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MECHANISMS AND CONSEQUENCES OF INTERSPECIFIC COMPETITION BETWEEN TWO STREAM INSECTS

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SUMMARY

(1) Grazing larvae of the net-veined midge, *Blepharicera micheneri*, and filter-feeding larvae of blackflies, primarily *Simulium virgatum*, occupy rock surfaces in fast-flowing water in Rattlesnake Creek, California, U.S.A. Based on observations of aggressive behaviour by *Simulium* toward *Blepharicera*, we conducted a series of field experiments to determine the presence, mechanisms and consequences of competition for attachment space between these two dipteran insects.

(2) There was an inverse relationship between abundances of the two taxa, and when *Simulium* was removed from natural substrates, blepharicerid densities increased. Despite blackfly aggression, co-occurrence was common. To estimate the cost of co-occurrence, we measured behavioural, feeding and fitness responses of blepharicerid larvae to manipulated simuliid abundances.

(3) *Simulium* caused *Blepharicera* to spend $5 \times$ more time in avoidance responses than when alone, resulting in a 20% reduction in time spent feeding. Distance travelled was also increased by simuliid interference. The interactions were strongly asymmetrical in favour of *Simulium*, being reversed only when *Simulium* was much smaller than *Blepharicera*.

(4) Diatom ingestion by *Blepharicera* was reduced 60% by the presence of *Simulium*. In mesocosms adjacent to the stream, blackflies inhibited the growth of blepharicerids and increased mortality and time to pupation, resulting in decreased blepharicerid production.

(5) *Baetis* mayflies and higher *Blepharicera* density also tended to inhibit blepharicerid growth, probably via exploitative competition, but these effects were secondary to interference competition with *Simulium*.

(6) The importance of interspecific competition varies within and between years, because *Blepharicera* and *Simulium* co-occur for a longer period in years of high rainfall, but may not overlap in dry years. Both taxa depend upon flood disturbance to open space and reduce competition from other taxa (macroalgae and the caddis *Hydropsyche oslari* Banks). Contrary to prevalent conceptions, competition in streams may be a common and important factor structuring populations and communities, while disturbance determines the form of interspecific competition rather than eliminating it.

INTRODUCTION

Much of the debate concerning the importance of interspecific competition in determining patterns of animal community organization centres on the frequency that competition

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is expressed. One view holds that competition is an omnipresent force driving past evolution and present distributions of populations (Schoener 1982) vs. the opposing view that predation and/or physical harshness tend to keep populations at sufficiently low densities that competition between species is rare, or intermittent (Wiens 1977; Connell 1983; Grant 1986). To test these ideas adequately requires not only the identification of contested resources and the mechanisms by which species compete, but also evidence that significant consequences exist over time for population distributions and/or reproductive output. Organisms which compete for space should provide clearer tests of competitive effects than those which share both space and food (Roughgarden 1986). But even with this single contested resource, it is instructive to consider the effects of competition not just for those animals which have been competitively excluded, but also for those which continue to co-occur in close proximity (den Boer 1985).

In stream communities, physical factors (e.g. substrate type, current speed, flood scour) may set the template for the structure of biotic assemblages (Edington 1968; Rabeni & Minshall 1977). Within this context, interspecific competitive interactions are quite common, with stream taxa apparently competing for food (e.g. Malas & Wallace 1977; Nilsson & Otto 1977; McAuliffe 1984b; Hawkins & Furnish 1987; Dudley & D'Antonio 1990) and space (Harding & Colbo 1981; McAuliffe 1984a; Hart 1985; Dudley, Cooper & Hemphill 1986; Hemphill 1988; Hershey & Hiltner 1988). Interactions may be common because densities are often high with a large overlap in use of both resources by potential competitors. The actual mechanisms of competition (interference vs. exploitation vs. pre-emption of space) are seldom identified, often because of the difficulty in quantifying resources that are shared (e.g. space and food for semi-sessile and/or filter-feeding taxa). Only McAuliffe (1984b) has clearly isolated competitive mechanisms: exploitative reduction of periphyton by a caddisfly led to reduced abundances of grazing mayflies (cf. Hart 1986, 1987a for examples of intraspecific exploitative and interference competition).

The observation of competitive interactions does not, however, prove that such interactions have important consequences for individuals, populations, and stream communities. Intraspecific competition can inhibit growth of grazing (Hart 1987a; Lamberti, Feminella & Resh 1987; Hill & Knight 1988) and predaceous (Cooper 1984) invertebrates, but similar fitness consequences have not been assessed for interspecific competitors. Likewise, local competitive effects need to be studied in a manner which will allow extrapolation to their impacts on population and community structures, and among a range of patch types occupied by competitors (Schmitt 1985).

The larvae of net-winged midges (Blephariceridae) and of blackflies (Simuliidae) inhabit rock surfaces in swift-flowing sections of small streams. Blepharicerids scrape diatoms and other periphyton from these substrates, while blackflies filter food particles from the water column. Despite differences in their feeding habits, the restricted habitat preferences of these two insects can cause them to encounter each other frequently, e.g. Gibo (1964) described simuliids as sharing the same habitat as, but outnumbering, blepharicerid larvae. Blackfly larvae interact aggressively with conspecifics and other taxa (Gersabeck & Merritt 1979; Harding & Colbo 1981; Wiley & Kohler 1981; Hart 1987b), although they are competitively subordinate to a common net-building caddis larva (Hemphill 1988). In this study we examined behavioural interactions between blepharicerids and simuliids, and test the consequences of competition for growth and reproductive potential of blepharicerids.

STUDY SITE AND ORGANISMS

Rattlesnake Creek (34°27'30''N, 119°41'10''W) is a second order coastal stream draining *c.* 8.2 km² of the Santa Ynez Mountains in southern Santa Barbara County, California, U.S.A. The study section runs through sandstone–shale deposits at *c.* 325 m above sea level. The stream has a well-developed riparian canopy (alder, *Alnus rhombifolia* Nutt.; bay, *Umbellularia californica* (H. and A.) Nutt.; live oak, *Quercus agrifolia* Nee.; willow, *Salix* spp.; sycamore, *Platanus racemosa* Nutt.) and dense chaparral upslope. Discharge is highly variable, with high flows (< 100–> 1500 l s⁻¹) occurring during the wet season (Nov.–March) and baseflow is *c.* 1–5 l s⁻¹ or absent in late summer and autumn. The gradient through the study reach is *c.* 5%, mean bed width *c.* 2–3m, and morphometry is primarily determined by large boulders (> 1 m diameter) and trees. During low flows the stream consists of broad pools connected by narrow riffles or falls flowing over cobble and boulders. The fast-flowing sections in which our study was conducted comprised roughly 5% of the stream length at this site. Further descriptive information is given in Cooper, Dudley & Hemphill (1986).

