

## Search mechanism of a stream grazer in patchy environments: the role of food abundance

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**Summary.** The search behavior of the grazing stream insect *Baetis tricaudatus* (Ephemeroptera: Baetidae) was examined in field and laboratory experiments. Regardless of food abundance in experimental habitats, nymphs spent significantly more time in food patches than predicted if they had moved randomly with respect to patches. A significant reduction in movement rate within patches relative to movement rate between patches largely accounted for these results. The movement pattern within patches was highly systematic and in agreement with predictions of optimal foraging theory since food was uniformly distributed within patches. Between-patch search movements were affected by food abundance in the most recently grazed patch. Search intensity after departure from a patch was positively related to food abundance in the patch while movement rate after patch departure was inversely related to patch food level. These effects produced between-patch movement patterns that were suboptimal in the experimental habitats because they resulted in revisitation of previously depleted patches. However, differences between experimental and natural habitats in the spatial occurrence of patch types suggest that *Baetis* between-patch search behavior may be adaptive in natural habitats.

### Introduction

The food resources of many foragers are patchily distributed in the environment. If feeding efficiency is an important determinant of fitness, natural selection should favor behaviors which promote efficient location and utilization of patchily distributed food. The strategic rules which animals should follow to maximize feeding efficiency in patchy habitats (e.g., Charnov 1976, McNamara 1982) have been translated, for some cases, into within- and between-patch movement rules that should be employed to maximize net rate of energy intake (e.g., Pyke 1978a, 1978b, 1979, 1981; Zimmerman 1979, 1982). The appropriate optimal movement rules depend upon the amount of information a forager has available and can use in making decisions, the distribution of food resources within patches, and the distribution of patches in a habitat (Oaten 1977; Pyke 1978a). Studies of Pyke and Zimmerman explicitly demonstrate the intimate relationship between search behavior and foraging efficiency. However, such relationships have been examined

for a relatively restricted group of animals (largely nectarivores) and further developments in optimal foraging would benefit from a broader treatment of behavioral mechanisms used to solve foraging problems (Krebs 1978).

The microdistribution of attached microalgae on which most stream grazers feed is poorly known. Considerable variation in periphyton (largely diatom) abundance between stones (Jones 1974; Pryfogle and Lowe 1979) and within stones (Munteanu and Maly 1981) apparently occurs in streams, yet little is known if such variation is perceived as patchiness by grazers. Recent studies (Hart and Resh 1980; Hart 1981) indicate that the larval caddisfly grazer *Dicosmoecus gilvipes* perceives and responds to patchiness in periphyton abundance both between stones and on single stones. Similarly, movement patterns of the mayfly grazer *Baetis tricaudatus* on the top surface of stones (Wiley and Kohler 1984) suggest an allocation of foraging effort largely to relatively small areas, a pattern that would be expected if *Baetis* movements reflect responses to patchiness in periphyton abundance. The objectives of this study were: 1) to test the hypothesis that *Baetis* forages efficiently (sensu Sih 1982) in patchy habitats by spending more time in patches than predicted if individuals moved randomly (with respect to patches) in a habitat, 2) to define the search mechanism of *Baetis* through examination of search behavior in response to variation in resource abundance and patchiness, and 3) to compare observed within- and between-patch movement patterns with those predicted by optimal foraging theory to evaluate the adaptiveness of the *Baetis* search mechanism.

### Study animal

*Baetis tricaudatus* Dodds is a relatively small, lotic mayfly that occurs commonly and often abundantly in small to intermediate sized streams throughout North America (Bergman and Hilsenhoff 1978; Morihara and McCafferty 1979). In the study area it is bivoltine with spring- and summer-emerging generations. It occurs largely on the top and sides of stones throughout the day and night in regions of relatively fast current velocity (Kohler 1983). *Baetis tricaudatus* gut fraction (mass of gut + contents/body mass) shows little diel variation (S.L. Kohler, personal observation). Therefore, I assume that nymphs graze periphyton more or less continuously and that all movement patterns discussed below are foraging-related.

## Field experiments

### Methods

Research was conducted at Hunt Creek on the grounds of the Hunt Creek Trout Research Station (Michigan Department of Natural Resources), Montmorency Co., MI. Within the study area, Hunt Creek is a second order stream with relatively stable flow and thermal regimes. Summer water temperature seldom exceeds 16° C although diel fluctuations may reach 6–7° C. McFadden et al. (1967) give a more detailed description.

The study site was a 15 m long riffle between two small, moderately shallow pools that was characterized by relatively uniform current and depth. Summer current velocity at 2.5 cm above the bottom ranged between 25 and 45 cm/s while depth ranged between 15 and 25 cm.

Cement artificial substrates (9 × 11 × 2 cm) were used in all experiments. Substrates were placed so as to create differences in food abundance between two groups of substrates. One group of 12 substrates was placed on the stream bottom in a region that was shaded for most of the day. Another group of 12 substrates was elevated 10–15 cm above the bottom in a region that was not shaded. Each elevated substrate was held by a buret clamp attached to a steel rod driven into the stream bottom. There were two columns of rods; each column containing three rods. Each rod supported two substrates with the top surface of substrates oriented parallel to the current. Substrates were given 3–4 wk for periphyton colonization. Substrates placed on the stream bottom were subject to grazing pressure from the dominant grazers in Hunt Creek, *Glossosoma nigrior* (Banks) (Trichoptera: Glossosomatidae) and *Baetis tricaudatus*. Elevated substrates, however, were not colonized by *Glossosoma*. Preliminary studies showed that this difference allowed elevated substrates to attain significantly greater periphyton biomass levels than non-elevated substrates. This difference was augmented by increasing phosphate levels delivered to elevated substrates as phosphorus is known to be limiting to primary producers in streams (Elwood et al. 1981). A 19 L carboy was placed on a scaffold about 2 m upstream of each column of elevated substrates. Carboys contained approximately 3000 mg PO<sub>4</sub>-P/L solutions made from phosphoric acid and stream water. Solutions were released slowly from about 0800 to 2000 (carboys were refilled when necessary) for 4–7 days before the start of an experiment. During this period, animals (largely blackfly larvae and *Baetis*) were removed daily from elevated substrates.

