

## EMERGENCE PATTERNS OF LARGE STONEFLIES (PLECOPTERA: *PTERONARCYS*, *CALINEURIA*, *HESPEROPERLA*) IN A MONTANA RIVER

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**ABSTRACT.**—Emergents of *Pteronarcys californica*, *Calineuria californica*, and *Hesperoperla pacifica* were captured with replicated emergence traps at 3 sites along the banks of Rock Creek, Montana. *Pteronarcys* emergence in early June was short (88% of individuals in 6 d) and attained rates of 5 m<sup>-1</sup> d<sup>-1</sup> (shoreline distance) and cumulative densities up to 19 m<sup>-1</sup> yr<sup>-1</sup>. *Calineuria* emerged synchronously (89% in 9 d) 2 wk later at densities up to 7 m<sup>-1</sup> d<sup>-1</sup> and 40 m<sup>-1</sup> yr<sup>-1</sup>. The less numerous *Hesperoperla* (5 individual m<sup>-1</sup> yr<sup>-1</sup>) had a longer emergence period partially coinciding with *Calineuria*. Median males of *Pteronarcys* and *Calineuria* emerged 2–3 d before median females; protandry was not significant in *Hesperoperla*. Sex ratios were female-biased in *Pteronarcys* and *Hesperoperla* but male-biased in *Calineuria*. Size trends through emergence were very weak although females showed a greater tendency toward larger size early in emergence.

*Key words:* Plecoptera, phenology, emergence traps, sex ratio, size.

Emergence, the transition from the aquatic growth phase to the reproductive and dispersal activities of terrestrial/aerial adulthood, is a critical event for aquatic insects (Macan 1958, Corbet 1964, Zwick 1990). For the biologist, collection of emergents provides a census of readily identified individuals at a defined point in the life history. Thus, emergence data are essential for life history studies and are potentially useful for monitoring. Statzner and Resh (1993) synthesized a large set of emergence studies in an analysis of species richness and other properties of stream communities; this paper, however, emphasizes population biology.

In the western United States, emergences of the stoneflies *Pteronarcys californica* Newport (Pteronarcyidae), *Calineuria californica* (Banks), and *Hesperoperla pacifica* (Banks) (Perlidae) are notable for the numbers and visibility of the large, colorful, diurnally active adults. (To avoid confusion involving the *californica* epithet, I refer to these species by their generic names throughout this paper.) As “salmonflies” (*Pteronarcys*) and “golden stoneflies” (*Calineuria*, *Hesperoperla*), these insects are important in angling lore and literature (Leiser and Boyle 1982). The nymphal biology of these taxa is moderately well known (Stewart and Stark 1988, Freilich 1991, DeWalt and Stewart

1995) but, aside from investigations of drumming behavior (Stewart and Maketon 1991) and *Calineuria* flight behavior (Poulton and Stewart 1988), little has been written about adults since Muttikowski (1929) described emergence of *Pteronarcys* and *Hesperoperla* in the Yellowstone River.

Emergence of stoneflies has been described from sweepnet catches (Sheldon and Jewett 1967) that confound adult longevity with emergence timing, counts of exuviae (Haro et al. 1994, Alexander and Stewart 1996), and captures in traps of various designs (Kerst and Anderson 1974, Zwick 1977, Kuusela 1984, Ernst and Stewart 1985, Bagge and Hynynen 1995, Giberson and Garnett 1996). I used catches from emergence traps, designed for this project, to describe phenology, abundance, and size and sex composition of adult *Pteronarcys*, *Calineuria*, and *Hesperoperla* in Rock Creek, Montana.

### METHODS

Rock Creek, a noted trout stream, originates in the Anaconda Range of western Montana and flows north 110 km to its confluence with the Clark Fork River (46°43'N, 113°41'W). Three sampling stations were established: Valley

