Predator-Prey Interactions

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I. INTRODUCTION

Streams may be viewed as open, nonequilibrium systems, having multiple patches connected by migration (Cooper *et al.* 1990, Forrester *et al.* 1999, Palmer *et al.* 1996; see also Chapter 21). Since most theory describing predator effects on prey communities has been developed for closed, equilibrium systems (e.g., Slobodkin 1961), historically, ecologists did not consider predation an important determinant of the structure of stream communities (Allan 1983a, 1983b, 1995). However, recent models (e.g., Caswell 1978, Diehl *et al.* 2000, Nisbet *et al.* 1997) predict that predation can have a major influence on prey populations in nonequilibrium systems, underscoring the value of studying predator-prey interactions in streams. As background for studies on predator-prey interactions in streams, below is an introduction to the types of effects that predators can have on prey populations and communities, and some of the mechanisms that may explain those effects.

In many streams fish are the top predators, feeding on invertebrates on the stream bottom or drifting in the water column (Hyatt 1979; see also Chapters 21, 22, and 26). Depending on the system, fish consume representatives of many orders of stream insects including mayflies (Ephemeroptera), dragonflies and damselflies (Odonata), stoneflies (Plecoptera), hellgrammites (Megaloptera), caddisflies (Trichoptera) and true flies (Diptera), and other macroinvertebrates such as amphipods (Allan 1995, Peckarsky 1982; see Chapters 20 and 25). Most studies of predation in streams have been conducted on drift-feeding fish (e.g., trout: Allan 1981, Healey 1984, Metz 1974) or benthic-feeding stoneflies (e.g., Allan 1982a, Malmqvist and Sjostrom 1980, Molles and Pietruszka 1983,

1987, Peckarsky 1985, Walde and Davies 1987). Thus, less is known about the effects of other predators in streams.

Predators can affect prey populations and communities by direct predator-induced mortality or by direct and indirect effects on prey behaviors and life histories (Sih 1987, Strauss 1991). For example, predators can have indirect community level effects ("top-down" cascading trophic effects) if reducing prey abundance increases resources used by prey (Carpenter *et al.* 1987, Power 1990). Alternatively, predators can have direct but nonlethal effects on prey populations through predator-induced changes in prey behavior or life history (Peckarsky *et al.* 1993, 2002). In this case interactions between predators and prey that do not result in prey death can have negative consequences on prey population growth (McPeek and Peckarsky 1998). This may occur if predator-avoidance behavior is costly to prey in terms of lost feeding time, shifting to unfavorable food patches, or shifting to less favorable feeding times (Peckarsky 1996). Alternatively, prey may alter their development to reduce exposure to dangerous predators (Crowl and Covich 1990, Peckarsky *et al.* 2001). Thus, the impacts of predators in streams can be studied from two general perspectives: (1) effects of predator-induced mortality on prey populations and communities and (2) consequences of antipredatory behavior and life histories on prey fitness and prey population growth.

The effects of predators often depend on whether predators are selective (i.e., consume certain prey types disproportionate to their abundance). Community ecologists are interested in whether selective predation alters the relative abundance of prey, which often has indirect effects on other components of communities (Connell 1975, Paine 1966). Selective predation may result from concentration of predator search in the preferred habitat of the prey, selection of prey types most frequently encountered, active rejection of some encountered prey individuals, or differential prey vulnerability (Allan and Flecker 1988, Fuller and Rand 1990, Greene 1985, Sih 1987). These alternative mechanisms of selective predation can be differentiated by measuring predator-prey encounter rates, attacks per encounter, and captures per attack, which are the major components of the predator-prey interaction (Peckarsky *et al.* 1994).

Behavioral ecologists often focus on the significance of differential prey defenses (Cooper 1985, Greene 1985, Peckarsky and Penton 1989), while population and evolutionary ecologists study the fitness consequences of predator-induced changes in prey behavior or life history (Crowl and Covich 1990, Peckarsky *et al.* 1993). If strategies to avoid predation result in reduced prey fecundity, demographic models predict that predators may affect prey population growth more strongly via nonlethal effects than by predation (McPeek and Peckarsky 1998). These predictions have been corroborated by field studies (Peckarsky *et al.* 2001), and experiments (Peckarsky and McIntosh 1998, Peckarsky *et al.* 2002), suggesting that in streams, predator effects on prey behavior and life history may be more important than on prey mortality.

The impact of predators on different prey species depends on relative prey vulnerability, immigration rates, and tendency to emigrate from patches where predators are foraging (Forrester 1994, Lancaster *et al.* 1991, Peckarsky 1985). Thus, it is important to know the prey *exchange rate*, the rate at which prey move in and out of areas where predators are feeding (Cooper *et al.* 1990). In streams with fast flowing riffles and high invertebrate drift rates (see Chapter 21) predation may be swamped by prey immigration (Cooper *et al.* 1990, Englund 1997). In streams with low rates of prey immigration, or where predators induce high rates of prey emigration (Sih and Wooster 1994), predators may have more substantial impacts (Cooper *et al.* 1990). In one striking example, a large-scale, long-term reduction of natural trout densities in a high-altitude stream had no detectable effects

on the abundance of invertebrate prey, possibly because high prey mobility obscured the effects of consumption by predators (Allan 1982b). Thus, the influence of predation on organisms living in open systems with extensive dispersal needs to be assessed relative to other influences on population dynamics (Palmer *et al.* 1996).

The purpose of this chapter is to introduce students and researchers to the study of predator-prey interactions from community, behavioral, and population perspectives. Methods are presented to (1) compare field measurements of predator consumption (gut contents) to estimates of prey availability to generate hypotheses on selective predation at the community level (Basic Method 1); (2) test those hypotheses by conducting mechanistic predation experiments to determine whether predators feed selectively on certain prey species (Basic Method 2); (3) conduct behavioral experiments to distinguish which components of predator-prey interactions explain observed patterns of selective predation (Basic Method 3); (4) compare field estimates of prey mortality to experimentally derived predation rates to generate hypotheses regarding the potential for predation to explain patterns of prey abundance in nature (Advanced Methods 1 and 2); and (5) measure effects of predators on prey behavior and life histories (Advanced Method 3).