Each group of substrates was subdivided into two groups: four experimental substrates and eight substrates for replicate periphyton biomass estimation. Experimental substrates were selected from elevated substrates for apparent uniformity in periphyton biomass and distribution. After removing all animals, periphyton patchiness was manipulated on experimental substrates by scraping areas of the substrates with a hard brush to remove periphyton. There were two patchiness treatments: 1) low patchiness = 20, 1 cm<sup>2</sup> periphyton patches/substrate, and 2) high patchiness = 9, 1 cm<sup>2</sup> periphyton patches/substrate. Patches were regularly spaced on top surfaces and were separated on all sides by 1 or 2 cm on low or high patchiness substrates, respectively. Scraped periphyton from top surfaces was rinsed into jars and preserved with 4% formalin. Periphyton

was also removed from the sides but was not saved. Two substrates were treated in this manner each day between 1400 and 1600 and placed in the stream at locations chosen for similar current velocities and depths. One substrate from each of the two-groups (non-elevated, elevated) was chosen at random each day. Each treatment combination was replicated once. Two non-experimental substrates from each group were sampled at random each day and periphyton was scraped from top surfaces, rinsed into jars, and preserved with 4% formalin.

Periphyton biomass was estimated gravimetrically using standard procedures (Clark et al. 1979). Periphyton was allowed to settle to the bottom of sample jars for several days before about 75% of the sample volume was decanted using a syringe. Samples were then centrifuged at 1,000 G, decanted, and rinsed several times with distilled water. Samples were transferred to tared crucibles, dried at 105° for 24 h to determine dry mass, and then ashed 1 h at 550° C to determine ash free dry mass (AFDM).

The foraging behavior of *Baetis* individuals colonizing experimental substrates was monitored continuously using time-lapse cinematography. A detailed description of the technique is given in Wiley and Kohler (1981). Briefly, each substrate was filmed at 2 frames/min using an 8 mm camera mounted on a tripod and focused through a plexiglass port which broke the surface of the water. Filming always commenced no later than 1800. Exposures were made with the aid of a strobe flash which provided very short duration (0.0005 s), low intensity (<20 lux) flashes. At a filming rate of 2 frames/min, such a flash has not been observed to affect *Baetis* behavior (S.L. Kohler, personal observation). A filming rate of 2 frames/min was chosen as it allowed continuous filming of each replicate without changing film during a trial and movements of individuals could easily be followed and subtle changes in activity levels detected. Each experimental substrate was filmed for about 18 h.

Films were analyzed frame-by-frame using an 8 mm analytical projector. *Baetis* movements were followed and recorded using a digitizing tablet interfaced with a microcomputer. Movement rate calculations were standardized by the body length of each individual to allow comparison of movement rate between *Baetis* generations.

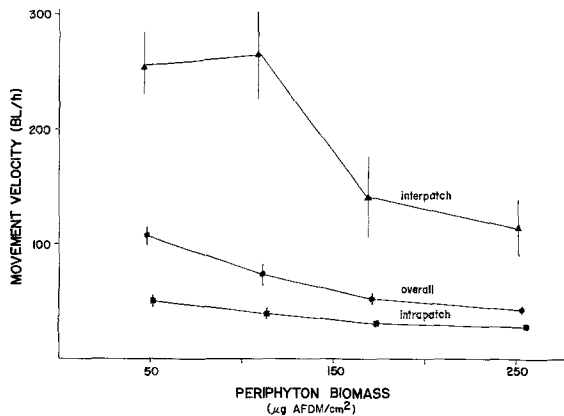
Experiments were conducted in May and September, 1981. These dates fell during the later stages of *Baetis* development in spring- and summer-emerging generations, respectively. Water temperature (daily range: May, 7–14° C; September, 9–14° C) and current velocity did not differ appreciably between dates. The September experiment was conducted to obtain information on *Baetis* foraging behavior at two additional levels of food abundance. As a result, observations were made at four levels of periphyton abundance. These will be referred to by their rank abundance with the lowest level assigned a rank of one. The lowest and highest periphyton abundance levels were attained in September. Also, high patchiness substrates were not sufficiently colonized by *Baetis* in May to merit inclusion of that treatment in the experimental design. Therefore, that treatment was omitted from the September study.

### Results

While on top surfaces, colonizing individuals spent most of their time within periphyton patches regardless of food abundance (Table 1). If nymphs moved at random across

**Table 1.** Time allocation of animals colonizing substrates of varying food abundance. Periphyton abundance is the mean value for manipulated, filmed substrates. Values in parentheses are the range observed on unmanipulated replicate substrates. Expected proportion of time spent within patches is the value predicted if animals moved randomly over the top surface of substrates. *P* value is the probability that the observed and expected proportions are equal (*t*-test)

Periphyton abundance ( $\mu\text{g AFDM}/\text{cm}^2$ )	Number of individuals observed	Total time observed (h)		Proportion of time spent within patches ( $\bar{x} \pm \text{SE}$ )		
		Day	Night	Observed	Expected	<i>P</i>
48(40–81)	7	0	3.8	$0.71 \pm 0.03$	0.20	<0.001
111(93–128)	6	13.1	7.1	$0.82 \pm 0.06$	0.20	<0.001
171(144–180)	8	6.1	7.5	$0.75 \pm 0.05$	0.20	<0.001
253(214–271)	14	7.6	43.1	$0.67 \pm 0.04$	0.20	<0.001



**Fig. 1.** Relationships between intrapatch, interpatch, and overall movement velocity ( $\bar{x} \pm \text{SE}$ ) at night and periphyton abundance

top surfaces, they would be expected to spend about 20% (i.e.,  $20 \text{ cm}^2/99 \text{ cm}^2$ ) of the time within patches. The proportion of time spent within patches was significantly greater than 20% in all cases (Table 1) and did not vary significantly between food levels (ANOVA of angular transformed proportions,  $P > 0.15$ ).

*Baetis* movements in patchy habitats can be divided into two categories: within-patch or intrapatch movements and between-patch or interpatch movements. Interpatch movement velocity at night (expressed as body lengths (BL) moved/h) was significantly greater than intrapatch velocity at all levels of periphyton abundance (Fig. 1; Mann-Whitney test,  $P > 0.05$ ). Intrapatch and interpatch movement velocity and, consequently, overall movement rate decreased significantly with increasing food abundance (Fig. 1; Kruskal-Wallis test,  $P < 0.05$ ). Dunn's nonparametric multiple comparisons procedure (Hollander and Wolfe 1973) showed that differences in intrapatch velocity were significant for periphyton abundance ranks 1 vs. 3 ( $P < 0.1$ ) and 1 vs. 4 ( $P < 0.05$ ). Interpatch velocity was significantly different for food level ranks 1 vs. 3 ( $P < 0.1$ ), 1 vs. 4 ( $P < 0.05$ ), and 2 vs. 4 ( $P < 0.05$ ). All possible overall movement velocity comparisons were significantly different at the 10% level or less except for the comparison of ranks 3 and 4. Overall movement velocity at the highest food level was sufficiently reduced relative to other resource levels such that it did not differ from intrapatch movement velocities at the lowest and second lowest food levels (Mann-Whitney test,  $P > 0.25$ ).

