

NATURAL HISTORY OF A RETREAT-BUILDING MIDGE, *PAGASTIA PARTICA*, IN A REGULATED REACH OF THE UPPER COLORADO RIVER

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ABSTRACT.—The retreat-building midge *Pagastia* prob. *partica* (Roback) is an abundant and conspicuous member of the benthic community of the upper Colorado River. We investigated the ecology and behavior of *P. partica* in this regulated stream using both qualitative observations and quantitative surveys. Our studies revealed that *P. partica* foraged primarily by grazing algae from their retreats and adjacent surfaces and exhibited territorial behavior toward other *P. partica* larvae. *Pagastia partica* were widely distributed among streambed surfaces but preferred those with higher biomasses of periphyton and swifter currents. The retreats of *P. partica* were composed largely of silk and colonized algae and were important structural habitat features for other benthic fauna. We found numerous small benthic invertebrates cohabiting retreats, while larger insects were observed to have distinct affinities for or aversions to retreat-structured surfaces. Our results indicate that *P. partica* is not only an abundant member of this benthic community, but also a habitat engineer whose retreats represent an important component of streambed habitat for upper Colorado River benthos.

Key words: Chironomidae, Diamesinae, *Pagastia partica*, retreat building, habitat engineering, biogenic structuring, benthic grazing, upper Colorado River.

The Chironomidae (Diptera) are a ubiquitous and diverse family of aquatic insects whose ecological importance is well documented (Oliver 1971, Pinder 1986). However, as Pinder (1986:1) stated, “[A]n enormous amount has been written about their biology, and yet the detailed ecology and life cycles of the great majority of species are unknown.” Indeed, given the scarcity of species-level biological information and their taxonomic difficulty (Pinder 1986), the importance of this group is likely understated.

Retreat-building midges in the genus *Pagastia* Oliver (Diamesinae) are perhaps a quintessential chironomid group. Although they appear to be a single species, *Pagastia partica* (Roback) (Oliver and Roussel 1982), identifications have been uncertain at best (e.g., *Pagastia* cf. *partica* in Pringle et al. 1988) and often erroneous (e.g., *Pseudodiamesa* cf. *pertinax* in Wiley 1978, Pringle 1985). Their ecological significance has been recognized in the strong influence of their retreat-building activities on periphyton communities (Pringle 1985, Pringle et al. 1988), their potential local abundance (Wiley 1978), and their capacity to contribute substantially to secondary benthic production (Berg and

Hellenthal 1991). Nonetheless, the basic ecology of these taxonomically challenging midges is poorly understood.

In the upper Colorado River, *Pagastia* prob. *partica* is an extremely abundant member of the benthic community, and its retreats are a visible component of the benthic landscape, or “benthiscape.” In our group’s ongoing investigation of the interaction between habitat heterogeneity and benthic herbivores in the upper Colorado River (see Wellnitz et al. 2000, Poff et al. 2003), we inevitably have come to suspect that this conspicuous, yet poorly known, insect is an important player in these interactions. The remarkable abundance of *P. partica* in this stream, along with its unique modification of the stone surfaces it inhabits, suggests its distinct role as a “benthiscape architect.”

In recent years ecologists have recognized the importance of certain organisms as habitat or ecosystem engineers (Lawton and Jones 1995, Power et al. 1996). Stream researchers have identified numerous habitat engineers, which include mammals that modify stream habitat at conspicuous landscape scales (Naiman et al. 1988), as well as many fish and benthic invertebrates that modify stream habitat, albeit less

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visibly, at finer scales (e.g., Flecker 1997, Wotton et al. 1998, Statzner et al. 2000, Cardinale et al. 2004). Because of this, our suspicion led to the present exploration of *P. partica*'s ecology and behavior, as well as to other studies considering its influence on insect distributions (Monroe 2002) and insect movement (Olden et al. 2004).

Our objectives in this investigation were to (1) determine *P. partica*'s trophic status, (2) describe its microdistribution in relation to biotic and abiotic streambed habitat components, and (3) document retreat characteristics and patterns of larval behavior. We used both quantitative surveys and qualitative observations to investigate these aspects of *P. partica*'s behavior and ecology in the upper Colorado River.

