USE OF BEHAVIORAL EXPERIMENTS TO
TEST ECOLOGICAL THEORY IN STREAMS

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INTRODUCTION

Direct behavioral observation of stream invertebrates was practiced extensively by aquatic entomologists in the early part of this century. Early descriptions of stream insect behavior were usually qualitative but of masterful literary style. Needham et. al. (1935) indulged in countless flowery descriptions of mayfly behavior, for example, this description of activities of close-clinging, stone-loving mayfly nymphs: "Under the stones we may find representatives of other ecological groups. Some dwell there; others are stranded there; others run in for shelter there. Every creature has a right to such shelter as he can find from the vicissitudes of life. In havens of refuge many strangers meet" (p. 182). Neave (1930) reported directly observing mass upstream migrations of mayfly nymphs along the banks of rivers, a behavior later reinvestigated by Hayden and Clifford (1974). Behavioral reports have an even older legacy as exemplified by writings of the habits of burrowing mayfly nymphs by the Dutch naturalist, Swammerdam (1737): "Of all species of insects, I never saw any one more mild, gentle, or innocent. For, in whatever manner it is treated, it is always calm and peaceful; and when left to itself, it immediately goes to work and begins to dig a cell for its habitation" (Needham et. al., 1935, p. 6).

The standards of the ecologists of the 1980's do not allow such qualitative indulgence, although much of the natural history of stream insects, written in this style, forms the basis for modern stream ecology. Unfortunately, the increasing emphasis on obtaining detailed quantitative distributional information has caused stream ecologists virtually to abandon behavioral work.
Not until recently have quantitative techniques and an experimental approach been utilized to study the behavior of stream insects. My objective in this paper is to show that a combination of direct behavioral observation, with quantification of insect activity and controlled experimentation, can provide rigorous data that can be interpreted in the context of general ecological theory. The primary advantage of behavioral experiments over other methods is that they can allow determination of mechanisms for observed phenomena.

Stream insect behavior can be observed in situ or in the laboratory. Observations of subjects in their natural habitat with minimal disturbance provide the most reliable data, but are often difficult because many stream insects are nocturnal or crepuscular. Field manipulations or laboratory experiments must be carefully designed and cautiously interpreted to avoid drawing erroneous conclusions from unnatural behavior stimulated by artificial conditions.

Altmann (1974) developed an observer's guide to behavioral sampling methods. This guide describes and lists recommended uses of all qualitative and quantitative techniques known at the time of publication. I will use her classification of quantitative methods in discussing behavioral studies addressing questions on a broad range of ecological concepts.

1. **Ad libitum sampling** - recording as much information as possible; typical field notes;

2. **Sociometric matrix completion** - supplementing ad lib sampling with additional observations on particular pairs of individuals;

3. **Focal-animal sampling** - recording all activities of one individual or a specified group;

4. **Sampling all occurrences of some behavior(s);**

5. **Sequence sampling** - recording the sequence of a particular interaction or occurrence;

6. **One-zero sampling** - occurrence or non-occurrence;

7. **Instantaneous and scan sampling** - preselecting a sampling frequency and recording current activities.

**INFLUENCE OF ABIOTIC FACTORS ON DISTRIBUTION**

Species of plants and animals are restricted to certain ecological ranges by constraints imposed by their abiotic
surroundings. Microdistributions of organisms are influenced further within prescribed ranges by variations in physical and chemical parameters. Stream invertebrate distributions are affected by substrate, current velocity, temperature, oxygen, detritus, and other variables. This generality has been supported primarily by data from traditional invertebrate survey techniques with simultaneous measurements of abiotic factors, or by manipulation of abiotic factors and assessment of its effect on invertebrate colonization. A few behavioral studies have provided convincing corroboration of mechanisms producing the observed field associations between benthic distributions and abiotic factors.