### Patch visitation

Nymphs remained significantly longer on substrate top surfaces as food abundance increased (Table 2; Kruskal-Wallis test,  $P < 0.01$ ). This largely resulted from a significant decrease in patch visitation rate (Table 2; Kruskal-Wallis test,  $P < 0.01$ ) and an increase in the amount of time spent within patches. The reciprocal of patch visitation rate times the mean proportion of time spent within patches gives an estimate of the average time spent within each patch per visit. This value ranged from 3.9 to 17.6 min for the lowest and highest resource levels, respectively.

*Baetis* frequently revisited patches. Revisiting a patch before locating a different patch will be referred to as immediate revisitation. This was considered when patch visitation rates were calculated. The effect of immediate revisitation on patch visitation rates increased with increasing food level (Table 2) because immediate revisitation frequency increased significantly with periphyton abundance (Table 3;  $\chi^2 = 17.3$ , 3 df,  $P < 0.001$ ). Patches were frequently revisited immediately more than once (Table 3). Pooling data for the two lowest and two highest food levels, the proportion of patches revisited immediately more than once was significantly greater at higher than at lower food levels ( $\chi^2 = 5.53$ , 1 df,  $P < 0.05$ ).

If a forager reduces the resource levels in a patch, subsequent visitors should spend progressively less time feeding in the patch. Foragers spent less time in patches during revisits (including immediate revisits) than during first visits more frequently than not (Table 4). If food levels are reduced during first visits, the proportion of revisits which are shorter than first visits should be greater than 0.5 for all food levels. This proportion was significantly greater than 0.5 for all food levels except the lowest periphyton level (Table 4). Nonetheless, foragers often spent more time in a patch during a revisit than during the first visit to the patch. This may partly be a function of the efficiency of the within patch search mechanism of *Baetis* for patches of the scale used in this study. Nymphs were rarely observed to thoroughly graze a patch before leaving the patch, even at the highest food level.

### Interpatch movements

Laboratory observations indicated that *Baetis* does not locate patches visually. Rather, interpatch areas are sampled by "grazing" and nymphs require mouthpart contact with algae to indicate that a patch has been located (S.L. Kohler, personal observation). Therefore, it is necessary to consider

**Table 2.** Time spent on top surface and rate at which patches are encountered (mean(SE)) at night as a function of periphyton abundance

Rank periphyton abundance	Time spent on top surface (h)			Patch visitation rate (#/h)	
	<i>n</i>	Mean(SE)	Range	Immediate revisits included	Immediate revisits excluded
1	7	0.49(0.14)	0.09–1.03	10.92(1.10)	10.48(1.21)
2	4	1.89(0.31)	1.24–2.62	6.68(0.91)	6.97(0.77)
3	5	1.93(0.49)	0.94–3.43	4.75(0.86)	3.50(0.53)
4	11	4.49(0.95)	1.03–10.68	3.32(0.29)	2.29(0.29)

**Table 3.** Proportion of patches visited which were revisited immediately (before a different patch was visited) once and more than once

	Rank periphyton abundance			
	1	2	3	4
Number of patches	41	51	36	99
1 immediate revisit	0.049	0.333	0.194	0.374
>1 immediate revisit	0.000	0.098	0.139	0.162

**Table 4.** Frequencies of patch revisitation in which foragers spent more or less time in the patch than the first time the patch had been visited. P value is the probability that the proportion of revisits shorter than the first visit is equal to 0.5 ( $\chi^2$  test)

Rank periphyton abundance	Number of revisits			<i>P</i>
	Longer than first visit	Shorter than first visit	Proportion shorter than first visit	
1	8	13	0.62	>0.25
2	8	31	0.79	<0.01
3	7	26	0.79	<0.01
4	14	87	0.86	<0.01

**Table 5.** Proportion of time that foragers moved to the nearest or second nearest patch. Moves which resulted in revisitation of the original patch are not included

Rank periphyton abundance	<i>n</i>	Nearest	Second nearest
1	33	0.79	0.18
2	43	0.72	0.26
3	29	0.66	0.24
4	101	0.78	0.17

general interpatch movement patterns to describe *Baetis* search behavior.

Eight patches generally surrounded a given patch on a substrate. The four patches immediately upstream, downstream, and to the right and left of a patch will be considered the nearest patches (excluding the original patch). Patches located diagonally from a patch will be considered the second nearest patches. Foragers moved to one of the four nearest patches on most occasions (Table 5) at all food levels ( $\chi^2 = 2.40$ , 3 df,  $P > 0.25$ ). The next patch that a forager encountered was rarely outside the eight patches that normally surrounded the original patch (4.9% of the time

**Table 6.** Overall directionality of interpatch movements. The proportion of interpatch movement sequences which result in visitation of the nearest patch in one of four possible directions relative to the original patch. Data pooled over all food levels

<i>n</i>	Upstream	Downstream	Left	Right
158	0.22	0.24	0.27	0.27

**Table 7.** Total distance (BL) moved ( $\bar{x} \pm SE$ ) between successive patches visited at the extreme levels of food abundance

Periphyton abundance	Periphyton abundance	
	Low	High
	Excluding immediate revisitation	Immediate revisitation only
	$5.72 \pm 0.51$ ( <i>n</i> = 30)	$8.86 \pm 0.67$ ( <i>n</i> = 94)
		$5.82 \pm 0.64$ ( <i>n</i> = 47)

for all food levels pooled). *Baetis* moved to either of the four possible nearest patches with equal probability (Table 6). This occurred even though nymphs generally maintained a positive orientation with respect to the current while moving in any direction.

