Fish Predation and The Evolution of Invertebrate Drift Periodicity: Evidence from Neotropical Streams

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FISH PREDATION AND THE EVOLUTION OF INVERTEBRATE DRIFT PERIODICITY: EVIDENCE FROM NEOTROPICAL STREAMS[1]

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Abstract. Drift activity of stream invertebrates typically is greatest during the nighttime hours in running waters throughout the world. Such diel periodicity may be an adaptive response that minimizes exposure to visually hunting, drift-feeding fishes. I tested this risk-of-predation hypothesis by examining drift behavior of mayflies in a series of Andean mountain and piedmont streams that vary in the abundance of drift-feeding fishes. Drift was primarily nocturnal in piedmont streams with natural populations of visually hunting predators. In contrast, mayfly drift activity did not differ between day and night in mountain streams that historically lack drift-feeding fishes. However, in naturally fishless Andean streams containing introduced rainbow trout, nocturnal peaks in drift were observed for the mayfly *Baetis,* suggesting a rapid evolutionary change in behavior in response to an exotic predator. When drift periodicity was examined along a gradient of predation regimes, activity was found to be increasingly restricted to the nighttime hours as predation risk became more intense. Diel periodicity was observed even when fish were experimentally excluded, suggesting that nocturnal activity has evolved as a fixed behavioral response to predation, and is not a direct ecological consequence of diurnal feeding by fishes. These observations support the hypothesis that predation risk is important in determining the timing of prey drift behavior.

Key words: Andes; drift; mayfly; neotropics; periodicity; predation.

INTRODUCTION

The diel periodicity of drift (i.e., the downstream transport of organisms in the water column of streams) has been extensively documented, yet its significance is not well understood (Brittain and Eikeland 1988). In many invertebrate groups and some fishes, drift numbers typically are low and constant during the day, followed by dramatic increases at night (e.g., Tanaka 1960, Waters 1962). Such nocturnally biased activity has been interpreted by some as an evolutionary response to minimize exposure to visually hunting, drift-feeding fishes (e.g., Anderson 1966, Allan 1978). This is similar to the hypothesis that the vertical migration of zooplankton between food-rich surface waters by night and deeper strata by day is an anti-predator adaptation to minimize encounters with planktivorous fishes (e.g., Zaret and Suffern 1976, Gliwicz 1986). Although many organisms display nocturnal behavior, there exist surprisingly few data that directly test whether the diel periodicity of activity is an evolutionary response to predation. This may in part be due to difficulties in determining the evolutionary origin of

fixed or "hard-wired" behaviors in present-day populations (Dill 1987).

The most convincing evidence that risk of predation constrains drift activity is the finding that prey size classes with the greatest risk to size-selective predators exhibit the greatest propensity for nighttime drift (e.g., Allan 1978, 1984, Stewart and Szczytko 1983, Skinner 1985). Allan (1978, 1984) reported that nymphs of several mayfly species, as they matured, became increasingly vulnerable to trout predation and displayed ontogenetic shifts towards nocturnal behavior. He posited that predation risk should be an important determinant of drift periodicity. A more direct test of this hypothesis is to compare drift between streams without vertebrate predators to systems that contain drift-feeding fishes, using taxa that typically are important in the diet of fish.

Here I report a series of tests of the risk-of-predation hypothesis conducted in the Andes of Venezuela. The Andes provide an unusual opportunity to study the evolution of drift periodicity because a wide range of predation regimes can be found in a relatively small geographical region. First, I investigated patterns of diel rhythmicity along a natural predation gradient by comparing drift among streams containing different assemblages of drift-feeding fishes. I then examined drift periodicity in Andean streams that are naturally devoid of drift-feeding fishes, as well as evaluating the effects of introductions of trout to otherwise fishless streams. Finally, I report findings from a field exper-

iment where native fishes were excluded from an Andean piedmont stream, in order to distinguish whether periodicity results from the direct consumption of drifting insects by day-active fishes, or is indeed an evolutionary response manifested in present-day drift behaviors.

Description of the study sites

The Venezuelan Andes provide a natural experiment (cf. Diamond 1986) for testing the evolution of diel drift periodicity. Streams in the lowland llanos (savannas) and Andean piedmont often contain diverse and abundant fish faunas. At higher elevations in the Andes, the density of fishes and number of species decrease (Nebiolo 1982a, b; A. S. Flecker, *personal observation*), and by ≈1500 m, drift-feeding fishes do not naturally occur.

Drift periodicity was examined in four Andean piedmont streams and four mid-elevation mountain streams. Piedmont streams were located between ≈180 and 630 m in Estado Portuguesa (Rios Saguas, Guache, and Las Marias) and Estado Barinas (Rio La Yuca). Sites were selected that were bordered by gallery forest, although considerable clearing of the natural deciduous dry forest has occurred throughout the Andean piedmont. All piedmont streams were stony bottomed and contained native populations of drift-feeding fishes (Table 1). Fish diversity and abundance varied among streams, and as many as 55 fish species were found per site (Flecker 1990). Most drift-feeding fishes were from the family Characidae, which generally are day-active hunters (Uieda 1984, Machado-Allison 1987; A. S. Flecker, *personal observation*). I also observed the knifefish, *Apteronotus* sp., a nocturnal predator that may feed on drifting invertebrates; however, they were never common at any of the piedmont sites and were absent from mountain streams. In addition to midwater drift predators, other fish feeding guilds included benthic insectivores, algal grazers, sediment-feeding detritivores, and piscivores. It should be noted, however, that most piedmont fishes cannot be readily classified into distinctive feeding guilds, but rather incorporate a variety of food items into their diets that often display considerable temporal variation (see Winemiller 1990). A more detailed description of piedmont fish assemblages is found in Flecker (1990).