To test the orientation of mayfly nymphs to light, Hughes (1966a) counted the number of four instar stages of *Baeotis harrisoni* (Baetidae) resting on their dorsal or ventral surfaces, given top or bottom illumination (focal animal sampling). Experiments were carried out in the laboratory in still water; thus, behavior may be an artifact of unnatural conditions. Nymphs were shown to maintain their dorso-ventral orientation using light as a proximal cue. Hughes also observed *B. harrisoni* repeatedly to release their hold of the substrate at low current velocity, swim upward, and fall back in a "somersaulting" behavior in the light beam. His interpretation of the importance of this response was that at low stream current velocities *B. harrisoni* nymphs thus created a current over their integument for respiratory purposes. However, he conducted no experiments to test this interpretation. Hughes (1966b) also tested the behavioral responses of *B. harrisoni* and another mayfly, *Tricorythodes discolor* (Tricorythidae), to light in an outdoor artificial stream (focal animal sampling). Both species were shown to use light as a proximal cue in the selection and maintenance of microhabitat.

Gallepp (1977) manipulated temperature, food availability (brine shrimp), and current velocity singly and interactively, and recorded the resultant behavior of the caddisflies *Brachycentrus americanus* and *B. occidentalis* (Brachycenridae) in a plexiglas insert in an artificial stream tank. He emphasized the importance of certain criteria in the choice of species for observation. Animals should be easy to observe (which eliminates many strongly photonegative or highly mobile species), should exhibit identifiable behavior patterns that allow ecological interpretation, should be adapted to life in the laboratory (in his case), and should be easy to collect in large numbers. Gallepp observed the percent of the larvae in his systems filtering (feeding), case-building, withdrawn inside cases, and unattached (crawling, drifting, or stationary) at established intervals (instantaneous and scan sampling). Results showed that *Brachycentrus* behavior was significantly affected by the abiotic variables, and by food availability, and that temperature and food
were of primary importance. These data can be used to identify the behavioral mechanisms mediating associations between the animal's environment and its distribution pattern. In other words, adaptive behavior categories, such as filtering and case-building, are restricted to certain ranges of food and temperature, with these variables overriding the effects of current velocity. Such behavioral experiments can be used to interpret more clearly patterns of caddisfly distributions observed in the field.

Mackay (1977) performed laboratory experiments designed to determine substrate choice by larvae of the caddisfly genus *Pycnopsyche* (Limnephilidae) under approximately natural conditions. She introduced specimens, evenly spaced, into plexiglas trays containing different substrate types, and noted their positions at designated intervals (instantaneous and scan sampling). She showed that substrate particle size may be an important abiotic factor limiting the distribution of *P. scabripennis*. As in the previous example, these behavioral data may be applied to identify the mechanisms producing observed associations between caddisfly distributions and substrate types in the field. However, they do not elucidate the relative importance of this variable, since other factors were not tested simultaneously.

Edington (1968) conducted laboratory experiments to corroborate field experiments and correlations suggesting a cause-effect relationship between current speed and the distribution of two net-spinning caddisfly species. *Hydropsyche instabilis* (Hydropsychidae) and *Electrocnemia conspersa* (Polycentropodidae) larvae were exposed to various current velocities in a laboratory tank for 24 hours, after which the number of larvae having constructed nets was counted (instantaneous and scan sampling). Net spinning activity of *H. instabilis*, the species with a larger mesh-size net, increased at higher current velocities; whereas *P. conspersa* net spinning decreased at higher flow rate. Edington concluded that current speed is an important variable limiting the distribution of these two species of caddisflies.

Wiley and Kohler (1980) observed the positioning behavior of four mayfly species in the laboratory in a small circular flowing-water chamber under several combinations of dissolved oxygen (DO) concentration and current velocity. Dissolved oxygen was reduced from saturation in 2 ppm decrements; nymphs were exposed to each DO level at three different current velocities for 15 minutes, after which the number of individuals on current-exposed surfaces of stone substrates was recorded (instantaneous and scan sampling). The design of their chamber allowed viewing of individuals on all stone surfaces. All four species moved to
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exposed substrate surfaces under respiratory stress, when gill ventilation was insufficient to meet respiratory needs.