II. GENERAL DESIGN

A. Site and Species Selection

The feasibility and specifics of these methods will depend on access to low (first–third) order rocky-bottom streams with riffle habitats containing abundant populations of large predatory stoneflies (Plecoptera: families Perlidae or Perlodidae) and potential mayfly prey species (Ephemeroptera: families Baetidae, Leptophlebiidae, Heptageniidae, Ephemerellidae). While it is possible to substitute other predatory taxa [e.g., benthic fish (see Kotila 1987), dragonflies, or hellgrammites] these methods were designed specifically for stonefly-mayfly interactions and, thus, have the highest probability of succeeding if those taxa are used. Basic Method 1 and Advanced Method 1 involve field collection of predators and prey, and will work best if predators are abundant (several predators per sample). For experiments (Basic Methods 2 and 3, and Advanced Methods 2 and 3) researchers should use the most abundant predator species and, for Basic Methods 2 and 3, three abundant alternative prey species — one overrepresented, one underrepresented, and one eaten in proportion to its availability in the predator's habitat (as determined by Basic Method 1). The prey species most abundant in predator diet should be used for Advanced Methods 2 and 3.

Predation experiments in Basic Method 2 and Advanced Method 2 can be carried out in enclosures placed in very shallow (<10 cm), moderately flowing (15–20 cm/s) riffles in the field, if such habitats are available and will not be disturbed overnight. Likewise, behavioral experiments (Basic Method 3 and Advanced Method 3) can be done in enclosures *in situ* but with less concern for disturbance, since they will not be left unattended. Alternatively, Basic Methods 2 and 3, and Advanced Methods 2 and 3 can be carried out in the laboratory if the researchers have access to dechlorinated water (e.g., well water or stream water) that can be distributed to replicate enclosures. However, best results will be obtained using circular, flowthrough enclosures set up streamside and using natural stream water.

B. Field-derived Electivity Indices — Generating Hypotheses for Community Level Effects

A simple method of estimating selective predation in the field involves comparing the proportion of prey in predator guts to relative prey abundance in the habitat (Chesson 1978). Although gut content data may provide an accurate record of undigested prey parts, there are many potential limitations to this method (see also Chapter 27). Variation in gut clearance time of different prey species (Hildrew and Townsend 1982) may lead to overestimation of prey with heavily sclerotized parts compared to soft-bodied prey. Partial consumption of prey may leave heavily sclerotized parts uneaten (Martin and Mackay 1982, Peckarsky and Penton 1985). Furthermore, ingestion of prey fragments, prey maceration, regurgitation during preservation, or alteration of gut contents by preservatives may also constrain our ability to quantify predator diets accurately from gut contents. Thus, gut contents show only part of what has been eaten, and could result in misinterpretation of the relative consumption rates of different prey species.

Field estimates of prey preferences also depend on the accuracy of estimates of prey abundance. A large literature deals with potential problems with the accuracy of benthic samples (Resh 1979 and see Chapter 20). Using samples of prey abundance to estimate their availability to predators assumes that (1) samples accurately reflect relative prey densities; (2) predators encounter prey at rates commensurate with measured prey density; and (3) the predator perception of available prey is the same as that of the investigator. Little is known about natural predator-prey encounter rates (Peckarsky *et al.* 1994) or predator perception of available prey in streams (O'Brien and Showalter 1993), since it is difficult to observe stream predators in their natural habitat. Consequently, hypotheses of differential predation based on data obtained by this field approach should be tested using other methods (see following).

To estimate selectivity from field data, investigators compare the relative importance of each prey item in predator gut contents to its relative abundance in the habitat. The simplest approach (correlation) involves comparing the ranks of prey types in the predator guts and in the habitat using Spearman's rank correlation analysis (Siegel 1956). A significant positive correlation indicates no selectivity (similar ranks of prey items in the diet and in the environment); no correlation or significant negative correlations suggest selective predation (feeding is weakly or strongly disproportionate to availability of prey in the environment). A second approach involves calculations of electivity indices (Chesson 1978, Ivlev 1961, Jacobs 1974, see also situation-specific modifications in Johnson 1980, Lechowicz 1982), which compare the proportion of each prey item in the predator's gut (r_i) to its proportion in the habitat (p_i). For preferred prey, $r_i > p_i$; $r_i < p_i$ suggests avoidance or prey unavailability; and if $r_i \sim p_i$, that prey item is being consumed in proportion its abundance in the environment. This method generally provides no significance tests (but see Lechowicz 1982) but can be used to compare the strengths of selection or avoidance among alternative prey. Finally, remember that this approach can only be used to hypothesize positive or negative selection for certain prey species, and that further tests are necessary to determine the reasons why specific patterns were observed.

C. Predation Experiments — Testing Hypotheses for Community Level Effects

An effective way to test hypotheses on selective predation generated from field data is to conduct predation experiments in the field or the laboratory, providing data that reveal cause and effect. Known numbers of alternative prey with contrasting patterns

of selectivity suggested by field data can be offered to predators in replicate enclosures closed to migration. Short-term prey disappearance rates can be measured and compared to prey disappearance from control enclosures containing the same prey numbers but no predators. Prey mortality rates (Dodson 1975) can be calculated for each prey species, and significance tests (analysis of variance) can be used compare predation rates among prey species (Peckarsky and Penton 1989). However, researchers must be aware of potential artifacts of enclosures (Hulberg and Oliver 1980, Peckarsky and Penton 1990), and interpret experimental data accordingly. For example, *in situ* mesh cages can slow stream flow and cause deposition of fine sediments, altering the behavior of predators or prey (Peckarsky 1985, Walde 1986). Nonetheless, correspondence between field and experimental data provide a powerful tool for answering questions about selective predation. If data from the two methods disagree, the investigator is then challenged to identify the artifacts biasing one or both methods (Peckarsky *et al.* 1997).