The larvae and pupae of the family Blephariceridae are found on smooth rock surfaces in fast-flowing water, in splash zones and at the base of waterfalls (Gibo 1964; Hogue 1973, 1983). Larvae are dorso-ventrally flattened, and bear six ventromedial hydrostatic sucking discs (one on each distinctly widened body division). This allows feeding on periphyton (mostly diatoms) while moving slowly on rocks in fast water. Pupation occurs in the same microhabitat as larval feeding, except that pupae are rarely found in water deeper than *c.* 1 cm.

Blepharicerids appear to have a univoltine life cycle. They survive summer and autumn in the egg stage, hatching when conditions are suitable. There are four larval instars, and most growth takes place in spring and early summer. There is, however, considerable variation in life cycles depending on flow conditions (Mannheims 1935; Hogue 1981). Gibo (1964) reported that at elevations between 600 and 900 m, *Blepharicera micheneri* Alexander larvae appeared in May and were present at the end of July, while adult numbers reached their peak in late June. In Santa Barbara, larvae are present from January until early summer and achieve a maximum length of about 9 mm before pupating.

The dominant blackfly in Rattlesnake Creek is *Simulium virgatum* Coquillet, with lesser numbers of *S. canadense* Hearle and *S. piperi* Dyar & Shannon. Larvae reach a length of 12 mm, and can form dense aggregations (> 400 per 100 cm²; Dudley, Cooper & Hemphill 1986) on nearly any substrate in fast currents. They attach a row of hooks on the terminal abdominal segment to webbing secured to the substrate and move by holding onto the substrate with their mouthparts, while re-attaching the anal hooks at a new location. Larvae aggressively maintain territories by nipping at neighbouring conspecifics (Hart 1986). Simuliid larvae feed by spreading cephalic fans in the water column to intercept suspended particles. Gut contents include primarily detrital material, but some diatoms are also present (T. Dudley, personal observation).

S. virgatum appears to be multivoltine in Santa Barbara County, with larvae and pupae present throughout the year (Hemphill 1989). Adults oviposit at the margins of fast water, and larvae develop quickly. Larvae are common by April, but reach highest densities in late spring and summer if flowing water is available.

Other macroinvertebrates occurring in riffles include grazer/collector-gatherers (mayflies *Baetis* and *Drunella*, caddis flies *Micrasema* and *Neophylax*, several chironomid

midges, dipterans *Maruina*, *Pericoma* and *Euparyphus*), filter-feeders (caddis *Hydropsyche* and *Rheotanytarsus* midges) and predators (caddis *Rhyacophila* (and *Hydropsyche*), and stoneflies *Calineuria* and *Isoperla*). None of these was abundant in habitats most preferred by *Simulium* and *Blepharicera*, and as long as macroalgae were not present.

In the smooth, fastest-flowing habitats favoured by *Simulium* and *Blepharicera*, few other invertebrates were abundant, although several insects from all functional groups (e.g. *Baetis* mayflies, hydroptychid, *Rhyacophila* and *Micrasema* caddis flies, psychodids) are found in adjacent riffle areas (Dudley, Cooper & Hemphill 1986; Cooper, Dudley & Hemphill 1986; Dudley & D'Antonio 1990). In the absence of macroalgae, their combined abundance rarely comprised more than about 10% of the individuals present. Consequently, we assumed their influences on competitive interactions between *Simulium* and *Blepharicera* were minimal.

METHODS

Habitat overlap in the field

We counted all insects within twenty, 10×10 cm quadrats on 4 May 1984, on rocks in fast-flowing sites (current velocity $> 66 \text{ cm}^{-1}$ measured with Bentzel tubes; Everest 1967). The quadrat was drawn onto a plexiglass viewing box, which could be placed over the substrate without causing animals to disperse. In addition, we compared blepharicerid and simuliid densities at different current velocities in randomly chosen quadrats on one date during the blepharicerid pupation period, calculating average densities for ten replicates from each of five velocity ranges (see below).

Behavioural interactions

To quantify behavioural interactions between simuliids and blepharicerids, we made direct observations of natural populations on boulders with sheetflow (wide, shallow flow with a largely unbroken water surface). A blepharicerid among a group of blackflies (c. 50–100 individuals per 100 cm^2) was first observed for 15 min. Then, a fine probe (00 minuten pin) was used to clear all simuliids within a 5-cm radius of the blepharicerid, without disturbing the substrate. The target larva was again observed for 15 min following a 2-min acclimation period. This procedure was repeated for seventeen blepharicerids.

Behavioural observations were recorded into a time-metred tape recorder, with each 5-s interval assigned to a behavioural category. Categories for *Blepharicera* included: (i) stationary, no observable movement; (ii) feeding, moving head in an arc while advancing forward (c. 2 mm min^{-1}); (iii) re-orientation, changing directions by alternately releasing and re-attaching anterior then posterior suckers and arching the body laterally; (iv) fast forward, forward motion ($\geq 2 \text{ mm min}^{-1}$) executed by releasing the posterior sucking disc and contracting the last abdominal segments as the next sucker is released, resulting in a caterpillar-like movement; (v) avoidance, lifting head and thorax away from the substrate, generally followed by re-orientation; (vi) looping, rapid lateral movement by alternately releasing and re-attaching anterior then posterior suckers (c. 5 arcs s^{-1}). The distance travelled by a blepharicerid and its angle of orientation to the current flow was noted. We also recorded the number of 'nips' by blackflies during each 5-s interval, the size of each blackfly that responded to the presence of *Blepharicera*, and the consequences of each interaction for both species.

