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Life history of five small minnow mayflies (Ephemeroptera: Baetidae) in a small tropical stream on the Caribbean slope of Costa Rica

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Life history characteristics of five species of Baetidae were investigated over a one-year period at Quebrada González, a warmwater stream in Braulio Carrillo National Park. Larvae of three species of *Baetodes* and two species of *Camelobaetidius* were collected at monthly intervals. Measurements of head capsules show a wide size range within each species throughout the year. For all species studied, mature larvae with black wings pads were found during all months. Fecundity averaged less than 1000 eggs per female for all species. The asynchronous development, multiple overlapping cohorts, and long emergence period with reproduction occurring throughout the year suggest a multivoltine life history for all five species. The high water temperatures (annual mean 21.4°C, ranging from 20.6°C to 22.1°C) throughout the year undoubtedly contribute to these life history patterns. The multivoltinism of these mayflies conforms to a general pattern of multivoltinism for aquatic insects in tropical regions.

Keywords: mayfly; Baetidae; life history; larval growth; emergence; fecundity

Introduction

Unfortunately, life histories of tropical species are generally less well known than their taxonomy, suggesting that taxonomic studies have progressed more rapidly than basic life history studies (Jackson and Sweeney 1995a).

Life history information is fundamental for most ecological studies of aquatic insects (Butler 1984). For example, its parameters are essential to estimating secondary production (Benke 1984), using insects as biological indicators for water pollution (Flowers and Hilsenhoff 1978; Johnson et al. 1993), and constructing models to predict the consequences of future conservation strategies (Rustigian et al. 2003).

In Costa Rica, two life history studies of mayflies have been published showing the total development times for five mayfly species (including one species of Baetidae) (Jackson and Sweeney 1995b) and presenting the first evidence of semivoltinism in a tropical mayfly (Sweeney et al. 1995).

Here we focus on the life history aspects of three species of *Baetodes* and two species of *Camelobaetidius*. These genera are very common in Costa Rica and the five species are most common species of Baetidae at Quebrada González.

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Methods

Study site

This research was conducted at Quebrada González, a first-order stream in Quebrada González Sector, Braulio Carrillo National Park. This 47,000 ha park is situated on the Caribbean slope of the Central Mountain Range, in one of the most rugged and wet areas of Costa Rica. The area receives an average annual precipitation of 7626 mm (measured between 1988 and 2008). This sector of the park was impaired (deforested) by anthropogenic activity 30 years ago but today it is reforested. The Braulio Carrillo highway (National Route 32) between San José and Guápiles crosses both the National Park and Quebrada González. The stream is a small tributary of the Río Sucio and part of the Río Sarapiquí watershed.

The study site in Quebrada González was located 2 km upstream of the confluence with the Río Sucio, 42 km north of San José (10°09.679′ N, 083°56.222′ W, 480 m a.s.l.). The stream has a steep slope and is characterised by cobble-boulder substrate. Flooding was common during all months. Two fish species, the small clingfish *Gobiesox nudus* (Gobiesocidae) and one undetermined species of live bearer (Poecilidae), were observed in the stream.

Water temperature was constant throughout year, ranging only between 20.6°C in January and 22.1°C in May/June (21.4°C annual mean). The average conductivity was 28 μS/cm between May and August 2007 using a WTW LF 330 conductivity.

Benthic fauna

Additionally to monthly collections of Baetidae, Quebrada González was sampled in October 2007 and in April 2008 for macroinvertebrates. All microhabitats were sampled using a D-frame aquatic net (500 μm mesh). All specimens were preserved in alcohol (70%) and then identified to genus level, in some cases only to family or subfamily (especially Diptera). Species level identification is not yet possible because most of Costa Rica's aquatic insect larvae remain undescribed and there are no identification keys available to species level.

Collection, taxonomic identification, larval growth patterns

Larvae of the five species of Baetidae were collected monthly from May 2007 to April 2008. We sampled for about 8 h along a 500 m stretch of stream. The technique consisted of sampling from one or more rocks and then removing all larvae from the net.

A key was constructed in order to separate all 'morphospecies' of *Baetodes* (seven in all) and *Camelobaetidius* (two in all) larvae present in the stream. We used colouration and body shape in conjunction with taxonomic characteristics of Nieto (2004) for *Baetodes* larvae and Nieto (2003) for *Camelobaetidius* larvae to achieve the taxonomic identification.

To determine larval growth patterns, head widths of all larvae were measured (to the nearest 0.025 mm) using a dissecting microscope with an ocular micrometer (at 40x magnification). Then we used size–frequency distributions and histograms to distinguish the size classes and to detect possible growth patterns of the species.

