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Foraging in a Patchy Environment by a Predatory Net-Spinning Caddis Larva: A Test of Optimal Foraging Theory

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Summary. The predatory larvae of the caddis *Plectrocnemia conspersa* (Curtis) cause significant prey depletion in a habitat in which prey are patchily distributed. Optimal foraging theory predicts that under these circumstances a predator should stay in any given patch until the prey capture rate there drops to a value equal to the average for the habitat as a whole. This was tested using a combination of field and laboratory data and the results were in broad agreement with the prediction. A second prediction is that the marginal capture rate should be higher in a habitat richer in prey and this was not supported. It is argued that by using a simple rule-of-thumb (constant giving-up-time) *P. conspersa* is able to approach the optimal solution for much of the time.

Introduction

The basic assumption of optimal foraging theory is that the behaviour which confers a forager with the greatest fitness is that which maximizes the net rate of energy gain (Pyke et al. 1977; Krebs 1978; Townsend and Hughes 1981). For a given distribution of food it is not especially difficult to work out the theoretical optimal allocation of search effort, by means of quite simple mathematical models. The question posed is whether real foragers perform like their hypothetical counterparts. If they do, support is gained for the assumption that the maximum rate of energy gain from food has been selected for in the evolution of foraging behaviour.

The net-spinning predatory larva of the caddis, *Plectrocnemia conspersa,* occurs in a habitat in which prey are very patchily distributed (Hildrew and Townsend 1976; Townsend and Hildrew 1979a). A large proportion of available prey, frequently 1–2%, is consumed each day in a simple stream community (Townsend and Hildrew 1978). The consequence of such prey depletion is that patch profitability declines with time and the predator may choose the point on the curve of diminishing returns when to leave one patch for another. In a habitat which contains patches of different profitability, optimal foraging theory predicts that a predator should stay in any one until the instantaneous net rate of energy intake there drops to a value equal to the average for the habitat as a whole (the marginal value theorem of Charnov 1976). We make the simplifying assumption that the average energy costs of setting up a net and of handling prey are constant in different patches and for different prey, so the form of prediction which we tested is that the marginal prey capture rate (the capture rate below which patches are abandoned) should be equal to the average for the habitat as a whole. This was tested using a combination of laboratory experiment to estimate marginal capture rate (reviewed briefly here but described fully in Hildrew and Townsend 1980) and field observation to assess average prey capture rates and predator distribution patterns. Ideally, the behavioural studies would also have been performed in the field but this was not practical and thus the inevitable element of artificiality was introduced.

Methods and Results

Average Capture Rates in the Field

We have gathered data on gut contents of a minimum of 30 fifth instar caddis larvae taken on each of 7 bimonthly occasions from the benthos of Broadstone stream (National Grid Reference TQ 436327), a small tributary of the River Medway in southern England (Hildrew and Townsend 1976). Experiments to determine half-lives of prey in the guts (corrected for prey size and stream temperature, details to appear in a later paper) have enabled us to convert diet figures into daily consumption rates. Table 1 shows the results for chironomid and stonefly prey, combined, on each occasion and averaged for the whole year. More than 65% of the diet of fifth instar *Plectrocnemia conspersa,* in numerical terms, consisted of larval chironomids and stoneflies. Most of the remaining prey were very small terrestrial items (Townsend and Hildrew 1979b). We have no data on gut half-lives in these cases but these are certain to be long because they are mainly heavily sclerotized litter mites and therefore resistant to digestion. Their contribution to overall number and biomass consumed per day is thus likely to be small.