STUDY SITE

The studied reach of the upper Colorado River runs through an arid shrubland valley on the western slope of Colorado's Rocky Mountains at an elevation of 2420 m. This reach receives regulated streamflows (via Granby dam located ca. 7 km upstream), which are highly stable and much reduced from those prior to impoundment (see Monroe 2002). The stream channel exhibits plane-bed characteristics (Wohl 2000), with alternating run and riffle channel units (Fig. 1A). The streambed is dominated, in both runs and riffles, by large stones that sit above a less conspicuous sublayer of gravels (Fig. 1B). Throughout the year, but particularly from early fall to early summer, the surfaces of these smooth granitic stones typically support dense colonies of the blue-green alga, *Nostoc*. From fall to early summer, *Nostoc* colonies are frequently inhabited by *Cricotopus* midge larvae, which form them into distinct ear-shaped pads (see Brock 1960).

METHODS

Observations

Over the summer of 2001, we recorded qualitative observations of *P. partica*'s larval behavior and retreat characteristics. These observations included over 150 hours in the stream (using a viewing tube) and numerous hours in streamside culturing channels (see Olden et al. 2004). We were particularly interested in foraging, movement, and retreat-related behavior, but we opportunistically recorded any note-

worthy behaviors. These observations spanned nearly the duration of the summer cohort's larval stage, excluding only very early (and unobservable) instars. Observational methods are suitable for mid- to late-instar *P. partica* because they are large relative to most chironomids (maximum length ca. 12 mm).

Trophic Relationships

We dissected 45 larvae (sampled in the August retreat survey, below) and homogenized and mounted their gut contents on individual slides using Taft's solution. We completely scanned each slide at 100X magnification, through repeated linear passes across a slide, and visually ranked the areal abundance of 5 diet categories, which were determined through preliminary inspections of the slides. Our diet categories, which classified nearly all the observed material, were blue-green algae, diatoms, filamentous algae, detritus, and sclerotized chironomid remains.

Habitat Relationships

We conducted a survey in July 2001 to explore habitat relationships of *P. partica* across 2 spatial scales. The spatial scales considered included the stone (i.e., stream stones) and surface (i.e., microhabitats within stream stones) scales (see Monroe 2002 for detailed description). We considered several habitat components across these 2 scales. At the stone scale, we measured the length of the intermediate, or beta, axis of stream stones to estimate their size. To characterize habitat at the surface scale, we measured depth, near-bed current velocity, and periphytic biomass. We separated periphyton into a coarse fraction, which contained elements such as *Nostoc* colonies and *P. partica* retreats, and a fine fraction that contained nonstructural periphytic components. Using this framework, we determined how well these abiotic and biotic variables explained *P. partica*'s surface-scale density and identified the primary habitat components (and associated scales) explaining the spatial distribution of *P. partica*.

We chose a representative riffle and run to sample streambed habitat, randomly selecting a transect across each. A total of 47 points were systematically located along transects every 0.5 m; all points falling on stones with beta axes greater than 6 cm were marked with lumber chalk. At each point we measured depth