Andean mountain streams were located within or nearby the Parque Nacional de la Sierra Nevada (Estado Mérida) at elevations between ≈1640 and 2200 m (Table 1). Streams in this region are historically devoid of drift-feeding fishes, although several genera of benthic-feeding catfish (*Chaetostoma, Trichomycterus,* and *Astroblepus*) naturally occur in some running waters. Beginning in the 1930s, rainbow trout (*Oncorhynchus mykiss*) and brook trout (*Salvelinus fontinalis*) were introduced to the Andes, and a series of hatcheries were constructed for both commercial production and stocking purposes (Hirogoyen 1976). As is characteristic throughout their distribution, trout are predators on drift in the Andes, where they feed heavily on stream insects (Bastardo 1990; A. S. Flecker, *personal observation*).

I sampled drift at sites from two Andean streams that remain devoid of drift-feeding fishes (Rio Albarregas, fourth order, and Quebrada La Fria, third order), and two streams with introduced trout. Andean sites were all pristine, stony-bottom, high-gradient streams flowing through tropical montane humid forest. Sites lacking drift predators are referred to as fishless in this paper, although Quebrada (Qda.) La Fria did contain some benthic-feeding catfishes in the most torrential reaches. The two trout streams were located near hatcheries that contained rainbow trout (Qda. Coromoto and Qda. Mucunutan, both third order).

METHODS

I tested the risk-of-predation hypothesis using a combination of natural and manipulative field experiments. These approaches included comparing drift along a natural predation gradient and at sites of trout introduction. Furthermore, drift periodicity was examined when native fishes were experimentally removed to separate the effects of direct consumption of nymphs by predators from behavioral responses of prey.

I chose to test the risk-of-predation hypothesis using stream mayflies (Order: Ephemeroptera). Mayflies were not only the most common members of the drift in both mountain and piedmont streams, but also comprised as much as 65% of the total benthic invertebrate fauna during the dry season months (Flecker 1990). Ephemeroptera provide a robust test of the hypothesis because they are commonly reported to display nocturnal drift activity. In addition, mayflies were important components of the diet of insectivorous fishes (A. S. Flecker, *unpublished data*; also Bastardo 1990), which is typical of many running waters throughout the world.

Comparisons along a natural predation gradient

I tested whether drift periodicity varies predictably according to predation regime by comparing diel patterns in each of the eight study streams from Andean piedmont and mountain sites. Patterns of diel periodicity were established on 3–5 dates for each stream. Drift was sampled every 4 h over a 24-h period. At each sampling period, two drift nets (dimensions: mouth opening = 0.1 m², length = 2 m, mesh = 307 μm) were suspended in the water column for 20–60 min. The duration of sampling period varied among dates and was adjusted as needed to minimize clogging of the nets by transported debris. The contents of each sample were preserved in 95% ethanol and insects were later separated from detritus in the laboratory. Drift was expressed as density (number per 100 m³), which was calculated by dividing the number of animals in the net by the volume of water sampled (Allan and Russek 1985). Water volume was estimated from the product

TABLE 1. Characteristics of Andean mountain and piedmont streams where drift collections were taken.

	Stream				
	Albar-regas	La Fria	Coro-moto	Mucu-nutan	Saguas
Stream type	Montane	Montane	Montane	Montane	Piedmont
Elevation of collection site (m)	2060	1680	2160	2200	630
Elevation of stream origin (m)	4240	4730	4970	5003	2200
Stream order	fourth	third	third	third	fourth
Drainage area (km²)	29.5	33.4	27.8	30.8	200.3
Width (m)	4–8	4–8	4–6	3–5	6–15
Temperature (°C)	11.0–14.7	14.0–16.5	11.0–14.5	10.2–12.0	17.3–20.5
pH	7.3	7.2–7.3	7.2	7.2	7.9
Hardness (mg/L)	54.3	30	30	20	60
Dissolved oxygen (mg/L)	7.8–8.6	8.0–8.8	8.1–9.1	8.2–8.7	7.5–8.4
No. fish species	0	3	1	1	11
No. species drift-feeding fishes	0	0	1	1	5
No. drift-feeding fishes/100 m²	0	0	5.6	7.0	46.9
No. drift sampling dates	3	3	3	3	3

of area of submerged net opening, current velocity in net opening, and duration of sampling period. Three estimates of current were made at the end of the sampling period using a General Oceanics (Miami, Florida) flow meter. Since moonlight could potentially affect night drift densities (Anderson 1966, Hynes 1975), sampling was conducted on nights during the dark phase of the lunar cycle. All drift collections were taken during the dry season (November to April), when water clarity was high and problems associated with drastic fluctuations in stream discharge from up-valley rainstorms were minimized.

In order to rank the eight streams relative to predation risk, the abundance and diversity of drift-feeding fishes were estimated by electrofishing during the dry season in 1988. At each site, a 5 × 2 m bag seine (mesh = 0.64 cm) was stretched across the stream, and eight to ten 50-m² reaches were fished using a generator-powered Coffelt electroshocker (Model VVP-II). These sampling methods provided a means to rank relative predator abundance among streams based on standardized effort, but clearly underestimated actual fish densities. Fishes were immediately preserved in 10% formalin and later identified and counted in the laboratory. Fishes were classified as drift-feeders based on underwater observations combined with stomach analyses. Voucher specimens were deposited in the Museo de Ciencias Naturales, UNELLEZ, Guanare, Venezuela.