Field rearing and larva–adult association

From the five species of Baetidae, mature larvae with black wings pads were collected directly off the rock surface. These larvae were then placed in a vessel with some water and then placed in rearing cages situated in the stream. The rearing cages were constructed using plastic cups with a lid, such as described by Edmunds et al. (1976). In most cases, we used one cage for each individual. However, mass rearing was used for the larvae of *Baetodes* sp. 1 and with the larvae of *Camelobaetidius* sp. 1, because both species were very abundant and easily recognised in the field. All reared subimagines were kept and allowed to undergo metamorphosis to adult. Each larval exuvia was preserved in alcohol (70%), together with the associated imago and subimago.

Fecundity

A total of 10 female mature larvae or adults were dissected to estimate fecundity (average number of eggs) for each species. For *Baetodes* sp. 2, only eight females were dissected because they were rare. Reared female imagines or subimagines were used in *Baetodes* sp. 1 and *Camelobaetidius* sp. 1, while mature larvae with black wings pads were used in the other three species. Although we reared some adult females of *Baetodes* sp. 3 and *Camelobaetidius* sp. 2, not enough individuals were available for dissection.

Results and discussion

Benthic faunal composition

We collected 1740 macroinvertebrates in 2007 and 1309 in 2008. The two samples contained 35 families and 58 genera of aquatic insects.

Ephemeroptera (mayflies) were the dominant aquatic insects at Quebrada González (Figure 1a, b), comprising 42.5% and 37% of the relative composition of macroinvertebrates collected in 2007 and 2008, respectively. Trichoptera, Diptera and Coleoptera were the next most abundant insect orders. The relative species composition of insects remained fairly constant in both. The dominance of mayflies at Quebrada González was due largely to large populations of some species of Baetidae. A very high percentage (75% or more) of all mayflies collected belonged to the family Baetidae (Figure 1c, d), and mainly to two genera in that family, *Baetodes* and *Camelobaetidius* (Figure 1e, f). In total, we found 13 morphospecies of Baetidae (Table 1). Although the species of Leptohyphidae and Leptophlebiidae were not the focus of the study, we also present a rough estimate of the number of species for each (Table 2), based on field observations and laboratory data. Thus, there are at least 24 species of mayflies in the study reach of this small stream.

It is very common that aquatic insects dominate the benthic fauna of rivers and streams at very high percentages. For example, previous studies in Central America have reported that insects may reach more than 90% of the composition of benthic samples (Pringle and Ramírez 1998; Fenoglio et al. 2004). Our result of more than 99% of the composition in Quebrada González is slightly higher than what has been reported by Fenoglio et al. (2004) for a small river in Nicaragua. In our study stream, some macroinvertebrates like shrimps and molluscs were absent from the samples. These two groups can be very abundant in lowland tropical streams. Studies in Costa