D. Behavioral Experiments — Testing Mechanisms for Behavioral Effects

Prey that are positively selected, avoided, or eaten in proportion to their abundance can be observed in enclosures to determine the precise components of the predator-prey interaction that cause the observed patterns. The biggest challenge in this approach is to design an enclosure similar to the natural environment that enables researchers to view interactions (e.g., Peckarsky *et al.* 1994). If compromises are made to observe organisms that are nocturnal or hidden under rocks, data need to be interpreted with caution. Removal of stream organisms from natural conditions and the presence of an observer can affect their behavior (Peckarsky 1983, Wiley and Kohler 1984). With this in mind, observers can conduct timed, replicated trials with one predator and identical densities of alternative prey species recording the numbers of predator-prey encounters, attacks, and captures per trial. Comparisons among prey species using significance tests (analysis of variance) enable researchers to determine whether prey taxa are selected or avoided on the basis of differences in encounter rates, attacks per encounter, or captures per attack. These data indicate whether prey selection is due to active choice by the predator or a passive consequence of prey attributes or behavior (Peckarsky and Penton 1989).

E. Field Estimates of Prey Mortality Rates — Generating Hypotheses for Population Level Effects

Methods developed by Kerans *et al.* (1995) can be used to estimate per capita daily mortality from sequential samples of one or more prey species in one or more stream sites. For this method sites should be sampled at one-week or two-week intervals during time periods when density of one cohort of an abundant prey species steadily declines, but before adult emergence could account for prey losses. Prey larvae can also be classified by developmental stage to estimate the development time of a cohort in each stream, which will also enable researchers to estimate the probability of surviving the larval stage.

F. Experimental Estimates of Predator-induced Mayfly Mortality — Testing Hypotheses for Population Level Effects

Investigators can estimate the proportion of larval mortality at each site that could be attributed to predation using predation experiments (similar to C above) and field

densities of predators (sampled at the same time as prey densities — E above) to estimate potential prey mortality that could be attributed to predation. Species pairs used in predation experiments should reflect known predator-prey interactions (B above), and temporal and spatial overlap between predators and prey species (Peckarsky and Cowan 1995). Functional response experiments (Elliott 2003, Kerans *et al.* 1995) measure the number of prey eaten across several prey densities to calculate daily predator-induced per-capita prey mortality rates, which can be compared to natural mortality rates estimated with field data (E above).

G. Effects of Predators on Prey Behavior and Life History — Testing Hypotheses for Non-lethal Fitness Effects

Experimental protocols similar to section D can be used to test the effects of non-feeding predators on prey behavior or life history by introducing cues from foraging predators into arenas without allowing predators to consume prey. Mouthparts of stoneflies can be glued with Barge Cement, if they forage naturally in chambers with mayflies (Peckarsky *et al.* 1993). Chemical cues from brook trout feeding in separate chambers can be introduced into chambers containing mayflies (McIntosh and Peckarsky 1996). Using these protocols, feeding behavior (foraging on rock surfaces, drift among different rocks) and life history parameters (growth rates, development times, size at maturity) can be compared statistically with and without predator cues.

III. SPECIFIC METHODS

A. Basic Method 1: Electivity Indices

1. Field Protocols

Researchers should collect invertebrates using a sampler designed for sampling in stream riffles (D-frame net, Surber sampler, Hess sampler; see Chapter 20). Methods can be standardized either by sampling the same microhabitat or by using the same effort for each sample (or both). If available to the researcher, an electrofishing machine may be equipped with a smaller anode and placed inside a Hess Sampler to take samples of benthic invertebrates (Taylor *et al.* 2001).

1. Using methods described in Chapter 20 or in Taylor *et al.* (2001) collect macroinvertebrates from a prescribed area of substrate (including large cobbles) in a shallow (<30 cm) riffle with moderate flow (20–30 cms^{-1}). The size of the area disturbed, and the number of samples taken depends on the productivity of the stream with a goal of collecting at least 100 individuals. Samples may be combined for analysis or kept separate to preserve replication and estimate variation.
2. Place each sample in a shallow pan, and use forceps to remove and preserve all large predatory stoneflies in a jar or whirlpack containing 70% ethanol. If no predatory stoneflies are collected, discard the sample (no useful information will be obtained). Preserve the rest of the sample after removing large bits of detritus and inorganic sediment. One of the major advantages of the "electro-bugging" method is that samples contain much less debris, and can be sorted more efficiently than standard "kick" samples (Taylor *et al.* 2001).

2. Laboratory Sorting, Counting, and Reference Protocols

1. Sort each sample and record the numbers of individuals collected of each predatory stonefly and prey taxon on Table 24.1. Since stoneflies primarily eat midges, black flies, and mayflies (Peckarsky 1985), or sometimes caseless caddisflies (Stewart and Stark 1996), other taxa need only be identified to order (see Chapter 20). However, blackflies (Simuliidae), midges (Chironomidae), and mayflies should be identified at least to family (especially Baetidae, Leptophlebiidae, Heptageniidae, and Ephemerellidae).
2. Prepare a reference collection of the invertebrates found at the stream to facilitate this process and minimize errors in identification.
3. Calculate the total numbers of each prey taxon and the proportion of the total individuals in all samples combined (p_i), and record data on Table 24.1. Alternatively, proportions of prey taxa may be calculated for each sample to estimate variability of relative prey abundance.

3. Protocol for Gut Content Analyses

1. Use two pairs of forceps to pull the head from the prothorax of each individual of the most abundant predatory stonefly taxon. The foregut, which should remain intact and attached to the head, can then be dissected and examined for recognizable prey parts. If the foregut does not remain attached to the head, dissect the thorax (through the ventrum) and anterior abdomen to extract the foregut. Since large predatory stoneflies swallow their prey whole, prey should be identifiable, provided a short time has elapsed since the predator's last meal.[1]
2. Use the reference collection of potential prey taxa or taxonomic references to identify prey in the predator's foregut. Prey fragments (claws, mandibles, head capsules, etc.) can be identified by comparison to whole specimens.
3. Record numbers of each prey taxon found in each predator gut on Table 24.1; calculate totals for each taxon, and the proportion of the total prey individuals for all predators combined (r_i). Alternatively, stoneflies may be analyzed separately to estimate variation in predator diets.

