# Food Habits of Species of Ephemerellid Mayflies (Ephemeroptera: Insecta) in Streams of Oregon

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ABSTRACT: Data on food habits were obtained for 20 species in the mayfly family Ephemerellidae. Diet of a species often varied with site, habitat and size, but such variation did not completely mask differences among species. Adaptive radiation in diet is relatively great in this family, but species showed no distinct groupings when classified either on a functional basis or by traditional trophic categories.

## INTRODUCTION

Because aquatic insects are thought to be extremely facultative in the type of food they consume, many species are considered to be either trophic generalists (Cummins, 1973) or at best "selective omnivores" (Hutchinson, 1981). The difficulties that opportunistic feeding habits impose on development of trophic models have led some researchers to adopt alternative classifications of trophic relationships (*e.g.*, Cummins, 1973, 1974). Few studies, however, have been thorough enough to examine variation both within and among species, although such an approach is necessary if concepts of specialization and opportunism are to be meaningful (Fox and Morrow, 1981).

The purpose of this study was to describe the food habits of some species in the mayfly family Ephemerellidae. I was interested in the following questions:

1. What foods did different species ingest?
2. How did diet vary with location, habitat and size?
3. Were species food specialists or generalists?

Approximately 80 species of Ephemerellidae in eight genera are recognized in North America (Edmunds *et al.*, 1976; Allen, 1980). Twenty-four species occur in Oregon (Hawkins, 1982), 20 of which I examined in this study. Of the species collected, 10 were represented by fewer than 10 individuals (Table 1), however, they are included in analyses and comparisons whenever possible because data on their food habits are rare.

## METHODS

*Study sites.* — Individuals were collected from a variety of stream sites. Most sites were within the McKenzie River drainage basin in the Cascade Range of Oregon, but I also examined animals collected from other drainages in the state (Coast Range, Willamette Valley, Deschutes River). Size of the streams sampled varied from approximately 3-60 m bankfull width. Stream gradients ranged from 0.2-45%. Dominant substrates varied with site and included sand, gravel, cobble, boulder and moss. At some sites large woody debris was common.

Six sites were chosen for detailed comparisons because they varied markedly in the type and amount of vegetation surrounding the stream. Three sites (Upper Mack Creek = UMACK, Mack Creek = MAOG, Mill Creek) flowed through old-growth (≥ 450 years) coniferous forests. These sites are characteristic of heavily shaded streams in which the major source of organic matter in the stream is allochthonous litter (Hawkins *et al.*, 1982). Two other sites (Mack clear-cut = MACC, Fawn Creek) drained sections of watersheds in which the vegetation surrounding the streams had been removed 14 and 7 years earlier, respectively. The sixth site was on a reach of Lookout Creek that was naturally open to sunlight. The latter three sites are characteristic of streams in which the primary food base is of autochthonous origin (Lyford and Greg-

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TABLE 1. — Mean percent composition by area of different food classes and dietary niche breadth (B₁) for 20 species of western Ephemerellidae. Data are combined over all sites and habitats