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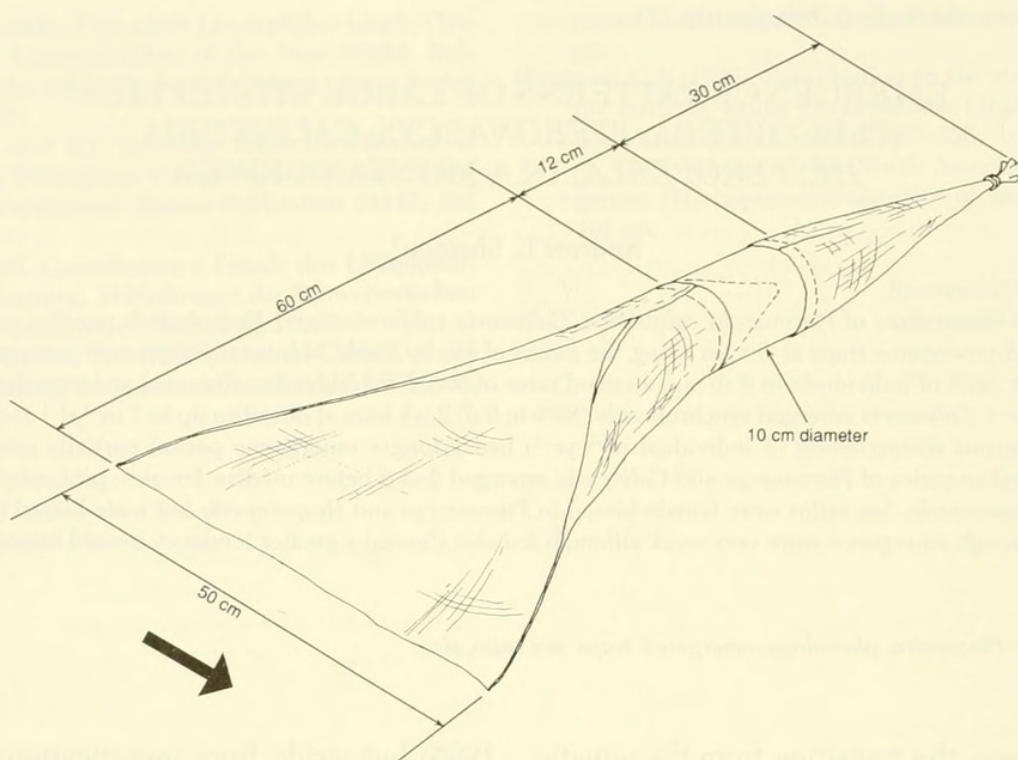


Fig. 1. Emergence trap used in this study. Arrow indicates direction of water flow along the shoreline.

of the Moon, stream km 4.0, 1095 m elevation; Ranch Creek, 20.0 km, 1207 m; Bitterroot Flat, 38.0 km, 1305 m.

The traps used (Fig. 1) were designed to intercept emerging stoneflies as they left the water. Cost was kept to a minimum since I used numerous replicates at each site and planned to sample at more sites. I also anticipated substantial trap loss from changing water levels and human interference. Traps were constructed of plastic window screen, PVC pipe, and duct tape. Each trap consisted of an apron leading upward to the PVC pipe which contained a screen funnel. Past the PVC collar, insects were captured in a stapled screen cylinder closed by a heavy rubber band which allowed easy access. Apron, funnel, and cylinder were attached to the PVC pipe with duct tape. Total cost was <\$2.00 per trap. More refined models with apron and cylinder attached by hose clamps and the funnel with epoxy resin were nearly twice as costly. However, duct tape was completely satisfactory except when the entire trap was submerged for hours.

In use, the edge of the apron was placed at or just below the water's edge and weighted with gravel and small stones. If needed, a large stone or two held the PVC pipe, and a stone at the rubber band end of the cylinder

anchored the entire trap. An informational sign was placed by each trap. Traps were tended daily and moved up or down to accommodate changing water levels. Stoneflies were collected from the cylinder and also from the apron and outer surface of the funnel since, especially on cold mornings, teneral and pre-ecdyial nymphs sometimes failed to pass through the funnel before the traps were tended. (Nymphs were included in numbers and sex ratios but not in size data.)

At each site 20 traps were placed at 15.2-m (50-ft) intervals along one bank since the opposite shore was inaccessible at spring discharge. Identification, sex determination, and size measurement (head width, including eyes, with dissecting microscope and ocular micrometer) were done in the laboratory. Data presented here are aggregated by site; a statistical treatment of between-trap variability and precision of this and other emergence studies is in preparation.

Preliminary fieldwork in 1989, using less retentive traps without funnels, began 5 June, midway in the *Pteronarcys* emergence, and ended 13 June. In 1990 I tended traps daily 29 May–30 June. This is a period of very heavy use by anglers, so I chose not to install recording thermometers although temperature data would have been very useful.



Statistical methods follow Sokal and Rohlf (1981) and Zar (1984).