4. Data Analysis

1. Using the combined samples (Table 24.1) compare the fractional composition of each item (i) in the guts of the stoneflies (r_i) to its fractional composition in the available food supply (p_i) using Ivlev's Electivity Index (1961):

$$E_i = (r_i - p_i)/(r_i + p_i) \tag{24.1}$$

Values of E_i can range from -1 to $+1$ indicating avoidance to preference, with values near zero indicating that the prey item is eaten in a similar proportion that it was collected in the environment. Record the electivities for each prey taxon on Table 24.1.

[1] For best results, samples should be taken in the morning because most predatory stoneflies are nocturnal feeders (Peckarsky 1982), and food items in the gut will be less digested.

TABLE 24.1 (Basic Method 1) Benthic Data and Predator Guts to Calculate Spearman Rank Correlation Coefficients or Ivlev's Electivity Index for Selective Predation Gray cells are not applicable.

	Number in benthic samples						Rank:	Number in predator guts						Rank:	(Eq. 24.1)
Samples	1	2	3	...n	total	p_i	Habitat	1	2	3	...n	total	r_i	Diet	Ivlev's E_i
Predator taxon:															
Prey taxa:															
Baetidae															
Ephemerellidae															
Heptageniidae															
Leptophlebiidae															
Other Ephemeroptera															
Plecoptera															
Trichoptera															
Chironomidae															
Simuliidae															
Other Diptera															
Total Prey															

2. Use these combined data to prepare a bar graph illustrating the electivities of each taxon, placing prey taxa on the horizontal axis in order of decreasing electivity. Alternatively, electivities may be calculated for predators in each benthic sample separately, in which case mean and variation around the mean can be plotted for each prey taxon.
3. Also using data from the combined samples, calculate a Spearman Rank Correlation Coefficient (Siegel 1956) to test for significant correlation ($p < .05$) between the ranks of potential prey taxa in the diets and in the habitat of the stoneflies (see Table 24.1).

B. Basic Method 2: Predation Experiments to Test for Selective Predation

1. Protocols for Field or Laboratory Trials

1. Collect predators and prey in the field and hold predators in aerated, cooled (10–15°C) or flowing water without prey for at least 24 hr to standardize hunger levels. For best results, minimize handling; predators should be handled with soft forceps, and prey individuals can be transferred between containers using large mouthed plastic pipettes.
2. Each set of replicates should include six enclosures (single prey trials), two each per three prey species containing 15–20 prey and either one predatory stonefly (predator treatment) or no stonefly (control).[2]
3. Choose three prey species from the available taxa identified in Basic Method 1. Preferably, they should include one overrepresented (positive electivity), one underrepresented in stonefly diets (negative electivity), and one eaten in proportion to its availability (electivity ~ zero). If three prey species are not available, this method can be accomplished with two prey species. Mayfly species are preferable, because they are easier to handle and manipulate than dipterans or caddisflies, which tend to slip through meshes (midges) or spin silken threads in which stoneflies get tangled (black flies and caddisflies).
4. Field enclosures should be rectangular with upstream and downstream ends covered with mesh (~800-μm openings: small enough to retain prey but large enough to minimize clogging). A simple design is a fabricated plexiglass box (Figure 24.1), but cheaper materials may be used, such as Rubbermaid® shoe boxes, with openings cut in the sides and screened with Nitex® attached to walls with hot-melt glue.
5. The floor of each enclosure should be covered with a standardized number of cobbles ranging from 5–15 cm in diameter with the same size distribution in each enclosure. It is best to use natural algal-covered stream substrata from which all invertebrates have been carefully removed. Such cobbles also provide food for prey, refuges for predators and prey, and anchor enclosures to the streambed.
6. The best design for laboratory enclosures is circular (10–15 cm diameter), which reduces edge effects. These can be made of plexiglass (e.g., Figure 24.2) or modified cylindrical food containers, and powered by water (Peckarsky and Cowan 1991, Walde and Davies 1984) or air pressure (Mackay 1981, Wiley and Kohler 1980). Air pressure necessitates recirculation of water and some type of refrigeration; water-powered chambers can use cold running water and central mesh-covered

[2] Number of replicates of treatments and controls should be maximized but may depend on feasibility. Number of prey included in each chamber will depend on the size of the chamber and should fall within the range of observed densities for each prey taxon in the field.