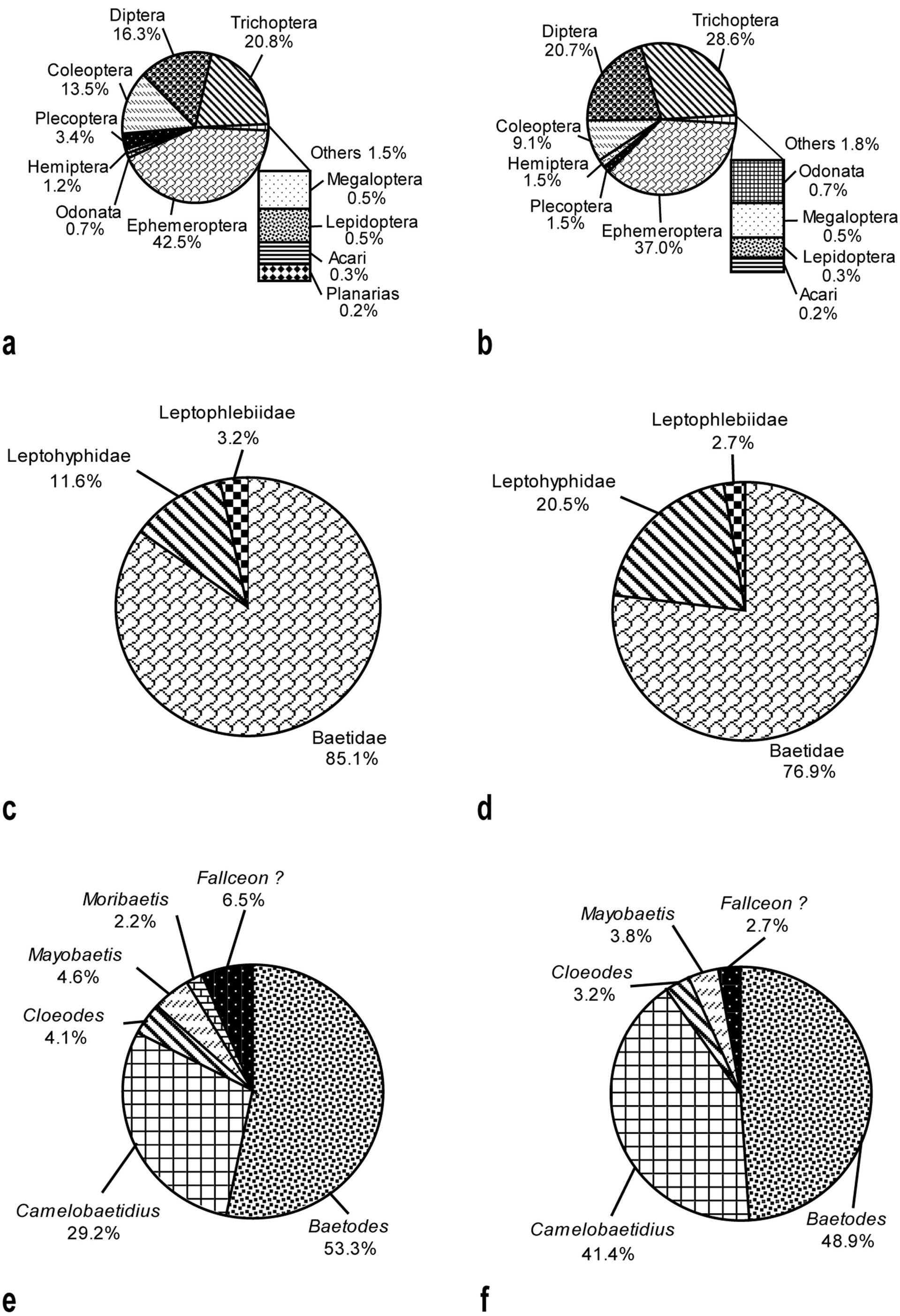

Figure 1. Faunal composition. All graphs show numbers of individuals. (a) Macroinvertebrates, October 2007; (b) macroinvertebrates, April 2008; (c) mayflies, October 2007; (d) mayflies, April 2008; (e) Baetidae, October 2007; (f) Baetidae, April 2008.

Table 1. Number of species within each genus of Baetidae collected at Quebrada González.

Genus of Baetidae	Species no.
Baetodes	7
Camelobaetidius	2
Cloeodes	1
Mayobaetis	1
Moribaetis	1
Fallceon ?	1

Table 2. Estimated number of species for others genera of mayflies collected at Quebrada González.

Family	Genus	Species no.
Leptohyphidae	*Asioplax*	1
Leptohyphidae	*Leptohyphes*	3
Leptohyphidae	*Tricorythodes*	3
Leptophlebiidae	*Farrodes*	2
Leptophlebiidae	*Thraulodes*	2

Rica showed that insects dominated drift in piedmont sites (90 m a.s.l.) but larval shrimp dominated in the lowlands (30 m a.s.l.) (Ramírez and Pringle 2001). Quebrada González, situated in the mountains, at 480 m a.s.l., may be above the altitudinal range for shrimps.

Despite its small size, this stream shows a high diversity of species of Baetidae, especially of the genus *Baetodes* (seven species). For example, Flowers (1991) collected a total of nine species of *Baetodes* (three identified at species level and another six species undetermined) from 42 streams in Panama. The diversity of this genus at Quebrada González is also greater than other studied sites in South America. For example, at the southernmost distribution limit of *Baetodes* (Argentina), the highest number of species collected in a given stream is four (C. Nieto, personal communication, June 11, 2008). In Brazil, only five species have been reported for its entire region (and two additional undetermined species) (Salles and Polegatto 2008). In Colombia, only three species have been reported (Zúñiga et al. 2004). Nieto (2004) proposed that the highest species richness of *Baetodes* occurs in mountain rivers of the Andean basal rain forest. However, based on the number of species reported (12) from Central America (Lugo-Ortiz and McCafferty 1995) and our data, we suggest that Central America rain forests can equal or exceed the *Baetodes* species richness of the Andean basal rain forest.

