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Intra- and interspecific competition among coexisting lotic snails

Wyatt F. Cross and Arthur C. Benke

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The competitive interactions of two lotic snails, *Elimia cahawbensis* and *Elimia carinifera*, were examined in a second-order spring-fed stream. We first demonstrated food limitation in laboratory microcosms where snails grew faster when exposed to enhanced periphyton levels. We then tested the magnitude and relative strengths of intra- and interspecific competition in similar stream and laboratory mesocosm experiments. Treatments were maintained in Plexiglas enclosures over a 7-week period with 0, 1 ×, 2 × and 4 × ambient biomass of each species alone, as well as mixed species treatments at 2 × and 4 × ambient. Snail responses to treatments were almost identical in field and laboratory experiments. Growth rates of both species were reduced by increased density of snails indicating strong intra- and interspecific competition among *E. cahawbensis* and *E. carinifera*. An analysis of the strengths of intra- and interspecific competition indicated minimal differences for either species, implying a lack of competitive dominance. Although periphyton biomass was generally highest without snails, there was little difference in periphyton biomass and snail production over the four-fold density range, regardless of species composition. These results suggest that *E. cahawbensis* and *E. carinifera* are functionally redundant with density-dependent responses in growth rate resulting in similar grazing pressure across a density gradient. This clearly demonstrates that species impact is not necessarily reflected by measures of abundance or biomass, and that secondary production should be considered.

W. F. Cross and A. C. Benke, Aquatic Biology Program, Dept of Biological Sciences, Univ. of Alabama, Tuscaloosa, AL 35487-0206, USA (present address of WFC: Inst. of Ecology, Univ. of Georgia, 711 Biosciences Bldg, Athens, GA 30602, USA [cross@sparc.ecology.uga.edu]).

The importance of interspecific competition as a mechanism capable of influencing community structure and function has been a topic of much debate (e.g., Schoener 1982, 1983, Connell 1983, Shorrocks et al. 1984, Sih et al. 1985, Gurevitch et al. 1992, 2000). Generally, competition is considered to be unimportant in variable environments dominated by stochastic abiotic events (Andrewartha and Birch 1954, Wiens 1977). These stochastic events are believed to maintain populations of potential competitors at low enough densities such that resources are abundant, encounters among individuals are rare, and competition is insignificant (e.g., Connell 1978, Sousa 1984). Similarly, predators may effectively reduce numbers of prey below levels necessary for competition (e.g., Paine 1966). As a consequence, species with varying competitive abilities and a high degree of niche overlap are able to coexist (e.g., Dayton 1971, Huston 1979, Sousa 1979, Dudley et al. 1990, Hemphill 1991). However, in ecosystems characterized as being relatively stable and containing few effective top predators, competitive interactions among organisms may become increasingly important as a result of the release of physical and predatory constraints on their distribution, growth, and reproduction. It is likely in these systems that competition is prevalent and potentially important in determining community structure and function.

Evidence of competition in nature comes primarily from terrestrial, marine, and lentic ecosystems (see reviews by Connell 1983, Schoener 1983, Sih et al. 1985,

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Gurevitch et al. 1992, Begon et al. 1996). In contrast, there have been relatively few studies of competition in stream ecosystems, and as in other systems, its prevalence and importance in structuring communities are debated (e.g., Hart 1983, Peckarsky 1983, Power et al. 1988, Grossman et al. 1998). Generally, streams are considered to be harsh environments in which community structure and function are determined by physical factors and stochastic events such as floods (e.g., Hynes 1970, Minshall and Minshall 1977, Reice 1981, Grossman et al. 1982, 1998, Resh et al. 1988). For benthic macroinvertebrates in particular, floods and predators are believed to reduce densities of competitively dominant species, such that competition is intermittent (e.g., McAuliffe 1983, 1984a, Hemphill and Cooper 1983, Hemphill 1991, Kuhara et al. 1999), or relatively unimportant (e.g., Minshall and Minshall 1977, Reice 1981). There is, however, increasing evidence of competition within stream invertebrate communities (e.g., Hart 1985, Harvey and Hill 1991, Kohler 1992, Kohler and Wiley 1997), suggesting that the relative importance of competition versus other factors in structuring stream communities is not yet understood.

In many stream ecosystems, invertebrates that feed on the attached periphyton assemblage (grazers) constitute a significant portion of the benthic invertebrate community. These grazers are capable of attaining extremely high densities at which they can deplete their food resources, show exploitative competition, and grow in a density-dependent manner (e.g., Hart 1987, Hill and Knight 1987, Lamberti et al. 1987, Feminella and Resh 1990). Grazers also have been shown to negatively influence densities of coexisting invertebrates via food exploitation (e.g., McAuliffe 1984b, Harvey and Hill 1991) or physical interference (e.g., Hart 1985, Hawkins and Furnish 1987). Most studies of competition among stream grazers have tended to focus on taxonomically dissimilar species (i.e., individuals from different classes or different phyla). It is common, however, for congeneric pairs of grazers to coexist, and competition seems most likely among these closely related taxa considering their similar resource requirements.