DISPERSAL MECHANISMS (DRIFT)

Wiley and Kohler's (1980) study not only provided information on proximal cues for microhabitat choice by stream insects, but also can be interpreted in the context of mechanisms for dispersal by stream insects. They observed active entry of all four mayfly species into the drift when dissolved oxygen (DO) fell below a certain critical level at which substrate-position and gill-ventilation behavior could no longer satisfy oxygen requirements (sampling all occurrences of some behavior). A Baetidae species (Pseudocloeon sp.) drifted at the highest DO, followed by Stenonema pulchellum (Heptageniidae), Ephemertella lata (Ephemerellidae), and Stenacron interpunctata (Heptageniidae). These responses were consistent with field distributional data and respiratory requirements, and reflected relative abundances of these taxa in traditional studies of stream drift. This study confirmed that an increase in exposure, and an active behavior might account for the entry of large numbers of individuals into the drift.

The active-passive drift controversy has been addressed by numerous authors (Waters, 1972). The adaptive significance of drift behavior is dependent, in part, upon whether it is an active dispersal behavior or an accidental removal phenomenon, and on the effect of drift on stream invertebrate community structure. Behavioral studies can effectively document mechanisms controlling entry into and resettling from the drift. Several papers have described experiments conducted within an elliptical artificial stream (e.g., Ciborowski et. al., 1977). Ciborowski and Corkum (1980) observed the settling ability of four mayfly species by introducing 50 live nymphs into the stream and recording the number suspended within the water column at one-minute intervals until 90% of the individuals had settled (instantaneous and scan sampling). Insects were then killed and the experiment repeated. An index of settling capacity (SC) was calculated for live and dead individuals of each species. Comparison of such indices allowed determination of the portion of the SC due to morphological characters (MC) and that due to the behavior of the individual (BC).

Ciborowski and Corkum showed that the relative contribution of behavior to the SC of an organism (the behavioral index, BI = BC - SC) was highest in Baetis vagans and intermediate in Ephemertella spp. and Paraleptophlebia mollis (Leptophlebiidae). These data and similar calculations from data of Elliott (1971) showed high behavioral indices for those individuals with a high
tendency toward diel periodicity (Ephemeroptera, Amphipoda) and low BI for some Plecoptera, Simuliidae, Chironomidae, and Elmidae, which showed less diel periodicity. The authors concluded that those species most prone to drift are best able to remove themselves behaviorally from the water column. They suggested that where the BI was minimal (Chironomidae, Simuliidae), capture in drift nets may be due to a low SC as well as a high propensity to drift. The behavior of these taxa should be studied under more controlled conditions before such conclusions be accepted without question.

Behavioral studies by Corkum and Clifford (1980) have documented effects of food, substrate type, light levels, and predators on the settling capacity of two mayflies. As in Ciborowski and Corkum (1980), the number of introduced nymphs of Baetis tricaudatus and Leptophlebia cupida suspended in the water column were counted at given time intervals (instantaneous and scan sampling) under different light, substrate, predator, and food regimes. Nymphs resettled faster during the day, larger nymphs resettled faster than smaller, and small Baetis settled more quickly when food or a predaceous stonefly (Isogenoides elongatus) were present. Such studies on resettling motivation provide more complete information on the role of drift in the redistribution and habitat choice of stream insects than do data from traditional drift net studies. Drift net contents only approximate numbers of organisms present in the water column over a given time interval. They do not allow identification of how far an insect drifted, why it resettled, or why it released hold of the substrate.

Other studies have implemented behavioral techniques to document release motivation. Corkum (1978) tested the departure rates of nymphs of Paraleptophlebia mollis and Baetis vagans under still water conditions in response to photoperiod and population density. She conducted nighttime observations of nymphs marked with luminous paint using a 40-W red bulb for illumination, which was shown not to affect nymphal activity. Nymphs were pipetted or poured through a funnel onto bricks, and total numbers leaving the brick were tallied at 10-sec intervals (instantaneous and scan sampling); or verbal tallies were made on a tape recorder of all departures from the brick (sampling all occurrences of some behavior). These experiments revealed that an increase in density did not result in an increased proportion of nymphs leaving the substrate but that behavioral type (B. vagans, swimmers; P. mollis, crawlers) was the most important determinant of drift behavior.