Abundance, larval growth patterns and emergence period

Baetodes sp. 1

This species was the most abundant during the year of study. Almost 6000 individuals were measured. Larvae of *Baetodes* sp. 1 were very abundant from May until November, showing peaks in September and in November (Figure 2). However, in December the population showed a considerable decrease in abundance, which continued through January and February, reaching its lowest number during March

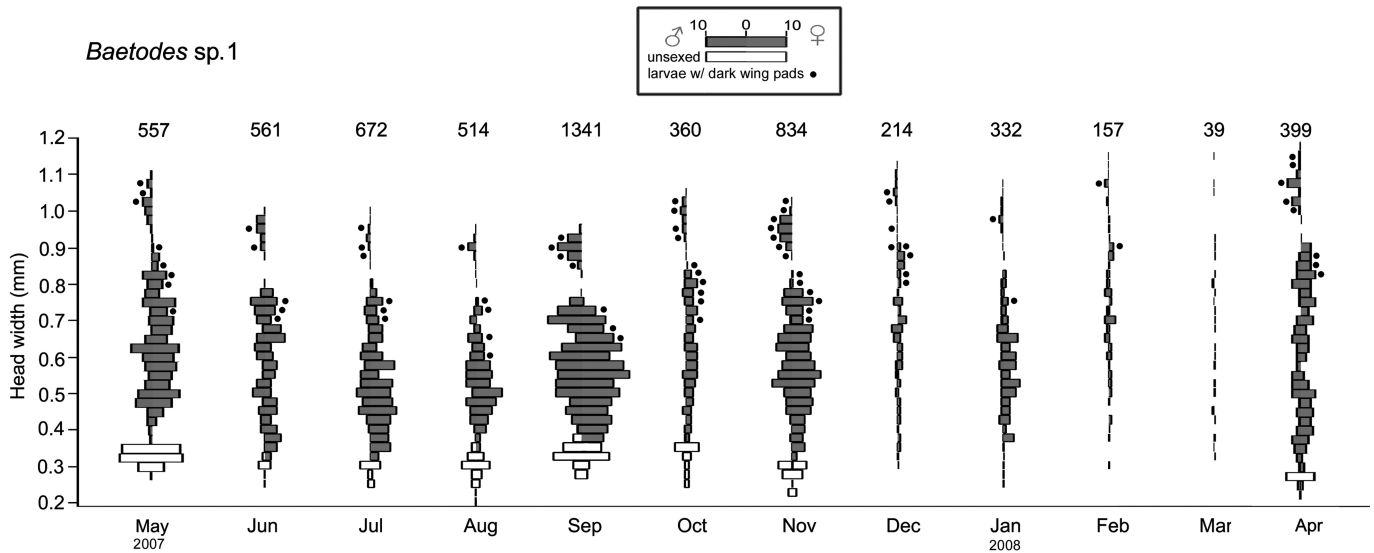

Figure 2. Monthly size–frequency distributions for *Baetodes* sp. 1. Width of bars represents numbers of individuals in each size class on a given sampling date. Bars represent male, female and unsexed larvae, respectively. Closed circles represent larvae with black wings pads. The number of larvae recorded at each month is given in the line above the graphs.

2008. We observed a new increase in the abundance of larvae in April of that year. Although mature larvae with black wings pads were found during all study months (except of March), this species had a large reproductive period between September and November, with a pronounced peak of reproduction at the end of November (Figure 3a). Although few individuals were collected in March, they showed a mixed size distribution similar to the one during the rest of the year. Therefore, the lack of mature larvae in that specific month is likely due to the low number of individuals found.

Baetodes sp. 2

This was the rarest of the three species studied of the genus *Baetodes*. In fact, we collected only one larva in February and none in March 2008. However, similar to what occurred with *Baetodes* sp. 1, the population of *Baetodes* sp. 2 increased during April (Figure 4). This species reached its maximum abundance between May and July 2007, with a second peak of abundance occurring during November and December. Mature larvae were collected during seven months. The population exhibited a high adult emergence at the end of May (Figure 3b).

Baetodes sp. 3

The abundance pattern of *Baetodes* sp. 3 differed from the other two species of *Baetodes* mainly in February and March 2008. During these months, larvae of *Baetodes* sp. 3 were relatively abundant (Figure 5). It appears that this species reproduces very well from January until April (Figure 3c). It is important to point out that in April the population had its peak abundance and highest reproduction. A second difference concerns July 2007, when only four individuals of this species were collected, while a high number of individuals of *Baetodes* sp. 1 and *Baetodes* sp. 2 were found.

Camelobaetidius sp. 1

Camelobaetidius sp. 1 was the second most abundant species with about 3000 individuals collected and measured. This baetid showed its maximum abundance during February, March, October and June (Figure 6). In July, November, and December, the population of larvae decreased. Mature larvae with black wings pads were common throughout the whole year (Figure 3d). This species was the easiest to rear. A total of 59 individuals (imagines and subimagines) were reared.

Camelobaetidius sp. 2

The abundance of this mayfly was relatively high most of the year, except in February and March, when the population of larvae decreased considerably (Figure 7). During March only four larvae were found. However, one month later over 500 larvae were collected. The reproductive period of *Camelobaetidius* sp. 2 showed an intense peak in September 2007 and another less intense in December of the same year (Figure 3e).