In this study we examined the competitive interactions of two lotic snails (Prosobranchia: Pleuroceridae) in a small spring-fed stream in Alabama. While there is evidence of competition between closely related snails from lentic (e.g., Brown 1982, Osenberg 1989) and intertidal marine ecosystems (e.g., Haven 1973, Underwood 1978, Creese and Underwood 1982, Fletcher and Creese 1985, Schmitt 1985), no experimental studies have tested the importance of competition between species of coexisting lotic snails.

Results from many previous studies of competition have been criticized for their failure to identify a limiting resource (i.e., competitive mechanism), failure to simultaneously consider both intra- and interspecific competition, and tendency to over-extrapolate laboratory results. Therefore, we designed experiments to: 1) test for food limitation of snails, 2) determine the influence of snails on their food resource (i.e., periphyton), 3) estimate the relative strengths of intra- and interspecific competition, and 4) determine whether identical experiments conducted in the laboratory and in the field can yield similar results. Such comparisons of laboratory and field experiments are crucial for understanding how accurately results from microcosm studies represent the complex dynamics of natural communities (e.g., Odum 1984, Lamberti and Steinman 1993, Lawton 1996, Kohler and Wiley 1997).

Study organisms

Pleurocerid snails often dominate the grazing invertebrate community in hardwater streams of the southeastern United States (e.g., Burch 1982, Newbold et al. 1983, Richardson et al. 1988, Rosemond et al. 1993, Huryn et al. 1994). They can reach densities as high as $7000/m^2$ (A. D. Huryn, Univ. of Maine, unpubl.) and constitute $>90\%$ of the total invertebrate biomass (e.g., Newbold et al. 1983, Richardson et al. 1988). In general, pleurocerids are long-lived, iteroparous organisms that exhibit relatively low rates of secondary production (Dazo 1965, Richardson et al. 1988, Brown 1991, Huryn et al. 1995). Growth can be continuous throughout the year (Huryn et al. 1994) or may be restricted to warmer months (Aldridge 1982, Huryn et al. 1995). Pleurocerids are feeding generalists (Aldridge 1983), capable of scraping organic material from various benthic substrates. Most ecological studies of pleurocerids have concentrated on their grazing influence, where they have been shown to affect periphyton biomass (e.g., Gregory 1983, Lamberti et al. 1989), production (e.g., Hill and Harvey 1990, Hill et al. 1992a, Rosemond et al. 1993), taxonomic assemblage and physiognomy (e.g., Lamberti et al. 1987, Steinman et al. 1987, McCormick and Stevenson 1989), and succession (e.g., Steinman et al. 1987, Tuchman and Stevenson 1991). Despite our current understanding of the influence of snails on periphyton communities (see review by Feminella and Hawkins 1995), few studies have considered the possible existence of exploitative competition between populations of pleurocerids and among snails and other coexisting invertebrates (but see Hawkins and Furnish 1987, Harvey and Hill 1991, Hill 1992).

Elimia cahawbensis (Lea) and *Elimia carinifera* (Lamark) (Prosobranchia: Pleuroceridae) are the only lotic pleurocerids present at Hendrick Mill Branch (see site description below), and together represent ca 75% of the total macroinvertebrate biomass (Huryn et al. 1995). Both species maintain extremely high densities

throughout the year, recruit new individuals at the same time of year (Huryn et al. 1994, 1995), have substantial overlap in their microdistributions, and do not appear to be controlled by predators. Annual secondary production of these snails is moderate (≈ 2500 mg/m^2), but in contrast to many other streams in Alabama, *E. cahawbensis* and *E. carinifera* continue to grow during the winter months at Hendrick Mill Branch due to relatively high winter temperatures (Huryn et al. 1995). Huryn et al. (1995) reported a strong negative relationship between growth rates and population biomass of *Elimia* in six Alabama streams (including Hendrick Mill Branch), and suggested that growth was limited by competition for periphyton. Thus, the dominance of two coexisting snails in Hendrick Mill Branch provides an ideal situation for testing hypotheses about competition in streams.

Methods

Site description

The field experiment was conducted at Hendrick Mill Branch, a second-order stream located in the Valley and Ridge physiographic province, Alabama, USA. The geology consists of long reaches of limestone and dolomite bedrock crossbedded by bands of erosion-resistant chert, and unconsolidated deposits of chert cobble, gravel, and sand (Osborne et al. 1988). The watershed is heavily forested by mixed hardwoods and pines, and during spring and summer months, light penetration through the dense riparian canopy is patchy. Hendrick Mill Branch is primarily spring-fed, causing temperature (mean = 15.3°C, range = 11.3–17.6) and discharge (mean = 66 L/s) to remain relatively constant throughout the year (Huryn et al. 1994). Spates are rare and generally restricted to the winter months. Nutrient levels are moderate compared to other streams of similar size in the Valley and Ridge province (127 μg/L NO_3-N, 6 μg/L PO_4-P, Methvin 1996).