Effects of interactions on ingestion

To determine whether the effects of *Simulium* on blepharicerid behaviour were translated into changes in food intake, we measured blepharicerid feeding rates in the field in the presence and absence of *Simulium*. Diatoms are the primary natural food eaten by *Blepharicera*, and those within guts of larvae can be counted by dissolving larvae in concentrated sulphuric acid, leaving only the siliceous frustules. Diatoms in the guts were first eliminated by providing, in the laboratory, an alternate food which did not occur in the field. Field-collected larvae were brought into the laboratory and held in a cold room at 14°C (c. average stream temperature). In 1984 they were placed in a waterbath with a re-circulating pump to simulate currents, and provided with clay tiles colonized by mostly green algae from a nearby pond. In 1985 we cultured two species of green algae (*Mougeotia* sp., *Chlorella* sp.), and a diatom (*Amphora venetus* Kütz) foreign to Rattlesnake Creek, in 400-ml beakers. Once the algae were abundant on the glass walls, beakers were placed in a gyratory shaker (to provide currents) and larvae were introduced. In both experiments larvae were fed in the laboratory for c. 48 h, and returned to the field in a container with a battery-powered aerator.

We ran paired tests in which a *Blepharicera* larva was allowed to feed in the presence of *Simulium* for 15 min, and then placed into the vial of acid. Blackflies were next removed from the same location with a probe and a second larva of the same size was allowed to feed for the same period, then placed into another acid vial. A third larva was size-matched with each pair and placed directly into acid without feeding to verify clearance of diatoms from guts. Diatoms in vials were washed and transferred to settling chambers, then the numbers of each type in fifty fields of view (at 200×) were counted with an inverted light microscope. Eight replicate triads were conducted each year.

Feeding trials were done on natural substrates in 1984 and in eight acrylic flow-through channels (each 10 × 10 × 40 cm) adjacent to Rattlesnake Creek in 1985. Stream water was diverted, and gravity-fed via PVC pipe to a common chamber, from which it flowed into the experimental channels at a 10% incline. The flow in each channel was about 0.2 l s⁻¹, with maximum velocity near 50 cm s⁻¹. Nylon screens (0.5-mm mesh) prevented drift into and retained animals within the channel, but allowed colonization by diatoms, and a barrier 8 cm high provided a small spillway with fast, turbulent flow at the channel head. Diatoms colonized the channels for 6 weeks, providing densities in excess of 5000 cells mm⁻², then 100 (± 10) mature blackfly larvae were transferred into each channel the day prior to experimental manipulations.

Effects on development

We assessed *Blepharicera* growth and developmental responses to competition with simuliids by rearing blepharicerids with varying simuliid densities in streamside channels (see above). The bottom of each channel was lined with two unglazed clay quarry tiles which had been in Rattlesnake Creek for 4 weeks prior to manipulations. Previous tests had shown that blepharicerids feed on these surfaces, and completed development in the channels.

Small-to-medium blepharicerid larvae (3–5 mm in length, c. 0.15 mg dry wt) were collected from Rattlesnake Creek on 29 April 1986, and distributed randomly to seven replicates of five experimental treatments. Treatments were: (i) control *Blepharicera* density, 25 individuals per chamber; (ii) high density, 25 larvae + 15 mature blepharicerid larvae (9–11 mm); (iii) 25 *Blepharicera* + 100 *Simulium* (5–10 mm); (iv) 25 *Blepharicera* + 250 *Simulium*; (v) 25 *Blepharicera* + 100 *Simulium* added 2 weeks into the

experiment. All densities are within, and substantially below maximum, natural levels (Dudley, Cooper-Hemphill 1986). The last treatment simulated the effect of increasing blackfly abundance after substantial blepharicerid development had occurred; this phenology was also observed in the field. A sixth set of chambers received only 100 *Simulium* each, as a control for *Blepharicera* effects on blackfly microhabitat use. This experiment was terminated after 2.5 weeks on 16 May, prior to blepharicerid pupation and only 4 days after 'late' simuliids were added, due to inadequate flows for all forty-two channels. All larvae were collected on this date, and dry-weighed (after 48 h at 65°C) to estimate effects of manipulations on larval growth.

Another experiment was immediately set up using only twenty-four channels with six replicates of four treatments: (i) *Blepharicera* alone, 25 medium larvae (5–7 mm in length, c. 0.4 mg dry wt); (ii) 25 *Blepharicera* + 100 small *Simulium* (< 5mm); (iii) 25 *Blepharicera* + 250 *Simulium* of all size-classes; (iv) 25 *Blepharicera* + 100 *Baetis* mayfly nymphs (3–10 mm). *Baetis* mayfly nymphs also feed on diatoms and may compete exploitatively with *Blepharicera*; no agonistic interactions were observed between these two taxa. Blepharicerid pupae were collected as they appeared, remaining larvae were collected on 11 June (after 25 days), and all were dried (2 days at 65°C) and weighed.

Effects of interactions on distributions

In the growth experiments, larval positions (spillway vs. bottoms vs. sides) were noted to detect influences of blackflies on blepharicerid microhabitat use. To verify that exclusion occurs on natural substrates, we also examined blepharicerid density responses to removal of blackfly larvae. On 24 April 1986, densities of both taxa were determined near the centres of each of twelve rocks and boulders (> 20 cm diameter) using a 10 × 10 cm quadrat. Blackflies were then removed from six rocks using a probe and forceps. After 10 days, densities were again measured, allowing time for blepharicerids to colonize from areas surrounding each experimental boulder.

A variety of statistical tests were used, as noted in the Results section, to analyse the data gathered in each of the experiments and patterns described above. For parametric tests, proportional data were arc-sine square-root transformed, and numerical data were log-transformed prior to analysis.

RESULTS

Distributions of Blepharicera and Simulium

In winter and spring of 1983, *Blepharicera* and *Simulium* larvae were abundant on smooth boulder faces in Rattlesnake Creek. *Blepharicera* was present in all sampled quadrats, while blackflies were absent in the two most turbulent sites. Abundances of the two species were negatively correlated ($r_{\text{Spearman}} = 0.81$, $P < 0.001$; Fig. 1). Both species are associated with the same high flow conditions (*Simulium*: 86% of seventy-seven haphazardly chosen larvae in flows > 118 cm s⁻¹, 98% > 66% cm s⁻¹; *Blepharicera*: 69% of 125 larvae in > 118 cm s⁻¹, 92% > 66 cm s⁻¹), so habitat segregation could not account for the observed negative correlation. Blepharicerid larvae in slower flows were adjacent to faster water, but were at the stream margins or splash zones very near substrates occupied by both species; of forty-six pupae observed, 80% were similarly distributed in slow water immediately adjacent to faster flows. These distributional patterns suggest that interactions between these species partly determine local abundances, yet coexistence continues due to the similarity of habitat requirements.

