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 Baetis
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 (Brachycentridae) 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 Plectrocnemia 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

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), Ephemerella 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
Ephemerella 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. phoebus (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, Ephemerellidae) 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, stricking 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 simuliids, and between simuliids
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 Rhagovelia scabra (Hemiptera:Veliidae) 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
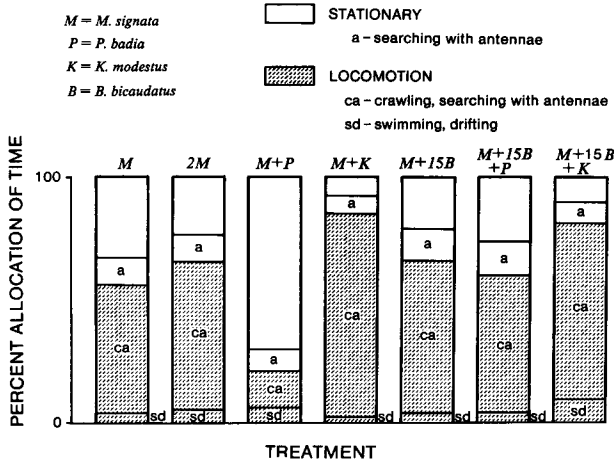knowledge, suggestive of exploitative competition among a guild of
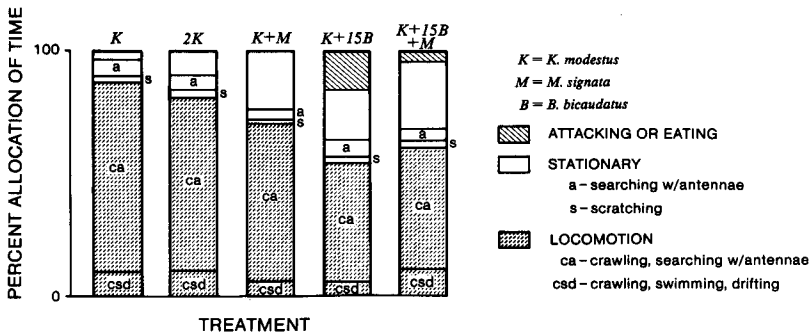
Fig. 1.   Activity of __Megarcys__ __signata__.

Fig. 2.   Activity of __Kogotus__ __modestus__.

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 excercised 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 acropedes grp (Rhyacophilidae) was observed capturing
some simuliid 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. Heptageniid
species crawled primarily in response to encounters with
predators. Such avoidance behavior may be an important mechanism
explaining biological patchiness of stream invertebrates.

     Ephemerellid 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

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, Ephemerella 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-catching 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
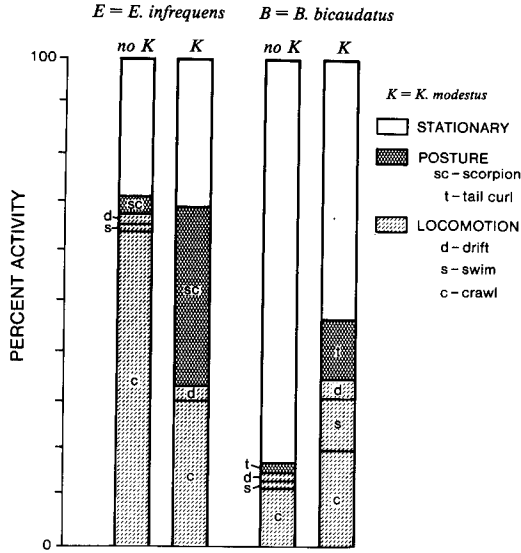a semi-aquatic lotic insect deserves discussion here.

Fig. 3.   Change in activity of Ephemerella infrequens and Baetis
          bicaudatus in the presence of Kogotus modestus.

     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 Denkl 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

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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