Marginal Capture Rates in the Laboratory

Hildrew and Townsend (1980) have demonstrated the tendency of larvae to abandon established nets (and drift from the "patch" in the flowing

Table 1. Daily consumption rates in the field by *Plectrocnemia conspersa* on chironomid and stonefly larvae combined

	Number · d^{-1}	Biomass $\mu g \cdot d^{-1}$
April 1974	0.24	33
June 1974	1.27	110
August 1974	2.52	168
October 1974	0.39	52
December 1974	0.38	43
February 1975	0.26	33
April 1975	0.16	19
Average	0.75	65

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Table 2. Average giving-up-times for 5th instar *Plectrocnemia conspersa* larvae after various feeding regimes (standard errors are given). The numbers of predators used are shown in brackets. There are no significant differences between the means

	Average giving-up-time (days)
Fed nothing (10)	1.76±0.38
Fed 1 chironomid on arrival (9)	1.23±0.37
Fed 3 chrinomids per day for 6 days (5)	2.81±0.55
Fed 6 chironomids per day for 6 days (7)	1.74±0.65
Average (31)	1.74±0.24

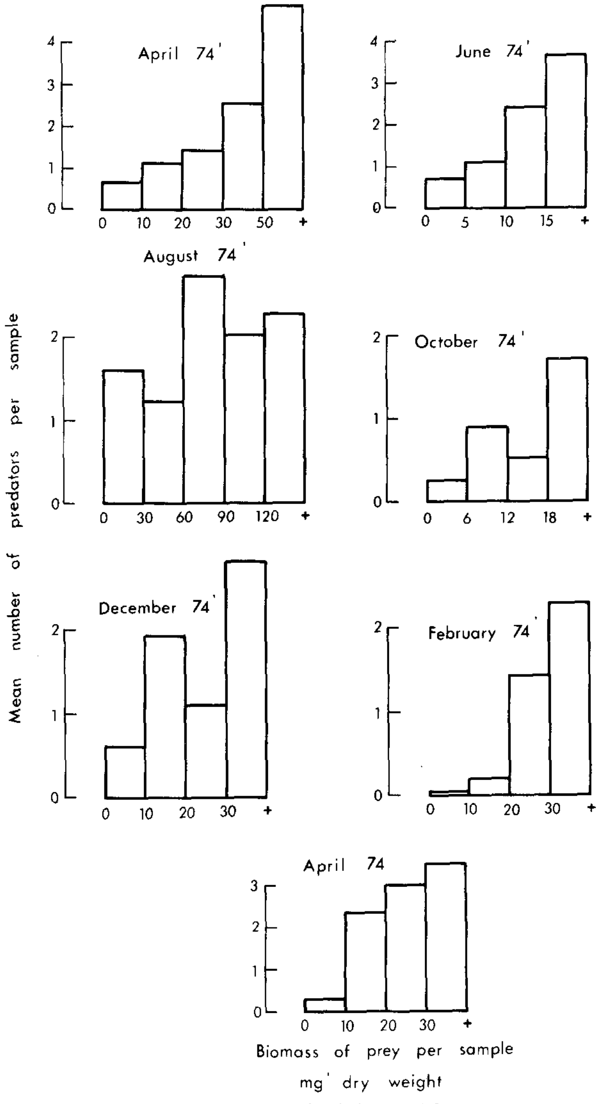

Fig. 1. Aggregative responses of 5th instar *Plectrocnemia conspersa* expressed as mean number of predators against combined biomass of chironomid and stonefly prey per 0.0625 m^2 sample of stream bed, in a number of prey biomass categories

column of water) if a prey item was not captured within a threshold time after a previous meal (the giving-up-time, g.u.t.). Four experiments were performed in artificial stream channels which provided appropriate environmental conditions of flow velocity, depth and temperature. In the first experiment, each fifth instar caddis was allowed to build a net but was not fed at all and the average time taken to abandon the net was calculated (this is not strictly a measure of g.u.t. but of time from establishment to abandonment). In the second experiment, each larva was fed on arrival in the "patch" with one prey item (a third instar larva of the chironomid *Heterotrissocladius marcidus* (Walker) with an approximate dry weight of 117 μg and representing the average sized prey item for fifth instar *P. conspersa*). Subsequently, it was not fed and the average time to net abandonment was calculated (g.u.t.). In the third and fourth experiments. larvae had been fed at a rate of 3 and 6 prey items per day for 6 days. Feeding then ceased and the g.u.t.s were measured. The results are shown in Table 2. There were no significant differences between the means (Kruskal-Wallis test, $p >$ 0.05). The overall average giving-up-time was 1.7±0.2 d. An estimate of marginal capture rate is given by the reciprocal of giving-up-time, provided prey do not vary much in size (Krebs et al. 1974). This assumption holds approximately so our estimate of marginal capture rate is 0.6 items or 69 μg dry weight per day.

