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Selective oviposition of the mayfly *Baetis bicaudatus*

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Abstract Selective oviposition can have important consequences for recruitment limitation and population dynamics of organisms with complex life cycles. Temporal and spatial variation in oviposition may be driven by environmental or behavioral constraints. The goals of this study were to: (1) develop an empirical model of the substrate characteristics that best explain observed patterns of oviposition by *Baetis bicaudatus* (Ephemeroptera), whose females lay eggs under rocks protruding from high-elevation streams in western Colorado; and (2) test experimentally selective oviposition of mayfly females. We surveyed the number and physical characteristics of potential oviposition sites, and counted the number and density of egg masses in different streams of one watershed throughout two consecutive flight seasons. Results of surveys showed that variability in the proportion of protruding rocks with egg masses and the density of egg masses per rock were explained primarily by seasonal and annual variation in hydrology, and variation in geomorphology among streams. Moreover,

surveys and experiments showed that females preferred to oviposit under relatively large rocks located in places with high splash associated with fast current, which may provide visual, mechanical or both cues to females. Experiments also showed that high densities of egg masses under certain rocks were caused by rock characteristics rather than behavioral aggregation of ovipositing females. While aggregations of egg masses provided no survival advantage, rocks selected by females had lower probabilities of desiccating during egg incubation. Our data suggest that even when protruding rocks are abundant, not all rocks are used as oviposition sites by females, due to female selectivity and to differences in rock availability within seasons, years, or streams depending on variation in climate and hydrogeomorphology. Therefore, specialized oviposition behavior combined with variation in availability of quality oviposition substrata has the potential to limit recruitment of this species.

Keywords Empirical models · Ephemeroptera · Recruitment limitation · Selective oviposition · Streams

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Introduction

Recruitment of new individuals is a critical process, because it establishes the initial size of populations. Some studies of marine invertebrates and terrestrial insects suggest that population dynamics may be a function of the rate of arrival of new recruits (Underwood and Fairweather 1989; Price et al. 1998; Cowen et al. 2000). Other work indicates that post-recruitment processes, such as competition and predation, dampen the effect of initial recruitment events (Palmer et al. 1996; Pfister 1996), and therefore better explain patterns of variation in the abundance of populations. Nonetheless, it is important to consider both recruitment and post-recruitment processes, because they each undoubtedly contribute to population dynamics.

Studies of insects have made a major contribution to contemporary theories in population ecology, and provide excellent systems for investigating the role of recruitment (by oviposition) as a possible mechanism underlying variation in abundance of individuals within populations. Furthermore, theoretical and empirical models of the evolution of oviposition behavior in insects have been used as a conceptual framework for studies of life history evolution (Singer et al. 1988; Resetarits 1996; Rosenheim 1999). For example, Bryant (1969) hypothesized that selective oviposition behavior should be advantageous to holometabolous insects, because their larvae are less capable of moving to locate sites that maximize their performance. In fact, empirical studies of many species of holometabolous terrestrial herbivorous insects demonstrate a strong link between female oviposition preference and offspring performance (Thompson 1988; Craig et al. 1989; Price and Ohgushi 1995). Alternatively, insects may also select oviposition sites that maximize their fitness by minimizing egg mortality from predation, parasitism or environmental stress (e.g., disturbance, desiccation) (Canyon et al. 1999; Faraji et al. 2002; Wissinger et al. 2003). Comparable studies of the relationship between oviposition preference and offspring performance have not been conducted using hemimetabolous insects.

Factors affecting choice of oviposition sites by female insects may include habitat characteristics like temperature, shape, orientation and size of the substrate (Higashiura 1989; Canyon et al. 1999; Reich and Downes 2003a, b). Some insects oviposit in places protected from snow cover (Higashiura 1989), and others avoid habitats with a high probability of desiccation (Juliano et al. 2002). Oviposition in egg aggregations has also been reported as a way of minimizing egg mortality from predation (Faraji et al. 2002; Damman and Cappucino 1991). Therefore, oviposition behavior can be adaptive and consequently have a fundamental influence on population dynamics in insects (Ohgushi 1995; Resetarits 1996).

In contrast to terrestrial insects, less is known about processes that affect oviposition of aquatic insects, and in particular, the role of adults in colonization and provision of new recruits (e.g., Caudill 2003; Macneale 2003). Instead, most studies have focused on the influence of post-recruitment processes (e.g., biotic interactions: competition, predation, larval movement) on the abundance of aquatic larvae (e.g., Richards and Minshall 1988; Forrester 1994; Fonseca and Hart 1996; McIntosh et al. 2002). Nevertheless, recent studies of adult behavior and dispersal have provided new insights regarding mechanisms of selective oviposition by aquatic insects (Chesson 1984; Pearman and Wilbur 1990; Peckarsky et al. 2000; Spencer et al. 2002) suggesting that recruitment may have important effects on aquatic insect populations (Bunn and Hughes 1997).

The objectives of this study were to: (1) develop an empirical model of the substrate characteristics that best explain observed patterns of oviposition of one species

of mayfly whose larvae live in high-elevation streams in western Colorado, (2) test experimentally the factors affecting selective oviposition by females.

Materials and methods

Study organism

Larvae of the mayfly *B. bicaudatus* Dodds (Ephemeroptera: Baetidae) are abundant algal grazers in high-elevation Rocky Mountain streams. Their biology and ecology have been studied extensively near the Rocky Mountain Biological Laboratory (RMBL) (e.g., Peckarsky et al. 2000, 2001, 2002). Populations at this location are univoltine, and oviposition occurs during the summer (June–August), after primarily upstream dispersal by winged females (Flecker and Allan 1988; Vance and Peckarsky 1997).

B. bicaudatus females exhibit specialized oviposition behavior (Peckarsky et al. 2000; Encalada 2004), which is unusual for mayflies (Brittain 1982). As in most of the reported species of *Baetis*, females land on rocks protruding from the water surface, then crawl under water on the downstream side of the rock to oviposit on the underside (e.g., Eaton 1888; Morgan 1911; Murphy 1922; Elliott and Humpesch 1980; Peckarsky et al. 2000). Each female lays one egg mass during her lifetime, with fecundity ranging over an order of magnitude (~200–3,000 eggs per female), depending on the size of the female (Peckarsky et al. 2000). Moreover, field surveys by Peckarsky et al. (2000) found that females did not lay eggs under submerged substrates, and egg masses were aggregated under large, unembedded, tall, granite rocks, suggesting that patterns of oviposition were not random.