Peckarsky (1980) recorded the results of encounters between several mayfly species and stonefly predators within plexiglas observation boxes in a Colorado and a Wisconsin stream (sampling
all occurrences of some behavior). *Baetis bicaudatus* (Colorado) and *B. pheobus* (Wisconsin) responded to encounters with predators by entering the water column actively, either drifting, swimming, or drift-swimming (releasing hold of the substrate, and drifting instantaneously, followed by active swimming behavior). Other mayfly types (Heptageniidae, Ephemereillidae) did not drift or swim in significant numbers in response to the predators. This simple behavioral experiment clearly documented that predator-avoidance is a motivation for active drift in some mayflies. Corkum and Clifford's (1980) study, described above, also showed that the presence of stonefly predators increased drift of mature *Baetis* and *Leptophlebia*.

**BIOLOGICAL INTERACTIONS**

The studies of Corkum (1978), Corkum and Clifford (1980), and Peckarsky (1980) added an interesting dimension to the testing of ecological theory in stream ecosystems. Data on such biological interactions as competition and predation in streams are conspicuously absent from the literature. Perhaps this lack of information is due to the difficulty of developing appropriate experimental designs to test such questions (see Hart, this volume). Most studies on predation or competition have been based on stomach-content analyses or interpretation of data on spatial or temporal overlap between closely related species. Controlled experiments, including those of a behavioral design, have been conducted only recently. These experiments have contributed significantly to the knowledge of predation and competition mechanisms in streams.

**Competition**

The frequency and importance of interference and exploitation competition in streams is not well understood. Few studies have investigated the role of competition in determining spacing patterns of stream invertebrates. (See chapters by Hart and McAuliffe in this volume for a thorough discussion of the application of competition theory to streams.) The behavioral experiments described below provide insight into the role of competition in structuring stream invertebrate communities.

Corkum (1978) examined the question of spacing of mayfly nymphs within the laboratory system described above. She observed nymphal movement on brick surfaces for *Baetis vagans* and *Paraleptophlebia mollis* during the first hour of every experiment (ad lib sampling). Contrasting responses to high density were observed between these two species (sociometric matrix completion). *Baetis* nymphs remained stationary until they swam or drifted from the brick; *P. mollis*, on the other hand, actively
crawled about the brick exhibiting intraspecific aggressiveness. Nymphs bent their abdomens in a horizontal plane from side to side, striking adjacent individuals; or when facing each other, they raised and lowered forelegs and antennae repeatedly in direct contact with another nymph. These interactions were followed by withdrawal behavior or by one nymph "chasing" the other over the brick. Drift rarely occurred from such encounters. Since this aggressive behavior was recorded under still-water conditions, it is possible that such interactions do not occur in the flowing-water habitat.

Others have recorded competitive or aggressive interactions among stream insects under still-water conditions. Glass and Bovbjerg (1969) studied aggressive behavior among groups of four caddisfly larvae (Cheumatopsyche sp., Hydropsychidae) forced into close contact in glass bowls. Encounters were classified as (1) avoidance (10%) - a head-on encounter, no contact; one retreats; (2) strike (15%) - mouth contact, but no biting; attacked larva retreats; (3) bite (50%) - mandibles close on attacked larva, which then retreats; and (4) fight (25%) - both animals strike or bite, one retreats. The percentage of each type of tension contact was recorded with and without the presence of pebble-refuges (sociometric matrix completion, sequence sampling). The authors also conducted spacing experiments by placing large numbers of larvae in a clump in a glass bowl. After a few hours, the population had become uniformly dispersed. Aggressive encounters were shown to mediate the spacing behavior, and were reduced by the presence of refuges.