## RESULTS

Emergence of these species occurs during peak spring runoff from snowmelt. Because high discharge covers rocks exposed at other seasons and limits emergence to the shoreline at the study sites, the entire emergent population was vulnerable to the traps. However, high and variable discharge washed away many traps on the gently sloping shore at the lower-most Valley of the Moon site in both years; thus, the quantitative data from that site cannot be used. One trap at Ranch Creek and, over the season, 3 at Bitterroot Flat were lost to flow and tampering. Analyses are based on data from traps persisting to the end of emergence for a particular species; i.e.,  $n = 19$  for *Pteronarcys* and  $n = 17$  for *Calineuria* and *Hesperoperla* at Bitterroot Flat.

In 1990 very few *Pteronarcys* adults were present at Ranch Creek when traps were installed 28 May; snow and low water temperature inhibited emergence over the next few days and again on 5 June (Fig. 2). However, *Pteronarcys* emergence was extremely synchronous, with 88% of adults emerging over 6 consecutive days. The first *Hesperoperla* adults emerged with *Pteronarcys*, but the majority were contemporaneous with the abundant *Calineuria*. *Pteronarcys* and *Calineuria* peaks were separated by a week with little activity. Although *Calineuria* emergence was protracted relative to *Pteronarcys*, 89% emerged during 9 consecutive days.

Emergence timing varied within and between years (Fig. 3). *Pteronarcys* emergence in 1990 at the upper 2 sites was in phase and controlled by cold weather in late May and on 5 June. Not shown in Figure 3 are 3 exceptionally late *Pteronarcys* emergents at Bitterroot Flat (males on 16, 18 June; female 24 June). Emergence at Ranch Creek in 1989 was slightly later than in 1990; anglers reported the first heavy emergence on 5 June. Spatial variation in timing was not adequately sampled with complete data from 2 sites only. Anglers rely on a steady upstream progression of the "hatch," and this is readily apparent in some years. In 1990 numerous adults were present on 28 May at the lower site, Valley of the Moon; a few were at Ranch Creek, and

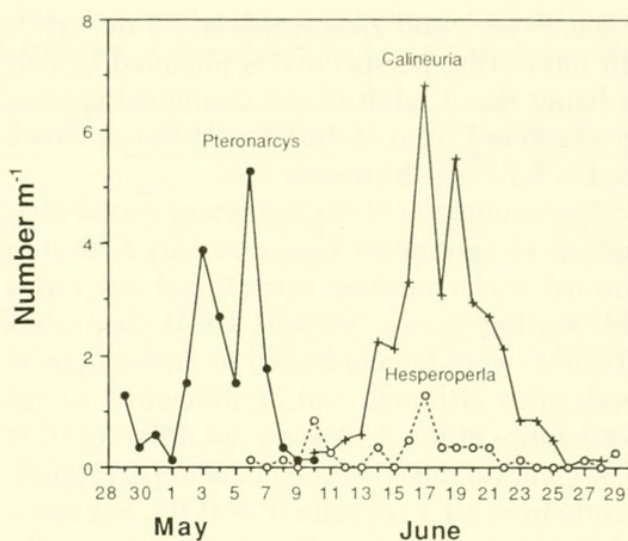


Fig. 2. Emergence (number  $m^{-1} d^{-1}$ ) at Ranch Creek, 1990. (Length is shoreline length; double these number to estimate number per stream length.)

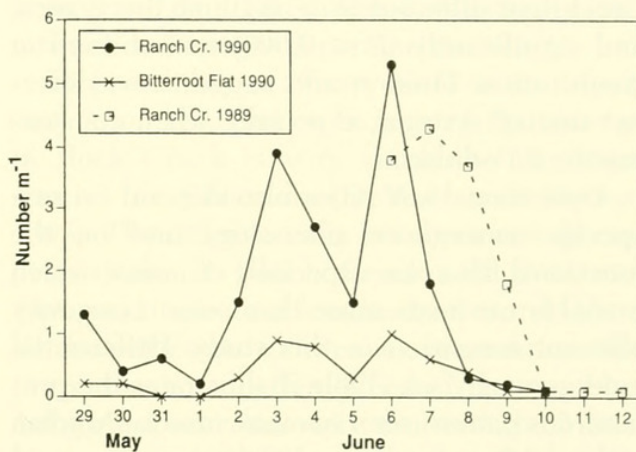


Fig. 3. Emergence of *Pteronarcys* at 2 sites in 1990 and at Ranch Creek in 1989 (no data before 6 June). Length measure is shoreline length.

no exuviae were found at Bitterroot Flat. In 1989 anglers and I observed massive emergence all along the lower 80 km of Rock Creek on 5 June.