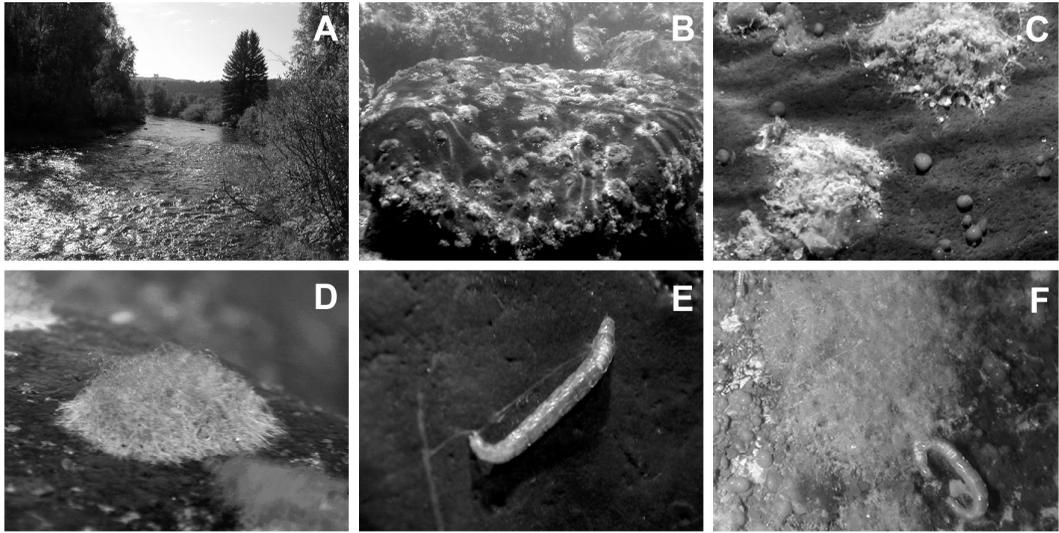


Fig. 1. A, The studied reach of the upper Colorado River; B, a large stone with numerous *P. partica* retreats; C, two early season retreats; D, a late-season retreat illustrating a silky lower layer and a filamentous algal overstory; E, a crawling larva advancing with the aid of a silk line; F, *P. partica* larva defending its retreat against another *P. partica* larva.

and near-bed current velocity, the latter using a Schiltknecht MiniWater 2 microprobe (probe diameter = 8 mm; temporal resolution = 1 s; measurement period = 7 s).

We removed stones from the stream and placed a firm rubber plumbing gasket (inner diameter = 58 mm) around each point mark. All invertebrates and periphyton in the contained 26-cm² area were removed with a nylon brush and pipette, and the sample was preserved in 10% formalin.

In the laboratory we observed samples under 10X magnification and identified and enumerated all visible invertebrates. To distinguish *P. partica* retreats and other structural periphytic components (e.g., *Nostoc* colonies) from more edible periphytic components (e.g., diatoms and green algae), we separated remaining periphyton into coarse and fine fractions by rinsing samples through a 250- μ m sieve and processing them for ash-free dry mass using standard methods (APHA 1992).

We used multiple regression analysis to model *P. partica* density as a function of the suite of scaled habitat variables, which included the stone-scale predictor, beta-axis, and the surface-scale predictors, depth, current velocity, coarse periphyton biomass, and fine periphyton biomass. Where necessary, we transformed variables (log or square root) to meet assumptions of normality and homoscedasticity.

Retreats, Their Spacing, and Associated Taxa

We conducted a survey in August 2001 to characterize the architecture, size, and taxa associated with late-season retreats and to examine relationships among retreat spacing, retreat size, scaled habitat components (as in the habitat survey, above), and larval size. To locate retreats for investigation, we placed points (as above) every 0.5 m along 2 separate transects, 1 across a run and the other across a riffle. For each point falling on a stone, we located and marked the nearest retreat and measured the depth and surface current velocity (as in the habitat survey) immediately adjacent to it. We removed the stone from the stream and measured the length and width of the retreat, as well as the linear distance to the 3 nearest neighboring retreats. We then carefully removed the retreat and its occupants from the stone and preserved them in 10% formalin solution, visually inspected the underlying stone surface for textural features such as depressions or grooves, and measured the stone beta axis. In the laboratory, retreats were examined under 10X magnification, and the presence or absence of architectural features such as a silk tube and structural elements (e.g., *Nostoc* colonies, pupal cases) was noted. We identified and enumerated all macroinvertebrates associated with each retreat and measured the

length and head capsule width of the resident *P. partica* larva.

We used averages, ranges, and percent occurrence (by retreat) to characterize retreat characteristics and associated taxa. We also constructed a multiple regression model for mean neighbor distance (of the 3 nearest neighbors) that used the stone-scale predictor, stone-beta axis, and the abiotic surface-scale predictors, depth and current velocity. Where necessary, we log-transformed variables to meet assumptions of normality and homoscedasticity.

RESULTS

Observations

APPARENT LIFE HISTORY.—We observed very small *P. partica* larvae (ca. 2 mm) in both mid-fall and late spring, and large larvae in mid-spring and late summer. This pattern suggests bivoltinism in this species, which has been found elsewhere (Berg and Hellenthal 1991). The summer cohort, on which we focus here, is far more abundant and more active in retreat-building. We noticed considerable variation in larval size in this cohort; however, pupation and emergence occurred relatively synchronously over an approximate 4-week period in late summer. Despite this concerted emergence, adults were surprisingly inconspicuous; large midge swarms were never observed.