Hildrew and Townsend (1980) quantified aggressive behavior between larvae of the predatory net-spinning caddisfly Plectrocnemia conspersa (Polycentropodidae) in an artificial laboratory stream with a 5 cm/s current velocity. Intruder larvae were introduced on substrate patches where a resident had established a catch net. If the intruder touched the resident's net, a confrontation was triggered. A "rearing up" behavior initiated the encounter, after which repeated mandibular striking and "rearing up" occurred. Severe biting occasionally resulted. The contest was terminated when one of the larvae retreated (sociometric matrix completion, sequence sampling). The resident retreated through its living tube; the intruder actively drifted in a characteristic movement pattern. Such mutual interference generally resulted in the larger of the two individuals "winning" the contest and a weak prior residency effect. Hildrew and Townsend interpreted these results in the context of a motive for active drift behavior, and as an explanation for the failure of P. conspersa to exhibit optimal foraging behavior in some seasons (see below).
Jansson and Vuoristo (1979) provoked fights between individuals of four *Hydropsyche* spp. (*Hydropsychidae*) within laboratory containers (40 X 25 X 12 cm) in which the water was aerated vigorously. They removed one larva, the "intruder," from its retreat, and introduced it into the net of a "defender." Observation vessels were placed on top of smaller containers so that larvae building retreats under rocks could be observed from underneath with mirrors. Fights were initiated when the intruder attempted to enter the defender's retreat. Biting behavior ensued, and the defender often backed into the retreat and began to stridulate. The authors recorded stridulation behavior with a hydrophone (sampling all instances of some behavior), and general behavior during fights (sociometric matrix completion). Larvae produced stridulation sounds by rubbing ventrolateral striations of the head (files) against specialized tubercles on the anterodorsal sides of the fore femora (scrapers). Upon the initiation of stridulation by the defender, the intruder either gave up or made further attempts to enter the retreat. Fighting continued with alternating bouts of biting and stridulation until one of the antagonists won. Stridulation by defenders increased the probability that they would win the fight, especially with larger intruders. These observations suggest that aggressive competition among stream-dwelling caddisflies may be an important density-regulating mechanism where sites for building catch-nets are limited.

Black fly (*Simuliidae*) larvae have been observed by Hart (1979) to bite at neighboring conspecifics, a behavior that may mediate observed spacing patterns. Wiley and Kohler (1981) devised a simple cinematographic technique with which they have recorded numerous interactions among epilithic species in a Michigan stream (*ad lib* sampling). This technique has tremendous potential for documenting biotic interactions among stream insects, although it is not an experimental manipulation. Analysis of 78 hours of film shot at 30-60 seconds/frame showed aggressive interactions between simulids, and between simulids and other taxa, the majority of which resulted in local displacement or migration of one of the antagonists (sociometric matrix completion).

Wilson et. al. (1978) conducted a simple field study on interference competition in a population of the tropical ripple bug *Ragoveilia scabra* (*Hemiptera:Velidae*) that feeds primarily on soft-bodied terrestrial insects floating on the surface of streams. The optimal location for food capture was at the head of pools where the current was swift. The authors noticed that 95% of the ripple bugs in this microhabitat were adult females. They conducted behavioral experiments to determine: (1) whether food capture was highest at the heads of pools, (2) whether the dominance of adult females occupying the optimal habitat was due
to their exclusion of adult males and juveniles, and (3) the mechanisms whereby interference among age and sex classes occurred. Their techniques involved recording capture rate of introduced fruit fly food (sampling all occurrences of some behavior), releasing individuals of adult males, adult females, and juveniles into a pool cleared of all R. scabra and observing the redistribution of each group alone and in combination with others at a designated time interval (instantaneous and scan sampling), and recording interactions between pairs of bugs for a five-minute period (focal animal sampling, sequence sampling). The results of these behavioral experiments showed clearly that the population of ripple bugs was structured by interference competition.

This convincing documentation of interference competition among stream insects suggests that such behavior is, perhaps, more prevalent in stream systems than had been previously suspected. In many hours observing the behavior of perlid and perlodid stonefly predators, I have often observed aggressive interactions between conspecifics or confamilials. Preliminary observations of the perlodid predators Megarcys signata and Kogotus modestus within observation boxes in a Colorado stream indicate that active avoidance of inter-individual contacts may be the mechanism mediating spacing behavior observed in experiments with substrate cages (Peckarsky, 1979; Peckarsky and Dodson, 1980). However, I cannot be certain that these experimental conditions produce "normal" aggressive behavior.