Fish exclusion experiments

In addition to natural comparisons, I examined patterns of drift periodicity after native fishes were experimentally excluded from Rio Las Marias, a piedmont stream with high densities of drift-feeding fishes. The rationale of these experiments was to distinguish whether low densities of daytime drift were due to: (a) direct consumption of drifting nymphs by day-active predators, or (b) behavioral suppression of drifting by mayflies during the daylight hours.

To test these alternative hypotheses, drift periodicity was examined among three experimental treatments: (1) fish exclusion, (2) cage control, and (3) natural stream conditions. Fish were excluded using mesh channels that were 10 m long × 1 m wide. Channels were constructed of plastic screening (mesh = 3.15 mm) that covered all four sides and the bottom, but allowed free access to mayflies. All channels were placed parallel to the current, and stones were placed on channel floors, in order to maintain structural integrity as well as provide natural substrate for benthic insects. Channel size was assumed to be of sufficient length to allow mayflies to make one to several complete drift trips, based on published estimates of mayfly drift distances (e.g., Elliott 1971, Larkin and McKone 1985, Allan and Feifarek 1989; also see Brittain and Eikeland 1988). Cage controls were of identical dimensions, but were open on the downstream end and had windows cut in the side screen walls. Fishes were frequently observed inside of the controls, as they were able to enter and exit freely. Finally, the uncaged stream served as the third treatment. Current velocity was measured inside of the channels and was generally less than in the open stream (Appendix). Each treatment had two replicates, which were sampled simultaneously at the downstream end during the collecting periods.

This experiment was first conducted on 23–24 December 1987, when drift was sampled for 1-h intervals, every 4 h over a 24-h period. It was repeated on 21 January 1988; however, I reduced the number of drift collections to 2 h at midday (1200–1400) and 2 h after nightfall (2000–2200). Differences between treatments in diel drift patterns were analyzed using repeated measures ANOVA (SAS 1990).

RESULTS

Natural comparisons

Mayflies from piedmont streams containing drift-feeding fishes displayed a clear nighttime bias in drift

TABLE 1. Continued.

	Stream	
Guache	La Yuca	Las Marias
Piedmont	Piedmont	Piedmont
210	210	180
1960	2300	1900
fourth	fourth	fourth
299.0	156.2	209.5
7–18	15–20	8–15
20.0–26.0	24.0–31.0	23.0–32.0
8.1	7.9–8.5	7.6
170–180	50–120	45–70
7.5–8.8	6.4–9.1	5.8–8.8
23	31	55
11	18	20
79.5	320.0	501.0
3	3	5

activity. At each site and sampling date, drift was low during the day and increased dramatically after dark (Fig. 1). Drift numbers generally remained high throughout the night, and at the following dawn returned to low densities similar to those observed during the preceding day. These differences between day and night generally were greatest in streams with the highest numbers of drift-feeding fishes (Rio La Yuca, Rio Las Marias, Fig. 1), where nocturnal densities often ex-

ceeded day values by two to several orders of magnitude.

In contrast to piedmont streams, mayflies did not exhibit nighttime activity peaks in Andean streams lacking drift-feeding fishes (Qda. La Fria, Rio Albarregas, Fig. 2). Few differences in drift densities were observed between sampling periods. Concordance between data sets was significant (Friedman's rank sum test, $W = 0.43$, $\chi^2 = 14.90$, $P < .011$, Siegel and Castellan 1988), because the first daytime samples (0730) generally contained a greater number of drifting mayflies than the late night collections (0330). However, this concordance value was low because drift was aperiodic during the other times of day.

Trout introduction streams

At the trout introduction sites (Qda. Mucunutan, Qda. Coromoto), mayfly drift densities showed slight but nonsignificant peaks immediately after dark (Fig. 3). However, only two mayfly taxa (*Baetis, Baetodes*) were common in these trout streams and they displayed different diel drift patterns. Drift of the mayfly *Baetodes* was generally aperiodic, as was observed in the fishless streams. In contrast, patterns of drift periodicity were highly consistent for *Baetis,* exhibiting a peak in drift activity immediately after dark, and a second
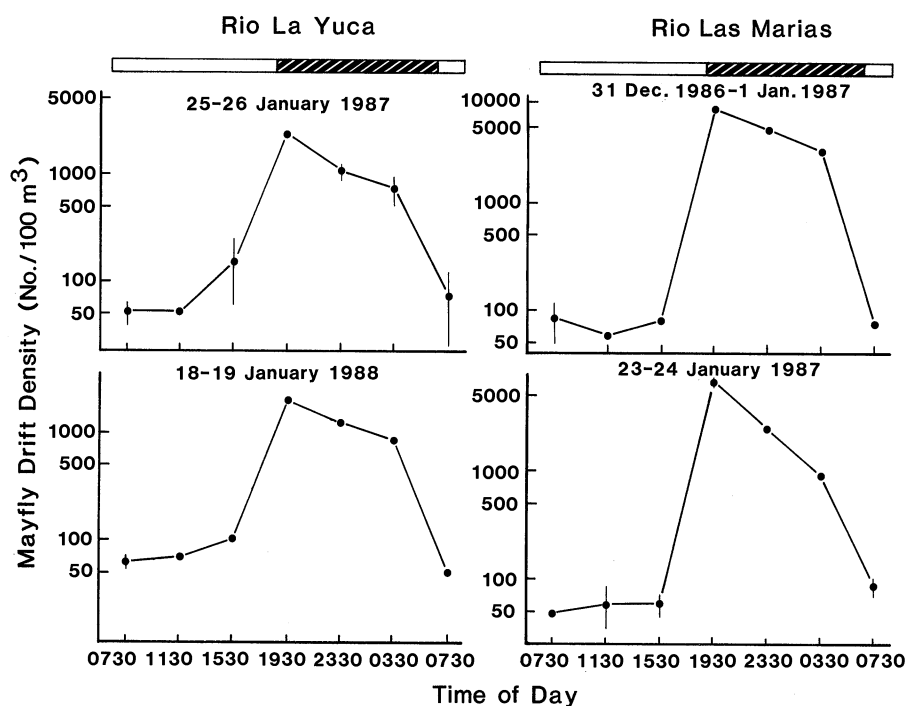