Finally, the fluctuations in the abundance patterns seemed to have been influenced, at least in part, by the amount of monthly precipitation. In general, some species such as *Baetodes* sp. 1, *Baetodes* sp. 2 and *Camelobaetidius* sp. 2 showed

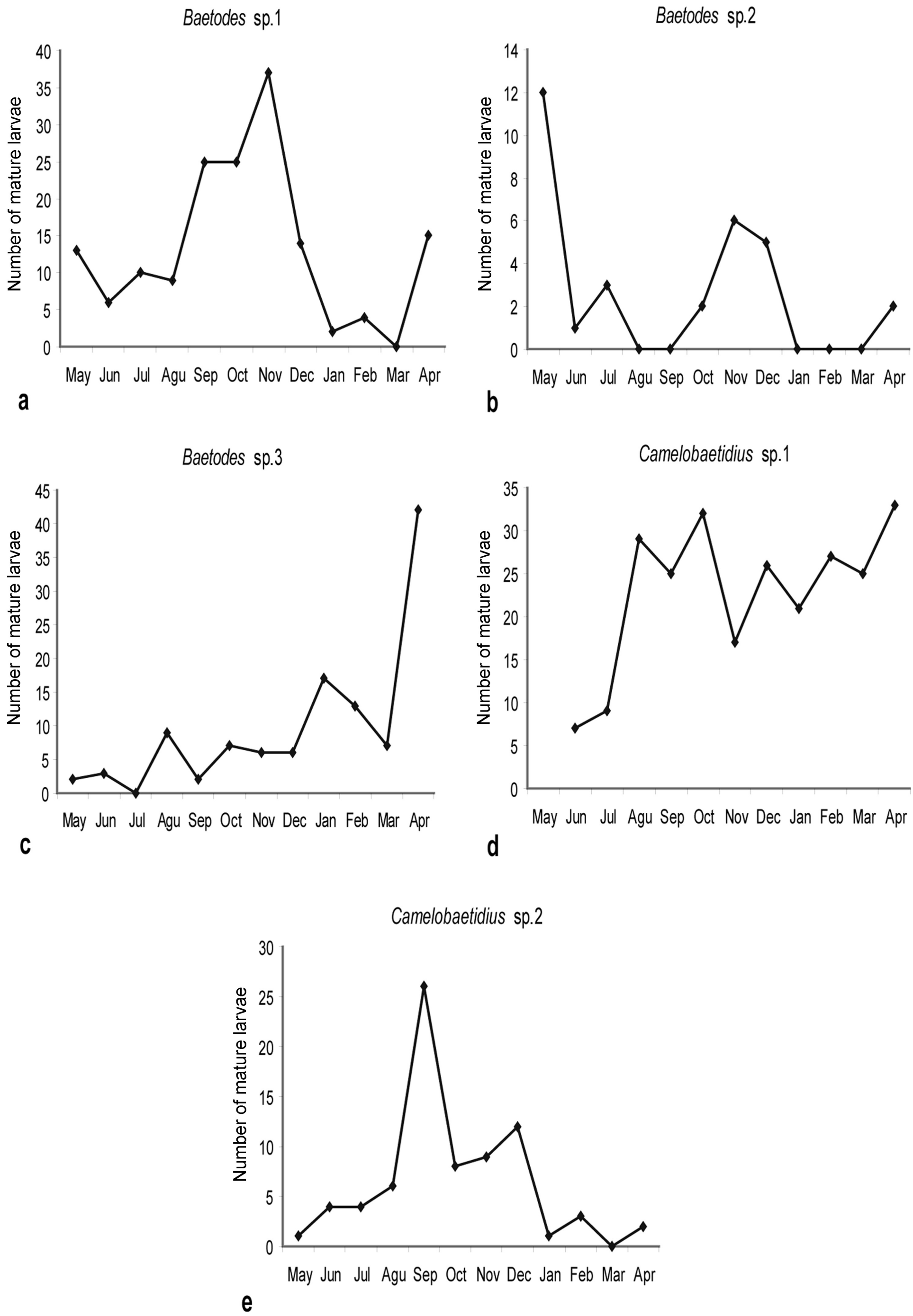

Figure 3. Number of mature larvae with black wings pads collected monthly. (a) *Baetodes* sp. 1; (b) *Baetodes* sp. 2; (c) *Baetodes* sp. 3.; (d) *Camelobaetidius* sp. 1; (e) *Camelobaetidius* sp. 2.