Laboratory experiments were carried out in the Experimental Mesocosm Facility on the Univ. of Alabama campus. This glasshouse facility contains large paddlewheel-driven recirculating stream mesocosms (water volume 1600 L; channel width 40 cm, depth 50 cm, total length ≈ 5 m). Each mesocosm is temperature controlled by heating-cooling units in conjunction with Campbell CR-10 dataloggers (Campbell Scientific Inc., Logan, UT) which record light and temperature data. Shading curtains on the ceiling of the glasshouse allowed us to simulate irradiance conditions at Hendrick Mill Branch (Laboratory ≈ 0–300 μE m^{-2} s^{-1}, Hendrick Mill Branch [1990] ≈ 0–500 μE m^{-2} s^{-1}; G. M. Ward, Univ. of Alabama unpubl.).

Experiment 1 – food limitation

A 5-week laboratory experiment was conducted from 24 April to 30 May 1998 to test for food limitation of *E. cahawbensis* and *E. carinifera*. Eight small air-driven recirculating streams served as replicate stream microcosms (modeled after Lawson 1982). These streams covered a bottom surface area of 0.1 m^2, had a volume of 10 L, and a flow of ≈ 5 cm/s. Microcosm streams were placed in one of two large mesocosm streams (four in each), which served as temperature control baths.

Each microcosm stream contained snails, periphyton-covered rocks (roughly 30, ≈ 5 cm diameter), and 9 L of stream water from Hendrick Mill Branch. Four microcosm streams received rocks collected directly from Hendrick Mill Branch. The other four microcosms received high biomass rocks from Hendrick Mill Branch that were incubated for 4 weeks in a nutrient-enriched mesocosm stream. Each microcosm received 156 snails (120 juveniles, 24 *E. cahawbensis* [six of each size class > 3 mm], 12 *E. carinifera* [three of each size class > 3 mm]), with maximum aperture widths ranging from 1 to 7 mm. Because total snail length averages $1.6\times$ and $2.4\times$ the maximum aperture width for *E. cahawbensis* and *E. carinifera* respectively, snail length ranged from about 1.6 to 11.5 mm (*E. cahawbensis*) and 2.4 to 16.8 mm (*E. carinifera*) (e.g., *E. cahawbensis* 3 mm aperture width = 4.8 mm total length). Densities in microcosms approximated the average density of snails at Hendrick Mill Branch (1560/m^2, based on averages from cobble habitat; Huryn et al. 1995). Realistic field temperature conditions (≈ 16°C) were maintained throughout the experiment. Fresh water and rocks from Hendrick Mill Branch or the nutrient-enriched stream were exchanged weekly in all microcosms to maintain treatment conditions and to prevent reduction of food supply by snails.

To estimate snail biomass growth rates, the aperture width of each snail was measured to the nearest 0.1 mm with an ocular micrometer before and after the experiment. Juveniles of both species (aperture width 1–3 mm) were pooled because of difficulty with identification at this stage. Larger snails (aperture width 3–7 mm) were individually marked with numbered microtags (Freilich 1989) to facilitate accurate estimates of individual growth rates. Ash-free dry mass (AFDM, including shell organic material) was estimated from aperture width measurements using previously established width-mass equations for these species (Benke et al. 1999).

For snails < 3 mm, daily growth rates were estimated from the average change in biomass over the duration of the experiment: $g = \ln(W_f/W_i)/\Delta t$, where W_i is the mean individual AFDM at the beginning of the experiment, W_f is the mean individual AFDM at the end, and Δt is the duration (in days) of the experiment

(Benke 1993). For the remaining size classes, growth rates were estimated for individual snails. Daily biomass growth rate (mg mg^{-1} d^{-1}) is a desirable response variable because it is adjusted for snail size and time interval, unlike absolute increases in length and mass, and thus allows comparisons among snails regardless of animal size or time interval. Furthermore, it can be used to convert biomass to estimates of daily production (see below).

At the end of the experiment, six large snails of each species (aperture width 5–7 mm) were collected from each microcosm, and frozen for subsequent neutral lipid analysis. Stored lipids are believed to increase reproductive fitness, and may allow individuals to survive periods of low food availability (sensu Hill et al. 1992b). Snails were removed from their shells, dried at 60°C to a constant mass, weighed, individually extracted for 2 d in 5 mL anhydrous ethyl ether, dried, weighed, ashed at 450°C for 4 h, and reweighed (Dobush et al. 1985, Hill 1992). Neutral lipid content was calculated as the dry mass lost after ether extraction.