Study site

Study streams are located at ~2,900 m elevation in the East River watershed near RMBL in Gunnison County, Colorado (latitude 38°959'N, longitude 106°989'W). Most of the streams are fed by snowmelt, but some are lake outlets or of groundwater origin. Streams in this watershed have similar water chemistry but vary in size and other associated physical characteristics (Peckarsky et al. 2001, 2002). The high-altitude location of these streams constrains the time for mayfly emergence and oviposition to the summer months. The rest of the year the environment can be quite hostile for flying insects, since snow, ice cover and very low air temperatures can occur from mid September to late May.

Temporal and spatial patterns of oviposition

To describe the temporal and spatial variation of *Baetis* oviposition relative to the availability of oviposition sites, we surveyed nine second- and third-order streams

(2000 and 2001) and 12 small headwater streams (2001 only) in the East River watershed. We sampled 30-m-long reaches of each stream 5 (2000) or 6 (2001) times approximately every 1.5 weeks. We estimated stream discharge on each survey date and recorded water temperature continuously with submerged Optic Stowaway data loggers (Onset Computer, Pocasset, Mass.) to relate those parameters with the timing of rock protrusion from the water surface and subsequent *Baetis* oviposition.

To evaluate potential oviposition sites available for females, in each survey we counted the number of rocks protruding from the water surface, and numbered rocks with paint markers (Speedball) to recognize them for subsequent sampling. We also counted the egg masses on each rock to determine if there was a pattern of female preference for certain rocks. Since each female oviposits only one egg mass during her lifetime, each egg mass represents oviposition by one female. By comparing maps of egg masses from one survey to the next we followed the fate of egg masses on each rock through the flight season, recording how many new egg masses appeared or old egg masses disappeared, and egg mass desiccation as water levels receded throughout each summer. To link female oviposition preference to substrate type we measured several characteristics of each protruding rock:

1. Total area: two-dimensional surface area of stream bottom covered by the rock estimated as width \times length.
2. "Landing area": area of rock protruding from the water surface estimated as width \times length.
3. Rock type: granite, sandstone, slate, marble.
4. Rock color: black, brown, red, white, gray.
5. Water depth upstream of each rock.
6. Splash associated with each rock: 0=no splash, 1=few bubbles, 2=moderate bubbles or white water, 3=abundant bubbles or white water.

We used splash as a surrogate for current velocity, because it may provide a more relevant visual cue for females than current velocity per se. Rock type, rock color and splash were considered categorical variables and were always recorded by the same person to avoid variation among observers. In 2001 we estimated rock height protruding from the water surface instead of landing area. We also used these data to explore the factors explaining the probability of rock drying.

Empirical model of oviposition preferences

Predicting the presence of egg masses from rock characteristics

To evaluate the factors explaining the probability of a rock being selected by a female (presence or absence of egg masses), we performed logistic regression on all

subsets, which finds the best predictor variables using a χ^2 -square model selection procedure. After testing for co-linearity among the variables we applied the multiple logistic regression model (PROC LOGISTIC) with the selected best predictor variables (SAS Institute 2003) using a binomial data set (1 = received eggs, 0 = no eggs) as a response variable. We performed this analysis for each stream and year separately because of intrinsic differences in geomorphology among streams, and to reduce the probability of getting significant effects as statistical artifacts of excessively large sample sizes (type I error). However, in 2001 data from 12 headwater streams were pooled and analyzed as one data set because they had similar geomorphology and hydrological conditions (Peckarsky et al. 2002) and were located in close proximity. Since rock area and landing area were highly correlated (Spearman correlation, $r=0.71$, $P<0.0001$), we removed rock area from the 2000 regression model to avoid co-linearity among these variables.

Predicting the density of egg masses from rock characteristics

To determine which variables best predicted the number of egg masses per square meter of rock surface area we performed a multiple negative binomial regression using GENMOD (Myers et al. 2002; SAS Institute 2003), because the data followed a negative binomial distribution and could not be normalized by transformation. For the model selection criteria we used the log likelihood ratio test, deleting one by one non-significant variables with the largest type-III-based P -value [$-2(\log$ likelihood reduced model $-\log$ likelihood full model)]; generalized linear model (GLM; SAS Institute 2003)]. Again, we performed these analyses for each stream and each year separately, but pooled the data from the headwater streams in 2001.

Predicting the probability of rock drying

We applied an all subsets logistic regression model to find the best predictors of the probability of a rock to dry, using a χ^2 -square model selection procedure (SAS Institute 2003). After testing for co-linearity among the predictor variables, we applied a multiple logistic regression model where the response variable was a binomial data set of either rock dried (1) or did not dry (0), and the explanatory variables were the total rock area and survey date. Again, we performed this analysis for each stream and year separately, but pooled the headwater streams for analysis.

Finally, we performed sign tests (Siegel 1985) to assess whether rock attributes were significant predictors of oviposition in more streams than expected by chance for each of the three empirical models separately (predicting the probability of egg presence, the density of egg masses and the probability of rock drying). For each attribute, a plus sign was assigned to a stream if the

variable was a significant predictor of oviposition, while a minus sign was assigned if it was not. Thus, a significant P -value ($P \leq 0.05$) indicates that a variable was significant in more streams than would be expected from a random distribution.

Experiments

Based on these and previous surveys of oviposition patterns of *B. bicaudatus* (Peckarsky et al. 2000), we manipulated oviposition sites to test experimentally several rock characteristics that could explain the proximate mechanisms of selective oviposition by these mayflies.