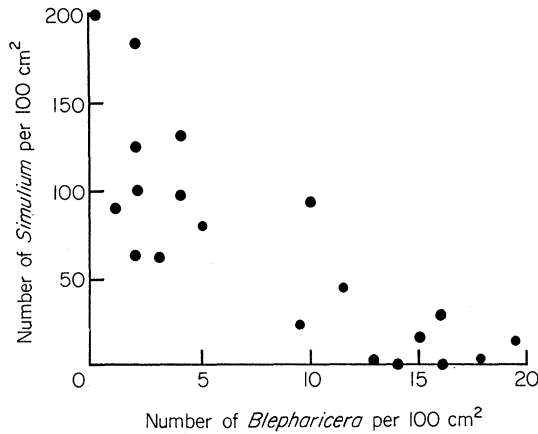


FIG. 1. Relationship between field densities of *Blepharicera* and *Simulium*.

Behavioural experiments

The presence of *Simulium* had clear effects on most blepharicerid behaviours for the eleven pairs suitable for analysis (Fig. 2). When blackflies were removed ($-S$), *Blepharicera* spent nearly the entire time feeding (92%), as compared with 74% when simuliids were present ($+S$). Blackflies 'nipped' at blepharicerids foraging adjacent to, and particularly upstream of their attachment site, often causing a 'looping' avoidance response. Nipping occurred without physical contact between larvae, as disruption of the current was sufficient to elicit blackfly aggression (a probe just upstream would elicit the same response). Occasionally the blepharicerid would respond with a low-intensity avoidance response rather than looping, and these two responses were combined as 'avoidance' responses in time-budget analyses. Significantly more time was spent in avoidance, fast forward and stationary behaviours in the $+S$ than in the $-S$ treatments (Fig. 2). Avoidance was typically followed by fast forward and then stationary behaviour during recovery from interactions.

The effect of blackfly interference on blepharicerid feeding is illustrated by the strong

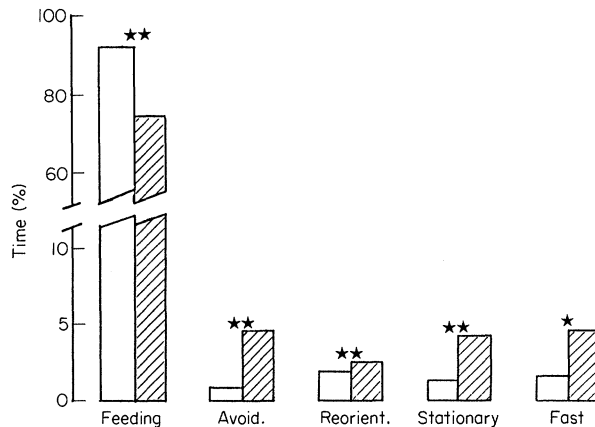


FIG. 2. Behavioural time budget for *Blepharicera* in the presence (▨) vs. absence (□) of *Simulium*. All category pairs are different (Wilcoxon paired sample tests: * $P < 0.005$; ** $P < 0.001$).

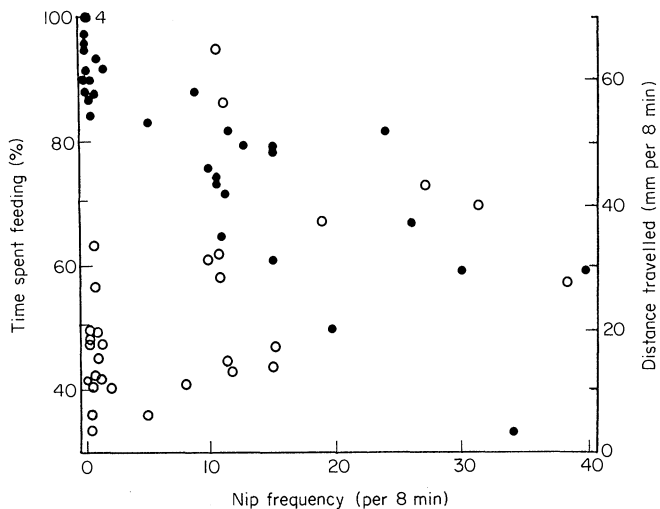


FIG. 3. Percentage of time *Blepharicera* spent feeding (●) and distance travelled (○) in relation to number of attacks by *Simulium*. A single larva is represented by two points for each relationship, one with *Simulium* present, and the other with most blackflies removed ($n = 17$ larvae).

negative correlation ($r_{\text{Spearman}} = 0.89$, $P < 0.001$) between feeding time and simuliid encounter (nip) frequency, which averaged thirty-four attacks per 15-min interval (Fig. 3). Some of the variation in blepharicerid response was due to diminution of the avoidance response following repeated nipping.

The behavioural consequences of these interactions were related to the relative sizes of interacting individuals (Fig. 4). Large blackflies induced both high and low-intensity avoidance responses (stationary/forward, low and looping responses were pooled for analyses) more frequently than did medium-sized larvae, which in turn elicited responses more than small simuliids (Kruskal-Wallis tests, $P < 0.01$ for small vs. other size-classes, $P < 0.05$ for difference between medium and large simuliids). Small blackflies were commonly ignored, or even displaced by *Blepharicera* ($P < 0.01$, 0.05 as above). Repeated nipping by an individual, however, reduced the small blackfly displacement rate and caused more avoidance responses than single nip attacks (Wilcoxon paired tests, $P < 0.001$; Fig. 4). Dislodgement of blepharicerids was uncommon, but was observed on more than ten occasions in response to nipping.

The presence of *Simulium*-caused *Blepharicera* not only to spend more time in avoidance reactions, but also to travel a greater total distance ($r_{\text{Spearman}} = 0.50$, $P < 0.005$; Fig. 3). In the absence of *Simulium*, *Blepharicera* spends virtually all of its time feeding while moving slowly in a downstream direction (Fig. 5). After each foraging bout, it turns and moves rapidly upstream in a straight line. With *Simulium* present, this movement pattern occurs (slow downstream, fast upstream), but with additional lateral components resulting from interspecific interactions.

