyed upon by fish (Leech & Chandler 1956) and by large aquatic invertebrates such as *Notonecta* (Giller 1986), both of which are common at the canal. Insectivorous fish are absent at Skipwith Ditch and other small bodies of water in the study area (Juliano & Lawton 1990). However, we know of no evidence linking dytiscid morphology to vulnerability to predation, and no evidence that these predators have a major impact on dytiscid populations, although fish predation has been shown to affect populations and communities of aquatic insects in general (e.g. Crowder & Cooper, 1982; Flecker 1984).

A second unanswered question about the canal assemblage is whether competition may be important among larval dytiscids. Larvae of small dytiscids are always rare at this site. Larvae of *Hyphydrus ovatus*, the largest species, are present in summer, but are always taken in lower numbers than adults. Larvae of *Hygrotus* and *Hydroporus* are extremely rare. It is possible that larvae occupy positions in the habitat (e.g in the substrate, or in deep water) where they are not easily sampled, or that most successful development of small dytiscids occurs in a few favourable places along the canal, and that adults occupy the whole canal by dispersing from these reproductive hot spots. Until the larvae are located, it is impossible to determine whether competitive interactions among larvae are important in the canal.

Wilson (1975) predicted that resource partitioning based on size should be rare among small predatory arthropods. In general, this has proved true, although there are several suggestive cases involving carabid beetles (Zant, Poulson & Kane 1978; Spence 1979; Pearson & Mury 1979; Pearson 1980). Our failure to discover significant effects of body

size on competitive interactions in small dytiscids supports Wilson's prediction, but only if these dytiscids can be shown to partition resources in some way other than by size. Wilson (1975) also predicted that competitive hierarchies, with larger species competitively dominant over smaller species, should be the rule for small predatory arthropods. Our experiment at the canal site provides no support for this prediction. There was no evidence that *H. ovatus* had a major competitive impact on the smaller *H. versicolor*, even at high densities where a general competitive effect was detectable.

The possibility remains, of course, that if we had chosen to study in detail other target species from these assemblages, we may have obtained different results. It is nevertheless true that failure to detect specific body-size effects on competition weakens, but does not yet completely refute, such effects as an explanation for the structure of dytiscid assemblages.

It is tempting to conclude that morphological patterns within assemblages are unreliable even as a means of generating hypotheses for experimental testing. We feel, however, that this conclusion would be wrong. Morphological patterns in several studies have provided direction for experimental work (e.g. Pacala & Roughgarden 1982, 1985; Munger & Brown 1981). A more appropriate interpretation is that non-random morphological patterns can result from a variety of processes. Understanding how natural assemblages are structured requires both a search for patterns and experimental tests of explanations of those patterns.

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