Rock size

To determine if *B. bicaudatus* females preferred to lay eggs under large versus small rocks, during summer 1999 we manipulated one 60-m-long reach of three third-order streams (East River, Copper Creek, Rustlers Gulch), and three second-order streams (Quigley Creek, Avery Creek and Lower Rock Creek). In each reach we placed 15 pairs of rocks adjacent to each other, one small (total horizontal surface area 150–450 cm²) and one large (650–4,500 cm²), and allowed *B. bicaudatus* females to choose among those rocks. All rocks originated from the test streams and were placed in the center of the reach in relatively fast current velocity locations (mean = 60 cm s⁻¹). We submerged all natural protruding rocks in the test reaches so that treatment rocks were the only oviposition sites available. Treatment rocks were numbered as in surveys to recognize them for subsequent sampling. Each pair of rocks was at least 5 m away from other pairs. We checked all rocks for egg masses after 7 and 14 days, which is the egg incubation period of *B. bicaudatus* (Peckarsky et al. 2000). We performed this experiment twice: near the beginning (early July) and end (early August) of the flight period of this species.

We used a mixed-model nested ANOVA to test the effects of rock size, stream size (order) and season as fixed factors, and rock pair nested within site as a random factor. This analysis enabled us to determine whether females selected rock size, and if selectivity differed between seasons or stream sizes. We performed this analysis using PROC MIXED in SAS (SAS Institute 2003). The response variable was ln number of egg masses oviposited per rock + 0.1. Higher numbers of egg masses on large rocks could simply result from more surface area available for female oviposition. Therefore, we also ran this analysis on ln number of egg masses per square meter of rock + 0.1 to test whether the density of egg mass was a function of rock size.

Rock size × current velocity

As a follow-up to the rock size experiment, we conducted a two-factor experiment to test for the interactive effects of rock size and current velocity on oviposition by

B. bicaudatus. On 1, 10 and 17 July 2000 we manipulated one 200-m stream reach of the East River north of RMBL. For each trial we placed 16 pairs of rocks (one small and one large as in the rock size experiment) in places with naturally fast current velocity (mean = 66.9 cm s⁻¹) and 16 pairs in places that had ~fourfold slower current velocity (mean = 15.5 cm s⁻¹). Rock pairs were distributed among eight locations (sites) separated by at least 12 m with two fast and two slow pairs at each site. Other naturally protruding rocks were submerged during the experiment. We allowed females to choose among those substrates and counted how many egg masses were oviposited on each rock after 7 days. We measured current velocity upstream of each rock at the end of each trial to ensure that fast and slow treatments remained different; locations of rocks were adjusted for subsequent trials if necessary. Over all dates, fast and slow velocity treatments were significantly different (t -test, $t_{62} = 23.49$, $P < 0.0001$).

We also estimated splash for each rock to obtain a range of current velocities for each splash category. Since current velocity is so variable around protruding rocks, this analysis also tested whether it was reasonable to use splash categories as a surrogate for current velocity.

To test for main and interactive effects of rock size and current velocity on the selection of oviposition sites by females we performed a mixed-model ANOVA, where the response variable was ln number of *B. bicaudatus* egg masses per rock + 0.1 and the predictors were rock size (large and small), current velocity (fast and slow) and trials (three dates) as fixed factors, and site (eight sites) as a random factor.

Aggregation experiment

We performed an experiment to test if ovipositing females aggregated on rocks as a function of the number of egg masses already present, or in response to rock characteristics. This experiment also tested whether aggregations provided a survival benefit to individual egg masses. In July 2003, we checked 60 protruding rocks for *B. bicaudatus* egg masses along a 200-m reach of the East River. Then we selected 15 rocks that had at least ten egg masses, and were characterized as “good” oviposition sites as predicted from results of the previous experiments and empirical models (> 500 cm², located in fast current velocity). Using maps of locations of egg masses on each rock, we counted new egg masses that were oviposited for 4 consecutive days after which all rocks had accumulated > 50 egg masses. Then we assigned randomly five rocks to each of three treatments: (1) removed all egg masses except one, (2) removed all egg masses except 20, and (3) removed all egg masses except 50. Each day for the next 4 days we counted new egg masses that were oviposited, and then removed those new egg masses to re-establish the treatments. This method enabled us to test if females responded to the

different egg mass densities or to the characteristics of the substrates.

We also used maps of locations of egg masses to calculate the daily survival of individual egg masses. We tested whether daily survival was a function of egg mass density using observational data from the 4 days before applying the treatments, and daily survival of egg masses at the manipulated densities for 4 days after treatments were established.

We performed a two-way repeated measures ANOVA using GLM (SAS Institute 2003), with the number of new egg masses per rock on each date as the response variable; the explanatory variables were: (1) treatment (before, after); and (2) egg mass density (one, 20 and 50 egg masses). The replicates were the 15 rocks and repeated measures were 4 days before and 4 days after the treatment. Finally, to detect density-dependent effects on egg mass survival, we regressed average egg mass density against egg mass survival expressed as a binary response (1=survival, 0=death), using a repeated measures logistic regression (GENMOD procedure, SAS Institute 2003).

Results

Temporal and spatial patterns of oviposition

Average stream discharge ranged from 0.003 to 4.41 m³ s⁻¹ among first- to third-order streams in this study. As discharge receded throughout the flight season more rocks protruded becoming potential oviposition sites. Consequently, stream discharge (averaged over all sites on each survey date) was inversely related to average rock availability (number of rocks per square meter) in both years (logarithmic regressions 2000, $y = 0.45 x^{-0.49}$, $F_{1,4} = 211.15$, $P < 0.0007$, $r^2 = 0.98$; 2001 second- and third-order streams, $y = 0.21 x^{-1.26}$, $F_{1,5} = 54.69$, $P < 0.002$, $r^2 = 0.93$; 2001 headwater streams, linear regression, $y = -141.9 x + 2216$, $F_{1,5} = 36.52$, $P < 0.004$, $r^2 = 0.90$). However, the spring-fed streams (e.g., Avery Creek) had more stable hydrographs with little change in either rocks available or discharge over the season (Encalada 2004).

The onset of oviposition varied among years, depending on the magnitude of the discharge early in the summer. For example, on 20 June 2000 when discharge was 20% higher than in 2001, females had oviposited in only two of nine streams as opposed to 2001 when five of nine streams had eggs by that date. However, peak oviposition date (~ 15–20 July) was similar in all streams during both years.