FIG. 1. Drift densities of mayflies sampled over 24-h periods from two Andean piedmont streams that contain natural populations of drift-feeding fishes. Only two dates are shown per site; however, the night: day drift ratio of individual mayfly taxa for all collections is shown in Fig. 5. Dots represent the mean of two drift collections, and vertical lines denote the ranges. In collections with minimal differences between replicate nets, the vertical bars fall within the dots. Darkened portion of horizontal bar at top of figure indicates night collections.
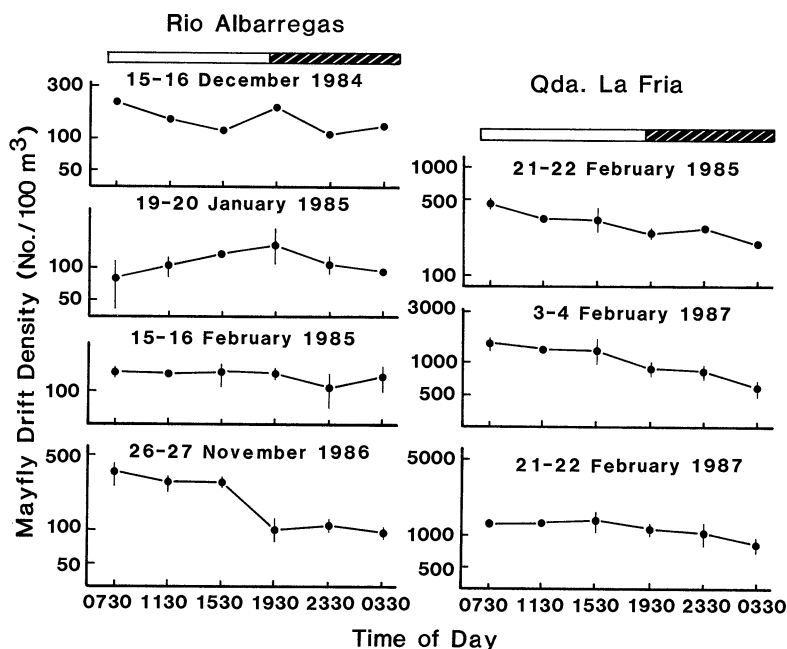
FIG. 2. Drift densities of mayflies sampled on seven dates over 24-h periods from two Andean montane streams that naturally lack drift-feeding fishes. Dots represent the mean of two drift collections, and vertical lines represent the ranges.

less pronounced peak at dawn (Fig. 4A). Drift density after nightfall was significantly greater (multiple comparison test based on Friedman rank sums, $P < .001$, Siegel and Castellan 1988) than densities from the midmorning and afternoon hours (i.e., 1130, 1530). Concordance between data sets was strong and highly significant ($W = 0.86$, $\chi^2 = 25.71$, $P < .001$), indicating that results were consistent and repeatable between different trout streams and sampling dates. This pattern differed from the fishless site, where *Baetis* drift was aperiodic (Fig. 4B).

Drift periodicity and the risk of predation

If fish predation is an important determinant of the timing of drift, then the degree to which activity is biased toward the nighttime hours should be positively correlated with the intensity of predation. A further test of the risk-of-predation hypothesis was performed by comparing the numbers of drifting mayflies at night vs. day among the eight streams with different fish assemblages. This gradient of predation regimes, as determined by electrofishing, ranged from fishless Andean streams to others containing at least 20 species of drift-feeding fishes and >500 individuals/100 m² (Fig. 5; Flecker 1990).

The night:day drift ratio was strongly correlated with the intensity of the predation regime (Fig. 5, Kendall's coefficient of rank correlation, $\tau = 0.697$, $P < .001$). Although drift always exhibited a nighttime bias in streams with native drift-feeding fishes, nocturnal drift propensity increased with predation risk. Among the eight study sites, I examined a total of 10 genera

from 4 mayfly families. Patterns of drift periodicity were more site than taxon specific, and at a given stream I found remarkably similar values of night:day drift for a wide variety of mayfly taxa.

Fish exclusion experiments

Distinct patterns of drift periodicity were observed in all experimental treatments, irrespective of the presence or absence of drift-feeding fishes (Fig. 6). When drift was recorded over a 24-h period, densities were low during the day, followed by increases of several orders of magnitude at night. During the daylight hours of the second day, drift numbers returned to low levels, similar to those observed initially. Drift densities differed significantly between night and day collections, whereas no significant differences were observed among treatments (repeated-measures ANOVA; treatment: $F_{2,3} = 0.18$, $P = .84$; time of day: $F_{6,18} = 111.06$, $P < .001$).