The variability in results for g.u.t. within each treatment is notable. This is an inevitable consequence of life in a relatively stochastic environment where there is an appreciable probability of dislodgement by the current at any time.

Aggregative Responses of the Predators in the Field

On each of the 7 bimonthly sampling occasions, forty samples were taken with a Surber sampler (sampling area 625 cm^2, mesh 330 μm) from random locations within a 500 m stretch of Broadstone stream. The numbers of fifth instar *P. conspersa* and biomasses of chironomid and stonefly prey, combined, were calculated for each sample. The aggregative responses (expressed as number of predators against dry weight of prey) of *P. conspersa* on each sampling occasion are shown in Fig. 1. There was a clear aggregation of predators in richer patches on occasions other than August, a month when prey abundance was particularly great. The aggregative responses of *P. conspersa* indicate that this predator perceives the area over which it "forages" as a patchwork, a condition necessary for the application of optimal patch-use theory. (Note that this predator responds directly to prey distribution. The aggregative response is not a result of common preferences by predator and prey for certain physical environmental parameters – Hildrew and Townsend 1976).

Discussion

The marginal capture rate estimated for fifth instar *Plectrocnemia conspersa* in the laboratory was 0.6 items·d^{-1} or 69 μg·d^{-1}. This corresponds quite closely to the annual average capture rate in the field of 0.75 items·d^{-1} or 65 μg·d^{-1} and the results are therefore in broad agreement with a prediction of optimal foraging theory. However, a further prediction of the theory is that marginal capture rate should be higher (and g.u.t. lower) in a habitat richer in prey. The g.u.t. of *P. conspersa* appeared to be unaffected by recent feeding history (Table 2) and this is consistent with its being invariable. The major peak in predator consumption rate in August corresponded to a dramatic rise in prey availability. For the predator to have performed perfectly optimally it should have had a shorter g.u.t. in August, in which case an aggregative response would have been evident then, as in other months. It can be argued that *P. conspersa* has a fixed g.u.t. with a value appropriate to the average rate of prey capture through the year. This behaviour is apparently sufficient to lead to aggregation of predators in prey-rich patches in all months except August.

Note that it follows from the marginal value theorem of Charnov (1976) that animals should completely ignore patches where the instantaneous net rate of energy intake would already be below the average for the habitat. Yet, animals would generally be expected to "waste" some time and energy before discovering that such a patch was not in the optimal set. This is particularly significant for a predator such as *P. conspersa* which needs to allocate a setting-up-time, in building a net, before beginning to exploit a patch. The problem appears to be minimized, however, by a tendency during the first 30 min to delay net building and wander quite widely (sometimes resulting in leaving the patch) unless a prey item is encountered (Hildrew and Townsend 1980). The period of wandering therefore serves as a rough sampling of the likely richness at a location.

Two alternative hypotheses which have been proposed to account for behaviour of foragers in patchy environments are (i) hunting by expectation (Gibb 1962a, b) where foragers learn to expect a certain number of food items per patch, and, having found the expected number, leave the patch; (ii) hunting by time expectation (Krebs 1973) where foragers learn to spend a constant amount of time in each patch. Neither of these hypotheses is supported in the case of *P. conspersa.* A predator is likely to remain indefinitely and consume a large number of prey (unless dislodged by the current) at a site where prey are taken regularly (at a rate equal to or greater than one every 1.7 d). In other words, our data correspond more closely to a model of foraging involving a fixed giving-up-time (the threshold time from last prey capture until leaving the patch), rather than one based on a fixed number or time expectation.

Optimal foraging theory appears to require animals to be capable of sophisticated procedures in gathering and storing information, computing an optimal solution and carrying it out. This is particularly so in what is a relatively fluctuating and unpredictable environment. In the case of this caddis larva a rather simple rule-of-thumb (constant giving-up-time) apparently results in the predator approaching an optimal allocation of search effort for much of the time.

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