The activity of M. signata and K. modestus was recorded continuously for 10-minute periods for single individuals, those in the presence of potential (conspecific or confamilial) competitors, of prey, and of prey and potential competitors (sequence sampling). The repertoire of behavior recorded included crawling with antennae searching the substrate, stationary with antennae searching, crawling, swimming, drifting, and stationary. The data showed that M. signata behavior was significantly affected by the presence of potential competitors, K. modestus and Pteronarcella badia, and that K. modestus behavior was altered by the presence of Baetis bicaudatus prey (Figs. 1 and 2). The presence of the potential competitor M. signata also significantly reduced the proportion of time that K. modestus spent attacking and eating prey. Murdoch and Sih (1978) recorded a 90% decrease in feeding rate by pool-dwelling Notonecta hoffmanni immatures in the presence of conspecific adults (focal animal sampling) in the laboratory. These observations suggest that "interference" with competitors may reduce the feeding efficiency of some stream-dwelling invertebrate predators.

Hart (1981) introduced the first behavioral evidence, to my knowledge, suggestive of exploitative competition among a guild of
grazing stream insects. He chose 12 focal animals of the caddisfly Dicosmoecus gilvipes (Limnephilidae) and quantified their activity by recording their behavioral state for 80 sequential 5-s intervals (instantaneous and scan sampling). Observations were made in pools of a California stream with facemask and snorkel on a mosaic of quarry tiles on which periphyton cover was manipulated. Grazers were shown to depress substantially food available for subsequent grazers, although grazer densities may have been artificially high. Individuals spent significantly more time on ungrazed food patches than on grazed areas. These data suggest that grazers can actually cause resource patchiness, and reduce the quantity of food available to
competitors, thereby generating a potentially negative effect on their fitness. These experiments, and those of McAuliffe (see elsewhere in this volume), suggest a resource-scramble or exploitative competition among stream grazers for a limited periphyton resource.

Predator-prey interactions

Little is known about the role of predator-prey interactions in determining patterns of species abundance and distribution in streams. Predator hunting strategies, prey preferences, prey escape mechanisms, and responses of predators to varying prey densities are poorly understood. (See chapter by Allan, this volume, for discussion of the application of predator-prey theory to streams.) The study of predator-prey interactions can be accomplished effectively by behavioral experimentation if the appropriate cautions are exercised in design of techniques such that observed predation events are not artifacts of unnatural conditions. Below is a summary of a few behavioral studies of stream invertebrates that have been conducted to address questions related to predator-prey theory.

Wiley and Kohler's (1981) photographic observation technique allowed the enumeration of predator-prey encounters, although experiments were not conducted. The predatory caddisfly, Rhyacophila acopedes grp (Rhyacophilidae) was observed capturing some simulid larvae and initiating the emigration of others. Peckarsky (1980) also quantified the responses of mayfly species in a Wisconsin and a Colorado stream to encounters with stonefly predators within plexiglas observation boxes (sampling all occurrences of some behavior). Baetidae species, as mentioned earlier, drifted, swam, or drift-swam in response to encounters with large stonefly predators in both streams. Heptagenioid species crawled primarily in response to encounters with predators. Such avoidance behavior may be an important mechanism explaining biological patchiness of stream invertebrates.

Ephemeroellid species in both streams exhibited a "scorpion posture," which may serve as a display behavior in response to encounters with predators. This posture acted as a deterrent to the tactile predators, presumably creating the "image" of a spiny creature of an unpreferred size and shape; it may also be a generalized stress response. Behavioral experiments are presently being conducted to determine the nature of stimuli producing this response, and its role in reducing the effectiveness of the predators.

Peckarsky (1980) also tested the hypothesis that mayfly species detect and avoid stonefly predators given non-contact cues. The positions of 15 mayflies of each test species were
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recorded in the observation boxes before, during, and after the presence of a stonefly predator in a screen tube or a test tube in the center of the box (instantaneous scan sampling). Results of these experiments showed that some species, including those that postured and the Colorado Baetis species, avoided a region of presumed high chemical stimulus downstream from the predator in the screen tube. This result has interesting implications for search and escape strategies for stream invertebrate predators and prey. If chemical cues can be detected indicating presence of a predator or prey, the predator should search in an upstream direction, and prey should escape downstream (such as in Baetis drifting). Also, Ephemera species may use a chemical sense to detect predators and assume their defensive posture before the predator comes into physical contact with them. These questions can be pursued by using in situ behavioral experiments.