Densities, expressed as emergents per meter of shoreline (estimated densities per meter of stream length will be twice these values), appear high although few data exist for comparison. At Ranch Creek, *Pteronarcys* and *Calineuria* attained peak emergences of 5–7  $m^{-1} d^{-1}$ . Cumulatives for Ranch Creek were *Pteronarcys* 19.6  $m^{-1} yr^{-1}$ , *Calineuria* 40.0  $m^{-1} yr^{-1}$ , and *Hesperoperla* 5.3  $m^{-1} yr^{-1}$ . Incomplete data for 1989 (Fig. 3) yielded 13.9 *Pteronarcys*  $m^{-1} yr^{-1}$ , of similar magnitude to 1990. Catches at Bitterroot Flat were considerably less: *Pteronarcys* 6.0  $m^{-1} yr^{-1}$ , *Calineuria*



7.6 m<sup>-1</sup> yr<sup>-1</sup>, and *Hesperoperla* 7.7 m<sup>-1</sup> yr<sup>-1</sup>. An interesting perspective is obtained by calculating that 1 adult of the combined species emerged in 1.5 cm of shoreline at Ranch Creek and in 4.7 cm at Bitterroot Flat.

Determination of sex ratios and sexual phenology of emergents is a necessary first step toward understanding operational sex ratios and mating tactics (Stewart 1994). Sex ratios (Table 1) were female-biased in *Pteronarcys* at both sites although not significantly so ( $\chi^2$  test); ratios at the 2 sites are not different ( $P > 0.99$ ), nor do the combined data depart significantly from a 1:1 sex ratio ( $P > 0.10$ ). Sex ratios of *Hesperoperla* were female-biased, significantly so for the larger collection, not different ( $P > 0.99$ ) at the 2 sites, and significantly ( $P < 0.005$ ) biased in the combined data. *Calineuria*, in contrast, was strongly male-biased at Ranch Creek, not different ( $P > 0.10$ ) at the 2 sites, and significantly ( $P < 0.005$ ) male-biased in combination. These results suggest very different mating systems, especially when comparing the 2 Perlidae.

Operational sex ratios also depend on sex-specific emergence phenology and on the functional life span, especially of males, which probably can mate more than once. Longevity was not measured in this study. Differential emergence by sex (Table 2) illustrates the protandrous pattern seen in many insects. Median males of *Pteronarcys* and *Calineuria* emerged 2–3 d before median females. Differences in distributions of emergence times of the sexes were tested with Kolmogorov-Smirnov tests (2-tailed). Contrasts involving *Pteronarcys* and *Calineuria* were significant except for *Pteronarcys* at Bitterroot Flat where sample size was small and where late emergents, mentioned above, included males. The pattern for *Hesperoperla* was quite different. Median emergence dates were very similar, especially in view of the extended emergence of this species (Fig. 2), and distributions of emergence times by sex were not significantly different.

Attributes other than sex may vary through the emergence period. A tendency for early emergents to be larger than later ones has been reported in stoneflies (Khoo 1964, Sheldon 1972) and other insects. Examination of size vs. time plots suggested that such patterns were weak or absent in these species. Formal tests and metrics were based on 2 × 2 tables

| TABLE 1. Sex composition by species and locations. |            |      |        |
|--|------------|------|--------|
| Species  | Location   | Male | Female |
| <i>Pteronarcys</i>                                 | Ranch      | 93   | 121    |
|  | Bitterroot | 25   | 34     |
| <i>Calineuria</i>                                  | Ranch      | 175  | 120    |
|  | Bitterroot | 37   | 37     |
| <i>Hesperoperla</i>                                | Ranch      | 16   | 29     |
|  | Bitterroot | 24   | 49     |

divided at medians of size and time. A significant  $\chi^2$  indicates that size and emergence time are not independent and the phi-coefficient (a nonparametric correlation coefficient with range -1 to +1) measures the strength and direction of the interaction. Size-time interactions (Table 2) were weak and only 3 of 11 tests were significant. Seven of 11 phi-coefficients were negative; i.e., later individuals were smaller, including all the significant cases. Effects on females were stronger than males in all species and locations. The collective result indicates little or no size change through the relatively short emergence periods of these species. If fitness attributes such as fecundity and mating success are size-dependent, quality of potential mates varies little over time. This conclusion may depend in part on the conservative contingency test used. Blackburn et al. (1993) showed that, in sampling from skewed size distributions, size and abundance were confounded. To avoid this effect, I used a nonparametric test. Applying the same test to comparable data (Sheldon 1972) on male *Skwala curvata* (Hanson) (Perlodidae) yields phi = -0.48,  $P < 0.005$ , a much stronger size-time interaction than observed in Rock Creek stoneflies. Although conservative, the tests can detect temporal size patterns where they exist.