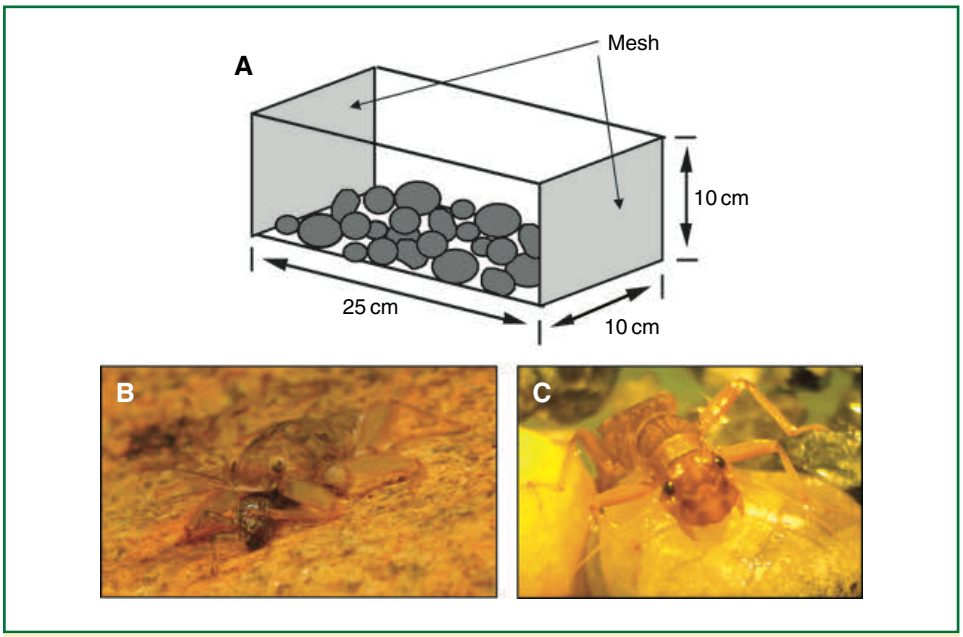

FIGURE 24.1 *In situ* enclosures. (A) Drawing of rectangular chambers for *Basic Method 2* (predation choice trials) that can be used in the field (from Peckarsky and Penton 1989). Shaded areas represent screen mesh or Nitex®. Photographs of (B) *Drunella doddsi* consuming *Baetis bicaudatus* (photo: Angus McIntosh), and (C) *Megarcys signata* foraging (photo: Michael Benton).

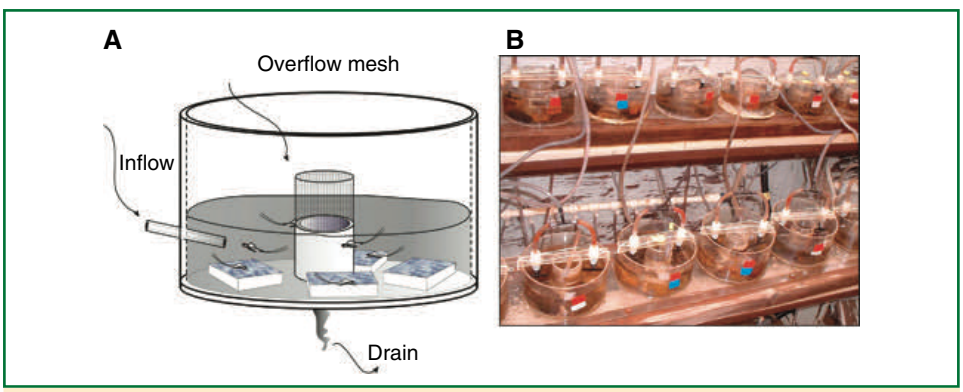

FIGURE 24.2 Small flowthrough streams for predation experiments. (A) Drawing (by Peter Ode) and (B) photograph of two different designs of circular chambers for *Basic Method 2* and *Advanced Methods 1 and 2* (predation experiments) that could be used in the laboratory or streamside.

standpipes to regulate water levels. These designs can be modified depending on facilities available, but cool temperatures (10–15°C) and good oxygenation are essential conditions to facilitate stonefly foraging. Again, natural algal-covered substrata can be collected from the stream and used for food and refuges for prey and predators.

7. Allow predators to feed in enclosures overnight or for 24 hr. It is advisable to conduct a pilot trial to determine the time during which predators eat detectable numbers of prey but do not deplete prey in any chambers (about 10–50% prey consumption is optimal). After the trial, record the numbers of prey remaining in each chamber on Table 24.2.

2. Data Analysis

1. Calculate a mean correction factor for losses of each prey species from controls, which are due to factors other than predation (see Table 24.2). Subtract that correction factor from numbers of prey missing from treatments with predators.
2. Calculate instantaneous prey mortality rates (m) for each prey species tested using the equation:

$$m = [\ln N_o - \ln N_f]/t \tag{24.2}$$

where N_f = final density of prey remaining in chambers (corrected for average number lost from all controls with that species), N_o = initial prey density (e.g., 15–20 individuals), and t = duration (days) of the trial (Dodson 1975). The units of this parameter (m) are prey mortality per prey per predator per day, which takes into account exploitation of prey over the time of the trial. Record these values on Table 24.2.

3. Using the data recorded on Table 24.2, prepare a bar graph of the mortality rate m, showing mean ± SE for each of the three prey species. Use a one-way analysis of variance (ANOVA) and multiple comparisons tests (e.g., Sokol and Rohlf 1995) to test for significant differences in predation rates among the three prey species. Compare these results to those predicted by hypotheses generated from the field data (Basic Method 1).
4. Alternatively, plot mean ± SE mortality rates in controls and predator treatments, and use a two-way ANOVA to compare mortality rates of prey species in controls versus predator treatments to test for significant predator-induced mortality on each species.

C. Basic Method 3: Behavioral Experiments to Test Mechanisms of Selective Predation

1. Field or Laboratory Trials

Using the same combinations of predators and prey as in Basic Method 2, conduct behavioral trials to determine which components of the predator-prey interaction are responsible for observed patterns of selective predation.

1. Containers used in Basic Method 2 can be used for these trials, except that substrate will have to be modified for viewing of behavior. Circular plexiglass chambers with natural substrata can be placed in elevated plexiglass trays and viewed by observers from the top and bottom (Figure 24.3). If such chambers are not available, use of

TABLE 24.2 (Basic Method 2) Data for Calculating Predator-Induced Prey Mortality (m).

	No. missing from controls			No. missing from predator treatments			Mortality due to predation		
	Prey sp. 1	Prey sp. 2	Prey sp. 3	Prey sp. 1	Prey sp. 2	Prey sp. 3	Prey sp. 1	Prey sp. 2	Prey sp. 3
Replicate no.									
1									
2									
3									
4									
5									
6									
7									
8									
9									
10									
...n									
	Correction factors			**Corrected number missing**			**Calculate using Eq. 24.2**		
Mean									
SE									
N									