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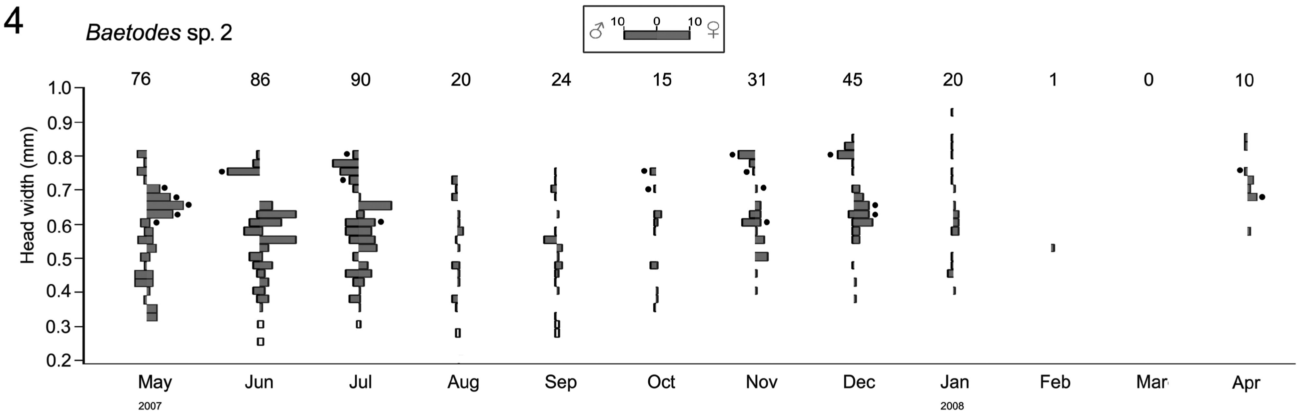

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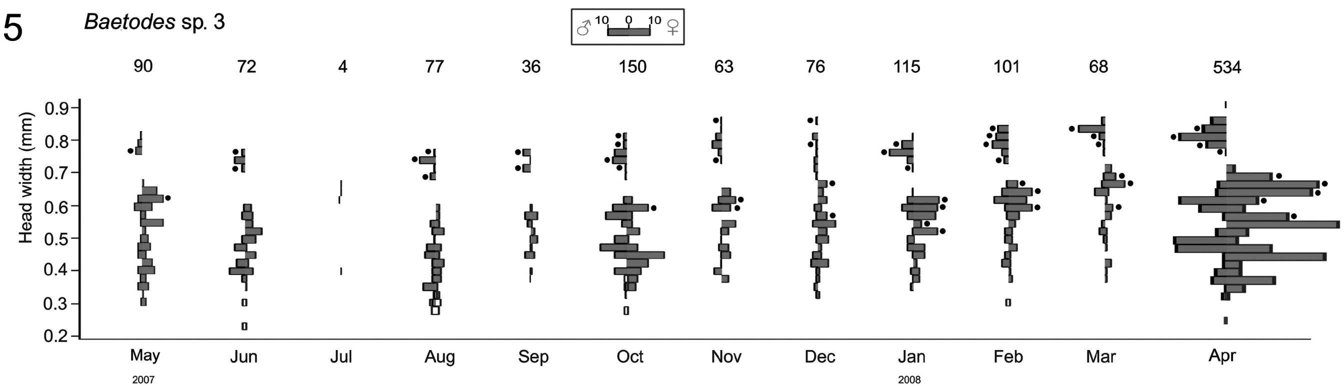
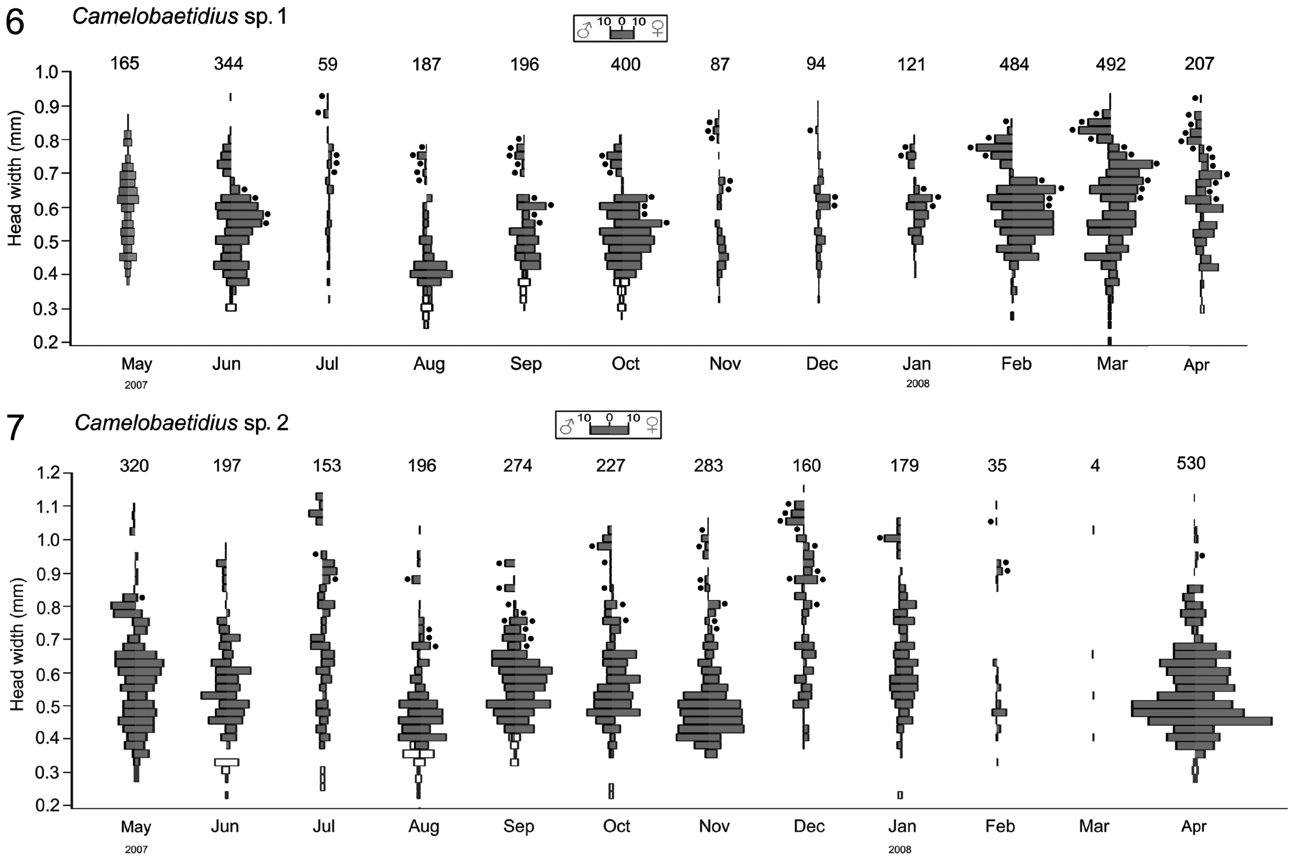


