Resource Partitioning by Two Species of Stream Mayflies (Ephemeroptera: Heptageniidae)

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ABSTRACT

We compared the phenology of nymph development, food type, and habitat selection of two stream mayflies, *Stenacron interpunctatum* (Say) and *Stenonema pulchellum* (Walsh) in Big Darby Creek, Ohio. Both species, which grow principally from autumn through early spring, emerged from the stream throughout the summer. The nymphs consumed the same sizes and types of food particles from deposits on stones, mostly in the form of detritus. As a result of morphological and behavioral adaptations, *S. pulchellum* lived on stones in swift water whereas *S. interpunctatum* lived on stones in a slower current.

Closely-related coexisting species often have similar resource needs, but because of divergent evolution they may differ in their use of resources. Such resource partitioning is common in ecological communities (Schoener 1974). In streams, for example, similar insect species partition the resources of time (Illies 1952, Hynes 1961, Grant and Mackay 1969), food (Sheldon 1971, Mackay 1972, Wallace 1975, Resh 1976), and space (Cummins 1964, Ulfstrand 1967, Madsen 1968, Mackay and Kalff 1973, Allan 1975).

Heptageniid mayflies are important components of the benthic invertebrate community of streams. They feed on algal and detrital particles deposited on stones and vegetation. Extensive systematic and biological studies of the *Stenonema* and *Stenacron* species, common in the eastern United States, have been made (Needham et al. 1935, Spieth 1947, Jensen 1974, McCafferty and Huff 1978); however ecological studies have been limited. Although the nymphs of these species have been used as indicators of water quality and pollution levels (Lewis 1974), comparative ecological studies of coexisting species have not been reported.

The purpose of this study was to compare two coexisting mayfly species, *Stenacron interpunctatum* (Say) and *Stenonema pulchellum* (Walsh), which inhabit central Ohio streams. We will discuss whether the species partition the resources of time, food, and space, and the morphological and behavioral differences that cause this partitioning.

METHODS

Field studies were conducted on Big Darby Creek (2 km south of Amity, Madison Co.) in central Ohio from May 1975 to September 1976. The stream is third order and flows through a 1437 km^2 watershed of the high-lime Wisconsin till region. Although organic wastes and soil sediments are present, the macroinvertebrates indicate that the stream is relatively pollution-free (Olive and Smith 1975).

Phenology of nymph development. From July 1975 to June 1976 nymph development was followed by obtaining samples from stones dipped in a white pan containing a weak acid-alcohol mixture (Britt 1955). Samples were obtained from 10 stones in each of four habitats (defined in Results section). Any nymphs that were dislodged by the removal of the stone

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from the stream bed were caught with an aquatic insect net. The specimens were killed in KAAD, and taken to the laboratory. At a later date, they were identified to species and the head capsule width was measured with an ocular micrometer mounted in a dissecting microscope.

Food type. On 28 April, large nymphs were killed in 80% ethanol. Analyses of the gut contents were made according to the method of Cummins (1973) within two days of collection. Briefly, this involved dispersing the contents of the gut in water, filtering the mixture through a millipore funnel fitted with a 0.45μ filter, and mounting the cleared filter on a permanent slide. Counts of the particles on the filter were made for five arbitrary categories which included algal cells and four size classes of detritus particles. The particle counts from six nymphs of each species were statistically compared using a multinomial chi-square test.

Habitat selection. A colonization experiment at the study site was used to compare habitat selection by the two mayflies. Common red brick ($6 \times 9 \times 20$ cm), which was found to be readily colonized by the nymphs, was used as an artificial substrate. Nine bricks were placed in a 3×3 grid pattern over 4 m^2 of stream bed in each of four habitats (defined in Results section). Current speeds were measured weekly by timing a float over a known distance (Welch 1948) and depths were also recorded. The bricks were placed on the stream bed on 19 April and were colonized for three months before their removal. During sampling the bricks were individually lifted from the stream and any loosened organisms were caught with an aquatic insect net. All organisms remaining on the brick and in the net were removed and transferred to 70% ethanol. In the laboratory all macroinvertebrates were identified and counted.