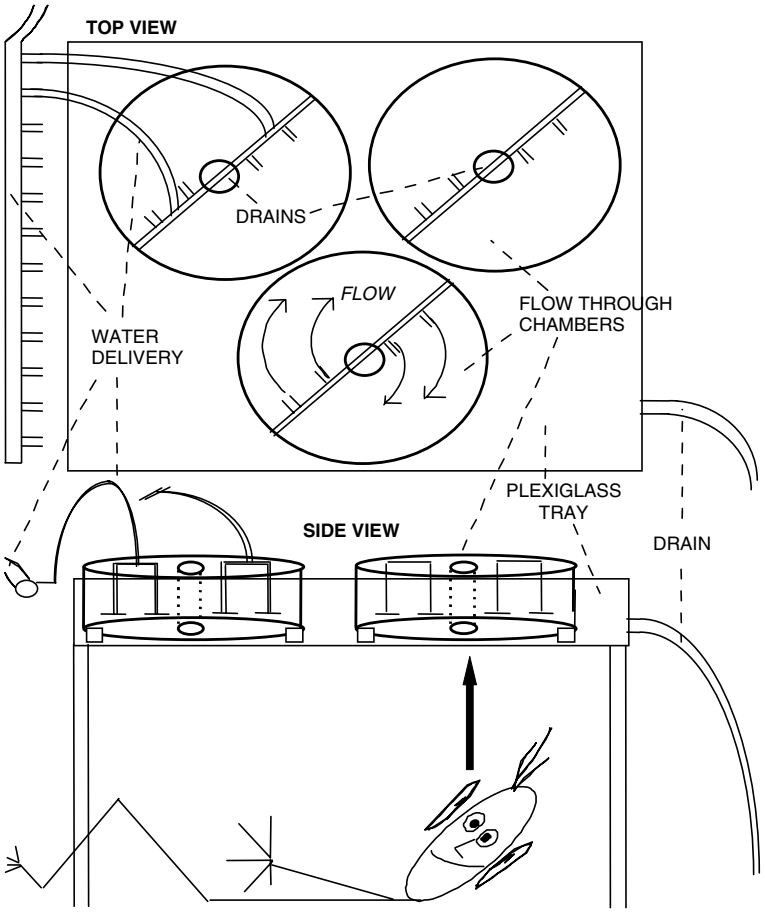

FIGURE 24.3 Drawing of plexiglass arenas for *Basic Method 3* (behavioral observations of predator-prey interactions) that could be used in the laboratory or field *(from Peckarsky et al. 1994).*

gravel or sand into which prey and predators cannot burrow is an alternative, but data may be biased by unnatural conditions (no refuges for predators or prey).

2. Each replicate should consist of three 10-min trials observing one 24-hr starved predator with 15–20 (same density as in Basic Method 2) individuals of each prey species one at a time (i.e., single prey species trials). Order of prey species observed should be randomized and replication should be maximized. Mixed prey species combinations can be used here and in Basic Method 2, but statistical analyses become complicated, necessitating the use of MANOVA (Peckarsky and Penton 1989). Trials should be conducted during natural feeding times of predators. If this is at night (typical for predatory stoneflies), observers should observe interactions using a flashlight covered with red acetate, and determine beforehand whether red light affects the behavior of stonefly or mayfly species (Peckarsky and Cowan 1995,

Peckarsky 1996). If replicates need to be run on different days, a repeated measures ANOVA should be used to test for effects of day on predation rates.
3. Observe each predator and set of prey only once, using careful handling techniques outlined in Basic Method 2. For each trial, record the number of encounters, attacks per encounter, and captures per attack on Table 24.3. If there are no encounters, a new predator should be observed, because there will be no useful data obtained from an inactive predator. However, the trial is useful if there are encounters but no attacks, but captures per attack are undefined.

2. Data Analysis

1. Prepare three bar graphs, one each for encounters, attacks per encounter, and captures per attack, to illustrate and compare the mean ± SE values (Table 24.3) for each of the three species.
2. Using the data from all observations (Table 24.3), compare each of the three parameters (i.e., encounters, attacks per encounter, and captures per attack) among the three different prey species using a one-way ANOVA and multiple comparisons tests.

D. Advanced Method 1 — Field Estimates of Prey Mortality Rates

Sequential samples of single cohorts of a prey species can be used to estimate loss rates over time under natural stream conditions. Observed loss rates may be attributed to mortality only if immigration and emigration are similar. Thus, investigators should also estimate drift into and out of a selected study reach to test this assumption (Chapter 21).

1. Field Collections

1. Select a time when 3–6 weekly or biweekly samples can be taken during the period of growth and development for one cohort of the most abundant prey species (Table 24.1).
2. On each day take 3–6 quantitative benthic samples using a fine mesh (200 μm) net and one of the devices described in Basic Method 1. Preserve all invertebrates in 70% ETOH. Maximize replication in time and space.

2. Laboratory Processing of Invertebrates

1. Record the two-dimensional surface area of the sampler so that predator and prey densities can be estimated (see Table 24.4A).
2. Record the number of predatory stoneflies (same species as used for Basic Methods 1–3) on Table 24.4A. Numbers of predators collected in all benthic samples may be combined for each date, or average number of predators per sample may be recorded. If samples are combined, record the total area sampled (area of one sampler × number of samples per site per date).
3. Count and stage mayfly prey using wing pad development (Stage I = no wing pads, Stage II = wing pads wider than long, Stage III = wing pads longer than wide, and Stage IV = black wing pads; Peckarsky *et al.* 2001). Calculate prey density per

TABLE 24.3 (Basic Method 3) Data on Number of Encounters, Attacks per Encounter, and Captures per Attack.

	Number of encounters			Attacks per encounter			Captures per attack		
	Prey sp. 1	Prey sp. 2	Prey sp. 3	Prey sp. 1	Prey sp. 2	Prey sp. 3	Prey sp. 1	Prey sp. 2	Prey sp. 3
Replicate no.									
1									
2									
3									
4									
5									
6									
7									
8									
9									
10									
...n									
Mean									
SE									
N									

TABLE 24.4 (Advanced Methods 1 and 2) Data to Compare Natural Prey Mortality to Predation Rates.