RETREAT CHARACTERISTICS.—*Pagastia partica* began building retreats as very small larvae in late spring. Retreats were almost always spaced to some degree (i.e., rarely contiguous) and were built exclusively on sunlit surfaces. Retreats were more common on larger stones (i.e., cobbles and boulders) and were rarely built on particles that were gravel-sized or smaller. Initially, retreats were constructed of a light brown spun silk and were conspicuous against the dark, oxidized surfaces of the streambed. Retreats were most often built among fine-scale structural elements, which were commonly the *Nostoc* colonies and *Cricotopus* pads that dominate upper Colorado River substrates in late spring. However, retreats were also built on smooth stone surfaces, in dense filamentous algae, in moss, and on wood. Like their foundations, the architecture of retreats was highly variable. Retreats often abutted or skirted around structural elements, whereas retreats on smooth surfaces were a low dome of silk with a roughly circu-

lar perimeter. Retreats lacked any distinct external features (e.g., ports), yet when dissected, most featured an internal tube of densely spun silk that was roughly the length and width of the resident larva. Inside the tube, distinct port-holes were usually apparent and occasionally very abundant (we observed as many as 15). The loosely spun silken matrix that surrounds this tube and comprises the majority of the retreat's volume appears to allow unrestricted movement, and it may function as surface area for algal colonization and perhaps capture of suspended material.

As the summer progressed, retreats changed in 2 notable ways. First, retreats became more conspicuous as they grew in size and as co-occurring *Nostoc* colonies and *Cricotopus* pads decreased in abundance. Second, low-profile, early season retreats that appeared to be largely silk and diatoms slowly accumulated filamentous algae to yield higher-profile, late-season retreats that had a current-swept over-story (Figs. 1C, D).

RETREAT-RELATED BEHAVIOR.—Retreat-building behavior of several larvae was observed from both above and below a smooth plexiglass substrate in a streamside flume. Retreat construction was initiated when the larva anchored its anal claws to the substrate to apply silk over its abdomen (Figs. 2A, B). In this manner, a small retreat consisting mainly of the central tube was completed in a matter of hours (Fig. 2C). Subsequent expansion of retreats occurred more slowly and appeared to be aided by algal colonization and accumulation of seston.

Pagastia partica individuals spent most of their time withdrawn inside the central tube. In streamside channels larvae in newly constructed, translucent retreats often made continuous undulating body movements while in this tube. Larvae occasionally extended much of their body length outside their retreat to engage in foraging or fighting (see below); however, they rarely exited completely. With the absence of distinct external ports, larvae would extend from nearly any point on a retreat. We observed larvae abandoning their retreats only when they lost an aggressive confrontation or when their home stone was removed from the water, in which case a delay of up to 1/2 hour was common.

FORAGING BEHAVIOR.—*Pagastia partica* appeared to forage primarily on periphyton,

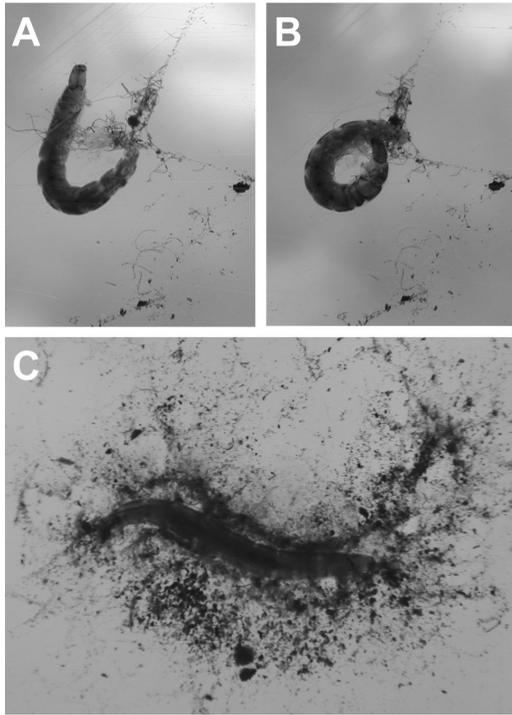


Fig. 2. Larvae initiate retreat construction by applying silk over the abdomen (A and B) and can build a basic retreat in several hours (C).

colonizing both retreats and adjacent stone surfaces. Although retreats themselves usually had distinct boundaries, surrounding foraging areas were not clearly delineated; we saw no visual evidence of foraging grounds or “gardens” observed from some other retreat builders (McAuliffe 1984, Hart 1985). Larvae emerged from their retreats and extended either out to forage from adjacent surfaces (surface foraging) or up to forage from retreat overstory (retreat foraging). Surface foraging appeared to be more extensive (i.e., larvae distributed bites over larger areas), whereas retreat foraging appeared to be more intensive (i.e., larvae concentrated bites in smaller areas). During surface foraging, larvae rarely extended more than half their body length from their retreat; during retreat foraging, larvae rarely extended more than their head. Foraging bouts were both brief (usually <5 seconds) and sporadic.