Morphological comparison. Twenty-five nymphs of various sizes of each species were fixed in KAAD to maintain proper measurements (Britt 1953). Measurements of head width, body length, profemur length, protibia length, and protarsus length were made using an ocular micrometer mounted in a dissecting microscope. Other structural differences were also noted.

Behavioral comparison. An aquarium simulating running water was used to explore behavioral differences. The aquarium contained a divider in the center and 19-litre/min pump to generate a current around the perimeter. To compare the ability of nymphs to land on substrate while drifting, two nymphs, one of each species, were released from a 2-dram vial just above and up-current of the brick substrate. Repeated with 25 different pairs of nymphs, the number of successful landings by each species was recorded.

RESULTS AND DISCUSSION

Phenology of nymph development. The youngest instars of both species were abundant in the autumn and most nymphs developed from autumn through early spring (Fig. 1). *S. pulchellum* nymphs were larger than *S. interpunctatum* nymphs on each of the sample dates except midsummer, which indicates some difference in their period of recruitment or time of maximum growth. Nonetheless, nymphs of all sizes of both species were found all year except during midsummer. Thus, the two species were not segregated by time of growth.

Adult emergence of both species began in late April and peaked in late May and early June. No *S. pulchellum* adults were collected after mid-August, although *S. interpunctatum* adults were collected through September. Both species appeared to be univoltine with recruitment and maturation spread over a long period of time.

Food type. The mouthparts of feeding heptageniid nymphs, armed with numerous spines and hairs, scrape and collect detrital and algal particles into the gut. Gut analyses indicated the size and type of food particles ingested by the nymphs. The counts of particles, classified by size and type, were totaled for each species (Table 1). Detritus particles accounted for 97% of the particles ingested. Using conversions for caloric content (Cummins 1973), the detritus composed 90.4% and 91.6% of the energy intake for *S. interpunctatum* and *S. pulchellum* respectively.

A significant difference in these enumeration data would be expected if the nymphs of each species preferentially fed in different microhabitats on the stone surface or if the mouthparts were sufficiently different to scrape different sizes of particles into the mouth. However, a multinomial chi-square test indicated no significant difference between species in the size and type of food particles ($P > 0.20$), thus the species did not partition the available food.

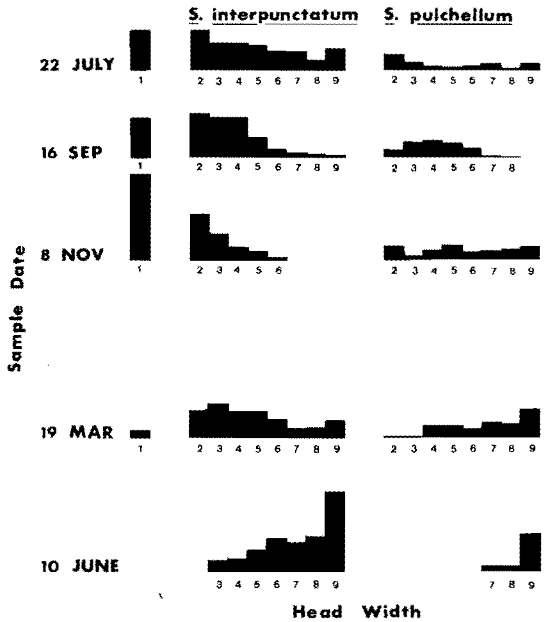

Fig. 1. Nymph development of the two mayflies illustrated by the head width frequency distribution for nymphs at each sample date. Very small nymphs could not be identified. Head width unit 1 is less than or equal to 0.50 mm, and each unit larger increases by 0.18 mm.

Table 1. Comparison of gut contents by particle counts.