Although food abundance did not appear to affect search attributes which determine the location of the next different patch located (i.e., the overall direction of movement), food level did appear to affect other aspects of interpatch movement. The mean total distance moved in each interpatch movement sequence was significantly longer at the highest than at the lowest food level (Table 7;  $t = 2.57$ ,  $P < 0.02$ ). In addition, foragers moved a similar distance in immediate revisits at the highest food level as they did in moving to a different patch at the lowest food level ( $t = 0.12$ ,  $P = 0.91$ ). This suggests that search intensity in the immediate vicinity of a recently departed patch is affected by food level in the patch. This may provide a simple explanation for the relatively high immediate revisitation frequencies observed at higher food levels.

**Laboratory experiments**

*Methods*

Food levels and between patch variation in food abundance could not be precisely controlled in the field. To obtain behavioral observations under more controlled conditions,

laboratory experiments which employed a membrane filter technique to create patches were conducted. All experiments were performed in a constant environment room that maintained water temperature at 12° C.

A diatom community was maintained on artificial substrates in small (19 L) flowing water systems (Gee and Bartnik 1969) which contained stream water and dechlorinated tap water. To create patches, diatoms were gently scraped off substrates into a beaker containing 200–400 mL of water. This suspension was thoroughly mixed and the cell density (cells/ml) estimated from counts of at least 36 fields in a Neubauer haemocytometer. The requisite suspension volume was then filtered through a 47 mm gridded membrane filter (0.45 µm pore size) using low suction to obtain the desired patch cell density (cells/cm<sup>2</sup>). The filter was then carefully placed on the surface of membrane-filtered water in a petri dish and the dish was covered, placed in a well illuminated area, and left undisturbed for at least 18 h. By this time, the diatoms became firmly attached to the filter and the filter could be submersed. The filter was removed from the dish and square patches (0.09 cm<sup>2</sup>) were cut from the filter along grid lines using a stencil knife. The filter and patches were kept moist during the cutting procedure. Using this procedure, diatom densities on filters were always within 5% of desired densities.

A template was used to mark the desired location of patches on a cement artificial substrate. A thin layer of silicon sealant was applied to each marked area and a pre-cut patch was placed on the sealant. Any excess sealant was scraped off. The sealant firmly held the patches in place but did not appear to adversely affect either diatoms or foragers. At the end of an experiment, patches could be removed from a substrate with a razor blade, placed on microscope slides, dried, and cleared with immersion oil for later inspection.

Artificial substrates contained 25 patches in a rectangular array with each patch separated by 1 cm on all sides. Three patch types were used: 1) low = 1 × 10<sup>5</sup> cells/cm<sup>2</sup>, 2) intermediate = 5 × 10<sup>5</sup> cells/cm<sup>2</sup>, and 3) high = 10 × 10<sup>5</sup> cells/cm<sup>2</sup>. A single substrate was used in each trial. The substrate contained two patch types (the low patch type was always used) arranged systematically so that two adjacent patches were not the same type. A substrate was prepared between 0730 and 0900 and placed in a small experimental stream (modified from Vogel and LaBarbera (1978)) containing stream water and dechlorinated tap water.

*Baetis tricaudatus* nymphs used in this study were collected from Hunt Creek, returned to the laboratory, and held in moderately large (150 L and 75 L) flowing water systems (Gee and Bartnik 1969) where they were fed diatoms *ad libitum*. Prior to a feeding experiment, several individuals were starved 24 h in a small flowing water chamber (Wiley and Kohler 1980). With the current velocity in the experimental stream set at 10 cm/s, a single individual was placed on the top of the substrate using a wide-bore pipette. The animal was pipetted into a plastic cylinder placed near a patch at the downstream end of the substrate. The cylinder had small rectangular regions removed from the upstream and downstream sides and replaced with netting to allow water to flow through it. The cylinder was removed after the animal became established on the substrate. The current velocity was then slowly increased to 20 cm/s.

Each foraging bout was recorded on film at a filming rate of 12 frames/min. A trial was stopped when the individ-

ual stopped feeding or moved off the top surface of the substrate. Three to five trials were conducted per day between 0900 and 1500. A new substrate was used after 12 or more patches had been depleted. Individuals were not used more than once.

These experiments provided information on search behavior within patches and after leaving a patch. An additional experiment provided data on search behavior prior to locating a patch. Two procedures were followed. The first was identical to that described above except that the substrate did not contain any patches. In the second procedure, three barren substrates were placed contiguously in the experimental stream and 30 individuals (all fed *ad libitum* or all starved 24 h) were introduced to the substrates in still water by pouring them from a beaker through a funnel over the substrates. The animals quickly became established on the substrates and the current velocity was slowly increased to 20 cm/s. Trials began 2.5 h before the end of the light cycle and lasted for another 2.5 h into the dark cycle of a natural photoperiod. The middle substrate was filmed at 2 frames/min using a strobe flash.

Films were analyzed frame-by-frame by projecting them onto tracing paper and plotting the movements of individuals. Movements were analyzed in 10 frame sequences for movement velocity and a measure of search intensity which relates the area searched to the area of the smallest circle which circumscribes the sequence of movements. Bond (1980) refers to this measure of search intensity as thoroughness, *T*, and indicates that it may be approximated by:

$$T = 1 - e^{-Lw/\pi D^2}$$

where *L* = path length, *w* = path width, and *D* = diameter of the smallest circumscriptive circle. I used body lengths as the unit of distance in all calculations. Path width was estimated to be equal to nymphal head capsule width which was closely approximated by 0.15 BL. Movement velocity and thoroughness were determined for 10 frame sequences for all between-patch movements. Within-patch search parameters were calculated for the entire sequence of within-patch movements. To allow comparison of movement velocity between all laboratory and field studies, it was necessary to calculate movement velocity for films exposed at 12 frames/min as though they had been exposed at 2 frames/min. That is, the position of an animal at every sixth frame was used to calculate movement velocity for films exposed at 12 frames/min.

## Results

Following terminology in Bond (1980), *Baetis* search behavior in patchy habitats can be classified into three modes corresponding to search prior to locating a patch (extensive search), within a patch (intensive search), and after leaving a patch (post-intensive search). Pooling all observations within each search category, measures of both search parameters analyzed varied between search categories (Table 8). The differences were highly significant (ANOVA, *P* < 0.001) as were all pairwise comparisons using the Scheffe method (*P* < 0.01).