MOVEMENT BEHAVIOR.—Although larval movement was rarely observed in situ, crawling and drifting behaviors were observed when larvae were introduced to streamside channels. Crawling movement consisted of a larva (1)

anchoring a silk line to the substrate with its mouthparts, (2) curling its abdomen to intercept the line with its anal claws, (3) anchoring its anal claws while lunging forward and playing a silk line out from its mouthparts (Fig. 1E), and (4) grasping the substrate with its prolegs and re-anchoring the silk line to the substrate. This protected crawling style effectively prevented larvae from being dislodged from erosional surfaces and resulted in silken trails across substrata, which became more conspicuous as they accumulated seston. Across smooth surfaces (here, bare ceramic tile), larvae moved rapidly (ca. 10–15 cm · minute⁻¹) and nearly linearly. On surfaces structured by *Nostoc*, retreats, or filamentous algae, larvae moved slower and in more tortuous paths. When structural elements were encountered, larvae always attempted to burrow into them by lunging in headfirst. Larvae occasionally made deliberate drifting movements by releasing from the substrate and drifting in a fully extended position. In slow currents (<ca. 10 cm · second⁻¹), drifting behavior often included swimming movements, in which a larva rapidly flexed its abdomen laterally back and forth to propel itself upward in the water column. Movement behavior always ceased when a larva either began building a retreat or overtook another larva’s retreat.

INTERACTIVE BEHAVIOR.—*Pagastia partica* larvae were never observed directly interacting with other benthic invertebrates, several of which (baetid and ephemereid mayflies and lepidostomatid caddisflies) were frequently found adjacent to or on their retreats. However, intraspecific interactions among *P. partica* larvae were frequently observed in streamside channels and occasionally observed in situ. These negative interactions occurred when either (1) two crawling individuals made tactile contact or (2) an individual attempted to enter another’s retreat (Fig. 1F). In nearly all of these encounters, both larvae would initially exhibit aggressive behavior, lunging off anchored anal claws and attempting to bite the other’s abdomen. These battles were always brief, with one larva quickly leaving the area. Successful bites were evidenced by the recoil behavior of the recipient, but they did not appear to inflict serious injury. In retreat intrusions, successful defenses and successful take-overs seemed equally likely, although larger larvae appeared to be superior fighters.

TABLE 1. *Pagastia partica* diet categories, their percent occurrence across 41 examined guts, their mode (or most frequent) rank within guts, and their description.

Diet category	% occurrence	Mode rank	Description
Blue-green algae	100	1	Predominantly <i>Nostoc</i>
Diatoms	78	2	Varied taxa
Detritus	78	3	Amorphous organic
Filamentous algae	51	4	Varied taxa
Chironomid remains	15	4.5	Head capsules

TABLE 2. Multiple regression predictors, their standardized regression coefficients, *t*-statistics, and *P*-values in explaining variation in *P. partica* density ($\sqrt{}$ transformed); $R^2 = 0.56$, $n = 47$.

Habitat predictors	β	<i>t</i>	<i>P</i>
STONE SCALE			
Beta axis length	-0.144	-1.06	0.294
SURFACE SCALE			
Depth	0.022	0.20	0.840
Log (current velocity)	0.366	3.24	0.002
Log (fine periphyton wt.)	0.929	3.51	0.001
Log (coarse periphyton wt.)	-0.217	-0.88	0.383

Trophic Relationships

Of 41 successfully mounted gut contents, all contained blue-green algae, 32 contained diatoms, 32 contained detritus, 21 contained filamentous algae, and 6 contained chironomid remains (see Table 1). Moreover, blue-green algae were most frequently ranked 1st, diatoms 2nd, detritus 3rd, filamentous algae 4th, and chironomid remains split between 4th and 5th.