| Species | | n | Diatoms | Detritus | Animal | Moss | Wood | Fungus | Other algae | $B_1$ |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Food class | | | | |
| Caudatella cascadia | Allen & Edmunds | 21 | 37 | 41 | 0 | 20 | 1 | 1 | 0 | 2.9 |
| C. hystrix | Traver | 23 | 44 | 35 | 4 | 15 | 2 | 0 | 0 | 2.9 |
| C. edmundsi | Allen | 17 | 55 | 26 | 0 | 19 | 0 | 0 | 0 | 2.5 |
| C. heterocaudata | McDunnough | 6 | 39 | 30 | 15 | 15 | 0 | 0 | 1 | 3.5 |
| Serratella teresa | Traver | 21 | 33 | 48 | 1 | 17 | 0 | 1 | 0 | 2.7 |
| S. tibialis | McDunnough | 13 | 32 | 58 | 10 | 0 | 0 | 0 | 0 | 2.2 |
| S. velmae | Allen & Edmunds | 9 | 56 | 43 | 1 | 0 | 0 | 1 | 1 | 2.0 |
| Ephemerella infrequens | McDunnough | 60 | 18 | 55 | 5 | 8 | 12 | 1 | 1 | 2.8 |
| E. inermis | Eaton | 3 | 20 | 73 | 0 | 0 | 0 | 0 | 7 | 1.7 |
| E. verruca | Allen & Edmunds | 3 | 25 | 75 | 0 | 0 | 0 | 0 | 0 | 1.6 |
| E. aurivillii | Bengtsson | 2 | 0 | 96 | 0 | 0 | 0 | 2 | 2 | 1.1 |
| Drunella spinifera | Needham | 34 | 21 | 27 | 48 | 3 | 1 | 0 | 0 | 2.9 |
| D. doddsi | Needham | 36 | 57 | 9 | 31 | 0 | 0 | 1 | 1 | 2.3 |
| D. pelosa | Mayo | 29 | 72 | 26 | 0 | 2 | 0 | 0 | 0 | 1.7 |
| D. coloradensis | Dodds | 65 | 53 | 19 | 25 | 1 | 2 | 1 | 0 | 2.6 |
| D. grandis | Eaton | 5 | 17 | 50 | 23 | 4 | 0 | 1 | 5 | 3.0 |
| Attenella delantala | Mayo | 6 | 1 | 99 | 0 | 0 | 0 | 0 | 0 | 1.0 |
| A. margarita | Needham | 3 | 20 | 80 | 0 | 0 | 0 | 0 | 0 | 1.5 |
| Eurylophella lodi | Mayo | 2 | 0 | 99 | 0 | 0 | 0 | 0 | 1 | 1.0 |
| Timpanoga hecuba | (Eaton) | 4 | 46 | 54 | 0 | 0 | 0 | 0 | 0 | 2.0 |

ory, 1975; Gregory, 1980). A detailed description of four of these sites (MAOG, MILL, MACC and FAWN) is given in Murphy et al. (1981) and Hawkins et al. (1982), and a general description of the region is given by Hawkins and Sedell (1981). Within a site, different habitats were also sampled. These included cobble riffles, depositional habitats dominated by sand and gravel, the tops of large boulders, submerged patches of moss, and submerged woody debris. All habitats were sampled with a D-frame kicknet (0.5 mm mesh).

*Food habits.*—I determined gut contents of individual animals by the methods described in Coffman et al. (1971). After noting the length of each animal, the foregut was removed. Contents were then filtered onto a 13-mm Millipore filter (0.45$\mu$m). After clearing with immersion oil, a permanent slide was prepared. Each slide was examined to determine the proportions of diatoms, detritus, animal matter, moss, wood, fungal mycelia and other algae (unicellular and colonial green, and bluegreen forms). The number of diatom frustules observed within an entire ocular grid (196 squares = 2.46 x $10^{-2}$mm² at 450 power) was counted in 10 randomly chosen fields. At 100 power the number of squares (1 square = 2.50 x $10^{-3}$mm²) within the grid that were covered by the other food sources was noted for five randomly chosen fields.

The area of filter covered by each food class was calculated based on direct measures of area except for diatoms which were counted and converted to area. The most commonly observed diatoms in guts were large *Achnànthes* and *Melosira* spp. I assumed that each diatom covered 2 x $10^{-4}$ mm² of filter. This value was based on occasional measurements of individual diatoms and literature values for these taxa. If significant numbers of smaller diatoms were observed, they almost always were present as dense aggregations. In this case, I estimated area directly in the same manner described for detritus.

*Analysis.*—Analysis of variance and t-tests were used to determine whether diet was dependent on site or habitat. Correlation analysis was used to determine whether diet varied with size. Dietary niche breadth was calculated by the formula of Levins (1968) where:

Niche breadth $(B_i) = 1/\Sigma p_j^2$

and $p_j$ = the proportion of food $j$ consumed by species $i$, and $p^2js$ are summed over $j$ food types. Estimates of niche breadth were calculated based on mean individual diets as given in Table 1.

