

Short Communication

Foraging Strategies and Co-existence in a Seasonal Environment

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Competition theory suggests that there should be a minimum ecological difference between stably coexisting, resource limited species. Species similar in most respects have generally been found to overlap rather little along niche axes defining their use of important resources. Such differences may lie in the what (which type of resource), the where (the habitat in which it is taken) or the when (the timing of utilisation) of resource use. Here, we are concerned with differences in the timing of resource use. These can be brought about by the staggering of life cycles (Hildrew, 1978), often associated with differential adaptation to some seasonally fluctuating aspect of the physical environment. However, in this communication we argue that species may coexist by virtue of contrasting foraging strategies which yield different returns under seasonally fluctuating biotic conditions.

The stream-dwelling larva of the caddisfly, *Plectrocnemia conspersa* (Curtis), spins a net for prey capture. A sit-and-wait predator, it takes advantage of the preys' movement when they arrive in its net via stream drift or locomotion over the bed. The alderfly larva, *Sialis fuliginosa* Pict., is not as strongly committed to a specific location, but is a more active forager. These species coexist in an iron-rich stream with a very low prey species diversity (Hildrew and Townsend, 1976). We have estimated consumption rates of *P. conspersa* (Townsend and Hildrew, 1978) and have found that the population, amongst its effects on prey, reduces the number of larval chironomidae by 84% in the two months after the August peak of prey density. In view of the great impact on their prey populations it is likely that the two species are limited by food supply. The numerical taxonomic composition of the prey taken by all sizes of each species is shown in Fig. 1A. The predators are generalists and resource overlap is great. In addition, they are to be found in all patch types in their environment, and both occur at all times of the year. What permits their coexistence?

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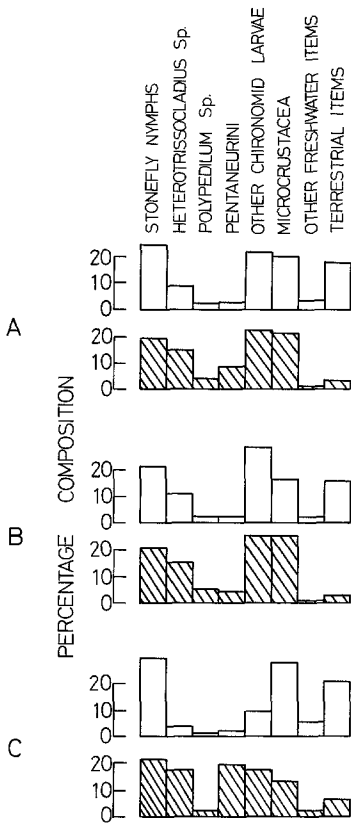


Fig. 1A-C. Numerical taxonomic composition of the diets of *Plectrocnemia conspersa* (open histogram) and *Sialis fuliginosa* (cross-hatched). A Overall; B June to October; C December to April

Those differences in diet which do exist can be attributed to the possession of a net by one of them. Firstly, quite a large component of the diet of *P. conspersa* is of terrestrial origin (mainly litter mites and winged insects). These items are washed downstream and caught in the caddis net. *S. fuliginosa* only rarely takes terrestrial prey. Secondly, *P. conspersa* takes larger stonefly nymphs and a greater proportion of small chironomid larvae in its diet than similar-sized *S. fuliginosa* (Fig. 2). The large stoneflies can only be subdued by use of the net and the small chironomids are more readily detectable when struggling in the net.

Differences in the foraging behaviour of the two predators are of particular significance in a seasonal context. In the summer, prey are very abundant and diet overlap is at a maximum (Fig. 1B). In the winter and early spring, prey numbers are very low, mainly as a consequence of losses to the predators. At this time of year chironomids are few and relatively immobile (some are tube-dwelling forms). Under these conditions *S. fuliginosa* has the more appropriate foraging strategy since its mobility will bring it into contact with chiro-

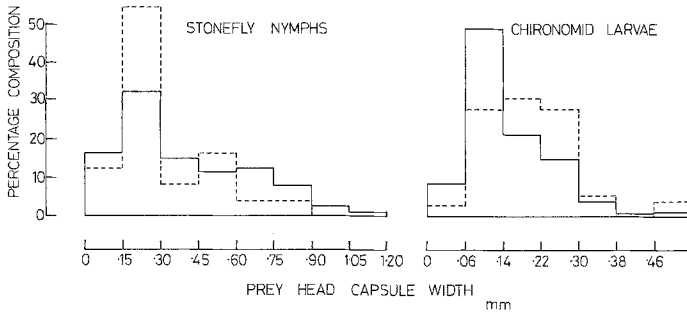


Fig. 2. Size class composition of diets of *Plectrocnemia conspersa* (solid line) and *Sialis fuliginosa* (dashed line). *P. conspersa* consumes significantly more chironomids smaller than 0.14 mm head capsule width (contingency table $\chi^2_{(1)} = 16.55$, $P < 0.001$) and more stoneflies larger than 0.58 mm head capsule width ($\chi^2_{(1)} = 4.55$, $P < 0.05$) when compared with *S. fuliginosa*

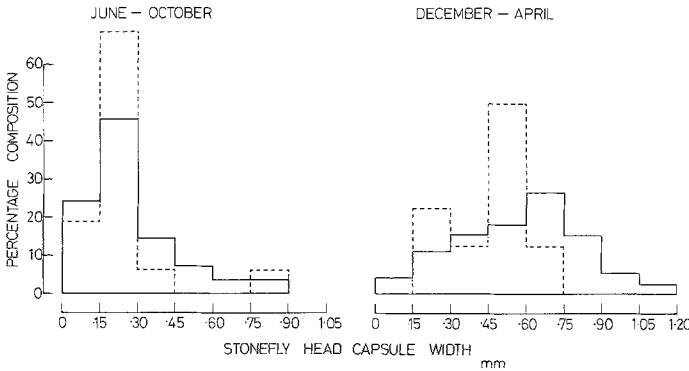


Fig. 3. Size class composition of stonefly prey taken by *Plectrocnemia conspersa* (solid line) and *Sialis fuliginosa* (dashed line) during the periods June to October, and December to April

nomid prey. In fact, it does do relatively better than *P. conspersa*. In the period December to April, chironomids still make up 57% of the diet of *S. fuliginosa* but only 16% of that of *P. conspersa* (Fig. 1C). At this time the diet of *P. conspersa* contains a greater proportion of stoneflies than *S. fuliginosa*'s, and only *P. conspersa* can take stoneflies which are reaching their maximum size (Fig. 3). It consumes 9 times more biomass of stonefly prey per unit weight of predator than *S. fuliginosa*. Both species can therefore be said to have a seasonal prey refuge (Reynoldson and Davies, 1970). At a time of year when food may be critically short, the different foraging strategies make separate food resources available, even in an environment with apparently little scope for specialisation.

Within a single generation, therefore, different foraging strategies may be important in the avoidance of competitive exclusion. We may further speculate that longer term changes in prey composition and abundance could alter the relative competitive advantage of contrasting predator species. This would increase the likelihood of their coexistence in a manner analogous to that suggested by Hutchinson (1961) for plankton species in a fluctuating abiotic environment.

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