Effects of interactions on ingestion

In 1984, the presence of *Simulium* caused a significant reduction (mean 27%) in ingestion of the dominant diatom, *Cocconeis*, by *Blepharicera* when compared with ingestion when *Simulium* was absent ($P < 0.05$, Wilcoxon signed rank, seven of nine pairs in the hypothesized direction). We chose *Cocconeis* for the comparison because it was the

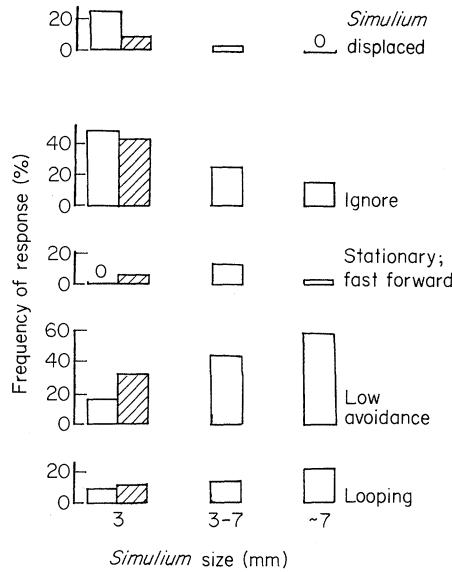


FIG. 4. Consequences of encounters between *Blepharicera* ($n = 17$ larvae) and *Simulium* in relation to blackfly size (length in mm). Lower four rows give frequencies of blepharicerid responses; top row is the reciprocal effect of blepharicerids on simuliids. Cross-hatched histograms represent cases of multiple nips by single simuliids.

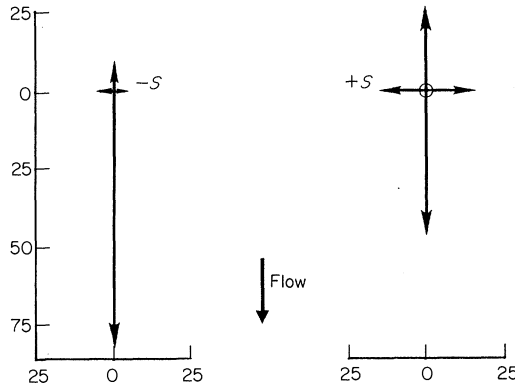


FIG. 5. Percentage of total time *Blepharicera* spent oriented in each direction (90° quadrants) in the absence ($-S$) vs. presence of *Simulium* ($+S$). Four directional vectors add to 100% in each graph.

dominant diatom in guts, accounting for 75% of total cells ingested. Other species present in substantial numbers were *Navicula* (12%), *Achnanthes* (8%), *Meridion* and *Eunotia* (each 2%).

The 1985 results gave further evidence that interference by *Simulium* reduces *Blepharicera* ingestion (Table 1). Control animals had almost no diatoms in their guts, since the laboratory-fed diatom was sparse in guts and the green algae ingested in the laboratory was digested by the acid. Both *Cocconeis* and total diatoms showed significant differences between treatments (Wilcoxon paired sample test, $P < 0.005$, $n = 8$). *Cocconeis* comprised $> 85\%$ of total diatoms ingested, and other genera in guts included *Navicula* (10%), *Gomphonema*, *Eunotia*, *Achnanthes* (each 1%) and *Amphora*, the laboratory-fed

TABLE 1. Ingestion of diatoms by *Blepharicera* in the presence and absence of *Simulium* during 15 feeding trials. Data are mean number of cells in guts (\pm S.E.) estimated from 6% subsamples

	<i>Blepharicera</i>	<i>Blepharicera</i> + <i>Simulium</i>	Control (unfed)
<i>Cocconeis</i>	6360 (2448)	2520 (2064)	16 (16)
Total diatoms	7232 (2496)	2976 (2240)	32 (32)

diatom (1%). While the behavioural experiments showed approximately a 20% reduction in time blepharicerids spent feeding owing to the presence of simuliids (Fig. 2), the reduction in ingestion was closer to 60% (i.e. ingestion was 2.5 \times greater when simuliids were absent). Interference by *Simulium* probably caused *Blepharicera* 'feeding' to be relatively inefficient, due to more time spent in a recovery phase, an altered harvesting technique, and/or relegation to grazing in resource-poor patches. In these feeding trials, *Blepharicera* often moved to the edge of the stream channel when simuliids were present, as was observed under field conditions.

Effects of interactions on growth and development

After less than 3 weeks in experimental channels, blepharicerid larvae were about 27% smaller when reared in the presence of *Simulium* (Fig. 6). Blepharicerid weight in high and low-density blackfly treatments did not differ, suggesting that strong competition occurs at densities substantially lower than those found in the field (see Fig. 1). There was little effect of blackflies introduced late in the experimental period, because there were only 4 days before experiment termination. Simuliids tended to reduce blepharicerid survival (Fig. 6). We observed blepharicerids forced into the drift by encounters with simuliids, and dead larvae were occasionally collected from downstream screens. Survival did not differ statistically, but pooling of treatments without competitors for most of the experiment (C + LS) vs. the two blackfly treatments (S + SH), simuliids reduced blepharicerid survival by about 25% (58.4% vs. 42.4%, ANOVA $F=3.8$, $P=0.02$). Blepharicerid growth and survival were also reduced by intraspecific competition, but tending towards a lesser effect than that caused by interspecific competition with simuliids (Fig. 6).

Simuliids also prolonged the duration of the blepharicerid larval stage (Table 2). At the end of the second growth experiment, all larvae had pupated in treatments without blackflies, but about 10% of those with blackflies remained as larvae. Pupal biomass did not differ among treatments because prolonging the growth period allowed larvae with simuliids to 'catch up' to those reared alone, although individuals exposed to simuliids tended to be smaller.

We estimated secondary production of blepharicerids by calculating the growth of animals from each channel (mean final – mean initial weight), and dividing by the mean date of pupation or expected pupation for all surviving individuals (assuming remaining larvae would pupate in 2 days). While acknowledging the many assumptions made in these calculations, the cumulative effects of blackflies on blepharicerid behaviour and development appeared to result in a nearly 50% reduction of secondary production (0.16 vs. 0.29 mg day⁻¹ per channel; Table 2).