Habitat Relationships

Pagastia partica larvae were present in 39 of 47 point samples, with an average density of 3.70 ($s_{\bar{x}} = 0.52$) per 26 cm². Our multiple regression model explained 56% of the variation in *P. partica* density and indicated that point-scale current velocity and fine periphyton weight explained the majority of this variation (Table 2) as positive predictor variables. Stone-scale beta axis explained little variation in *P. partica* density, but higher densities did appear to be associated with larger stones. Likewise, depth and coarse periphyton weight were poor predictors of *P. partica* density. However, the poor performance of coarse periphyton weight was, in fact, a statistical artifact of the strong positive correlation between the coarse and fine periphyton fractions. In 2 separate linear regression models explaining *P. partica* density, fine periphyton weight ($R^2 = 0.44$) and

coarse periphyton weight ($R^2 = 0.31$) were both significant positive predictors ($t = 5.93$, $P < 0.001$; $t = 4.52$, $P < 0.001$, respectively).

Retreats, Their Spacing, and Associated Taxa

Table 3 shows that, architecturally, distinct silk tubes were present in almost half of the sampled retreats, *Nostoc* colonies were always associated with retreats, and cased Trichoptera pupae were occasionally incorporated in retreats. Retreats were not typically located on textural stone features. The mean retreat length and width were 14.7 mm and 9.6 mm, respectively. Of the taxa associated with retreats (summarized in Table 4), Chironomidae (other than the resident *P. partica*) were the most commonly found, being present in all retreats and often in great abundance. Baetidae and Lepidostomatidae were also common, being present on 67% and 38% of retreats, respectively. Oligochaeta were present on 18% of retreats, whereas remaining taxa were all found on less than 10% of the sampled retreats.

Our multiple regression model explained 24% of the variation in mean neighbor distance (Table 5). Current velocity is the only variable that explained a significant amount of variation in mean neighbor distance, indicating that retreats in swifter velocities were more closely spaced.

TABLE 3. Retreat architectural and morphometric components and their respective percent occurrence or mean length (mm) for the 45 sampled retreats.

Retreat feature	% occurrence (by retreat)	Mean length (range)
ARCHITECTURAL COMPONENTS		
Silken tube	42	
<i>Nostoc</i> colonies	100	
Cased Trichoptera pupae	4	
Stone feature	16	
RETREAT LENGTH		14.8 (9–22)
RETREAT WIDTH		9.6 (5–19)

DISCUSSION

Autecology

Pagastia partica larvae were widely distributed across the range of sampled benthic habitat, occurring in 83% of the habitat survey samples. This broad distribution suggests extensive dispersal via oviposition or the drift of early instars; crawling appears to be a rare and potentially costly mode of movement. *Pagastia partica* density was also highly variable (ranging from 0 to 16 larvae · 26 cm⁻²). Our multiple regression model accounted for a little more than half of this variation in density, which was best explained at the surface scale by current velocity and periphytic biomass. The swifter currents that passed over surfaces with higher *P. partica* densities likely enhanced local algal production via increased colonization and nutrient delivery rates. This speculated flow enhancement is supported by the higher biomasses of fine periphyton that existed on surfaces with greater *P. partica* densities, which were doubtless elevated further by *P. partica*'s retreat-building activities. Swifter currents also may have passed more oxygen over respiring larvae and perhaps delivered more suspended food particles to retreat surfaces. *Pagastia partica* densities were far less explained by the stone scale of habitat structure, and this suggests that larvae may not respond as directly to this coarser scale of habitat variability.

The spacing of retreats was likewise best explained by surface-scale current velocity. The closer retreat spacing associated with swifter currents illustrates that, along with the larvae, *P. partica* retreats were denser in these microhabitats. Interestingly, the more crowded retreats were often larger (Fig. 3), thus decreasing surface foraging space and increasing

TABLE 4. Taxa associated with *P. partica* retreats, their percent occurrence across 45 retreats, and their range of abundance per retreat. The Chironomidae do not include *P. partica*.

Associated taxa	% occurrence	Abundance range
TRICHOPTERA		
Lepidostomatidae	38	1–3
Hydropsychidae	7	1–1
Brachycentridae	2	1–1
EPHEMEROPTERA		
Baetidae	67	1–10
Ephemerellidae	7	1–1
DIPTERA		
Chironomidae	100	2–135
Tipulidae	4	1–4
Empididae	4	1–2
Simuliidae	2	1–1
COLEOPTERA		
Elmidae	7	1–1
OLIGOCHAETA	18	1–10
HYDRACHNIDA	2	1–1