Figures 4–5. Monthly size–frequency distributions for (4) *Baetodes* sp. 2 and (5) *Baetodes* sp. 3. Width of bars represents numbers of individuals in each size class on a given sampling date. Bars represent male, female and unsexed larvae, respectively. Closed circles represent larvae with black wings pads. The number of larvae recorded at each month is given in the line above the graphs.



Figures 6–7. Monthly size–frequency distributions for (6) *Camelobaetidius* sp. 1 and (7) *Camelobaetidius* sp. 2. Width of bars represents numbers of individuals in each size class on a given sampling date. Bars represent male, female and unsexed larvae, respectively. Closed circles represent larvae with black wings pads. The number of larvae recorded at each month is given in the line above the graphs.

a clear decrease in their populations in the months of February and March 2008, precisely coinciding with the lowest precipitation period of our year of study. Monthly mean precipitation from the last 20 years indicates that those are the months with less rain in Quebrada González (Figure 8). During those months, we found a few microhabitats with strong currents in the stream; also the water level was very low, which may have caused a lack of resources (food/habitat). Under those conditions, we collected only 39 larvae of *Baetodes* sp. 1 in March, despite the very intense sampling effort. In contrast, more than 1300 larvae were collected in September. Furthermore, the three species showed an increase in their populations in April, a month characterised by the transition between the two months with less rain and a long rainy period. In another species, *Camelobaetidius* sp. 1, the population seems to take advantage of the low rainfall period to increase its abundance. In contrast, in months with high rainfall, such as July and November of the year 2007 (more than 1200 mm of rainfall per month), the population decreased.

Another possible explanation of the observed variation in abundance along the year, especially during the dry period, could be the high mortality associated with the large spates that occurred just prior to low flow periods. However, in this case, spates were observed throughout the year, though more common from May to December. Besides this, larvae of Baetidae were found in the same substrates after the flooding events. We believe that contrary to some other aquatic insects, these baetid species are able to withstand drifting thanks to their morphological adaptations, resulting in a higher rate of survival.

Flowers and Pringle (1995) studied the yearly fluctuations in a mayfly community of a lowland stream near to Braulio Carrillo National Park. In that study, populations of larvae of all common species showed large fluctuations. Similar results were found in adult Ephemeroptera populations, in a study on the Atlantic coast of northwest Panama (Wolda and Flowers 1985). Lauzon and Harper (1988) affirmed that yearly fluctuations are doubtless reflections of changes in weather patterns and stream conditions, particularly flow and substrate.