To compare similarity in food consumed by the different species, I first constructed a matrix of pairwise dietary overlaps and then clustered species based on this matrix. I calculated dietary overlap using the formula of Pianka (1973) where:

$$O_{ij} \text{ (overlap)} = \sum_a^n p_{ia}p_{ja}/[(\sum_a^n p^2_{ia})(\sum_a^n p^2_{ja})] \frac{1}{2}$$

and p = proportional consumption of food $a$ by two species $i$ and $j$, and n = number of resource classes.

An average-linkage algorithm was then used to generate clusters (Dixon, 1981).

## RESULTS

Diatoms and detritus were the food items most commonly consumed and together composed 48-100% of material ingested among the 20 species examined (Table 1). Animal matter was an important (23-48%) component in four of the five *Drunella* species and comprised 15% of ingested material in *Caudatella heterocaudata*. Five species had 15% or greater of total gut contents represented by moss. Of these species, four belong to the genus *Caudatella*, the other to *Serratella*. Wood, fungal mycelia and other algae were poorly represented (<12% but usually <5%) in all species.

Dietary niche breadths varied from 1.0-3.5. The most highly specialized species were all detritivores ($B_i = 1.0 - 1.7$) with the exception of *Drunella pelosa* (1.7) which mainly consumed diatoms. The most general feeders ($B_i > 2.8$) were species of *Caudatella* and *Drunella*.

For five species, enough animals were collected to compare diet as a function of site, habitat or both. Consumption of moss by *Caudatella cascadia* varied significantly with site. Analysis of variance, based on 16 individuals from upper Mack Creek (UMACK), Mack Creek (MAOG) and Mack clear-cut (MACC), indicated that consumption of moss was highest (37%) in UMACK ($F_{2, 13} = 8.01$, $P < 0.01$). In this stream most bottom substrates were covered with a thick carpet of several moss species. Consumption of moss was lowest (0%) in the clear-cut section of Mack Creek (MACC), a site with practically no moss on bottom substrates. The slightly larger section of Mack Creek flowing through the old-growth forest (MAOG) had patches of moss and consumption of moss was intermediate here (10%). Proportions of detritus in guts of *C. cascadia* varied inversely with that of moss (33, 40 and 69%, respectively) but was not significantly different among sites. No significant differences in consumption of other food items existed among sites.

To examine variation in diet as a function of site for the four other species, I compared diet of individuals from shaded sites with those from sections open to light. The diet of *Ephemerella infrequens* clearly depended on site. In shaded areas, proportions of moss (15%) and wood (31%) in the diet were significantly greater than for individuals from open sites (4 and 0%, $t = 2.29$, $P < 0.05$ and $t = 4.05$, $P < 0.001$, df = 57, respectively). In open sites relatively more diatoms (22 vs. 13%) and detritus (70 vs. 46%) were consumed ($t = 2.45$, $P < 0.02$ and $t = 3.11$, $P < 0.01$, respectively) than in shaded sites. Two species of *Drunella* (*coloradensis* and *spinifera*), however, showed no significant shift in diet with site (n = 64 and 25, respectively). The diet of a third species, *D. doddsi*, was weakly dependent on site. More detritus was consumed in shaded sites than open sites (24% vs. 4%, $t = 2.98$, $P < 0.01$, df = 27). However, the most important dietary items, diatoms and animal matter, did not differ between sites.

Two species were collected often enough to examine consumption patterns among habitats as well. For *Ephemerella infrequens,* proportion of detritus in the diet was greatest for individuals from gravel habitats (75%), followed by cobble substrates (57%), and was least important in animals from wood (24%) ($F_{2, 28} = 17.5$, $P < 0.001$). Moss was consumed only by individuals from cobble substrates (10 vs. 0%, $F = 3.47$, $P < 0.05$), and only animals collected on wood had large proportions (52 vs. 0%) of wood in their guts ($F = 15.4$, $P < 0.001$).