The demonstration of food limitation rests on the assumption that snails in the treatment stream received more food per unit area than in control streams. Therefore, periphyton AFDM and chlorophyll *a* on treatment rocks were quantified throughout the experiment. Periphyton AFDM was estimated from three rocks of each treatment three times during the experiment. AFDM was quantified by scrubbing the upper surface of each rock with a toothbrush, and rinsing this slurry into a plastic tray. A known volume of slurry was filtered onto a precombusted glass fiber filter (Whatman GFF, pore size 0.7 μm), dried to a constant mass at 60°C, weighed, ashed at 450°C for 4 h, and reweighed. AFDM was calculated as the difference between dry mass and ash mass. Chlorophyll *a* was estimated weekly from four rocks of each treatment five times during the experiment. Rocks were frozen to lyse algal cells and submerged in 90% alkaline acetone solution overnight in a dark coldroom. Chlorophyll *a* was analyzed spectrophotometrically according to Wetzel and Likens (1991). To estimate AFDM and chlorophyll *a* on an areal basis, rock surfaces were covered with aluminum foil, and a foil weight-surface area relationship was used. To determine the effect of snail grazing on periphyton biomass in between weekly rock exchanges, both AFDM and chlorophyll *a* were measured after being exposed to snails for each of three weeks.

Experiment 2 – field competition

A 7-week field experiment was conducted from 6 August to 26 September 1998. Ten Plexiglas flow-through enclosures, each consisting of three parallel channels (0.05 m^2 bottom surface area in each channel), were used to manipulate snail densities. Each enclosure was constructed of a common bottom piece (50 cm × 36 cm) with four vertical parallel walls (30 cm high) spaced 11 cm apart extending above the water surface. Wire mesh (1-mm mesh window screen) was glued with silicon to each end of the enclosures to prevent immigration and emigration of snails, yet allow realistic flow conditions. Enclosures were distributed in a shallow (mean depth 11 cm), non-turbulent 20-m stretch of Hendrick Mill Branch, and firmly anchored with rebar stakes. Current velocity in experimental channels was 5.3 cm/s ± 1.8 SD (measured at the beginning of the experiment with a Marsh McBirney portable flow meter). Any periphyton or debris which accumulated on the enclosures (usually minor) was removed at least weekly. To simulate stream substrate conditions, previously dried sand and gravel, as well as freshly collected periphyton-covered rocks (≈ 5-cm diameter) were placed in each enclosure. Conspicuous invertebrates were removed from rocks by hand.

Ten snail density treatments, each replicated three times, were randomly assigned to channels in the enclosures (Table 1). Mid-sized snails of both species (aperture width 2.5–5.5 mm) were used in the experiment. The "A" or "B" treatments (treatments 1 and 7, Table 1) represent mean annual biomass of each species alone (calculated from quarterly samples in Huryn et al. 1995), and can be considered a control density under the null hypothesis of no interspecific interactions (Underwood 1978). The "A + B" treatment (treatment 4, Table 1) represents natural ambient biomass. The high density treatments (4A, 4B, A + 3B, B + 3A) represent a doubling of natural ambient biomass. Juvenile snails

Table 1. Density treatments for *Elimia cahawbensis* (A) and *Elimia carinifera* (B) and relevant comparisons for intra- and interspecific competition experiments (experiments 2 and 3).

	Experimental treatment									
	1	2	3	4	5	6	7	8	9	10
E. cahawbensis	A	2A	4A	A	A	3A	–	–	–	–
E. carinifera	–	–	–	B	3B	B	B	2B	4B	–
Total no. of snails	18	36	72	36	72	72	18	36	72	0
	Relevant treatment comparisons									
	Intraspecific competition						Interspecific competition			
E. cahawbensis	3 vs 2 vs 1						5 vs 4 vs 1 and 2 vs 4			
E. carinifera	9 vs 8 vs 7						6 vs 4 vs 7 and 8 vs 4			

(< 2.5 mm aperture width) were not used because of their potential to move through the mesh, and large snails (> 5.5 mm) were not used because growth is negligible in older pleurocerids (Huryn et al. 1994). Densities used, however, reflect total average biomass of each species (including juvenile and large snails). *Elimia cahawbensis* and *E. carinifera* had roughly similar average biomass, so the same number of each species (18) were used for the "A" and "B" density treatments.

For each treatment containing snails, the aperture width of 18 "target" snails was measured in the laboratory with a dissecting microscope, and snails were tagged with microtags. In treatments other than controls, additional untagged "treatment" snails of either species were added. For example, treatment 5 (Table 1) consisted of 18 individually tagged *E. cahawbensis* and 54 untagged *E. carinifera*. All growth analyses were conducted on target individuals. The range of densities used in the experiments (18–72/channel or 360–1440/m^2) falls well within the range of naturally occurring densities ($\approx$ 100–3000/m^2, Huryn et al. 1994), and thus provided a realistic estimate of density effects.

After 4 weeks, six target snails were collected from each channel and replaced with untagged snails of the same species and similar size to maintain treatment densities. Biomass and growth rates of the six target snails were estimated as described for experiment 1. Two rocks were also sampled from each channel to estimate chlorophyll *a* and periphyton AFDM, and replaced with nearby stream rocks to maintain the same amount of substrate in each channel. From each rock, a subsample (5 cm^2) was removed by brushing with a toothbrush. Subsamples from each channel were pooled and brought back to the laboratory on ice for subsequent analysis of chlorophyll *a* and AFDM. Algal slurries were homogenized and split into two portions. Periphyton AFDM was estimated from one portion as described for experiment 1. To estimate chlorophyll *a*, the other portion was filtered onto a glass fiber filter (pore size 0.7 μm) and frozen. Filters were then soaked in 10 ml of 90% alkaline acetone solution overnight, and extracted pigments were analyzed spectrophotometrically as in experiment 1.