When the experiment was repeated on a second date, drift densities again were much greater by night than day, independent of the experimental treatment (Fig. 6, repeated-measures ANOVA, treatment: $F_{2,3} = 0.21$, $P = .82$; time: $F_{1,3} = 483.07$, $P < .001$). These results establish that diel periodicity is not due to consumption of drifting nymphs by fishes during the day, but is rather a fixed behavioral pattern of mayfly nymphs dwelling in high-predation environments.

DISCUSSION

An important insight in community ecology has been that many interesting effects of predators result from interactions that are not necessarily lethal to prey (see
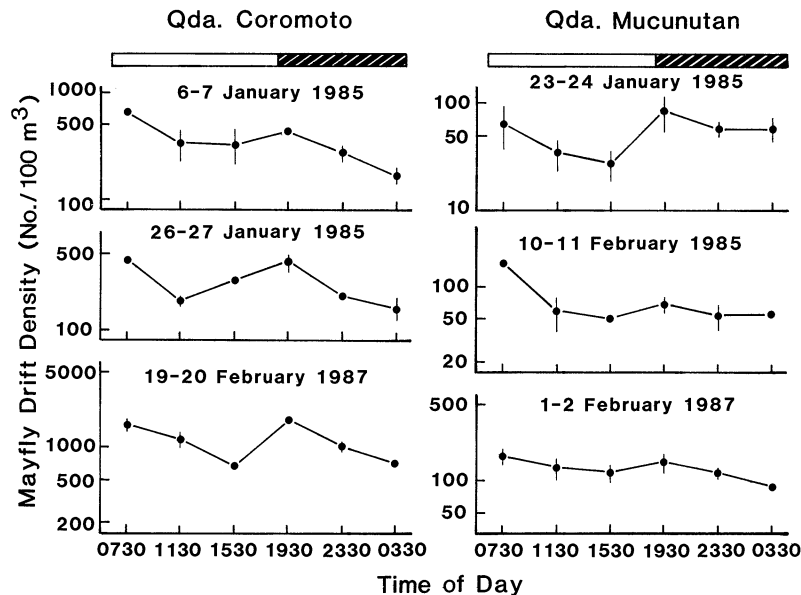
FIG. 3. Drift densities of mayflies sampled on six dates over 24-h periods from two Andean montane streams that contain introduced trout. Trout were observed to feed heavily on stream insects at both of these sites (H. Bastardo, *personal observation*, 1990). Dots represent the mean of two drift collections, and vertical lines represent the ranges.

Kerfoot and Sih 1987). In recent years, much of the focus of predator–prey interactions has shifted from the influence of predation on patterns of prey abundance, to the consequences of predation on prey behaviors. In running-water communities, such nonlethal effects have not been well explored, although a number of examples do exist (e.g., Peckarsky 1980, Cooper 1984, Gilliam and Fraser 1987, Power 1987, Peckarsky and Penton 1989). For instance, several workers have shown that fishes can influence foraging patterns of stream insects (e.g., Soluk and Collins 1988, Feltmate and Williams 1989, Kohler and McPeek 1989). Our understanding of behavioral responses to predation is based largely on those behaviors that are flexible in that they are modified by the presence of a predator. The very nature of their flexibility allows for ready demonstration that habitat or resource use can vary according to the presence or absence of predators. However, some behaviors are hard-wired or fixed, presumably when there is a "prohibitively expensive cost" in assessing risk (i.e., high probability of mortality) (Sih 1987). It is difficult to ascribe adaptive significance to any behavior that is fixed. For example, linking cause and effect of fixed predator-avoidance behaviors is limited by the ineffectiveness of short-term experimental manipulations of predators. This is because a change in a fixed behavior would not be expected in the absence of predators. Instead, tests of adaptive hypotheses of hard-wired behaviors rely heavily on the comparative method, and long-term manipulations of sufficient time scale to measure evolutionary change.

The Venezuelan Andes provide a series of natural experiments for testing whether diel activity patterns are an adaptive response to predation. In the present study examining differences in patterns of drift periodicity along a predation gradient, I found that in streams with native populations of drift-feeding fishes, mayflies displayed a nighttime bias in their drift activity. In contrast, few differences in activity were observed between day and night in Andean streams that have historically lacked drift-feeding predators. This aperiodicity is not unique to the Venezuelan Andes, as a similar phenomenon has been reported for a fishless stream in Ecuador (Turcotte and Harper 1982). Such differences between streams that vary in the presence vs. absence of fishes support the notion that predation has been a major driving force in determining the timing of prey activity.