Baetis mayflies had little effect on most measured components of *Blepharicera* fitness;

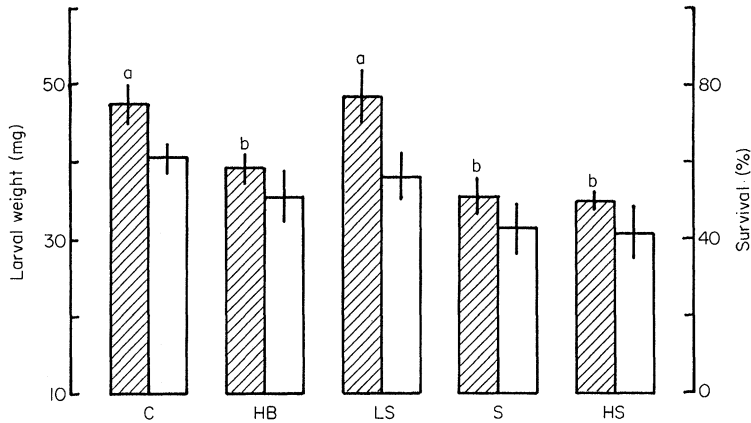


FIG. 6. Mean weight (▨) and survival (□) (\pm S.E.) of *Blepharicera* at different densities of intraspecific and interspecific competitors. C, control *Blepharicera* density; HB, high blepharicid density; LS, *Simulium* added late in the experiment; S, moderate *Simulium* present throughout; HS, high *Simulium* density throughout. Unmatched letters = statistically different weights (Duncan multiple range test, $P < 0.05$).

however, time to pupation was significantly greater and growth tended to be reduced in control vs. *Baetis* channels (Table 2). Interspecific competition for food with a non-aggressive competitor appears to be less consequential than interference with access to that food by a more aggressive competitor. The effects of *Blepharicera* on *Simulium* growth could not be assessed because of initially high variability in blackfly size. The frequency of simuliid nipping at blepharicerids was extremely low ($\ll 1$ nip min^{-1}), however, compared to the frequency of interactions between congeners (often > 10 nips min^{-1}), so reciprocal interspecific effects of blepharicerids on blackflies were assumed to be minor compared to possible intraspecific effects among simuliids.

TABLE 2. Mean pupal weight, frequency and time to pupation, survival and production (\pm S.E.) of *Blepharicera* in the presence vs. absence of *Simulium* or *Baetis* in experimental channels. C, *Blepharicera* control; S, *Blepharicera* with *Simulium*; HS, *Blepharicera* with high *Simulium* density; B, *Blepharicera* with *Baetis*. Data on the distribution of blepharicerid larvae and pupae vs. simuliid larvae, on 27 May 1986, are included. Asterisks indicate significant differences between treatments and the control

	C	S	HS	B
Number pupating	12.0 \pm 1.5	11.7 \pm 1.7	9.0 \pm 1.3	12.2 \pm 1.4
Pupal wt (mg)	79.6 \pm 6.7	72.9 \pm 1.8	71.4 \pm 4.2	74.5 \pm 4.4
Larvae remaining at end (%)	0	5.7 \pm 1.9**	10.2 \pm 2.6**	0
Survival (%)	48.0 \pm 6.0	50.0 \pm 6.6	39.9 \pm 5.8	48.8 \pm 5.6
Days to pupation	18.3 \pm 0.3	19.5 \pm 0.2**	20.7 \pm 0.5**	19.5 \pm 0.4*
Biomass pupated	10.1 \pm 1.4	9.5 \pm 1.2	7.4 \pm 1.0	9.9 \pm 0.8
Production per channel (mg day ⁻¹)	0.29	0.23	0.16	0.26
Larvae on walls (%)	5.5 \pm 3.2	14.8 \pm 4.2	17.3 \pm 7.3	5.7 \pm 3.7
Larvae in fast water (%)	30.4 \pm 9.7	1.3 \pm 1.3**	4.0 \pm 4.1**	23.4 \pm 4.0
Pupae in fast water (%)	72.5 \pm 14.0	0**	0**	55.3 \pm 12.5
<i>Simulium</i> in fast water (%)	—	89.6 \pm 4.5	87.3 \pm 4.6	—

* $P < 0.05$; ** $P < 0.01$ (Duncan multiple range test).

Effects on habit association

Both *Blepharicera* and *Simulium* preferred the upper portions of the experimental channels where water velocity was greatest. When alone, blepharicerid larvae and pupae were commonly found in this micro-habitat, but c. 90% of the blackfly larvae resided here regardless of the presence of blepharicerids (Table 2). Simuliid distributions were identical in both the presence and absence of blepharicerids. With blackflies present, *Blepharicera* was more frequently found on the side walls, just out of the flowing water.

When simuliids were removed from natural substrates, both taxa re-colonized the removal sites. Nevertheless, after 10 days a 70% mean *Simulium* reduction in removal plots (net change of 185 larvae per 100 cm²) resulted in an increase of 12 (S.E. 7.0) *Blepharicera* larvae per quadrat (Mann-Whitney *U*-test, $P < 0.01$). Control densities were highly variable but remained nearly constant during the experiment (mean increase of c. 5 larvae per 100 cm², initial range 26–250 larvae). There was a strong negative relationship between the changes in densities of the two taxa before and 10 days after manipulations ($B = -14.5S + 0.14$, $R^2 = 0.84$; $B = \text{Blepharicera}$, $S = \text{Simulium}$). Those areas with high simuliid and low blepharicerid densities often had adjacent 'splash' zones where blepharicerid densities were as high as 100 individuals per 100 cm². Apparently, blepharicerids were excluded from their preferred microhabitat by *Simulium*.

DISCUSSION

Mechanisms of competition between Simulium and Blepharicera

Competition for space between these two study insects was readily documented for two reasons: (i) both taxa have similar, discrete habitat associations (smooth stone surfaces in fast-flowing sections of streams); (ii) they do not share food resources so space is the only apparent limiting resource (*Blepharicera* grazes on epilithic microflora and *Simulium* is a filter-feeder). There is anecdotal evidence of simuliids feeding on benthic algae (Burton 1973; Craig 1977), but exploitation can be dismissed as a mechanism of competition because they tend to remove microalgal filaments that interfere with filtering, not diatoms. Aggressive interference for attachment space was clearly the most important mechanism to explain the interspecific effects observed. Contests were commonplace because, unlike truly sessile space competitors which partition space following intense interactions (Roughgarden 1986), these insects are slow moving and are subject to encounters for long periods of time.