		Number of particles (%)	
Type	Size (μ)	*S. interpunctatum*	*S. pulchellum*
Algae	> 2	3	3
Detritus	1.4– 2.8	58	56
Detritus	2.8– 5.6	27	26
Detritus	5.6–11.2	10	12
Detritus	11.2–22.4	2	3

[a]Based on total counts of 1710 particles for *S. interpunctatum* and 1427 for *S. pulchellum*.

Habitat selection. Four habitats were subjectively defined by relative current speed. Habitat A was in the slowest section of the stream in a shallow pool area along one edge. Habitats B and C were intermediate in current speed, with C having the faster current of the two. Habitat D was in the swiftest section of the stream. Measured water depths and current speeds illustrated that these habitats were not distinct (Table 2), but rather that they existed on a continuum from slow to fast current. Since the habitats were in close proximity most chemical characteristics would have remained approximately constant, however some chemical and physical characteristics correlated with current rate would have varied (Hynes 1970). Biological data from the colonization experiment reflected the difference between the habitats. Each invertebrate species maximally colonized a particular habitat while their numbers diminished in the faster or slower habitats (Table 3). Of the 14 species collected, one was collected most in habitat A, two in habitat B, four in habitat C, and seven in habitat D.

Table 2. Characteristics of the four habitats during the colonization experiment.

	Current Speed (cm/s)		Water Depth (cm)	
Habitat	Range	Mean	Range	Mean
A, shallow pool	3– 29	8	4–17	7.6
B, run	8– 55	18	25–40	29.9
C, run	25– 72	33	24–40	29.6
D, riffle	80–150	94	13–28	17.7

Table 3. Number of each species collected in the four habitats during the colonization experiment.[a].

		Number of Individuals				
		Habitat				
Order	Species	A	B	C	D	Total
Ephemeroptera	*Stenacron interpunctatum*	54	200	115	66	435
Ephemeroptera	*Stenonema pulchellum*	0	1	14	44	59
Ephemeroptera	*Caenis* sp.	1	16	5	3	25
Ephemeroptera	*Isonychia* sp.	2	0	8	11	21
Odonata	*Argia* sp.	4	6	16	3	29
Coleoptera	*Psephenus herricki*	1	6	8	6	21
Coleoptera	*Stenelmis* sp.	49	56	95	136	336
Trichoptera	*Protoptila* sp.	0	1	27	0	28
Trichoptera	*Hydropsyche* sp.	0	1	1	13	15
Trichoptera	*Cheumatopsyche* sp.	0	1	58	315	374
Trichoptera	*Chimarra* sp.	0	0	0	13	13
Diptera	Chironomidae	0	7	37	1	45
Gastropoda	*Goniobasis* sp.	8	17	18	21	64
Amphipoda	*Hyalella azteca*	8	0	0	0	8

[a]Species of which less than five individuals were collected are not shown.

The colonization experiment showed a highly significant difference in the selection of habitats by the two heptageniid species (Table 3, multinomial chi-square test, $P < 0.001$). *S. interpunctatum* was collected in all habitats, but was most numerous in habitat B where current speed was relatively low. *S. pulchellum* was almost completely absent from habitats A and B, but was most numerous in habitat D with a high current speed. Although the colonization experiment only sampled the summer distribution, the nymph development samples during the other seasons produced similar results. With one exception, *S. pul-*

chellum was mostly confined to areas of fast current, while *S. interpunctatum* was usually distributed throughout the stream. During the winter and early spring the current speed and volume increased greatly in Big Darby Creek. Samples taken at that time showed *S. pulchellum* distributed more generally across the stream bed, while *S. interpunctatum* was largely found in areas of slower current near the stream edge.

In habitat D, 89% of the nymphs were collected from bricks with both species. Moreover, the distribution of nymphs on the nine bricks showed an insignificant correlation (Spearman's test, $P > 0.20$) between the number of each species on each brick. Thus, the distribution of one species was independent of the other.