The five species of Baetidae studied showed very similar larval growth patterns. Measurements of head capsules clearly revealed the presence of large, medium and very small larvae at any time of the year (Figures 2, 4–7). The wide size range within

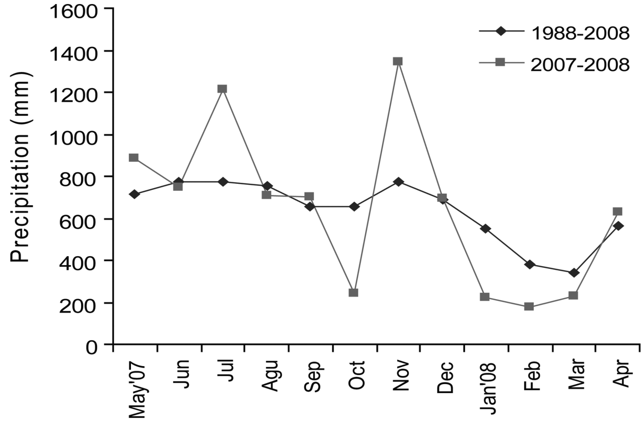


Figure 8. Monthly mean precipitation over the last 20 years at Quebrada González and monthly mean precipitation of the year of study.

each species likely represents the concurrence of multiple generations and also an asynchronous development. Moreover, mature larvae with black wings pads were found during all months, indicating continual emergence throughout year. Emergence of subimagines occurred in the late afternoon, mainly from 18:00 to 18:30 h. Reared subimagines lived for about 10 h or less until adult emergence at approximately 04:00 h. Adults survived about 3 d in laboratory. However, not all Baetidae from Quebrada González follow this emergence behaviour. Reared subimagines of the genus *Mayobaetis* emerged before dawn and lived more than 24 h until adult emergence. We observed one adult individual that lived six days.

We were not able to recognise cohorts from the histograms and concluded that many generations occur during the year. Our results suggest a multivoltine life history for all five species. Similar observations in the field and the laboratory suggest the same for other Baetidae of Quebrada González.

Multivoltine life histories seem to be typical for many species of tropical and subtropical streams mayflies. For example, Jacobi and Benke (1991) concluded that in a subtropical river a high fraction of snag-dwelling mayflies were multivoltine (including Baetidae and also members of others families). They suggested that the high mean annual temperature was the main reason for multivoltinism. Benke and Jacobi (1986) determined high growth rates for *Baetis* spp., which allow complete development in about 19 d and therefore several generations over a six months period with stream temperatures higher than 20°C. Over the past 30 years, very similar results for other species of Baetidae have been reported. Reared *Cloeon triangulifer* completed development in 27 d at 25°C and in 45 d at 20°C (Sweeney and Vannote 1984). In a tropical stream from Australia, larvae of *Cloeon fluviatile* had a life span of about four weeks at an average temperature of 30°C, but at certain times it may have been as short as two weeks (Marchant 1982). Finally, larval development times measured for *Fallceon quilleri* of less than two weeks in a southwestern USA desert stream (Gray 1981) suggest that the equivalent of at least 10 generations per year are possible in warm water environments.

Our data are also consistent with another study in northwestern Costa Rica, where Jackson and Sweeney (1995b) examined total development times for 35 species of aquatic insects (including five mayfly species). The combination of rapid development and the absence of diapause suggests that all these species have multivoltine life histories. In that study, relatively short development times (28 d) for *Americabaetis* sp. was reported.

Fecundity

Table 3 shows the average of eggs per female for each of the five species of baetids. All species produce less than 1000 eggs per female (in average). In general, most

Table 3. Average of eggs (and range) for each species (N = female dissected).

Species	Average of eggs	n	Stage
Baetodes sp. 1	795 (426–1106)	5/5	adults/subimagines
Baetodes sp. 2	981 (702–1295)	8	mature larvae
Baetodes sp. 3	708 (406–1045)	10	mature larvae
Camelobaetidius sp. 1	638 (341–1054)	10	adults
Camelobaetidius sp. 2	405 (247–610)	10	mature larvae

species of Ephemeroptera produce 500 to 3000 eggs, but values range from less than 100 to 12000 (Brittain and Sartori 2003).

Given these results, we conclude that the relatively high water temperature of Quebrada González throughout the year allows for rapid development and growth of the populations of larvae of the most common Ephemeroptera in this tropical stream. Although we do not know how many generations occur in the species studied, the data obtained show evidence that many overlapping generations occur during the year. Baetid species in this stream seem capable of reproducing continually during all months of the year, with increases and decreases in their populations showing some correlation with the amount of rainfall. Despite the fact that the Quebrada González Sector is considered as non-seasonal and of stable climate, fluctuations in the abundance patterns of Baetidae indicate otherwise.

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