Contested space is, however, used differently by the two competitors. Blepharicerids require the two-dimensional feeding surface, but *Simulium* appears to be defending a three-dimensional space upstream of a larva, through which food is delivered by streamflow. A blepharicerid (or any other object) creates turbulence, which reduces filtering efficiency (Kurtak 1978; Craig & Chance 1982). Hydrodynamic interference, rather than simple food availability (cf. Hart 1986), is likely to be responsible for the common observation of simuliids nipping at conspecifics and other taxa (Harding & Colbo 1981; Wiley & Kohler 1981; Hart 1986; Hemphill 1988). Similarly, the consequences of interference for *Blepharicera* are indirectly related to access to limited food (see Sebens 1983); undisturbed larvae spent virtually all of their time feeding and our results suggested that baetid mayflies inhibited growth by food exploitation, so interference inhibited maximal exploitation of algal resources.

Interactions between *Blepharicera* and *Simulium* are asymmetrical (*sensu* Lawton &

Hassell 1981), as blackflies returned immediately to filtering following an encounter, whereas blepharicerids exhibited a variety of detrimental responses. Nevertheless, the reciprocal effects are not entirely neutral. All size-classes of both taxa were often present, and blepharicerid larvae displaced blackflies that were substantially smaller than themselves. Because there is also strong hierarchical size dominance within the simuliid assemblage (Gersabeck & Merritt 1979), small larvae are displaced to the same edge areas as blepharicerids (Colbo & Moorhouse 1979). Here blepharicerids may exclude small blackflies, although the actual effect on blackfly populations is uncertain because small larvae use a wide variety of substrates, such as algal filaments, that are unavailable to large conspecifics and blepharicerids (Dudley, Cooper & Hemphill 1986).

Intraspecific effects on development were significant among blepharicerids, but it is unclear whether such effects are sufficiently strong to override interspecific effects (cf. Connell 1983; Fletcher & Creese 1985). While intraspecific competition may be critical to maintaining simuliid distributions (Hart 1987a), the greater aggressiveness of *Simulium* in the preferred habitat may overwhelm exploitative competition between blepharicerids under field conditions (agonistic interference among blepharicerids was rarely observed). It is in the marginal habitats to which *Blepharicera* are excluded, and in which habitat or resource quality is presumably poorer, that intraspecific effects may become important.

Consequences of competition

The distributional consequences of competition represent a continuum from complete exclusion and ultimate mortality to continued coexistence, with attendant interactions, within a preferred zone. Complete exclusion from an entire habitat may be rare or infrequently documented (den Boer 1985), but smaller-scale distributional responses are common (Werner & Hall 1979; McAuliffe 1984a; Hart 1987a). Although the absence of exclusion (e.g. Reice 1981) is often taken as evidence that competition is insignificant (cf. Birch 1979; den Boer 1985; Cooper & Dudley 1988), on-going interactions may have important effects on survival and growth of competitors without altering distributions. Local exclusion of *Blepharicera* by *Simulium* certainly occurs, as our removal experiments indicated. Encounters occasionally caused blepharicerid dislodgment, and despite a remarkable ability to re-attach to smooth substrates in very fast water, the rarity of suitable habitat reduces the probability of re-attachment. Those larvae displaced or emigrating from riffles may experience high mortality because substrates are unsuitable and predator densities are high in slow-water sections (pools) of Rattlesnake Creek (Cooper, Dudley & Hemphill 1986). No larvae have ever been collected outside smooth substrates in fast water, and we have recovered one larva from the gut of a trout living in a pool. The importance of large-scale exclusion of *Blepharicera* in the field is unresolved, but coexistence with *Simulium* clearly incurs ecological costs.

For *Blepharicera* co-occurring with *Simulium*, the fitness components of growth and time to first reproduction were negatively affected by the presence of competitors. Size at pupation was not significantly reduced, but we suspect that greater replication would have yielded greater statistical power. Reduction of pupal and adult size and thus fecundity result from larval competition in other Diptera (Prout & McChesney 1985). By estimating the total biomass of pupae (c. 25% lower in blackfly treatments compared to controls), and dividing growth during the experiment by average time to pupation, we estimated that *Simulium* may have reduced daily production of reproductive blepharicerids by approximately 45% (see Table 2). As this value incorporates growth reductions as well as mortality, the composite effect of competition on population production is greater

than that predicted simply from individual performance. The quantitative effect of interspecific competition on *Blepharicera* fitness in the field will require estimation of the proportion of time larvae are exposed to encounters with simuliids vs. the proportion of time within refuges, along with performance in both situations.

It is important for *Blepharicera* to pupate as soon as possible because larvae, like tadpoles in temporary ponds (Wilbur & Collins 1973), are essentially in a race to pupate and emerge before waters recede with the onset of the dry season. Minor inhibition of growth by *Simulium* potentially results in mortality (due to desiccation or loss of fast water) before pupation is possible, with a greater effect on individual reproductive success than our results suggest. Furthermore, pupation without blackflies occurs in the larval habitat, but in their presence blepharicerids pupate away from the main current. In previous studies which documented negative rheotropism (avoiding current) by blepharicerid pupae (Mannheims 1935; Gibo 1964), pre-pupae may have been relegated by competition to marginal locations. When rocks with pupae were moved from fast-flowing sites to locations with slow currents, at least some imagoes (three out of *c.* twenty-five) did not successfully emerge (all pupae in the control location successfully emerged), further suggesting that competition can have both chronic and acute negative effects.

Temporal variation in competition

The role of competition between *Simulium* and *Blepharicera* varies within and between years, because the life cycles of the two insects sometimes have little overlap in Rattlesnake Creek. Initial hatching of diapausing *Blepharicera* eggs appears to be under external, probably photoperiodic, control because early instar larvae have been first observed during the first 3 weeks of January in six successive years (1983–88). In contrast, we observed that larvae disappear at very different times in different years (August, June, May, June, May, May, respectively; unpublished data). *S. virgatum* larvae are present throughout the year but show considerable seasonal and interannual variation in density (Dudley, Cooper & Hemphill 1986; Hemphill 1989). Because *Simulium* larvae often do not increase until spring, they often have little effect on *Blepharicera* from January to April. The period of overlap depends largely upon rainfall. In dry years (e.g. 1985, 1987, 1988) this overlap is usually no more than 1 month, if at all, while in wet years (e.g. 1983) blepharicerid populations were present even into August (*c.* 4 months coincidence between species). This variation in overlap was related to the duration of fast-flowing water over smooth substrates. The extensive temporal overlap between species in 1984, a dry year, was related to high groundwater inputs resulting from very high rainfall the preceding year. Blepharicerid larvae disappear when current speeds decline below some threshold; in some years before *Simulium* increase.