Morphological comparisons. *S. pulchellum* nymphs were significantly wider than *S. interpunctatum* nymphs of the same body length (ratio of head width to body length for *S. pulchellum*, 0.315; for *S. interpunctatum*, 0.289; Rank Sum Test, $P < 0.01$). Thus, for *S. pulchellum* the ventral surface area in contact with the substrate and thus frictional resistance to the current was greater. Also, *S. pulchellum* measurement of the profemora, protibiae, and protarsi in comparison to body length were significantly shorter than *S. interpunctatum* measurements ($P < 0.05$), which also increased frictional resistance.

S. pulchellum nymphs had a ring of hairs around the anterior margin of the head. This ring was absent in *S. interpunctatum* nymphs (Fig. 2). Normally, the nymphs faced the current and these hairs helped seal off the ventral side of the head from the current. Thus, *S. pulchellum* was able to withstand a greater current speed than *S. interpunctatum*.

Behavioral comparisons. When nymphs of both species were placed in an aquarium with moving water, *S. pulchellum* landed on the substrate sooner than *S. interpunctatum*. A controlled experiment (see Methods section) tested this response. Out of 25 paired trials in a 35 cm/sec current, seven *S. pulchellum* successfully landed on the substrate while only one of the *S. interpunctatum* nymphs was successful. A Fisher Sign Test for paired replicate

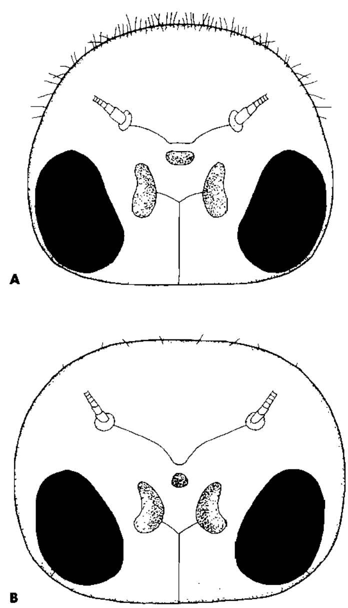

Fig. 2. Dorsal views of nymph heads, illustrating the presence of absence of hairs on the anterior margin: (A), *S. pulchellum*, (B) *S. interpunctatum*.

data showed a significant difference between the species responses (P = 0.035, one-tailed test). Characteristics on the nymphs' legs explained the difference. *S. pulchellum* legs were hairy and in particular had several stiff spines laterally on the tibia, whereas *S. interpunctatum* legs lacked spines (Fig. 3). When the *S. pulchellum* nymphs drifted, they kept their legs against their body and the tibiae parallel to the substrate. Thus, when contact with the substrate was made, the nymphs could use the tibial spines to land on the substrate.

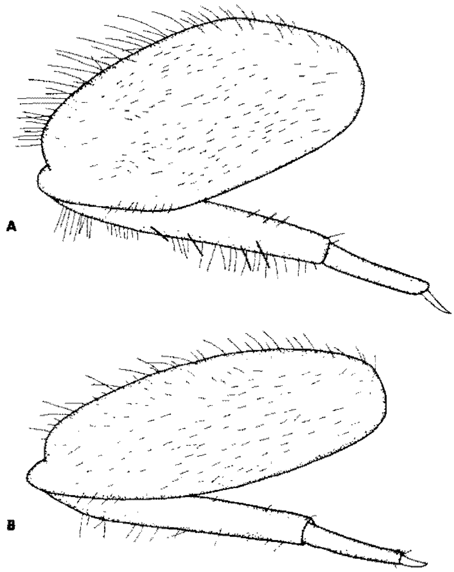

Fig. 3. Dorso-lateral view of the right hind legs of nymphs, illustrating the presence of spines on the tibia of *S. pulchellum*: (A) *S. pulchellum*, (B) *S. interpunctatum*.

CONCLUSIONS

These two mayfly species in Big Darby Creek significantly differed in their use of the space resource. *S. pulchellum* inhabited stones in swift water whereas *S. interpunctatum*, because of behavioral and morphological differences, primarily inhabited stones in calm water. Thus, the partitioning of the resource dimension of space by the two species resulted in fewer interactions between *S. interpunctatum* and *S. pulchellum*.

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