Diet among individuals of *Drunella coloradensis* did not vary as much among habitats. A trend for ingestion of more animal matter (27, 40 and 68%) and fewer diatoms (57, 40 and 17%) occurred with increasing substrate size (gravel to cobble to boulder), but these differences were not statistically significant (n = 38). However, diets of animals collected on wood differed from those collected on rock substrates by the presence of moderate amounts of wood (16 vs. 0%), $F_{3, 34} = 11.1$, $P < 0.001$).

Seven of 11 species showed significant correlations between size and percent of at least one food class (Table 2). All species did not respond in the same manner, but when all individuals were examined over all species, consumption of animal matter was positively correlated with size. Conversely, percent diatoms in the gut was negatively correlated with size.

Three species (*Caudatella hystrix, Drunella coloradensis* and *D. pelosa*) had significant negative associations between size and percent consumption of diatoms. In *Serratella teresa* the relative amount of diatoms consumed increased as size increased. Of all 11 species, eight showed negative (although not necessarily significant) correlations between size and percent ingestion of diatoms, a result not expected by chance alone (P = 0.03, two-tailed test, Binomial distribution).

The proportion of detritus consumed also tended to decline with size. Two species,

*Serratella teresa* and *Caudatella edmundsi*, showed significant negative correlations; and among all 11 species, seven correlations were negative (P = 0.11).

Both animal matter and moss often increased in relative abundance with size. Percent animal matter in *Drunella coloradensis* was strongly correlated with size, and percent moss was significantly correlated with size for both *Ephemerella infrequens* and *Caudatella edmundsi*. The number of species exhibiting positive correlations for either animal matter or moss was eight in both cases. When considering all species, such results were probably not due to chance (P = 0.01 for animal matter, P = 0.03 for moss).

The cluster analysis based on data in Table 1 described quantitative differences in diet among species (Fig. 1). It is possible to make a gross distinction between those species in which diatoms are a major component of the diet (first 10 species) and those in which detritus is a major component (next nine species). In general, however, species and subclusters of species showed gradual differences in percent similarity of diet.

DISCUSSION

*Food habits.* — Examination of gut contents can lead to insights regarding food requirements only if such static measures are truly representative of the dynamic relationship between ingestion, assimilation and growth. Because so few studies exist describing such relationships, I have assumed that gut contents do reflect ingestion of usable and thus "nutritious" food items. Although the validity of this assumption is open to criticism, some correspondence between ingested food and assimilable food is expected if animals maximize their fitness through their feeding behavior (Calow, 1977; Cummins and Klug, 1979).

When I considered all individuals and taxa, species differed rather markedly in their gut contents (Table 1). It is possible that chance differences (*e.g.,* associated with small sample size) can be erroneously interpreted as significant and thus of ecological importance. Nevertheless, these data seem to indicate that among species in this family, preferences for certain food items exist that transcend variability within taxa due to differences in site or habitat.

Comparison of my data with that of others supports this conclusion. Gilpin and Brusven (1970) presented another comprehensive data set on gut contents of Ephemerellidae from western North America. Comparison of their data with mine show similar diets for most species, although there are also some major differences. For example, *Ephemerella infrequens/inermis* (they lumped these species) have similar food habits in both data sets, as do *Serratella tibialis, Drunella grandis, Attenella margarita,* and *Timpanoga hecuba*. In contrast, *D. doddsi* and *D. coloradensis/flavilinea* (lumped) show distinct differences.