After 7 weeks, enclosures were removed from the stream bottom. The remaining tagged snails were collected for growth rate measurements. Periphyton was removed with a toothbrush from a single rock from each channel. These rocks and algal slurries were brought back to the laboratory for subsequent analysis of chlorophyll *a*, AFDM, and rock surface area.

Experiment 3 – laboratory competition

A 7-week laboratory experiment, conducted from 24 October to 15 December 1998, was designed similarly to experiment 2, but was carried out in laboratory mesocosms. The same Plexiglas enclosures were placed in five paddlewheel-driven mesocosm streams (two enclosures or six channels per mesocosm). Stream water collected from Hendrick Mill Branch was distributed to each mesocosm stream ($\approx$ 400 L). Throughout the experiment, depth was maintained at 16 cm by replacing evaporative losses with deionized water. Previously dried sand and gravel, and freshly collected periphyton-covered rocks from Hendrick Mill Branch were placed into each of the 30 channels 1 day before snail introduction. Snails were collected and introduced into the appropriate channels as described in experiment 2.

Flow in experimental channels was maintained at 14.2 cm/s (SD = 4.4) throughout the experiment. Flow measurements taken before the experiment indicated low variability within and between enclosures in each mesocosm. Periphyton that accumulated on mesh screens was periodically removed with a brush to maintain similar flow regimes in all channels. Water temperature was maintained at 17.0°C. This temperature was slightly higher than the average daily stream temperature during the fall months (14.5°C), but was similar to stream temperatures during the summer field experiment.

After 4 weeks, target snails and rocks were sampled and replaced for analysis of snail growth rates, periphyton AFDM, and chlorophyll *a* as in experiment 2. After 7 weeks, one rock from each channel was sampled and analyzed for chlorophyll *a* and AFDM as in experiment 2. All remaining target snails were removed and measured. Treatment snails were also removed and counted to determine final densities.

Secondary production

We calculated snail production for each of the treatments in experiments 2 and 3 by multiplying individual growth rates by the geometric mean of their initial and final biomass (AFDM) (Benke 1984, Huryn et al. 1995). Secondary production for a particular channel was estimated by summing the production of individual target snails, multiplying that number by a factor to account for the target snails not removed (e.g., 18/6 at 4 weeks because only six target snails were removed), and multiplying by 2 or 4 depending on the total density of the channel. This assumes that growth rates of non-target snails were the same as target snails, and that production of non-target snails in high density mixed-species treatments (i.e., A + 3B and B + 3A) was identical to those in high density single-species treatments (i.e., 4B and 4A).

Statistical analyses

Experiment 1 – food limitation

A two-tailed t-test was conducted on mean growth rates for untagged juvenile snails (< 3 mm). Mean growth rates of larger snails (3–7 mm) were analyzed with three-way (species, size class, food level) analysis of variance (ANOVA). Post-hoc t-tests were performed on mean growth rates for each size class with respect to differences between food levels. For all t-tests, differences were considered significant at $P < 0.0125$ (Bonferroni-adjusted, Bland and Altman 1995). Neutral lipid data (as % of AFDM) were arcsine-transformed, and then analyzed by one-way ANOVA. A comparison of chlorophyll *a* between treatments among all five dates was made with a two-way ANOVA. Comparisons of chlorophyll *a* and periphyton AFDM between treatments, among dates, and before and after 1-week grazing periods were made with three-way ANOVAs.

Experiments 2 and 3 – field and laboratory competition

Experimental design and analyses on snail growth were done according to procedures developed by Winer (1971) and Underwood (1978) and subsequently used by others (e.g., Creese and Underwood 1982, Schmitt 1985, Kohler 1992; see Underwood 1997 for a complete description). This procedure essentially addresses two questions for each species: 1) does competition occur, and if so, 2) what are the relative strengths of intra- and interspecific competition for that species? The first question is answered by contrasting the control group with all of the other treatments (i.e., are growth rates affected by the presence of additional snails?). The sums of squares for the control versus other treatments were calculated as the difference between the sums of squares for all treatments and the sums of squares for all treatments except the control. The second question concerning the relative strengths of intra- and interspecific competition is addressed with two-way ANOVAs on all treatments excluding the control ("A" or "B" density, treatments 1 and 7, Table 1). This makes it possible to tease apart the effects of density and identity of the competitor (species) on snail growth rates. This type of analysis treats the data as two separate experiments. One looks at the influence of conspecifics and congeners on *E. cahawbensis*, while the other looks at the influence of conspecifics and congeners on *E. carinifera* (see Table 1). Significant ANOVAs were followed by Student-Newman-Keuls (SNK) multiple comparisons.