A. Advanced Method 1
Prey taxon:

Date	Cum.[1] Days	Area sampled (m^2)	No. predators	Predator density (N_P)	No. prey collected in benthic samples: Stage I	Stage II	Stage III	Stage IV	Total	Prey Density
1	0									
2										
3										
4										
5										
6										
…n										

[1]Total days from date 1 – n

mean		Daily Prey Mortality[2] (Eq. 24.2 – Field modification)
SE		
N		

[2]Assumes density declines from date 1 to n.

B. Advanced Method 2

Daily Per Capita Prey Mortality (Field)	Prey Density[3]	Predator-induced prey mortality[4] (M_P from experiments – Eq. 24.2)	Predation Rate (Experiments) Adjusted by Predator Density (Field)	Ratio of Adjusted Predation Rate to Field Mortality
	5			
From Advanced Method 1 (Table 24.4A)	10			
	15			
	20			
Averaged over all prey densities:				

[3]Adjust accordingly if different prey densities are used.

[4]Calculated as in Table 24.2

sample or combine all samples using the appropriate area sampled as described for predators above (see Table 24.4A).

3. Data Analysis

1. Estimate daily per-capita mortality (m) (as in Kerans *et al.* 1995): $m = (\ln [N]_t - \ln [N]_{t+1})/d$ (modification of Eq. 24.2), where N = density of all stages combined; t and t+1 = the first and last dates of time series of samples during which density steadily declined, but before adult emergence could account for losses; and d = days between samples. Record that value in Table 24.4A.
2. Depending on the stage structure of the mayflies during the sampling period, and the synchrony of development, investigators may also be able to estimate the development time (D) of larvae as the number of days to advance from stage II–stage IV. If this is possible, the probabilities of surviving the larval stage (K) can also be estimated.

$$(K = e^{-mD}) \tag{24.3}$$

assuming constant mortality rate (m) during a larval period of duration D.

3. Estimates of mortality, development time, and probability of surviving the larval stage can be plotted using bar graphs of means and standard errors to illustrate comparisons of taxa or streams. These parameters can be compared among species of mayflies or populations in different types of streams (e.g., fish and fishless) using MANOVA on log-transformed data.

E. Advanced Method 2 — Experiments to Test for Predator-induced Mortality Rates at Different Prey Densities

Natural larval mortality (measured in Advanced Method 1) of different prey species or sites can be compared to estimates of predation rates using instantaneous attack rate coefficients from small-scale functional response experiments (Kerans *et al.* 1995) combined with field estimates of natural predator densities (from Advanced Method 1). Investigators could also use trout as predators in larger arenas (Figure 24.4) and estimate trout densities by electrofishing (Chapter 22). The following protocol describes methods for predatory stoneflies and mayfly prey.

1. Design of Predation Rate Experiments (Functional Response)

1. Conduct overnight or 24-hr predation trials using the same protocol as in Basic Method 2 (preferably the circular chambers — Figure 24.2, which provide more accurate estimates of mortality due to predation), but this time varying the prey density (e.g., 5, 10, 15, and 20 prey per chamber) with one stonefly predator, and the same prey densities with no predators as controls.
2. Species pairs and densities used in experiments should reflect known prey preferences (Basic Method 1), known temporal and spatial overlap between predators and prey species (e.g., Peckarsky and Cowan 1995), and the natural range of prey densities (Advanced Method 1).

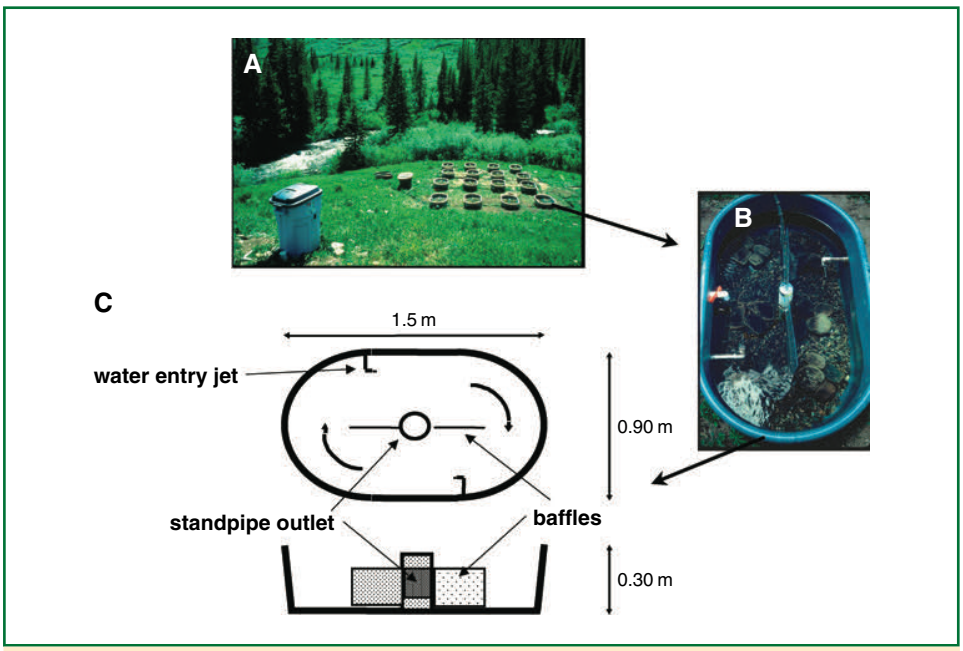

FIGURE 24.4 Large artificial streams useful for *Advanced Methods 2 and 3* (predation experiments with fish). (A) Artificial streams at Rocky Mountain Biological Laboratory, Colorado, are gravity-fed with water from a nearby fishless stream, which provides a source of fishless water for controls. Fishless water can also be gravity-fed to a 110-L holding tank (shown at left) containing two brook trout and then dripped into tanks allocated to a fish-cue treatment. Alternatively, fish can be added directly to streams. (B) Single artificial stream; fish water drips in through spout with orange ribbon. (C) Schematic diagram of an artificial stream in top and side views *(from McIntosh and Peckarsky 1996).*