TABLE 2. — Correlations between size (mm) and percent composition of different food items in the gut. Percentages transformed (arcsin) prior to analysis. Values given are correlation coefficients (r). P<0.05 = *, P<0.01 = **

| Species | n | Diatoms | Detritus | Animal | Moss | Wood | Fungus |
|---|---|---|---|---|---|---|---|
| C. cascadia | 18 | 0.191 | 0.149 | — | -0.369 | 0.027 | -0.518* |
| C. hystrix | 23 | -0.550** | 0.166 | 0.203 | 0.398 | -0.213 | -0.117 |
| C. edmundsi | 17 | -0.115 | -0.609** | 0.313 | 0.573* | — | — |
| S. teresa | 21 | 0.660** | -0.550** | -0.183 | 0.001 | — | -0.412 |
| S. tibialis | 13 | -0.095 | -0.199 | 0.160 | 0.424 | — | — |
| E. infrequens | 60 | -0.129 | -0.177 | 0.109 | 0.295* | 0 | 0.080 |
| D. spinifera | 33 | 0.037 | 0.050 | -0.016 | -0.057 | -0.035 | -0.128 |
| D. doddsi | 36 | -0.067 | -0.324 | 0.211 | -0.255 | — | -0.165 |
| D. coloradensis | 65 | -0.313** | -0.138 | 0.433** | 0.144 | -0.168 | -0.142 |
| D. pelosa | 29 | -0.463* | 0.256 | 0.179 | 0.330 | — | — |
| D. grandis | 5 | -0.863 | -0.371 | 0.394 | 0.245 | — | 0.158 |
| All species | 359 | -0.115* | -0.099 | 0.257** | 0.008 | -0.034 | -0.067 |

Also, when dietary niche breadths for species studied by others are plotted against niche breadths that I observed for the same species, a positive relationship was observed (Fig. 2). Points that were not close to the theoretical line predicting exact correspondence were derived from data based on small sample size (white circles on graph).

Other examples exist that suggest ephemerellid species often consume a restricted range of food types. Shapas and Hilsenhoff (1976) report that *Ephemerella aurivillii* in Wisconsin consumes between 85-100% detritus depending on the season; the rest of the diet was composed of diatoms (4-15%) or filamentous algae (4%). In Oregon, I found that this species consumed 96% detritus, 2% filamentous algae and 2% fungal mycelia (Table 1). Gray and Ward (1979) found that *E. inermis* consumed between 68 and 98% detritus and 2-31% diatoms depending on the season. The overall value they gave for one site was 82% detritus and 18% diatoms; for another site the percentages were 98 and 2, respectively. Both sites produced results similar to those that I observed.

The observation that both site and habitat affected proportions of ingested material lends credence to the conclusion of Muttkowski and Smith (1929), later echoed by Cummins (1973), that "local conditions beget local results." Fox and Morrow (1981) showed similar variation among terrestrial insects and provided a cogent discussion of such phenomena. It must be noted, however, that even though the percent of a food class consumed varied with locality for some species, such variation did not appear to be sufficient to completely mask differences that exist among species.
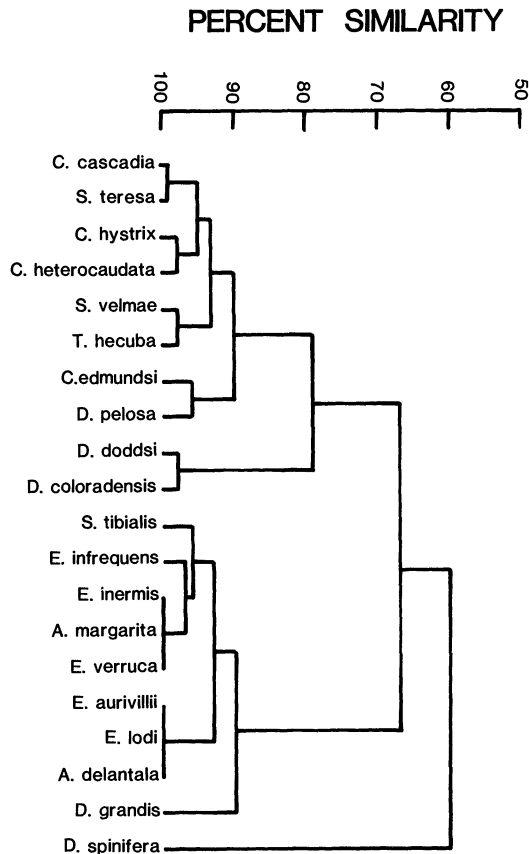
## PERCENT SIMILARITY