### Intensive search

High intrapatch thoroughness values result from a dramatic decrease in movement velocity relative to between-patch

**Table 8.** Overall search parameter values ( $\bar{x} \pm \text{SE}$ ) for each search category. Results are based on observation of 60 individuals, of which 30 are from the day-night extensive search trials

Search category	<i>n</i>	Thoroughness	Movement velocity (BL/h)
Extensive	51	$0.033 \pm 0.003$	$190.78 \pm 15.6$
Intensive	30	$0.741 \pm 0.014$	$35.04 \pm 1.47$
Post-intensive	208	$0.123 \pm 0.007$	$314.47 \pm 14.6$

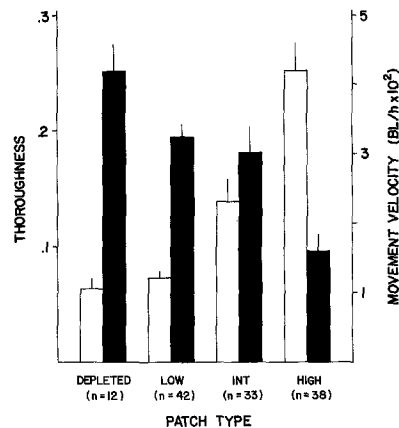
rates combined with a highly systematic pattern of movement within patches. Higher (or lower) thoroughness values could conceivably be attained but it is not immediately clear if changes in *T* relative to those values observed would be advantageous (in terms of net rate of energy intake) to foragers. For a given patch, *D* has an upper bound so *T* can be increased only by increasing *L*. However, increasing *L* increases the probability that resource points already visited and depleted within a patch will be revisited. Since food was uniformly distributed within each patch, an optimum *L* exists which minimizes revisitation but ensures that the total surface area of the patch will be grazed. If *S* is the length of a square patch, *L* is optimized when  $L = (S/w)S$ . Assuming no overlap between the *S/w* paths and, as before, that  $w = 0.15 \text{ BL}$ , the optimum *L* for square patches results in  $T = 0.72$ . This is very close to the observed value of 0.74 (Table 8).

#### Extensive search

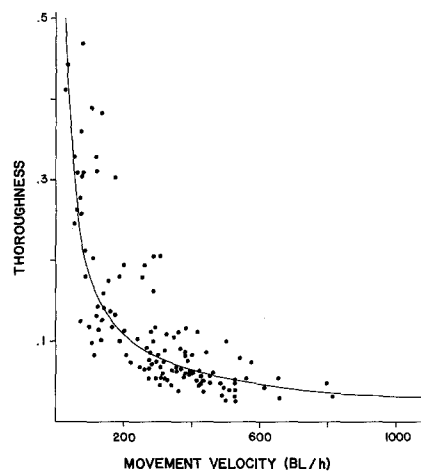
Information on extensive search (Table 8) is presented only for data from the day-night studies. The results are derived from individuals that moved from side to top surfaces of substrates at night and proceeded to move across top surfaces, apparently searching for food. Such diel microdistributional changes have previously been observed in mayflies (e.g., Elliott 1968; Bailey 1981) and have been suggested to be involved with feeding on algae which is most abundant on top surfaces (e.g., Chapman and Demory 1963; Elliott 1967; Hynes 1970; Waters 1972). Therefore, I assume that these movement patterns best reflect *Baetis* extensive search on natural substrates. Low extensive search thoroughness results from the tendency of nymphs to move more or less in straight lines at relatively high movement velocities (Table 8). There were no differences between starved or recently fed animals with respect to either thoroughness of search ( $t_{49} = 1.10$ ,  $P > 0.2$ ) or movement velocity ( $t_{49} = 0.65$ ,  $P > 0.2$ ).

#### Post-intensive search

The hypothesis that patch quality affects search intensity after leaving a patch was tested by comparing search parameters over all patch types for the first 10 frames (50 s) after a patch was departed (Fig. 2). In some cases, the measures were based on <10 frame movement sequences if a patch (either a different patch or the same patch) was located in <50 s. Visits and subsequent departures from patches which had previously been visited and grazed to depletion (i.e., the entire patch surface was white; inspection under a compound microscope showed that >90% of the diatoms had been removed) were included in the analysis. Search intensity immediately after leaving a patch increased significantly with increasing patch quality (AN-



**Fig. 2.** Relationships between movement velocity (solid bar), thoroughness (open bar), and patch type for the first 50 s after leaving a patch. Depleted patches are patches which had previously been grazed to depletion. Error bars are 1 SE

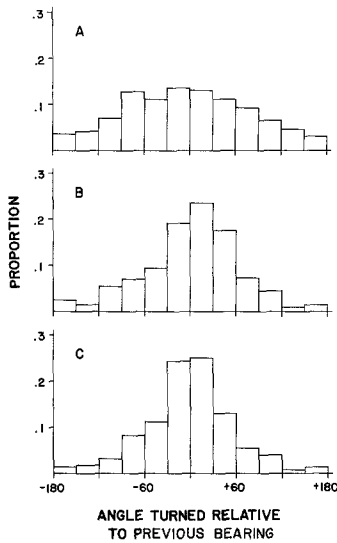


**Fig. 3.** Relationship between thoroughness (*T*) and movement velocity (*V*) for all 50 s post-intensive search sequences. The relationship is described by the equation  $T = 7.56V^{-0.8}$ ,  $R^2 = 0.68$ ,  $P < 0.001$

OVA,  $P < 0.001$ ). All possible pairwise contrasts (Scheffe method) were significant at the 5% level except for the comparison between depleted and low food patches. Conversely, movement velocity after patch departure decreased with increasing quality of the preceding patch (Fig. 2; ANOVA,  $P < 0.001$ ). All pairwise comparisons were significant ( $P < 0.05$ ) except that between low and intermediate patch types.

The relationships presented in Fig. 2 suggest a negative relationship between search intensity and movement velocity immediately after patch departure (Fig. 3). It seems intuitive that rapid movement through an area should preclude thorough search. However, low movement velocity does not necessarily ensure thorough search. For example, the thoroughness value for an individual that takes 10 movements in a straight line at 50 BL/h is 0.045. From Fig. 3, this thoroughness value would be expected for a substantially greater movement velocity. Therefore, differences in movement velocity are not sufficient to account for differences in search intensity and patterns of movement after patch departure must be considered.