Although the number of rocks with eggs could be predicted from the number of rocks protruding (2000, $r^2 = 0.38$, $F_{1,44} = 26.46$, $P < 0.0001$; 2001, $r^2 = 0.35$, $F_{1,53} = 27.62$, $P < 0.0001$; headwater streams 2001, $r^2 = 0.19$, $F_{1,69} = 15.73$, $P < 0.0001$), this relationship was weak, because after initially increasing, the number of

rocks with eggs eventually leveled off despite continued increases in rocks available (Fig. 1). Consequently, the number of rocks available throughout the summer did not explain a high proportion of the variance in the number selected by females. Alternatively, substrate and stream characteristics better explained the variation in number of rocks selected by females.

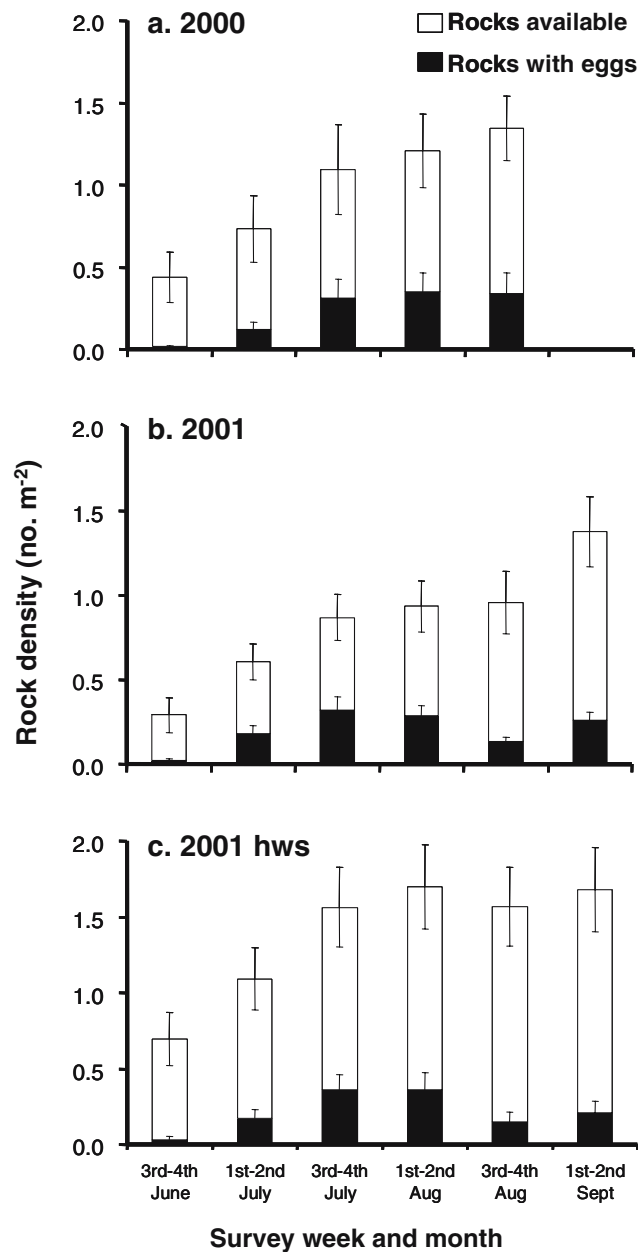


Fig. 1a–c Density of protruding rocks available and protruding rocks with mayfly (*Baetis bicaudatus*) eggs (number per square meter of stream surface area) during June–September 2000 and 2001 in western Colorado. Data from nine second- and third-order streams in **a** 2000, **b** 2001, and **c** 12 headwater streams (*hws*) in 2001. *Aug* August, *Sept* September

Empirical models

Predicting the presence of egg masses from rock characteristics

As in Peckarsky et al. (2000), frequency distributions of the number of rocks receiving egg masses in all the streams followed a negative binomial distribution, indicating that most of the protruding rocks received none or a few egg masses and a few rocks received most of the egg masses (Fig. 2). The proportion of protruding rocks used by females did not differ between years (0.24 of > 3,000 rocks sampled in 2000 and 0.26 of > 4,000 rocks sampled in 2001) (t -test, $t_{16} = -1.67$, $P = 0.11$). However, the proportion of rocks that received at least one egg mass varied by an order of magnitude among streams

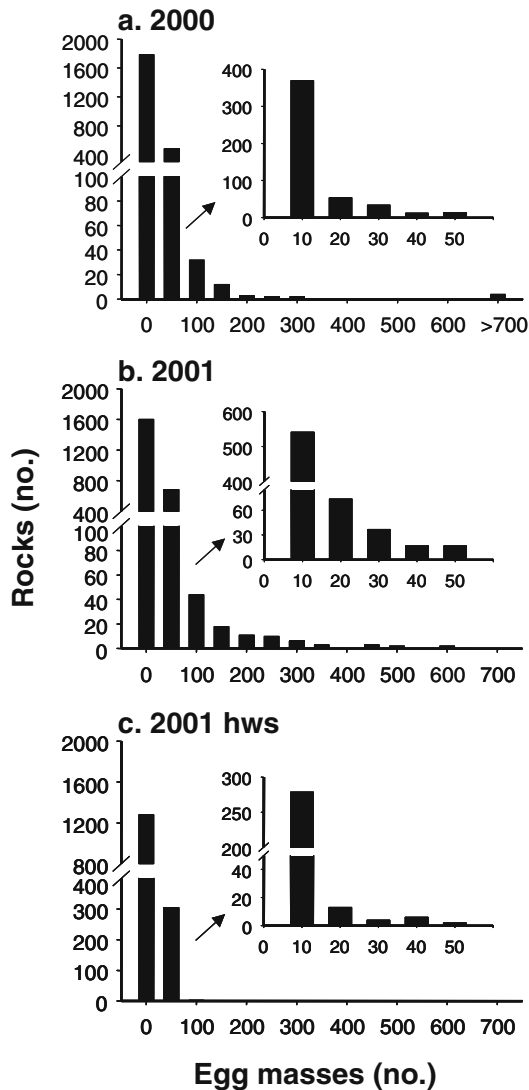


Fig. 2 Frequency distributions of *B. bicaudatus* egg masses per protruding rock for nine second- and third-order streams in **a** 2000 and **b** 2001, and in **c** 12 hrs in 2001 from the East River drainage basin. The *first bar* of each histogram shows number of rocks with zero egg masses, and histograms thereafter represent intervals of 50, (1–50) in **(a)**, **(b)** and **(c)** or 10 (1–10) in *insets*

and over the season, ranging from 0.06 to 0.60 during peak oviposition.