A further line of evidence for the risk-of-predation hypothesis is the observation that in Andean streams where trout have been introduced, the common mayfly *Baetis* displays nighttime drift peaks, whereas drift is aperiodic in nearby fishless streams. Trout were introduced to the Venezuelan Andes over the last 60 yr; thus, it appears that the length of time necessary for diel periodicity to become established can be relatively short. Likewise, in a study conducted on the Atlantic island of Madeira, Malmqvist (1988) reported that *Baetis* exhibited different patterns of drift behavior from two irrigation channels that differed in the presence of trout. Whereas drift was aperiodic in a fishless channel, a proportionally greater number of mayflies drifted at night in a nearby channel that contained introduced trout. In each of these cases, the ability of insects to assess the presence of predators and adjust their behaviors accordingly could produce differences in pe-
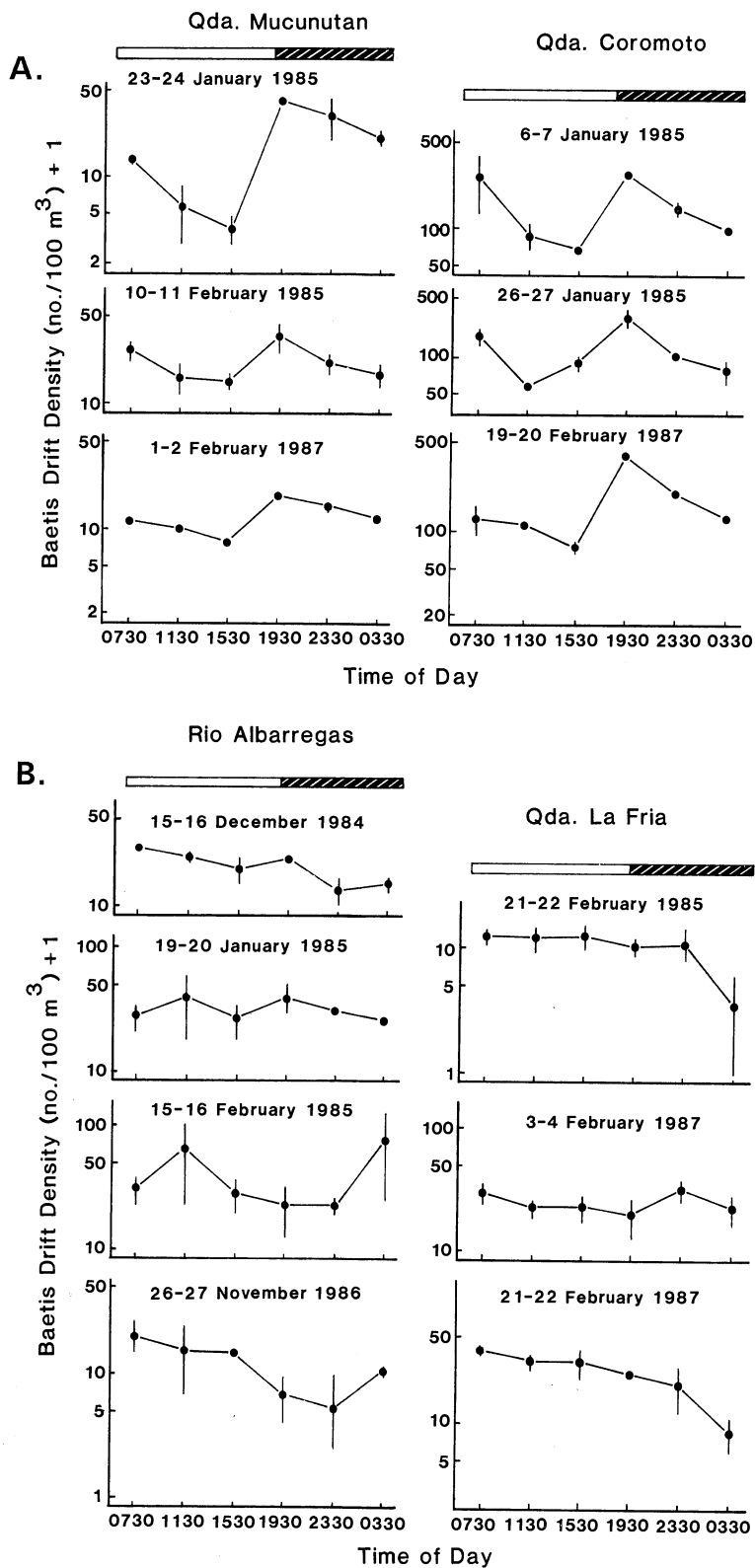
FIG. 4.   Drift densities of *Baetis* sampled from Andean montane streams. The upper panels (A) are from two streams that contain introduced trout. Lower panels (B) are from streams devoid of drift predators. Dots represent the mean of two drift collections, and vertical lines represent the ranges.
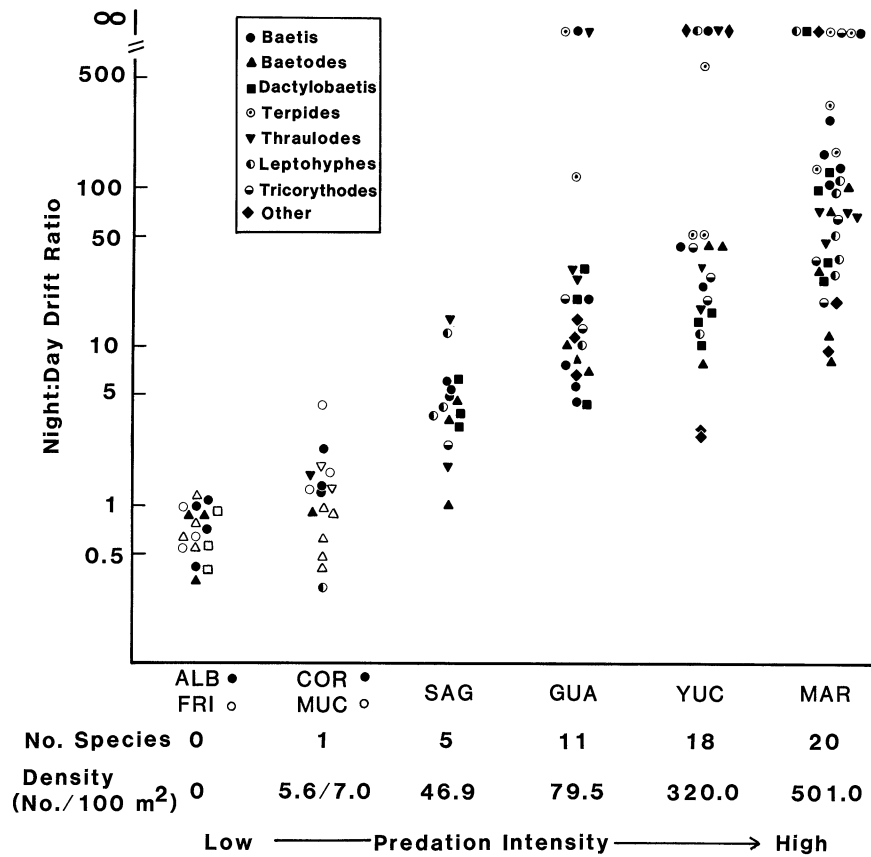
FIG. 5. Ratio of mayfly drift densities from night vs. day drift samples (night : day drift ratio) collected in a series of streams that represent a predation gradient. Streams are ranked according to relative abundance and diversity of drift-feeding fishes. Predation intensity increases from left to right. The number of drift-feeding fish species and densities are shown below stream names. The density of drift-feeding fishes was determined by electrofishing, and represents a relative measure of predation intensity. The Andean piedmont streams were Rio Saguas (SAG), Rio Guache (GUA), Rio La Yuca (YUC), and Rio Las Marias (MAR). Night : day drift densities also are shown for "fishless" Andean montane sites [Rio Albarregas (ALB), Qda. La Fria (FRI)] and for mountain streams with introduced trout [Qda. Mucunutan (MUC), Qda. Coromoto (COR)]. Note that fishless (ALB, FRI) and trout streams (MUC, COR) are treated jointly along the gradient.