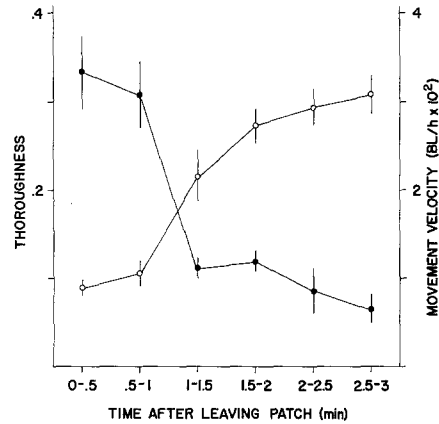
Frequency distributions of the angle turned relative to



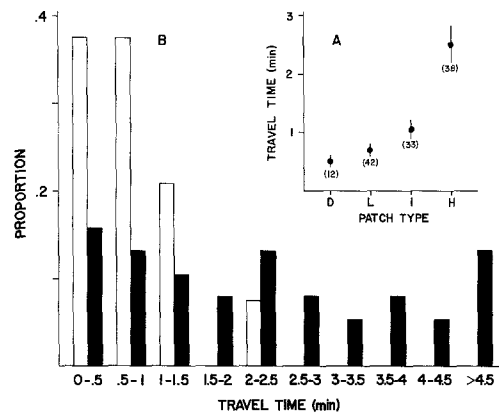
**Fig. 4.** A–C. Frequency distributions of the angle turned relative to the previous bearing for: **A** the first 50 s after leaving a high patch type ( $n=259$ ), **B** the first 50 s after leaving low and depleted patch types ( $n=204$ ), and **C** extensive search movements ( $n=276$ ). A turning angle of  $0^\circ$  indicates no change in direction between movements. Positive and negative angles denote right and left turns, respectively

the previous bearing were significantly different from uniform for post-intensive (Fig. 4a, b) and extensive (Fig. 4c) search ( $\chi^2$  test,  $P<0.001$ ). In all cases, turns resulting in a reversal of direction (i.e.,  $+90^\circ$  to  $+180^\circ$ ;  $-90^\circ$  to  $-180^\circ$ ) were rare. However, the proportion of such turns after leaving the high patch type was significantly greater than during extensive search ( $\chi^2=21.7$ , 1 df,  $P<0.001$ ) or than after leaving low quality and/or depleted patches ( $\chi^2=10.4$ , 1 df,  $P<0.01$ ). If only turns between  $-90^\circ$  and  $+90^\circ$  are considered, the frequency distribution of turning angles for movements after leaving the high patch type does not differ from a uniform distribution ( $\chi^2=3.345$ , 11 df,  $P>0.25$ ). The other frequency distributions are significantly nonuniform between  $-90^\circ$  and  $+90^\circ$  ( $P>0.25$ ) but are not significantly different (Kolmogorov-Smirnov two-sample test,  $P>0.1$ ). Also, movements after leaving the high patch type have a greater tendency to be in the same direction as that of the previous movement (52%,  $n=230$ ) than movements prior to encountering a patch (45%,  $n=257$ ), but the difference is not significant ( $\chi^2=1.9$ , 1 df,  $P>0.1$ ). Therefore, extensive search movements and movements after leaving low quality or depleted patches are more directional and have a greater tendency to alternate right and left turns than movements after leaving high quality patches. Both of these factors will tend to produce movements in more or less straight lines (Pyke 1978a) which, as shown in the example above, will result in low search intensity, independent of movement velocity. Movements after leaving high quality patches are not strongly directional and are more likely to result in a reversal of direction relative to the previous movement. At low movement velocities, this produces movements concentrated around the previously grazed patch and increases the probability that the patch will be encountered again.

Search intensity and movement velocity after departure from high quality patches decayed rapidly to values similar to those observed for movements after departure from low



**Fig. 5.** Changes in thoroughness ( $\bullet$ ) and movement velocity ( $\circ$ ) over time after leaving a high quality patch. Values are mean  $\pm$  SE. Sample sizes are 16 for the first two time intervals, 14 for the second two time intervals, and 10 for the final two time intervals



**Fig. 6.** A, B. Relationships between the time taken to locate the next, different patch and the quality of the previously grazed patch. **A** Travel time ( $\bar{x} \pm$  SE) to the next patch after leaving depleted **D**, low **L**, intermediate **I**, and high **H** patch types. Sample sizes in parentheses. **B** Frequency distributions of travel times after leaving low (open bar) and high (solid bar) patch types

quality patches (Fig. 5). However, the initial response to having just grazed a high quality patch (i.e., low movement velocity, high search intensity) was maintained for a sufficient duration that the amount of time taken to locate the next, different patch (travel time) increased with increasing quality of the previously grazed patch (Fig. 6a). Travel time differed significantly between all patch types (Mann-Whitney test,  $P<0.05$ ) except for comparisons between depleted and low quality patches ( $P>0.25$ ) and between low and intermediate patch types ( $P>0.1$ ). These results are in agreement with relationships between movement velocity, search intensity, and identity of the preceding patch shown in Fig. 2. As a result of these relationships, the average travel time between patches in a habitat will depend upon the range of patch types available and their respective probabilities of encounter. The greater the range of patch types, the greater will be the variance associated with the mean travel time in a habitat. The stochastic aspects of travel time are more apparent when frequency distributions of travel time are considered (Fig. 6b). Travel time is reasonably predictable if the preceding patch is of low quality (75% of the values are  $<1$  min), but not if the preceding patch

is of high quality. The frequency distribution of travel times after departure from high quality patches is not different from uniform ( $\chi^2 = 2.53$ , 4 df,  $P > 0.25$ ) which indicates that the probability that the travel time will take on any value over the range of travel times is equal for all possible values and very small. Therefore, mean travel time in a habitat may be highly unpredictable due to variability between and within patch types in the time taken to locate another patch if the preceding patch of a given type.

## Discussion

The hypothesis that *Baetis* perceives and responds to spatial heterogeneity in periphyton abundance was strongly supported. Individuals spent on average >70% of their time within periphyton patches when food was present on only 20% of the surface area of a habitat. Upon encountering a patch, the rate of movement was sharply reduced and the degree of turning between moves increased relative to search movements between patches. Similar results were reported by Hart (1981) for the stream caddisfly grazer *Dicosmoecus gilvipes* and similar movement patterns, characteristic of area-restricted search (Krebs 1978), have been frequently observed in other insect predators, parasitoids, and herbivores (Jones 1977; Hassel and Southwood 1978). Area-restricted search is simple behavioral mechanism which may allow foragers to optimally allocate time to patches of varying quality in a habitat (Krebs 1978). Conclusions concerning optimal patch use by *Baetis* are not warranted from data presented here and will be considered elsewhere (Kohler in prep.). However, it is possible to address questions concerning the adaptiveness of the *Baetis* search mechanism in patchy habitats from these data.