The all-subsets regression procedure selected three main parameters for 2000 data, landing area, splash, and landing area \times splash; and three parameters for 2001 data, rock area, splash, and depth. The multiple regression models showed that the probability of a rock of being selected by a female consistently increased with the rock size and in some streams and years, with the splash surrounding that rock (e.g., Fig. 3). Rock area (all streams) and landing area (eight of nine second- and third-order streams) were significant predictors of the probability that a rock would receive eggs (Table 1, Electronic Appendix A). The other two variables selected by the model (splash and area \times splash interaction) were significant predictors in some streams and years, but not in others. In fact, the sign test indicated that those rock attributes significantly predicted oviposition in fewer streams than would be expected by chance (Table 1).

Predicting the density of egg masses from rock characteristics

The density of egg masses per square meter of rock was also highly variable among streams and years, ranging from 0.7 to 30 egg masses per square meter of rock area in 2000 and 0.34–33 egg masses per square meter or rock in 2001. Interestingly, the density of egg masses per square meter of stream reach was neither a function of the area of stream sampled (reach size) (Pearson correlation, 2000, $r = -0.56$, $P = 0.12$; 2001, $r = 0.33$, $P = 0.15$) nor the number of protruding rocks per reach (Pearson

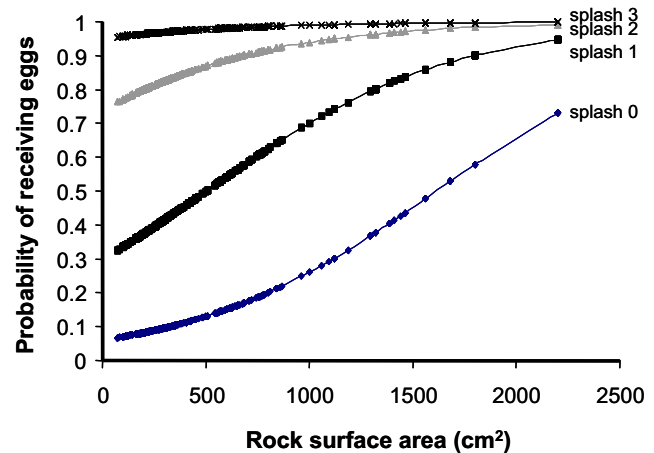


Fig. 3 Probability of a rock of receiving egg masses increases with rock surface area and splash level in the East River 2001. Data based on the logistic equation: $P(\text{rock with eggs}) = \{\exp[-2.74 + (0.0017 \times x1) + (1.9 \times x2)]\} / \{1 + \exp[-2.74 + (0.0017 \times x1) + (1.9 \times x2)]\}$, where $y = 1$, if egg masses present; $y = 0$, if egg masses absent, $x1 = \text{rock area}$, $x2 = \text{splash}$ [no splash (*splash 0*), few bubbles (*splash 1*), moderate bubbles or white water (*splash 2*), abundant bubbles or white water (*splash 3*)]. Model goodness-of-fit test ($\chi^2 = 212.93$, $P = 0.32$, PROC LOGISTIC, SAS). See Appendix A for details

Table 1 Results of sign tests assessing whether rock attributes were significant predictors of oviposition in more streams than expected by chance for each empirical model^a. Blanks appear where variables were not included in the model

Parameters	Empirical models					
	Predicting presence of egg masses		Predicting density of egg masses		Predicting probability of a rock to dry	
	2000	2001	2000	2001	2000	2001
Rock area		0.001***	0.746	0.011*	0.06	0.965
Landing area	0.02*		0.254			
Height				0.377		
Depth			0.998	0.989		
Survey					0.773	0.035*
Splash	0.91	0.623	0.5	0.172		
Rock area×Splash	0.998		0.98	0.989		
Landing area×Splash		0.999				

* $P < 0.05$, *** $P < 0.001$

^aDetails of the models are given in Electronic Appendix A (probability of egg presence—logistic regression model), Electronic Appendix B (density of egg masses—negative binomial regression model) and Electronic Appendix C (probability of rock drying—logistic regression model)

correlation 2000, $r = -0.11$, $P = 0.78$; 2001, $r = -0.02$, $P = 0.94$), suggesting that the density of egg masses in any given stream reach was a function of the quality rather than the quantity of oviposition substrates. Since substrate characteristics depend on the geomorphology of each stream, streams with high rates of oviposition in 2000 also had high oviposition in 2001 (Pearson correlation egg masses per square meter of stream reach in 2000 versus 2001: $r = 0.71$, $P = 0.047$).

The multiple negative binomial regression enabled us to predict the rock characteristics that best explained egg mass densities. The log likelihood ratio tests showed that the best predictors of egg mass density varied among streams, which also reflected the intrinsic variability among sites. As in the analysis of presence/absence of egg masses, rock area (four of nine streams in 2000, eight of nine streams in 2001 plus the headwater streams), landing area (six of nine streams in 2000, five of nine streams and the headwater streams in 2001), and splash (five of nine streams in 2000, six of nine streams in 2001 and the headwater streams) were the most consistent predictors of egg mass density (Electronic Appendix B). Nevertheless, in year 2000 sign tests indicated that all three variables were significant predictors of oviposition in fewer streams than expected by chance; and in 2001 rock area was the only rock attribute that was a significant predictor in more streams than expected by chance (Table 1).

In summary, data from these surveys and empirical models are consistent with the hypothesis that *B. bicaudatus* females prefer to oviposit under relatively large rocks in streams across the landscape. Furthermore, splash around rocks, and the interaction between splash and rock size significantly predict oviposition only in some streams.