Fig. 1. — Dendrogram showing results of cluster analysis

Data of Gray and Ward (1979) and of this study suggest that diet of stream inverte-brates may not always vary within species as much as previously thought. Gray and Ward showed that diet of herbivore-detritivore taxa did not differ significantly between their study sites, although sites differed markedly in type of food available to con-sumers. I compared diet of 11 species studied by Gilpin and Brusven (1970) to diet of the same species in my study by calculating overlap in diet (as described above) between these different populations. Mean overlap among populations for these species was 0.858. Mean pairwise overlap among all combinations of the 20 species that I studied was 0.764. These results also indicate that populations of the same species are more alike in their diets than are populations of different species ($P < 0.05$, n = 11, t-test after arcsin transformation). In an earlier study, Coffman *et al.* (1971) suggested "that avail-ability of food is the dominant factor influencing composition of the diet." Coffman *et al.* qualified their statement by implying differences in diet may occur mainly within food categories (*i.e.*, detritus, algae, etc.). It seems apparent, however, that far more detailed and comprehensive data are necessary in order to determine the relative influence of lo-cality (*i.e.*, food availability) and the dietary constraints specific to a species.

Consumption of certain food items also varied with size of the animal, often in a systematic manner. Age- or size-specific variation in feeding habits is well-documented (Coffman *et al.*, 1971) and has been cited as evidence of the opportunism of feeding (Cummins, 1973). Coffman *et al.* (1971) noted that the percent of diatoms and algae in
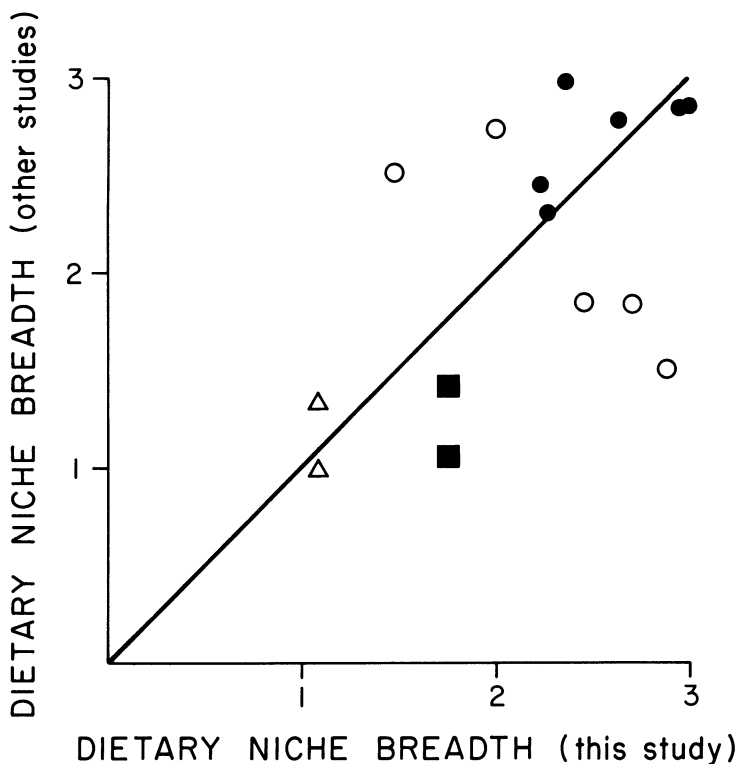


Fig. 2.—Relationship between dietary niche breadth of species observed in this study com-pared with other studies. Circles represent comparison of my data with that of Gilpin and Brusven (1970). Triangles are comparison of data with Shapas and Hilsenhoff (1976). Squares are comparison of data with Gray and Ward (1979). Open symbols represent values derived from data based on small sample size

guts increased as size increased. This trend was not evident for most of the species that I studied (Table 2). The causes responsible for the relationship that I observed likely involve changes in feeding efficiency or ability with size. As size increased, animal material (live prey) and moss increased in relative abundance in guts, whereas detritus and diatoms decreased. Both fine detritus and loose diatoms can be ingested by small larvae. On the other hand, to engulf animals or to shred large pieces of plant material, organisms require larger gapes, more powerful mouthparts, or both.