2. Data Analysis

1. As in Basic Method 2 (Table 24.2), calculate the daily predator-induced per-capita prey mortality rates (M_p) using a modification of equation 24.2: $M_P = (\ln[N_I] - \ln[N_F])(P)^{-1}(d^{-1})$, where N_I = initial prey density, N_F = final prey density, P = predator density, and d = days of the feeding trial. Use the area of the experimental unit to estimate predator and prey densities. Record estimated predation rates for each prey density treatment on Table 24.4B.
2. To compare these estimated predation rates to natural prey mortality estimated in a particular stream, first adjust predator-induced mortality (M_P from Table 24.4B) by average predator density measured in that stream (N_P from Table 24.2A, Advanced Method 1); then calculate the ratio of the adjusted predation rate to the loss rate of prey from that stream (m from Advanced Method 1) as $M_P \times N_P/m$. Record this value in Table 24.4B. If the predation rates at each prey density differ, select the prey density that best approximates that of the study stream. Otherwise, use the average estimated predation rate (Table 24.4B).
3. To compare multiple streams or multiple prey species or predator species, the ratios of adjusted predation rates to total prey mortality can be compared graphically and statistically using ANOVA on transformed data or nonparametric analysis of variance.

F. Advanced Method 3 — Experiments to Test Predator Effects on Prey Behavior and Life History

1. Design of Experiments

1. Set up replicate circular arenas similar to those used in Basic Methods 2 and 3 (Figure 24.2) using dechlorinated water (well water or stream water) in the laboratory or preferably by diverting natural stream water into streamside artificial streams (Peckarsky and Cowan 1991), which enables natural light and temperature regimes to be maintained.
2. Add 5–10 prey of a selected species to chambers with algal-covered natural rocks, or unglazed tiles can be substituted for ease of viewing. For behavioral trials, arenas should be left uncovered. If rearing prey to maturity, arenas should be covered with mesh emergence nets that allow light to penetrate.
3. To measure effects of stonefly predators on prey behavior/life history, use a thin wire or toothpick to place a small drop of Barge Cement on the mouthparts of a stonefly while it is anesthetized in a weak suspension of alka seltzer and water (Peckarsky *et al.* 1993). Allow glued stoneflies to recover in a holding chamber before using them in experiments. To start the experiment, place one stonefly in each chamber randomly allocated to the predator treatment, and a small piece of gravel with Barge Cement in chambers allocated to controls.
4. Observe and record feeding behavior (instantaneous scan of numbers of individuals foraging on the surface of substrates) or drift behavior (number drifting per unit time) of prey several times during a 24-hour period in chambers with and without glued stoneflies. Nighttime observations should be made using dim red light. Numbers of stoneflies visible foraging should also be recorded and compared to known natural feeding periodicity of the predators (determined in preliminary observations with nonglued stoneflies.)
5. To measure effects of glued stoneflies on prey life histories, prey should be reared to maturity (black wing pad — Stage IV) under these same treatments, and then preserved for analysis of size and fecundity (numbers of eggs per female).
6. Using a similar experimental design, chemical cues from brook trout feeding in separate chambers can be dripped to experimental arenas to test the effects of those cues on prey behavior and life history. Small chambers (Figure 24.3) allow greater replication, but larger chambers (Figure 24.4) provide a more realistic environment in which to measure prey life histories and behavior (McIntosh and Peckarsky 1996, Peckarsky and McIntosh 1998).

2. Data Analysis

1. Numbers of prey individuals foraging on rock surfaces and prey drift rates can be compared between predator treatments and controls graphically and statistically using MANOVA on multiple, interdependent response variables, and subsequent ANOVAs on individual response variables if the MANOVA is significant (Peckarsky and McIntosh 1998). Data should be transformed to meet the assumptions of parametric statistical tests.
2. Similarly, life history parameters (i.e., growth rates, development times, and size at emergence) can be compared graphically and by MANOVA (see Peckarsky *et al.* 1993) to test whether prey life histories respond to predator cues.

IV. QUESTIONS

1. What are the strengths and limitations of field-generated electivity indices? Predation experiments? Behavioral observations?
2. What hypotheses were suggested by the electivity indices or by correlations between gut contents and benthic data? Did these methods generate the same hypotheses?
3. What can you conclude about selective predation by stoneflies from predation experiments?
4. What did behavioral experiments reveal about the importance of encounter rates, attacks per encounter, and captures per attack as mechanisms explaining patterns of selective predation by stoneflies?
5. Is prey selection by stoneflies active or passive? Explain.
6. Are data from different methods to test for selective predation consistent? Describe any discrepancies. If data are not consistent, what conclusions would you draw? Do you trust some methods more than others? Why?
7. Why should investigators include controls and replication when designing experiments?
8. Were predation rates (estimated by functional response experiments) high or low compared to prey mortality observed in the field? What are the implications of your findings for the potential of predators to regulate of prey populations in nature?
9. What are the potential fitness costs of lower growth rates, longer development times, and/or smaller size at maturity associated with avoiding predators? Alternatively, how might prey increase their fitness by accelerating their development, even if they emerge at smaller sizes in streams with dangerous predators? (Consider probability of surviving the larval stage.)
10. What did behavioral observations tell you about the possible mechanisms of observed effects of predator cues on prey life history?

V. MATERIALS AND SUPPLIES

For field collections (Basic Method 1 and Advanced Method 1)

Collecting jars or whirlpaks
Collecting devices (D-nets, Surber sampler, Hess sampler, electrobugging machine)
Shallow sorting pans
Plastic eyedroppers and soft forceps

Additional supplies for experiments (Basic Methods 2 and 3, and Advanced Methods 2 and 3)

Enclosures/rearing chambers/observation chambers
Holding chambers (for predators)
Flashlights with red acetate to produce dim red light for nighttime observations
Various plumbing supplies and a first name basis with the local hardware store
Water or air source (for circulating flow in chambers if trials are done in the laboratory)

Laboratory Equipment

Petri dishes for sorting samples
Dissecting microscope
Dissecting forceps
Invertebrate identification guide (see Appendix 20.1)

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