Predation strategies of net-spinning caddisflies (Plectrocnemia conspersa) have been studied by several authors. Tachet (1977) designed an apparatus that vibrated an artificial lure (a bristle) so that the frequency and amplitude of the net-vibrations could be varied independently while the larva was in its prey-catch net (in still water). A sophisticated coding system was implemented for recording from a large repertoire of behavior (focal animal sampling). A number of behaviors related to prey-capture were recorded in sequence (sequence sampling). Larvae of P. conspersa exhibited a characteristic sequence of responses to vibrations of their nets, including waiting, awakening of interest, orientation and movement toward prey, mandibular capture, withdrawal of prey, examination of prey, ingestion of prey, and egestion of feces. Tactile stimulation of the nets provided sensory cues for prey capture by this predator.

OPTIMAL FORAGING THEORY

Hildrew and Townsend (1980) and Townsend and Hildrew (1980) examined predatory behavior of P. conspersa using behavioral techniques. They recorded net-building behavior, widespread movement (wandering), ventilation behavior, incidence of stationary behavior, and agonistic behavior of one or a pair of larvae (focal animal sampling, sociometric matrix completion, sequence sampling). The authors found that the availability of prey significantly affected the length of time a larva remained at an established retreat. Larvae abandoned sites after a certain threshold time during which they had not captured a prey (giving-up time, GUT). The authors interpreted the results of these experiments in the context of optimal foraging theory, which predicts that predators should maximize their net energy gain per unit time (Krebs, 1978).
Optimal foraging theory assumes that animals have sophisticated data-gathering and data-assimilation capacity. Townsend and Hildrew (1980) showed that a fixed GUT could result in approximately optimal behavior consistent with the prediction that predators should leave a patch when the instantaneous rate of energy gain drops to the equivalent of the average of the entire habitat (Charnov, 1976). This marginal value theorem was derived by assuming a variable GUT. However, Townsend and Hildrew's (1980) observations suggest that a simpler behavior can approximate an optimal solution. One possible problem with this study is that the average field prey-capture rate was calculated as a seasonal mean. High seasonal variability in capture rate might cast doubt on the accuracy of this estimate.

Others have interpreted stream-insect behavior in the context of optimal foraging theory. Hart and Resh (1980) recorded behavior of the grazing caddisfly Dicosmoecus gilvipes in a pool of a California stream by a number of methods involving observations by SCUBA. This study did not involve experiments, however. They mapped the distribution of tagged individuals twice daily (instantaneous scan sampling), and recorded their behavior each five seconds, for 3.5-minute intervals (sequence sampling), from a repertoire including feeding on periphyton, feeding on leaves, walking, withdrawing inside case, holding onto substrate, and falling. The purpose was to determine how these larvae partitioned their time budget among various activities. Results showed that greater than two-thirds of the time was spent feeding. The authors interpreted the pattern of movement of D. gilvipes to be influenced by the spatial heterogeneity of the available periphyton. Larvae remained in one area for several days, then moved long distances, rarely feeding while on long walks, and settled on another patch for an extended period of time. The amount of movement across small-scale food patches was negatively correlated with the amount of periphyton per patch (determined subjectively). This "area-restricted search" behavior is consistent with optimal foraging theory (Krebs, 1978).

In an elegant study of the predatory bug Notonecta hoffmanni (Notonectidae) that inhabits stream pools, Sih (1980) demonstrated that conflicting demands, such as prey-search and predator-avoidance, may require predators to assume a suboptimal strategy as far as energy intake is concerned. Adult N. hoffmanni are cannibalistic on immatures, both of whom consume dipteran prey. Sih recorded the amount of time spent in regions of high and low prey (Drosophila) density by sampling at 30-minute intervals (instantaneous and scan sampling). After 24 hours he recorded the survival and feeding rates of the adults and nymphs. First-instar Notonecta spent more time in the low prey-density area, but actually consumed more prey in this region than in the region of high prey density. Older instars and adult N. hoffmanni spent
more time and consumed more prey in the area of high prey density. Sih concluded that juvenile N. hoffmanni balanced the conflicting demands of predator-avoidance and prey-search by feeding in areas apart from adults. Since optimality is maximizing fitness, a behavior balancing energy intake and predator avoidance may be optimal. Each instar preferred the microhabitat with higher associated fitness. Sih suggested that this information should be incorporated into optimal foraging models. Hildrew and Townsend (1980) showed, similarly, that suboptimal foraging behavior by P. conspersa larvae might be a result of mutual interference between foragers. Aggressive interactions could have caused a lack of aggregation of P. conspersa in regions of high prey density during an August sampling period. Such a lack of a positive numerical response by stonefly predators (Peckarsky and Dodson, 1980) could also be attributed to interference with competitors that has been observed in behavioral experiments.