It is apparent that site, habitat or size can influence composition of the diet for some species. It is therefore understandable that stream insects have often been considered trophic generalists or opportunists. The relationship between locality and consumption may indeed reflect a certain degree of flexibility in what is consumed. The relationship with size is apparently more systematic and often describes shifts toward larger food. In part, this trend may reflect a tendency to take in more nutritious food (animal prey; *see*, *e.g.*, Anderson, 1976).

It is unclear whether moss is preferentially consumed because of its food value or if pieces are bitten off when attached diatoms are fed upon. Of the aquatic macrophytes that occur in streams (not including macroalgae), mosses are more often eaten than others (Hynes, 1941; Chapman and Demory, 1963; Gaevskaya, 1969), and two species of European Ephemerellidae have been shown to consume copious amounts of moss (Percival and Whitehead, 1929). It would therefore be surprising if these species were not deriving some direct benefit from the consumption of such quantities of moss.

*Feeding guilds.* — I attempted to identify different feeding groups or guilds (Table 3) within this family based not only on what species eat (Fig. 1) but also on how they forage (Root, 1967, 1973). In all but one case, a combination of traits was necessary to define a guild (*cf.*, Cummins, 1973, 1974; Cummins and Klug, 1979; Hawkins and Sedell, 1981; Hawkins *et al.*, 1982). Species were placed into a guild based on the following criteria: degree to which they (1) scraped diatoms (SC); (2) shredded (chewed) moss ($SH_m$); (3) shredded coarse detrital material ($SH_d$); (4) consumed loose fine detritus (CG), and (5) engulfed living prey (P). These guilds are tenuous, because I lack detailed or quantitative data describing feeding method or behavior for most species. I offer them as a tentative description of the major avenues along which Ephemerellidae have evolved to exploit food resources. An alternative approach based only on food eaten (*see* MacMahon *et al.*, 1981) would be to define guilds strictly on traditional groupings of herbivore, detritivore and predator. However, the cluster analysis (Fig. 1) and inspection of Table 1 showed that clear distinctions among species did not exist.

The two attempts to classify species into groups are interesting because they clearly indicate that attempts to either classify animals on a simple functional basis (*sensu* Root, 1967; Cummins, 1973) or classify them according to traditional trophic categories may significantly misrepresent real differences in feeding ecology. If the renewed interest in trophic structure and food webs (Pimm, 1982; Paine, 1980; Pianka, 1980; Cohen, 1978; Heatwole and Levins, 1972) is to lead to meaningful generalizations about ecological communities, the specific data on which analyses are based must accurately portray real feeding relationships among species. The extent to which our classifications

TABLE 3. — Feeding guilds among western Ephemerellidae

| SC | SC/$SH_M$ | SC/$SH_D$/CG | SC/P | P/$SH_D$ | $SH_D$/CG |
|---|---|---|---|---|---|
| *Drunella pelosa* | *Caudatella cascadia* | *Serratella tibialis* | *Drunella doddsi* | *Drunella spinifera* | *Ephemerella verruca* |
| | *C. hystrix* | *S. velmae* | *D. coloradensis* | *D. grandis* | *E. aurivillii* |
| | *C. edmundsi* | *Attenella margarita* | | | *Attenella delantala* |
| | *C. heterocaudata* | *Timpanoga hecuba* | | | *Eurylophella lodi* |
| | *Serratella teresa* | *Ephemerella infrequens* | | | |
| | | *E. inermis* | | | |

SC = diatom scraper, $SH_M$ = moss shredder, $SH_D$ = detritus shredder, CG = fine particle collector-gatherer, P = predator

misrepresent the real world should be an important concern to those involved in both theory and application.

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