Predicting the probability of rock drying

If eggs oviposited under larger rocks are less likely to desiccate, then female oviposition preferences could

confer a fitness benefit. Both the percent of protruding rocks that dried (0–33% in 2000 and 0–52% in 2001) and egg mass desiccation (0.33–88% in 2000 and 0–54% in 2001) were variable among streams (Encalada 2004) and years, and increased through the flight season in both years as discharge declined (Fig. 4). However, the number of dry rocks per stream was a significant, but poor predictor of egg mass desiccation (2000, $r^2 = 0.17$, $F_{1,43} = 8.57$, $P = 0.0054$; 2001, $r^2 = 0.11$, $F_{1,38} = 4.46$, $P = 0.0414$).

Multiple logistic regression showed that for five of seven second- and third-order streams in 2000 and two of eight in 2001 (some streams in both years had neither dry rocks nor dry egg masses), rock area was the best predictor of probability that a rock would dry (Electronic Appendix C). However, a marginally non-significant sign test suggested that rock area was significant predictor in more streams than expected by chance in 2000, but not in 2001 (Table 1), when stream discharge did not decline as dramatically over the flight season (Fig. 4). Interestingly, in 2001 the date of the survey was a significant predictor that a rock would dry in more streams than expected by chance (six of eight streams), but only in three of seven streams in 2000 (Table 1).

In summary, logistic regression models suggest that during the 2 years of this study, the probability of a rock to dry decreased either with increasing rock size (e.g., Fig. 5) or throughout the flight season as discharge declined. These results are consistent with the hypotheses that by selectively ovipositing on large rocks or by ovipositing early in the flight period, females reduce the probability that their egg masses will desiccate.

Experiments

Rock size

Significantly more *B. bicaudatus* females oviposited under large rocks than small rocks ($F_{1,263} = 55.19$,

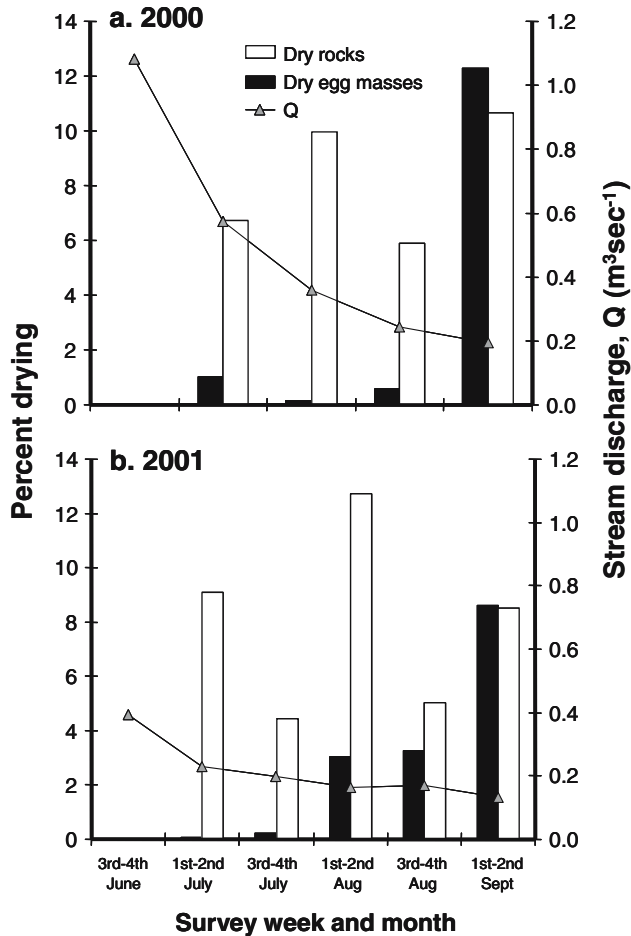


Fig. 4 Percentage of total rocks protruding from all streams that dried and percentage of all *B. bicaudatus* egg masses that desiccated, for each survey date, during summers **a** 2000 (June–August) and **b** 2001 (June–September), as stream discharge (Q); scaled on the right y -axis) declined throughout the season. For other abbreviations, see Fig. 1

$P=0.0001$; Fig. 6), independent of season and stream size, supporting the hypothesis suggested by the surveys. This pattern was not the result of large rocks having more space for egg masses than small rocks, because we obtained the same result when we standardized the number of egg masses by square meter of rock area ($F_{1,263}=4.32$, $P=0.038$; Fig. 6).

Rock size \times current velocity

Current velocity and splash were highly correlated ($r=0.77$, $P=0.001$), and more females oviposited under rocks in fast than slow current velocities (velocity, $F_{1,179}=213.95$, $P<0.0001$). In fact, oviposition under the slow flow rocks was negligible for all trials. Thus, in all three trials (trial, $F_{2,179}=0.74$, $P=0.48$) females preferred to oviposit under large rocks over small ones (rock size, $F_{1,179}=89.09$, $P<0.0001$) only if the large

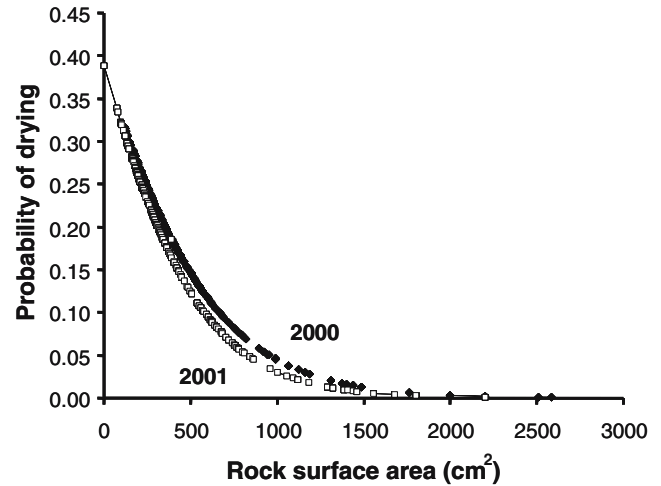


Fig. 5 Relationship between rock surface area and probability of drying, from logistic regression models for rocks surveyed in the East River 2000 and 2001. For 2000: $P(\text{dry rocks}) = \{\exp[-0.42 + (-0.003 \times x_1) + (-0.04 \times x_2)]\} / \{1 + \exp[-0.42 + (-0.003 \times x_1) + (-0.041 \times x_2)]\}$; goodness-of-fit test (scale deviance = 540.9, scale deviance/ $df=0.97$; GENMOD SAS). For 2001: $P(\text{dry rocks}) = \{\exp[-0.37 + (-0.003 \times x_1) + (-0.08 \times x_2)]\} / \{1 + \exp[-0.37 + (-0.003 \times x_1) + (-0.08 \times x_2)]\}$; (scale deviance = 784.5, scale deviance/ $df=0.77$; GENMOD SAS); where $y=1$, if rock not dry; $y=0$, if rock dry, x_1 =rock area, x_2 =survey. See Appendix C for details

rocks were located in fast velocity (significant size \times velocity interaction, $F_{1,179}=81.79$, $P<0.0001$).