retreat foraging space. This pattern suggests that retreat foraging by *P. partica* may become particularly important on crowded surfaces, and it may be explained by the increased resources delivered by the swifter currents that pass over them (e.g., algal growth resources, suspended food particles). The benefits of retreat foraging, which could include reduced exposure to predators and aggressive conspecific larvae (see Hershey 1987), are further substantiated by the abundance and diversity of other invertebrates found on and in them. Nonetheless, even the most crowded retreats exhibited spacing; the lowest mean neighbor distance measured was 4.3 mm—roughly half the length of larger *P. partica* larvae. Although the ultimate cause of inter-retreat spacing may involve the territorial inclusion of at least some surface grazing space, spacing is likely maintained by the extremely aggressive behavior *P. partica* larvae exhibit toward one another. This behavioral pattern has been observed in other retreat builders (see McAuliffe 1984, Hart 1985, Matczak and Mackay 1990, Wiley and Warren 1992, Keiper and Espeland 2000), and this further influences the surface-scale distribution of *P. partica* in the upper Colorado River.

Although these results reveal some specializations in *P. partica*'s behavior, they also reveal extreme plasticity in its environmental relationships. *Pagastia partica*'s sedentary retreat-dwelling behavior is a specialization that has

TABLE 5. Multiple regression predictors, their standardized regression coefficients, t -statistics, and P -values in explaining variation in mean neighbor distance ($\sqrt{}$ transformed); $R^2 = 0.24$, $n = 45$.

Habitat predictors	β	t	P
STONE SCALE			
Beta axis	-0.141	-1.02	0.314
SURFACE SCALE			
Depth	0.186	1.55	0.128
Log (current velocity)	-0.324	-2.48	0.017

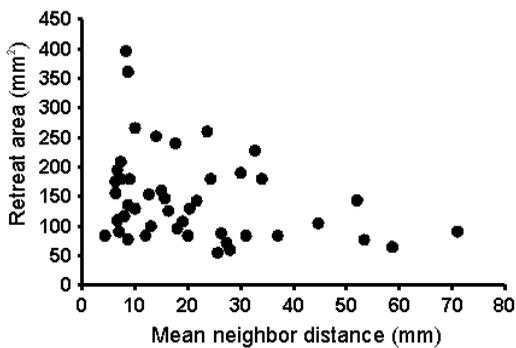


Fig. 3. The relationship between mean neighbor distance (of the 3 nearest neighbors) and retreat area (retreat length \times retreat width) for *P. partica* retreats.

not been reported in other *Pagastia* species (Oliver and Roussel 1982), and its expansive retreats are distinct from the narrower, tube-like retreats of other chironomids (Pringle 1985, Chaloner and Wotton 1996). Its exclusive use of stable sunlit substrates and the predominance of algae in its diet are indicative of an obligate herbivore, but its high-profile, "sticky" retreat and substantial consumption of detritus suggest it may be a facultative filterer as well as an opportunistic predator (see Pringle 1985). Its density varies along gradients of many benthic habitat components, particularly fine-scale current and algal conditions, but it generally persists at some density across the length of these gradients. Indeed, *P. partica* occurs on nearly every stable sunlit surface in the studied reach, representing a substantial proportion of benthic biomass (in both the large larvae and their retreats) and forming a more conspicuous component of upper Colorado River benthoscapes.

The remarkable abundance of this retreat-builder in the studied reach is of interest in itself. We suspect that *P. partica*'s high densi-

ties are actually facilitated by the regulation of this stream. Reduced frequencies and magnitudes of high-flow events have doubtless decreased the movement of large cobble/boulder substrata and the scouring of their surfaces (Rader and Ward 1989). These 2 disturbance mechanisms (scour and stone rolling) can reduce *P. partica* densities by destroying retreats and, perhaps more importantly, removing coarse algal components that aid in retreat building and rebuilding (J. Monroe unpublished data). It is likely that *P. partica* benefits further from increased primary productivity provided by clear, nutrient-enriched waters released from upstream impoundment.

Synecology

Pagastia partica's influence on the biomass and distribution of stream periphyton has been well demonstrated in other research (Pringle 1985). By providing both increased substrate microstructure and an enriched nutrient source in fecal material, retreats host far more productive and diverse algal communities than do adjacent surfaces (Pringle 1985). In the upper Colorado River, these facilitated algal communities appear to be dominated by diatoms in early summer and filamentous green algae in late summer. By modifying the distribution and composition of periphyton, *P. partica* presumably exerts strong control over the distribution of both food and structural habitat in this strongly autotrophic stream. This critical role is played by numerous retreat-building insects, with consequences for food availability (Pringle 1985, Bergey 1995) and food web dynamics (Power 1990, 1991), and this role may even be assumed by some mobile case-building insects (Poff and Ward 1988).