riodicity between fishless and trout sites. However, studies demonstrating nocturnal increases in drift in laboratory streams where fish are absent indicate that diel activity patterns are fixed behaviors with a presumably underlying genetic basis (e.g., Corkum et al. 1977, Ciborowski 1983, Kohler 1985).

I found that drift periodicity differed among sites that varied in fish faunal composition. Although differences between fish assemblages are in part confounded by elevation, variation in diel periodicity among sites is not easily explained by other changes, such as changes in physical factors associated with an altitudinal gradient. Drift periodicity of mayflies is a well-documented phenomenon under a wide variety of geographical and physical settings in streams throughout the world. Whereas drift exhibited no differences between night and day in fishless mid-elevation Andean sites studied here, substantial evidence exists from other montane regions of pronounced diel periodicity in high-altitude streams containing drift-

feeding fishes (e.g., Pyrénées, France, Elliott 1973; Beskydy Mountains, Czechoslovakia, Zelinka 1976; Rocky Mountains, USA, Allan 1978, 1984, Stewart and Szczytko 1983). Furthermore, if physico-chemical factors are the major determinants of diel periodicity, it is difficult to account for night : day differences in drift activity from systems where diel fluctuations of physico-chemical variables are minimal (e.g., Pawmpawm River, Ghana, Hynes 1975; Tai Po Kau Forest Stream, Hong Kong, Dudgeon 1983; River Dan, Israel, Allan et al. 1988). Finally, it is hard to explain based on a physico-chemical model why drift is suppressed during nights that are well lit by moonlight (e.g., Anderson 1966, Hynes 1975). Rather, these observations support the hypothesis that risk of predation is the major force responsible for night : day differences in mayfly drift activity.

The fish exclusion experiments conducted in Rio Las Marias suggest that differences in night : day drift densities are not a consequence of the consumption of

nymphs by day-active predators. One explanation is that experimental channels were not of sufficient length to prevent predation on drift originating outside of the channels from overshadowing potential effects of the fish exclusion treatment. This would be especially problematic if channel length was considerably shorter than average drift distance. However, this seems unlikely since mayfly drift distances are believed to be rather short (i.e., several metres; see Brittain and Eikeland 1988) based on a variety of experimental studies (e.g., Elliott 1971, Larkin and McKone 1985, Allan and Feifarek 1989). Instead, the fish exclusion experiments are highly consistent with the notion that nymphs exposed to fish predation may have evolved fixed diel activity cycles in which drift entry generally occurs during hours of darkness. The finding that drift activity becomes increasingly nocturnal with progressively greater predation risk (Fig. 5) further implies that some cost is involved to individuals that restrict drift activity to the nighttime hours. Although the causes and consequences of drift are not entirely clear, there is evidence that drift represents for at least some mayflies a mechanism to actively search for high-quality, algal-rich food patches (Kohler 1985). Such a trade-off between patch search behavior and predator avoidance could lead to site-specific variability in nocturnal drift propensity as a function of predation risk. In order ultimately to understand drift, it may be necessary to evaluate the importance of trade-offs between foraging gain and predation risk in explaining decision-making processes of stream insects (Dill 1987). Likewise, vertical migration in zooplankton may be best explained within a similar evolutionary framework (e.g., Zaret and Suffern 1976, Gliwicz 1986, Stirling et al. 1990).