The question of relative allocation of time among various activities, such as foraging and predator-avoidance, also has been examined by Peckarsky (1980). The behavior of six mayfly nymphs was recorded in observation boxes in the Colorado and Wisconsin streams before and after the introduction of three stonefly predators. Behavior was enumerated each minute for 15 minutes from a repertoire including crawling, swimming, drifting, drift-swimming, stationary, and posturing (instantaneous and scan sampling). Prey that were relatively stationary in the absence of predators became highly active in their presence (Baetis spp., Heptageniidae spp.), and vice versa (Ephemerellidae spp.) (Fig. 3). These responses suggest that different mayflies allocated different energy resources to predator-avoidance. In addition, such observations revealed an increase in certain behaviors in the presence of predators, such as the "scorpion" posture in Ephemerella and a "tail curl" behavior in B. bicaudatus, in which the mayflies flexed their abdomens laterally, usually in the direction of the predator. Further behavioral experiments can be designed to identify the function of these responses in defense against predation, and their role in maximizing fitness.

REPRODUCTIVE BEHAVIOR

Few aquatic insects breed in the stream habitat. Only representatives of the Hemiptera and Coleoptera have aquatic adults. Most studies of mating behavior in aquatic insects including those of courtship displays, acoustical signalling, and paternity assurance have been conducted on lentic Hemiptera or Coleoptera (see Jansson, 1973; Ryker, 1976; Smith, 1979). However, one truly elaborate study of the reproductive behavior of a semi-aquatic lotic insect deserves discussion here.
Male riverine water striders (Gerridae, Hemiptera) produce calling signals of a wide range of frequencies by generating surface waves using their pro-, meso-, and metathoracic legs (Wilcox, 1972, 1979). Females also signal, but only at low frequencies using their forelegs. Wilcox conducted numerous experiments to document the call sequence in courtship and mating of two species of Gerridae. To do so, he used a variety of ingenious gadgetry and techniques, including recording mating behavior in total darkness by connecting a galvanometer and float system to a Rika DenkI Model B-1 activity recorder, generating artificial courtship signals with the galvanometer, blindfolding males with custom-made rubber masks, and gluing to the foreleg of a female a tiny samarium-cobalt magnet through which a signal simulating the frequency and amplitude of the male signal could be transmitted from an IMSAI 8080 microcomputer. His entire computerized recording system could be converted to battery operation for field use.

Female or male responses were scored from a range of behaviors. Female responses included approaching the male, signalling, touching the male, spanning and moving laterally to the mid- or hind-leg of the male, grasping a float that the male inhabited, and ovipositing on the float (Wilcox, 1972). Male responses included grasping an object (float), releasing the object, attempts to copulate, backing away, and various signalling
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responses. Behavior was recorded on videotape (ad lib sampling, sociometric matrix completion, sequence sampling). Results showed that surface waves produced by males and females entirely communicated the information required for sex-discrimination, courtship, mating behavior, and oviposition in Gerridae.

CONCLUSIONS

Simple to very complex behavioral experiments on stream insects have provided valuable data that can be interpreted in the context of general ecological theory. Careful quantification of behavior can be used to address questions of abiotic limitations to invertebrate distributions, the mechanism and role of dispersal within streams, competitive and predator-prey interactions, optimal foraging behavior, and reproductive behavior. This review demonstrates clearly the need for more rigorous behavioral experiments designed to test general ecological theory. Such data will allow us to evaluate the adequacy of the present conceptual framework for explaining phenomena occurring in streams.

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