### Within-patch search

The within-patch movement pattern which maximizes the net rate of energy gain by a forager is largely determined by the distribution of food within patches (Pyke 1978c). If food is uniformly distributed within patches, the optimal search behavior is to move through a patch in a highly systematic fashion such that all points in a patch are visited and previously visited points are not revisited (Pyke 1978c). Such behavior ensures that the net energy intake rate within a patch of given quality is maximized since all resource points within the patch are utilized in a minimum amount of time. In the laboratory experiments, the technique used to establish patches ensured that the distribution of diatoms within patches was nearly uniform, although some heterogeneity undoubtedly occurred. It is unlikely that such heterogeneity was detected by *Baetis* for two reasons. First, diatoms covered virtually the entire surface of patches except at the lowest cell density where the distance between cells was still considerably less than *Baetis* head capsule width. Second, observations of *Baetis* grazing movements indicated that cells were consumed in groups (estimated at up to 750 cells per "bite" at the highest cell density) which, together with the first observation, would mask over micro-scale variation in diatom abundance within patches. Therefore, *Baetis* within-patch movements should have been highly systematic. Mean intrapatch search thoroughness was nearly equal to the optimal thoroughness value calculated assuming systematic search. Therefore, *Baetis* search behavior is consistent with a movement rule that should maximize net energy intake rate within patches.

### Between-patch search

*Baetis* movements between patches in these studies were affected by the quality of the most recently grazed patch. After leaving a high quality patch, movement velocity was slower and movements were less directional than after leaving a low quality patch. This resulted in more intensive search of the area near a recently grazed patch if that patch was of high rather than low diatom cell density. If another patch was not encountered shortly after a high quality patch had been departed, movement velocity increased and search thoroughness decreased rapidly until values similar to those observed after leaving low quality patches were approached. Bond (1980) observed similar decays in velocity and thoroughness in movements of green lacewing larvae after larvae had contacted prey.

In the field and laboratory studies, these movement patterns resulted in frequent immediate revisitation of high quality patches while low quality patches were rarely revisited. Pyke (1978a, 1978c) suggested that interpatch movements of optimal foragers should be strongly directional to minimize the probability of revisitation. Zimmerman (1979, 1982), however, showed that movements can be random with respect to direction and still result in maximization of net rate of energy intake if the probability of re-encountering a patch during a foraging bout is low. Clearly, the structure of a habitat (i.e., the distribution of patches and patch types) determines which interpatch movement pattern results in maximized foraging efficiency. *Baetis* interpatch movements were not optimal for the habitat structure used in the laboratory and field studies as they often resulted in revisitation of depleted patches. These results could be used to test optimality predictions for interpatch search only if: 1) the habitat structure employed in the experiments is similar to that experienced by *Baetis* in nature, or 2) foragers had sufficient experience with the experimental habitats to be able to compensate for any structural differences between experimental and natural habitats (McNamara and Houston 1980). Since all foragers were naive with respect to the experimental habitats, the latter condition was not met. There is also evidence that the first condition was not met. Munteanu and Maly (1981) found that the upstream and downstream thirds of glass microscope slides oriented parallel to the current supported significantly higher diatom densities than the center third. They suggested that eddy formation at the upstream and downstream edges of slides, and a corresponding reduction in shear stress in these areas relative to the center, could account for these abundance patterns. Stevenson (1981) observed diatom accumulation on substrates and modified to create five distinct flow regimes across substrate surfaces and found over eight-fold differences in diatom abundance between upstream and downstream regions with highest concentrations occurring in regions of eddy formation with turbulent flow and relatively low shear stress. These studies suggest that patches of a given general type (i.e., relatively high or low cell density) are likely to be distributed contiguously in natural habitats (e.g., on stone top surfaces) with relatively high quality patches occurring largely in upstream and downstream regions and relatively low quality patches occurring largely in center regions. Patch types did not have clumped distributions in the laboratory habitats (see Methods). While this precludes testing optimality predictions for interpatch search, observed movement patterns can be com-



pared with those expected in habitats having contagiously distributed patch types to provide a preliminary evaluation of the adaptiveness of the *Baetis* interpatch search mechanism.

Interpatch movements patterns exhibited by *Baetis* in the experimental habitats seem well suited to exploit habitats where patch types are contagiously distributed. If, after grazing a high quality patch, the probability of locating a similar patch nearby is high, search intensity should be high (i.e., low movement velocity and directionality) upon leaving the patch. Similarly, search intensity should be low after grazing a low quality patch if the probability of encountering a similar patch nearby is high. *Baetis* movements after patch departure were consistent with these predictions. Movements after leaving a low quality patch in natural habitats should incorporate a strong upstream-downstream directionality component as this would increase the probability that the next patch located is of higher quality than the previous patch. Interpatch movements after leaving low quality patches were strongly directional (Fig. 4b) and resulted in the next patch located being immediately upstream or downstream of the previous patch three times as frequently as it was immediately to the right or left of the previous patch. Also, while searching for another patch, post-intensive search parameters quickly decayed and approached asymptotes characteristic of extensive search. *Baetis* extensive search movements were highly directional and were predominately upstream-downstream oriented in 24 of the 30 individuals observed. If high quality patches occur largely in upstream and downstream regions of stones, extensive search movements that are largely upstream-downstream oriented should maximize the probability that a high quality patch will be located in a given search time. In general, between-patch search behavior of *Baetis* appears adapted to exploit habitats in which patch types are contagiously distributed. Note that it is the location of *patch types* on stone top surfaces that may be predictable and not the location of *individual patches*. Consequently, the observed effects of previous patch quality on travel time may apply to natural habitats but should depend strongly on the density of patches within patch type regions. Therefore, determining the extent that deterministic patch choice models (e.g., Schoener 1974) apply to *Baetis* foraging behavior will require further information on periphyton distribution patterns. As Hart (1981) suggested, more information regarding periphyton heterogeneity on several spatial scales (e.g., between stones, within stones, within stone top surfaces, within regions on stone top surfaces) would allow better interpretation of the adaptiveness of grazer search behavior in stream habitats.