As alternatives to fixed behaviors, drift patterns could result if: (1) day-active fishes directly consume invertebrates and thereby deplete drift numbers during the daylight hours (Bishop and Hynes 1969), or (2) drift behavior is sufficiently flexible that insects respond to local variation in predation regimes. Results of the fish exclusion experiments do not support either of these alternative hypotheses, as diel periodicity was observed even when fish were removed. Furthermore, Allan (1982) reported pronounced drift periodicity, even after fish densities were greatly reduced from a 1.2-km section of a Rocky Mountain stream over a 5-yr period.

Although fish exclusion experiments have failed to reveal changes in drift behavior, these results would not be unexpected if insects are responding principally to chemical cues. While neither my fish exclusion nor Allan's removal experiment eliminated water-borne chemicals, laboratory studies provide the best evidence that chemical cues are unlikely controls of mayfly drift rhythmicity. Experiments conducted in artificial stream channels show that mayflies exhibit drift periodicity even in the absence of fish (e.g., Böhle 1978, Kohler 1985). Chemical exudates from fish appear to reduce total drift activity of the amphipod *Gammarus* (Wil-
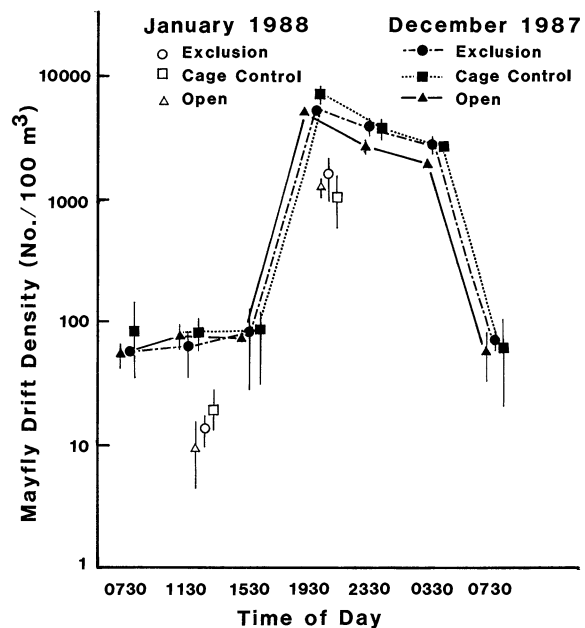

FIG. 6. Drift densities of mayflies from field experiment examining the effects of fish consumption on diel periodicity. In the experiment conducted 23–24 December 1987 (closed symbols), drift was collected every 4 h during a 24-h period. Circles represent the mean of two replicate cages for fish exclusion, squares represent cage control, and triangles represent collections from open stream. Vertical bars denote the range of measured densities. In the experiment conducted 21 January 1988 (open symbols), drift was collected for 2 h at midday (1200–1400) and after dark (2000–2200).

liams and Moore 1985, Andersson et al. 1986), rather than cause shifts in drift activity to the nighttime hours. Chemical compounds may therefore play a role in influencing drift propensity, but do not appear to control the periodicity of drift activity. In addition, the importance of light as a proximate cue affecting drift periodicity has been well established in both laboratory and field studies (e.g., Waters 1972, Müller 1974, Haney et al. 1983).

A number of other patterns of drift behavior further support the risk-of-predation hypothesis. To date, the most convincing evidence has been the discovery that as mayflies mature and become more vulnerable to size-selective predators, they display an increasing bias toward nocturnal behavior (e.g., Anderson 1966, Allan 1978, 1984, Skinner 1985). On well moonlit nights, however, drift can be suppressed, presumably due to increased visibility (e.g., Anderson 1966, Bishop and Hynes 1969, Hynes 1975). Interestingly, moonlight has been reported to inhibit the largest nymphal size classes most severely (Anderson 1966). In contrast, reductions in visibility during daylight hours with increased turbidity may result in escalated drift. Pearson and Franklin (1968) found that a sudden increase in the turbidity of a large river was accompanied by higher mayfly drift

rates, even though no change in stream discharge was noted. It would be intriguing to test whether drift periodicity is generally less pronounced in turbid rivers where visibility is continually limited.

In conclusion, I argue that fish predation has been an important evolutionary force in shaping drift behavior of lotic mayflies. Until recently, studies on the effects of fishes in stream systems have generally focused on the direct consequences of predators via consumption. It has been difficult to demonstrate a clear role of fish predation in influencing patterns of lotic community structure (e.g., Allan 1982, Flecker and Allan 1984, Reice and Edwards 1986, Thorp 1986, Flecker 1990). Immigration via drift appears to play a major part in obscuring the effects of prey consumption by predators (e.g., Cooper et al. 1990, Flecker 1990). These very immigration processes have been subject to selection by predators. My findings suggest that evolutionary effects of predation in natural communities may be important; however, these impacts are not necessarily coupled with strong ecological effects expressed in the currency of species abundance and diversity (Flecker 1990).

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APPENDIX

Current velocities (cm/s) within experimental treatments on each of two dates in the fish exclusion experiments. Current was measured using a General Oceanics mechanical flow meter.

Treatment	23–24 December 1987	21 January 1988
Exclusion		
Replicate 1	46.1	14.7
Replicate 2	36.1	28.9
Cage control		
Replicate 1	33.4	17.3
Replicate 2	40.0	13.2
Open stream		
Replicate 1	68.6	28.4
Replicate 2	49.0	19.2