Aggregation

There were no significant differences in the number of new egg masses oviposited among the three density treatments or between pre- and post-treatment time periods (Table 2), suggesting that females did not respond to the presence of other egg masses under rocks. However, within-subjects analysis showed a significant day effect (day 1 up to an including day 4), because the number of new egg masses increased significantly from day 1 to day 2 and from day 2 to day 3.

Proportional egg mass survival throughout the experiment was very high (97.7%) and independent of egg mass density. There were no effects of egg mass density or time on egg mass survival (repeated measurements logistic regression: treatment, $\chi^2=0.16$, $P=0.68$; time, $\chi^2=0.64$, $P=0.43$). Therefore, we found no evidence of density-dependent survival, density-dependent mortality or maximum survival at intermediate egg mass densities (Encalada 2004).

In summary, the results of the experiments show that high densities of egg masses observed on some rocks can be explained by female selectivity for rocks with certain characteristics (large size and high current velocity), rather than by behavioral aggregation of females. Furthermore, the third experiment provided no evidence that egg mass aggregations reduced egg mass mortality.

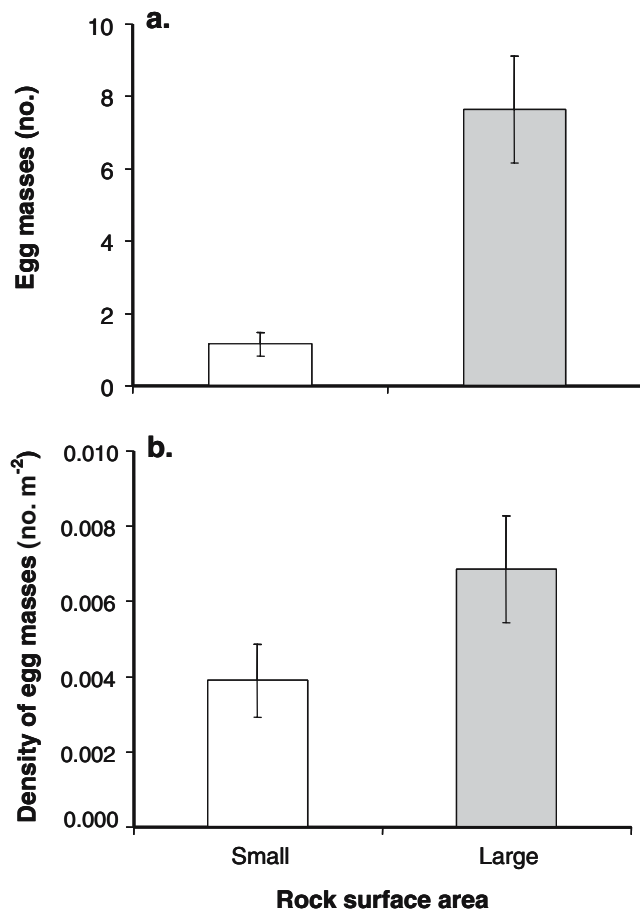


Fig. 6 **a** Number of egg masses oviposited by females of *B. bicaudatus* per rock, and **b** density of egg masses per square meter for rocks with small surface areas (*Small*; horizontal surface area 150–450 cm²) and large surface areas (*Large*; horizontal surface area 650–4,500 cm²) in six different streams of the East River drainage basin in 1999 (mean \pm 2 SE)

Discussion

Observed spatial and temporal variability of *B. bicaudatus* oviposition can be explained by a combination of selective oviposition behavior of females, seasonal, annual and spatial variation in hydrology (discharge), and intrinsic variation in geomorphology among streams of the upper East River drainage basin. Experimental data agreed with patterns from surveys and provided unequivocal evidence that females preferred to oviposit under large rocks in locations with high current velocity, which was positively correlated with splash, and may attract females via visual or mechanical (or both) cues.

In our study both the onset of oviposition and the availability of oviposition sites were affected by stream discharge, which varied annually and throughout the flight season of *B. bicaudatus*. For example, high early season discharge delayed the onset of oviposition in 2000, since high water levels covered potential oviposition sites for females ready to oviposit. Therefore,

climatic factors, such as patterns of precipitation and snowmelt can strongly influence recruitment of aquatic insects like *B. bicaudatus* that exhibit specialized oviposition behavior tied to stream hydrology and geomorphology.

Both surveys and experiments showed that oviposition by *B. bicaudatus* was not random, and that a few rocks with certain physical characteristics received most of the eggs. Other aquatic invertebrates and vertebrates have been reported to select oviposition sites using physical characteristics of oviposition substrates (Golini and Davies 1975; Kupferberg 1996). In our study rock size was consistently a good predictor of presence and density of egg masses, as observed by Peckarsky et al. (2000). Reich and Downes (2003a) also found that Trichoptera females were more likely to oviposit their eggs under large emergent rocks. Large rocks have been shown to be more stable and to roll less often than small ones (Peckarsky 1991; Downes et al. 1998). Therefore, selection of large substrates for oviposition might confer a higher probability of egg survival by reducing scouring and damage associated with rock movement.