To further quantify the relative strengths of intra- versus interspecific competition, the growth rates of snails in the A + B, 2A, and 2B treatments were converted to proportions of maximum growth. This was accomplished by dividing the growth of each target snail by the mean growth of conspecifics in the low density treatment (A or B). These data were analyzed by a one-way ANOVA followed by SNK multiple comparisons.

The relationship between periphyton biomass (chlorophyll *a* and AFDM) and snail density was analyzed by one-way ANOVA followed by SNK multiple comparisons. Because *E. cahawbensis* and *E. carinifera* similarly influenced these variables (two-way ANOVAs on all data except channels without snails; factors: density and species; species term $P > 0.05$, density term $P < 0.05$), total snail density was used as the fixed factor irrespective of species.

Secondary production data were analyzed with one-way ANOVA followed by SNK multiple comparisons.

Results

Experiment 1 – food limitation

Treatment effectiveness

Periphyton AFDM was 8–15 times higher on high biomass rocks than on low biomass rocks (average high biomass: 1.3 mg/cm^2; average low biomass: 0.1 mg/cm^2). Similarly, chlorophyll *a* was 5–11 times higher on high biomass rocks than on low biomass rocks (average high biomass: 12.4 μg/cm^2; average low biomass: 1.9 μg/cm^2). Treatment differences for chlorophyll *a* and periphyton AFDM were significant throughout the experiment (ANOVA, $P < 0.001$), and no differences were detected among dates (ANOVA, $P > 0.05$).

Periphyton AFDM was not significantly influenced by snail grazing between weekly rock exchanges (ANOVA, $P > 0.05$). Chlorophyll *a*, however, was significantly reduced between weekly rock exchanges on one date (ANOVA, $P < 0.05$), but large differences were still maintained between treatments.

Snail growth

Daily growth rates of juvenile snails (aperture width < 3 mm) were significantly higher in microcosms with high biomass periphyton (average 2.5%/d $\pm$ 0.02 SE) than in microcosms with low biomass periphyton (average 1.7%/d $\pm$ 0.08 SE) (two-tailed t-test: $P < 0.001$). These growth rates were among the highest reported in this study.

Growth rates of larger snails (size classes III–VI, aperture width 3–7 mm) were significantly different among size classes, between species, and between periphyton biomass treatments (Fig. 1A, B, three-way ANOVA, $P < 0.001$ for all main effects). Growth rates of *E. cahawbensis* were significantly higher (2.4–5.4 ×) in high biomass microcosms for all size classes except VI (Fig. 1A, Bonferroni-adjusted t-tests, $P < 0.001$). Growth rates of *E. carinifera* were higher in high biomass microcosms, and although differences between treatments were not significant, they were nearly so for

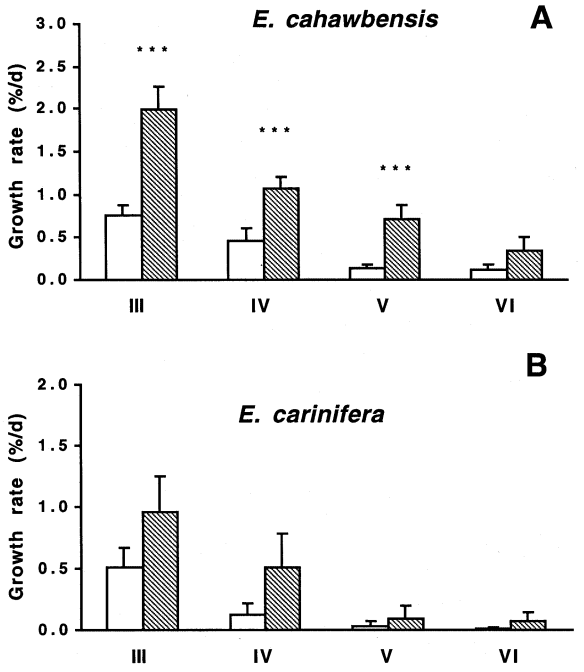

Fig. 1. Mean daily growth rate (%/d) + 1 SE ($n = 4$) of *Elimia cahawbensis* (A), and *Elimia carinifera* (B) in low biomass periphyton (white bars) and high biomass periphyton (cross hatched bars) microcosm streams. III–VI represent 1 mm aperture width size classes (i.e., 3–4 mm, 4–5 mm, etc.). *** $P < 0.001$.

size classes III and IV (Fig. 1B, Bonferroni-adjusted t-tests; III: $P = 0.03$, IV: $P = 0.04$). In general, as snail size increased, growth rates declined in both low and high biomass treatments (Fig. 1). Growth rates of both species approached zero around size classes V and VI (Fig. 1), potentially making differences among treatments difficult to detect.

Snail neutral lipid content

No significant differences were found in neutral lipid content among treatments for either species (ANOVA, $P > 0.05$). At the end of the experiment, *E. carinifera* had accumulated slightly more neutral lipid than *E. cahawbensis* for both treatments, but this difference in means was not significant (*E. cahawbensis*: low biomass – 2.2%, high biomass – 2.8%; *E. carinifera*: low biomass – 7.1%, high biomass – 4.6%).