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## References

- Bailey PR (1981) Diel activity patterns in nymphs of an Australian mayfly *Atalophlebioides* sp. (Ephemeroptera:Leptophlebiidae). *Aust J Mar Freshwater Res* 32:121-131
- Beck SD (1968) Insect photoperiodism. Academic Press New York
- Bergman EA, Hilsenhoff WL (1978) *Baetis* (Ephemeroptera:Baetidae) of Wisconsin. *Great Lakes Entomol* 11:125-135
- Bond AB (1980) Optimal foraging in a uniform habitat: the search mechanism of the green lacewing. *Anim Behav* 28:10-19
- Chapman DW, Demory RL (1963) Seasonal changes in the food ingested by aquatic insect larvae and nymphs in two Oregon streams. *Ecology* 44:140-146
- Charnov EL (1976) Optimal foraging, the marginal value theorem. *Theor Pop Biol* 9:129-136
- Clark JR, Dickson KL, Cairns J (1979) Estimating Aufwuchs biomass. In: Weitzel RL (ed) *Methods and measurements of periphyton communities: a review*. American Society for Testing and Materials ASTM STP 690:116-141
- Elliott JM (1967) Invertebrate drift in a Dartmoor stream. *Arch Hydrobiol* 63:202-237
- Elliott JM (1968) The daily activity patterns of mayfly nymphs (Ephemeroptera). *J Zool Lond* 155:201-221
- Elwood JW, Newbold JD, Trimble AF, Stark RW (1981) The limiting role of phosphorus in a woodland stream ecosystem: effects of P enrichment on leaf decomposition and primary producers. *Ecology* 62:146-158
- Gee JH, Bartnik VG (1969) Simple stream tank simulating a rapids environment. *J Fish Res Bd Canada* 26:2227-2230
- Guillard RRL (1973) Culture of phytoplankton for feeding marine invertebrates. In: Smith WL, Chanley MH (eds) *Culture of marine invertebrate animals*. Plenum Publishing Corporation New York, pp 29-60
- Hart DD (1981) Foraging and resource patchiness: field experiments with a grazing stream insect. *Oikos* 37:46-52
- Hart DD, Resh VH (1980) Movement patterns and foraging ecology of a stream caddisfly larva. *Can J Zool* 58:1174-1185
- Hassel MP, Southwood TRE (1978) Foraging strategies of insects. *Ann Rev Ecol Syst* 9:75-98
- Hollander M, Wolfe DA (1973) *Nonparametric statistical methods*. John Wiley and Sons New York
- Hynes HBN (1970) *The ecology of running waters*. University of Toronto Press Toronto
- Jones JG (1974) A method for observation and enumeration of epilithic algae directly on the surfaces of stones. *Oecologia (Berlin)* 16:1-18
- Jones RE (1977) Search behaviour: a study of three caterpillar species. *Behaviour* 60:237-259
- Kohler SL (1983) Positioning on substrates, positioning changes, and diel drift periodicities in mayflies. *Can J Zool* 61:1362-1368
- Krebs JR (1978) Optimal foraging: decision rules for predators. In: Krebs JR, Davies, NB (ed) *Behavioural ecology: an evolutionary approach*. Blackwell Scientific Publications Oxford
- McFadden J, Alexander G, Shetter D (1967) Numerical changes and population regulation in brook trout, *Salvelinus fontinalis*. *J Fish Res Bd Can* 24:1425-1459
- McNamara J (1982) Optimal patch use in a stochastic environment. *Theor Pop Biol* 21:269-288
- McNamara J, Houston A (1980) The application of statistical decision theory to animal behaviour. *J Theor Biol* 85:673-690
- Morihara DK, McCafferty WP (1979) The *Baetis* larvae of North America (Ephemeroptera:Baetidae). *Trans Amer Ent Soc* 105:139-221
- Muteanu N, Maly (1981) The effect of current on the distribution of diatoms settling on submerged glass slides. *Hydrobiologia* 78:273-282
- Oaten A (1977) Optimal foraging in patches: a case for stochasticity. *Theor Pop Biol* 12:263-285
- Pryfogle PA, Lowe RL (1979) Sampling and interpretation of epilithic lotic diatom communities. In: Weitzel RL (ed) *Methods*

- and measurements of periphyton communities: a review. American Society for Testing and Materials ASTM STP 690:77-89
- Pyke GH (1978a) Optimal foraging: movement patterns of bumblebees between inflorescences. *Theor Pop Biol* 13:72-98
- Pyke GH (1978b) Optimal foraging in hummingbirds: testing the marginal value theorem. *Amer Zool* 18:739-752
- Pyke GH (1978c) Are animals efficient harvesters? *Anim Behav* 26:241-250
- Pyke GH (1979) Optimal foraging in bumblebees: rule of movement between flowers within inflorescences. *Anim Behav* 27:1167-1181
- Pyke GH (1981) Optimal foraging in hummingbirds: rule of movement between inflorescences. *Anim Behav* 29:889-896
- Schoener TW (1974) The compression hypothesis and temporal resource partitioning. *Proc Nat Acad Sci USA* 71:4169-4172
- Sih A (1982) Optimal patch use: variation in selective pressure for efficient foraging. *Am Nat* 120:666-685
- Stevenson RJ (1981) Microphytobenthos accumulation and current. Dissertation. The University of Michigan Ann Arbor
- Vogel S, LaBarbera M (1978) Simple flow tanks for research and teaching. *BioScience* 28:638-643
- Waters TF (1972) The drift of stream insects. *Ann Rev Entomol* 17:253-272
- Wiley MJ, Kohler SL (1980) Positioning changes in mayfly nymphs due to behavioral regulation of oxygen consumption. *Can J Zool* 58:618-622
- Wiley MJ, Kohler SL (1981) An assessment of biological interactions in an epilithic stream community using time-lapse cinematography. *Hydrobiologia* 78:183-188
- Wiley MJ, Kohler SL (1984) Behavioral adaptations of aquatic insects. In: Resh VH, Rosenberg DM (eds) *The ecology of aquatic insects*. Praeger Scientific Publications New York
- Zimmerman M (1979) Optimal foraging: a case for random movement. *Oecologia (Berlin)* 43:261-267
- Zimmerman M (1982) Optimal foraging: random movement by pollen collecting bumblebees. *Oecologia (Berlin)* 53:394-398

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