Interestingly, our experiments also showed that large rocks were selected by females only if they were located in high-velocity places that had a high probability of persistent flow during the egg incubation period. Therefore, minimizing egg desiccation could provide sufficient selection pressure to maintain *B. bicaudatus* preference for ovipositing under rocks with lower probability of drying. Similarly, some damselflies select oviposition sites based on current velocity and this selectivity has been associated with higher hatching success (Gibbons and Pain 1992). Reich and Downes (2003b) also observed oviposition site selection of three caddisfly species based on flow characteristics; however, the mechanism underlying this behavior and its potential benefits has not been investigated.

The precise sensory cues used by female mayflies to select large rocks with high current velocity are unclear. Adult females of other aquatic insects have been shown to discriminate among oviposition habitats using a variety of sensory cues (McIver 1982). While it is unlikely that females directly detect current velocity, they could respond to the visual characteristics of faster flowing water (higher reflectivity). We speculate that high reflectivity associated with splash, which was positively correlated with current velocity, might be a reliable environmental cue for ovipositing females. Splash was clearly an important predictor of oviposition in the East River (Fig. 3) where the current velocity experiments were conducted. However, splash was not universally important, probably because the amount of splash varied among streams and over time (Electronic Appendices A and B).

Many insects navigate by detecting polarized light from objects or the sky (Schwind 1991; Wildermuth and Spinner 1991; Horvath 1995). Polarized light produced by the stream environment could attract females to a particular stream reach (Kriska et al. 1998), because

Table 2 Results of repeated measures ANOVA (general linear model procedure) testing the effects of treatment (before vs. after) and density (1, 20 and 50 egg masses per rock) on the number of

new egg masses on each rock at each date. The replicates were five rocks per treatment and repeated measures were 4 days before and 4 days after treatment. (SAS Institute 2003)

Source	df	Type III SS	Mean square	F-value	P > F		
Between-subjects effects							
Treatment	1	56.03	56.03	0.21	0.6471		
Density	2	348.87	174.43	0.67	0.5214		
Error	26	6,791.27	261.20				
Source	df	Type III SS	Mean square	F-value	P > F	Adjusted P > F ^a	
						G-G	H-F
Within-subject effects							
Time	3	2,014.60	671.53	12.78	< 0.0001****	< 0.0001****	< 0.0001****
Time×Treatment	3	48.43	16.14	0.31	0.8200	0.7037	0.7409
Time×Density	6	238.20	39.70	0.76	0.6068	0.5412	0.5610
Error(time)	78	4,097.27	52.59				

**** $P < 0.0001$

^aSince the sphericity test using Muchly's criterion was significant we used the adjusted P -values: Greenhouse-Geisser epsilon ($G-G$) (0.5724), or Huynh-Feldt epsilon ($H-F$) (0.6797) for the within-subject effects

turbulence reflects polarized light in many directions, potentially increasing its attractiveness. For example, Schwind (1984) found that flying corixids detected bodies of water using reflection of polarized light. Polarized UV light elicited a plunge reaction, whereas unpolarized light was ineffective even if it was several times more intense. Thus, mayflies might recognize splashy rocks as black areas in a sea of polarized light (the stream) (Gilbert, personal communication; Wildermuth and Spinner 1991), and use those visual cues to target suitable oviposition sites.

Alternatively, other insects are capable of detecting chemical and physical properties of oviposition sites (Blaustein and Kotler 1993; Millar et al. 1994); thus, female mayflies might use mechanoreceptors or chemoreceptors to find suitable oviposition sites. Gaino and Rebora (1998) showed that some mayflies of the family Baetidae contain flat-tipped sensilla on antenna and cerci, which possess a tubular body and dendrites extending along the shaft, supporting the hypothesis of a chemo-mechanosensory function. However, we have found no evidence that adult female mayflies respond to chemical signals from conspecifics or predators during oviposition, as has been shown in other insects (Blaustein and Kotler 1993; Pennuto and Stewart 2001). More detailed observations and experiments are needed to explore physiological and behavioral functions of sensilla on cerci and of ommatidia of adult females to understand fully the sensory mechanisms of oviposition selection.

Although *B. bicaudatus* egg masses were highly aggregated on preferred substrates, our experiments suggest that females were not attracted to the presence of other egg masses, but instead selected substrates based on their physical characteristics. Moreover, egg mass aggregation did not affect egg mass survival in a controlled experiment using preferred oviposition substrates where egg masses were not allowed to desiccate. These

results contrast with previous field studies where aggregations of *B. bicaudatus* egg masses on natural substrates had higher probabilities of survival (Peckarsky et al. 2000). Otto and Svensson (1981) suggested that caddisflies oviposit in aggregations to avoid egg mass desiccation. Similarly, under natural conditions in our study selective oviposition by *B. bicaudatus* resulted in egg mass aggregations under large rocks, thereby indirectly reducing the probability of mortality by desiccation.

Others have linked egg mass aggregations to fitness of offspring. For example, Hoffmeister and Rohlf (2001) attributed high offspring mortality in *Drosophila subobscura* to density-dependent factors such as intraspecific competition resulting from egg mass aggregation. Conversely, Wertheim et al. (2002) reported higher survival of larvae of *D. melanogaster* that hatched from aggregated eggs due to the "Allee effect" (Stephens et al. 1999). Higher hatching success of aggregated eggs and higher offspring survival may also be a consequence of predator satiation (Damman and Cappucino 1991; Rehfeldt 1992) or improvements in limiting conditions like temperature and humidity (Parrish and Edelstein-Keshet 1999; Lancaster et al. 2003). Whether aggregated egg masses result in higher offspring survival of *B. bicaudatus* is unknown.

Finally, selective oviposition may have a strong influence on population dynamics if it results in recruitment limitation, which has been reported for other insects (Craig et al. 1989; Price and Ohgushi 1995; Resetarits 2001) and marine invertebrates (Underwood and Fairweather 1989; Palmer et al. 1996; Cowen et al. 2000). Our study suggests that optimal oviposition habitat might be limited temporally (in some seasons and in some years) driven mostly by variation in climate and hydrology, and spatially (among streams) due to differences in hydrogeomorphology. Therefore, specialized oviposition behavior combined with temporal and spatial variation in availability of quality oviposition

substrata has the potential to cause recruitment limitation in these mayfly populations as has been addressed in detail elsewhere (Encalada 2004).

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