Experiment 2 – field competition

Snail survivorship and growth

Mortality of tagged snails in the experimental channels was very low (4% of total). It was not possible to assess the mortality of treatment snails because they were not removed before sample preservation. However, most preserved snails showed no signs of decomposition, and therefore density treatments were assumed to have remained constant throughout the experiment. Several tiny snails (< 1 mm aperture width), which presumably passed through the enclosure mesh, were found in all channels at the end of the experiment (typically 20–40), but it is unlikely that they influenced our results.

Both *E. cahawbensis* and *E. carinifera* were negatively influenced by increased densities of conspecifics and congeners at 4 weeks, and differences became more pronounced at 7 weeks (Fig. 2A, B, Table 2). There was no difference between the influence of intra- or interspecific competitors for either species (Fig. 2A: 2A vs A + B, 4A vs A + 3B; Fig 2B: 2B vs B + A, 4B vs B + 3A; Table 2: non significant species term). After 7 weeks, each increase in density had a significant reduction on snail growth rates, regardless of species (Fig. 2).

Periphyton

After 4 weeks, periphyton AFDM and chlorophyll *a* were much lower in channels containing snails (1.3 mg/cm^2 AFDM; 3.9 μg/cm^2 chl *a*) than in channels without snails (3.6 mg/cm^2 AFDM; 11 μg/cm^2 chl *a*) (ANOVA, AFDM: $P < 0.01$, chl *a*: $P < 0.01$). There were no differences, however, among channels containing varying densities of snails (SNK comparisons). At the end of the experiment (7 weeks), no significant

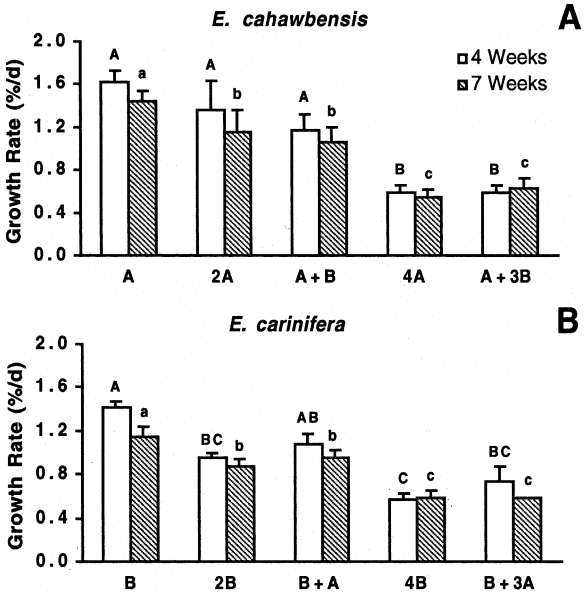

Fig. 2. Mean daily growth rates (%/d) + 1 SE ($n = 3$) of *Elimia cahawbensis* (A) and *Elimia carinifera* (B) at 4 and 7 weeks in the field competition experiment (see Table 2 for ANOVA). Treatments correspond to those described in Table 1. Significant differences were determined using SNK multiple comparisons; different letters indicate significant differences among treatments (capital letters – 4 weeks, lower-case letters – 7 weeks).

Table 2. Analysis of variance of snail growth rates for experiment 2 (field competition experiment) at 4 and 7 weeks.

	4 weeks			7 weeks		
Source of variation	df	MS × 10^4	*F*	df	MS × 10^4	*F*
Elimia cahawbensis						
All treatments	4	3.90	9.2**	4	4.28	9.2**
Control† vs other treatments	1	6.98	16.5**	1	8.57	18.3**
Species	1	0.17	0.4	1	0.00	0.0
Density	1	8.26	19.5**	1	8.30	17.8***
Species × Density	1	0.18	0.4	1	0.26	0.5
Residual	10	0.42		10	0.47	
Elimia carinifera						
All treatments	4	2.16	14.4***	4	1.77	12.8***
Control† vs other treatments	1	5.62	37.4***	1	3.74	27.0***
Species	1	0.43	2.9	1	0.50	0.5
Density	1	2.60	17.3**	1	3.23	23.4***
Species × Density	1	0.00	0.0	1	0.05	0.4
Residual	10	0.15		10	0.14	

† 18 snails alone, * $P<0.05$, ** $P<0.01$, *** $P<0.001$.

differences were found among any treatments (ANOVA, AFDM: $P>0.05$, chl *a*: $P>0.05$).

Experiment 3 – laboratory competition

Snail survivorship and growth

Snail mortality was also low in experiment 3 (4% of total). Overall, growth rates of snails in the laboratory were somewhat lower than field growth rates from experiment 2. Patterns of competition, however, were very similar. Growth rates of *E. cahawbensis* were influenced by densities of both conspecifics and congeners at 4 and 7 weeks (Fig. 3A, Table 3). The significant species term in the ANOVAs and SNK comparisons indicate that for *E. cahawbensis*, intraspecific competition was slightly stronger than interspecific competition. *Elimia carinifera* was also influenced by snail density at 4 and 7 weeks, but only in high density treatments (B vs 4B or B vs B + 3A, Fig 3B). The identity of the competitor, however, made no difference for *E. carinifera* (non-significant species term in ANOVA, Table 3, Fig. 3B).