Pagastia partica does not appear to interact behaviorally with other invertebrate species and, based on our in situ observations, certainly not with the larger mobile species often

occurring on or near retreats. This finding is in contrast to other reports of frequent inter-specific behavioral interactions between retreat-dwelling insects, including chironomid (Wiley and Warren 1992) and caddisfly larvae (McAuliffe 1984). Through its retreat-building behavior, however, *P. partica* may influence the distribution of many species. Our survey of *P. partica* retreats revealed that numerous organisms dwell on and in them.

Of the larger mobile herbivores in this reach, lepidostomatid caddisflies and baetid mayflies were most frequently found on retreats. These insects, along with ephemereid mayflies, were also frequently observed immediately adjacent to retreats and most often on the leeward side, where they presumably gained refuge from current and, beneath a trailing algal overstory, from predators (e.g., trout and sculpins). The affinities of lepidostomatids and ephemereids for retreat-structured surfaces, both of which have been experimentally shown via retreat removals (Monroe 2002), further appeared to involve increased resources (from retreat foraging) and increased clinging stability. Conversely, large physid snails, glossosomatid caddisflies, and heptageniid mayflies, which are all reasonably abundant in this reach, were never found on retreats and rarely found near them. Morphologically, these 3 herbivores exhibit low substrate clearance (e.g., the flat gastropod foot, the flat-bottomed glossosomatid case, and the flattened heptageniid body) that is more suited to moving over smooth stone surfaces (see Olden et al. 2004). Thus, in the context of invertebrate movement and dispersal through benthiscapes, the degree to which a surface is structured by retreats may determine the permeability of that surface for crawling species. Speculatively, even the drifting movements of some taxa could be influenced by high-profile, sticky retreats, which may be more easily intercepted and may cause localized hydraulic deposition zones (see Diamond 1986).

Of the smaller invertebrates associated with retreats, chironomids were by far the most prevalent (reaching abundances of 135 larvae per retreat), although oligochaetes were also abundant (up to 10 per retreat). These smaller organisms are less observable, but the fact that we never observed them on retreats indicates they likely dwell *in* retreats. The loosely spun silk that surrounds the central tube is the most

probable retreat habitat for these organisms and would afford them both a predator refugium and an apparent diversity of food resources (e.g., algae, detritus, fecal material, silk). Our gut content analysis indicated that retreat-dwelling chironomids can fall prey to *P. partica*; however, given the abundance of chironomids in retreats, they do not appear to be a preferred food source. Ultimately, the relationship between these associated organisms and *P. partica* remains unresolved: do they compete with their host (e.g., by consuming limiting resources) or facilitate their host (e.g., by increasing algal fertilization)?

Collectively, our observations and measurements have provided strong support for our suspicion that *P. partica* plays an important role in this benthic community. Indeed, our exploration of the ecology of *P. partica* has led us to view this species as a “benthiscap engineer” whose retreats are important structural habitat features for other epilithic invertebrates. The distribution of nearly every benthic invertebrate we have studied in this stream has shown a strong relationship, either positive or negative, with the abundance of *P. partica*'s retreats (Monroe 2002). Indeed, retreats appear to broaden the available space and trophic resources for some organisms (ephemereids, lepidostomatids, baetids, chironomids) and constrain the available space and resources for others (glossosomatids, physids, heptageniids). Although our results leave the mechanisms for these relationships largely unrevealed, we have given them sufficient speculation to aid not only our continued research, but that of other researchers studying similar systems. Indeed, retreat-building insects, particularly chironomids, are widely distributed in streams and are being increasingly considered in the context of habitat engineering (Chaloner and Wotton 1996).

In describing the characteristics of *P. partica* and its retreats in the upper Colorado River, we have illuminated the role of this species as an important habitat engineer with pervasive ecological influences. We also have demonstrated the utility of considering several scales when studying hierarchical systems, particularly those fine scales wherein benthic invertebrates influence each other most directly (McAuliffe 1984). Finally, we hope to have promoted the combined use of both observation and measurement in studying poorly known

organisms (see Polis et al. 1998, Power et al. 1998, Applegate 1999), wherein observations serve to both guide measurements and aid their interpretation.

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