Despite the ultimate importance of winter rains to *Blepharicera* life cycles, several proximate factors which vary with flow regime may affect populations (e.g. temperatures are lower in high flow years and may delay development). In 1983, heavy winter storms caused extensive scouring in Rattlesnake Creek, which can decimate the biota on benthic substrates (Fisher *et al.* 1982; Power & Stewart 1987). By opening new space and reducing densities of dominant species, disturbance can benefit early-colonizing taxa in many systems (Connell 1978; Sousa 1979), including streams (Hemphill & Copper 1983; McAuliffe 1984a; Power & Stewart 1987; Dudley & D'Antonio 1990). Macroalgae compete for space with *Blepharicera* which, in turn, increase in response to both natural and simulated disturbances that remove these plants (Dudley, Cooper & Hemphill 1986). Thus, scouring and increased discharge in 1983 resulted in a dramatic increase in total

blepharicerid abundance compared to other years. In 1983, smooth substrate was available throughout the spring and summer, except in a few well-lit locations where algae re-established. The lack of scouring in dry years allows algal populations to pre-empt space throughout the winter, thereby excluding or reducing densities of blepharicerid larvae (Dudley, Cooper & Hemphill 1986).

Simulium also depends upon disturbance, partly because it is more abundant on smooth surfaces, but also because scouring reduces abundance of *Hydropsyche oslari* (Hemphill & Cooper 1983; Dudley, Cooper & Hemphill 1986). This net-forming insect colonizes more slowly than *Simulium*, but is a superior competitor for attachment space. Simuliids benefit during high discharge years when hydropsychid densities are low (Hemphill 1989). During wet years, blackfly densities are high, macroalgal abundances are low, and flow and substrate conditions are favourable for both taxa. Therefore, it is in wet years that interactions with *Simulium* are of greatest consequence to *Blepharicera*.

Year-to-year variation in rainfall and associated disturbance results in switches in the relative importance of limiting factors to *Blepharicera* populations. In dry years, reduced habitat availability and competition with macroalgae result in low blepharicerid densities before competition with *Simulium* becomes important. In wet years, competition with blackflies, rather than with algae, is of greater importance. While both the form and degree of competition depend on physical regimes, it is unclear whether these effects carry over to the following year. A large blepharicerid population in 1983 following a low abundance year (Hemphill 1989) suggests that blepharicerids, and possibly other riffle taxa (Fisher *et al.* 1982), are able to produce sufficient propagules even in poor years to repopulate streams when suitable conditions arise. Where recruitment is not limited, competitive interactions may be important in determining community structure, because populations can rapidly achieve densities at which resources become limiting (Wiens 1977).

Interspecific competition in streams

The debate regarding the importance of interspecific competition in structuring natural communities hinges on the conditions under which competition is attenuated by other factors. Competition may be a rare and/or intermittent phenomenon in systems subject to 'harsh' conditions (Wiens 1977; Dunham 1980; Grant 1986). Certainly stream systems could be included in this category because they are frequently disturbed by flood or drought (Fisher *et al.* 1982). Ward & Stanford (1983) claim that only in the most constant or benign streams might competitors reach densities sufficiently high for interactions to cause significant alterations in populations, and McAuliffe (1984a) suggested that competition for space may have been common in his Montana stream because it was relatively undisturbed. Despite these assertions, many stream studies now imply that competitive interactions may be common and important determinants of species distributions and abundances (Wiley & Kohler 1981; Hart 1983, 1987a, b; Peckarsky 1983; McAuliffe 1984a; Hawkins & Furnish 1987; Lamberti, Feminella & Resh 1987; Hemphill 1988; and others). Detection of competition would probably be even more frequent, except that sampling is often conducted at a scale too large to identify the interactions (McAuliffe 1984a).

So how do we rectify the apparent commonness of competitive interactions with the perception that disturbance over-rides the effects of 'deterministic' processes like competition? In our system both *Simulium* and *Blepharicera* depend on disturbance to make space available that would otherwise be dominated by other competitors, but

ecological dogma holds that opportunistic organisms should be fugitives from competition and so are rarely limited by chronic competitive interactions (Pianka 1976). It is true that flooding may re-set stream communities to an earlier stage of succession (Fisher *et al.* 1982; Dudley, Cooper & Hemphill 1986; Power & Stewart 1987; Dudley & D'Antonio 1990), and that local disturbances continue to open new patches for colonization (McAuliffe 1984a; Robinson & Minshall 1986); yet, it does not necessarily follow that such disturbance is always sufficient to negate significant competitive modifications of communities, especially within patches of locally abundant species.

The period between storms may, in fact, provide a sufficiently long period of unimpeded exploitation of limited resources that competition becomes important. Connell & Sousa (1983) maintain that the importance of biological interactions may be a function of the time-scale of habitat suitability relative to generation time of the organisms, such that even short-lived species may experience major effects of competition if the environment remains benign for significant periods (cf. Huston 1979). Periodic catastrophic disturbance should favour small invertebrates with fast life cycles, as large, long-lived species may not survive frequent disturbance events. Rapid recruitment of stream organisms with overlapping food and/or spatial utilization can then reduce resources to limiting levels. Therefore, interspecific competition becomes a recurrent force modifying growth, distributions and abundances of many taxa, e.g. *Blepharicera*, *Simulium*, *Hydropsyche* and macroalgae, with weaker effects by many more vagile species (Hemphill & Cooper 1983; Dudley Cooper & Hemphill 1986; Hemphill 1988; Dudley & D'Antonio 1990).

Thus, competition for space (interspecific and intraspecific) among benthic stream assemblages appears to be intense and chronic, but the identity of competing species will depend on preceding hydrographic conditions and other factors (e.g. current, consumers, refuges) that determine the establishment of populations. While disturbance sets many conditions for interspecific interactions, the question remains whether disturbance, by eliminating biota before competitive exclusion can occur (Hubbell & Foster 1985), could also inhibit the evolution of mechanisms to avoid these interactions.

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