Natural history observations on post-emergents include the following. Adults are readily apparent on bushes where mating occurs. Oviposition flights, occurring as air temperatures rise, appear to be directed upstream, and many flying adults of *Pteronarcys* were observed several kilometers upstream from reaches where, from exuvial density and number of adults on bushes, significant emergence had occurred. Supporting Muttkowski's (1929) observations on predation, I saw numerous birds, especially flocks of 30–40 Western



TABLE 2. Emergence timing and size trends by sex (M, F) and location. Median dates are all in June 1990 and probabilities are from Kolmogorov-Smirnov contrasts of temporal distributions of emergence of the 2 sexes. Correlations (phi) are negative if later emergers are smaller; probabilities from  $\chi^2$ .

| Species             | Site       | Median date |    |        | Size-time (M) |        | Size-time (F) |        |
|---------------------|------------|-------------|----|--------|---------------|--------|---------------|--------|
|                     |            | M           | F  | P      | phi           | P      | phi           | P      |
| <i>Pteronarcys</i>  | Ranch      | 3           | 5  | <0.001 | -0.02         | >0.75  | +0.05         | >0.50  |
|                     | Bitterroot | 4           | 6  | >0.05  | +0.04         | >0.75  | -0.26         | >0.10  |
| <i>Calineuria</i>   | Ranch      | 17          | 20 | <0.001 | -0.17         | <0.025 | -0.30         | <0.005 |
|                     | Bitterroot | 15          | 18 | <0.001 | -0.17         | >0.75  | +0.13         | >0.25  |
| <i>Hesperoperla</i> | Ranch      | 10          | 11 | >0.40  | —             | —      | -0.14         | >0.25  |
|                     | Bitterroot | 13          | 13 | >0.90  | -0.11         | >0.50  | -0.32         | <0.05  |

Tanagers (*Piranga ludoviciana*), foraging in riparian vegetation and hawking at flying adults, particularly *Pteronarcys*.

DISCUSSION

The simple emergence traps worked well at the 2 sites where stream banks were steep enough that a moderate rise in water level did not submerge the entire trap. Daily maintenance was necessary to accommodate fluctuating discharge and to yield temporally precise emergence data. Data aggregated over longer periods can be very useful (Masteller 1983, Kuusela 1984) but miss the details of short, synchronous emergences.

Although common elements appear, each of the 3 species had unique elements in its emergence phenology. *Pteronarcys* and *Calineuria*, although intraspecifically synchronous, were temporally well separated whereas the less abundant *Hesperoperla* had a longer, less synchronous emergence overlapping the other two. Synchrony has been suggested as a tactic for satiating predators (Sweeney and Vannote 1982); perhaps *Hesperoperla* benefits from emerging with abundant *Calineuria*.

Patterns of size and sex ratio also vary between species. A general tendency toward protandrous emergence in insects is supported in *Pteronarcys* and *Calineuria*, species with short, synchronous emergence periods. The selective advantage (Fagerström and Wiklund 1982) of protandry apparently is reduced in the less common *Hesperoperla* with its protracted emergence. Size-time interactions were weak although females showed a greater tendency than males for early emergents to be larger. The conservative nonparametric statistics

used here may have failed to detect real phenomena. However, Blackburn et al. (1993) have shown that skewed size distributions and temporally varying collection sizes, as in most emergence data, can produce statistically “significant” artifacts with parametric tests.

Repeatability of observations is an important issue. Emergence biology of *Pteronarcys* in Rock Creek is very similar to the same species in Colorado (DeWalt and Stewart 1995). The differences in numbers and species proportions at Ranch Creek and Bitterroot Flat may indicate a longitudinal trend, but I attribute them to differences in pool:run:riffle proportions and other physical factors. Phenology and sex ratios were similar at the 2 sites. Haro et al. (1994) detected substantial variation of size and sex ratio of a perlodid stonefly among sites and years.

Emergence is a single event in a life history. Emphasis in this paper is on timing, identity, size, and sex of emergents. More generally, emergents are the product of the aquatic phase of the life history and input to the adult population. Emergence data could be a sensitive indicator of nymphal population biology and environmental conditions between years and locations (Haro et al. 1994). Of equal interest, the numbers and quality (sex, size) of emergents must influence mating behavior and reproductive success. Detailed studies of stonefly reproduction (Alexander and Stewart 1996) would be enhanced by a firm comparative base of emergence data. Such data are relatively easy to obtain and, for *Pteronarcys* and the perlids of Rock Creek, provide information at the time of high discharge when the stream itself is unworkable.



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