Periphyton

At 4 and 7 weeks into the experiment, periphyton AFDM and chlorophyll *a* were significantly lower in channels containing snails (4 weeks: 0.5 mg/cm^2 AFDM, 0.8 μg/cm^2 chl *a*; 7 weeks: 0.5 mg/cm^2 AFDM, 0.5 μg/cm^2 chl *a*) than channels without snails (4 weeks: 1.8 mg/cm^2 AFDM, 7.2 μg/cm^2 chl *a*; 7 weeks: 1.7 mg/cm^2 AFDM, 5.4 μg/cm^2 chl *a*). Channels without snails accumulated ≈2 times the amount of AFDM and up to 12 times the amount of chl *a* than channels with snails; these differences were significant (ANOVA, AFDM: 4 weeks, $P<0.001$; 7 weeks, $P<0.01$, chl *a*: 4 weeks, $P<0.001$; 7 weeks, $P<0.01$). Except for a small difference in the amount of AFDM on rocks at 4 weeks, there were no significant differences in periphyton among snail densities (SNK comparisons).

Relative strengths of intra- versus interspecific competition

Ratios of snail growth rates at ambient densities (e.g., treatments "A + B", "2B" or "2A") to 'maximum potential' growth rates (treatments "A" or "B") revealed that there was generally no significant difference between the effects of intra- and interspecific competition on individual growth rates for both species (Table 4). One exception, however, was in the laboratory experi-

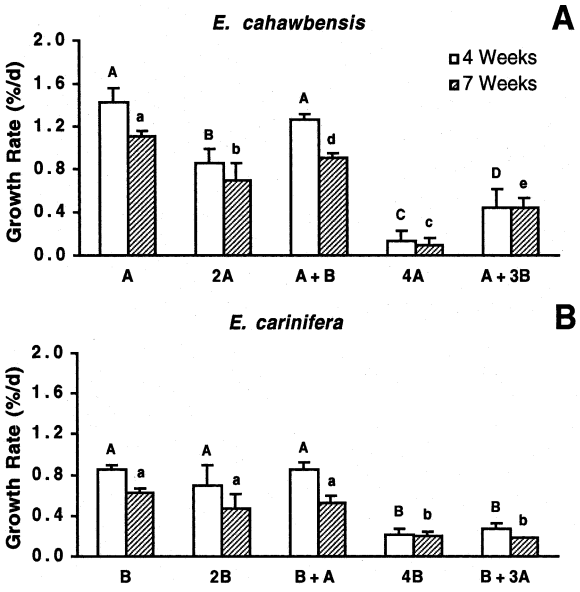

Fig. 3. Mean daily growth rates (%/d) + 1 SE ($n=3$) of *Elimia cahawbensis* (A) and *Elimia carinifera* (B) at 4 and 7 weeks in the laboratory competition experiment (see Table 3 for ANOVA). Treatments correspond to those described in Table 1. Significant differences were determined using SNK multiple comparisons; different letters indicate significant differences among treatments (capital letters – 4 weeks, lowercase letters – 7 weeks).

Table 3. Analysis of variance of snail growth rates for experiment 3 (laboratory competition experiment) at 4 and 7 weeks.

	4 weeks			7 weeks		
Source of variation	df	MS × 10^4	*F*	df	MS × 10^4	*F*
Elimia cahawbensis						
All treatments	4	7.23	19.9***	4	4.21	18.4***
Control† vs other treatments	1	11.1	30.7***	1	7.09	31.0***
Species	1	3.10	8.6*	1	2.06	9.0*
Density	1	14.6	40.2***	1	7.60	33.3***
Species × Density	1	0.07	0.2	1	0.11	0.4
Residual	10	0.36		10	0.23	
Elimia carinifera						
All treatments	4	2.20	7.4**	4	1.05	6.7**
Control† vs other treatments	1	1.78	6.0*	1	1.65	10.5**
Species	1	0.03	1.0	1	0.00	0.0
Density	1	6.68	22.4***	1	2.53	16.1**
Species × Density	1	0.04	0.2	1	0.03	0.2
Residual	10	0.03		10	0.16	

† 18 snails alone, * $P<0.05$, ** $P<0.01$, *** $P<0.001$.

ment at 4 weeks in which individual growth rates of *E. cahawbensis* were influenced more by its own density than by *E. carinifera*.

Secondary production

Secondary production was remarkably similar among all species and density treatments in the field competition experiment (Fig. 4). There were no significant differences ($P < 0.05$) among treatments for *E. cahawbensis* at 4 or 7 weeks, and only few differences among treatments for *E. carinifera*. The laboratory experiment also revealed relatively similar secondary production among treatments (Fig. 5). However, significant differences were revealed by SNK comparisons, particularly for the high intraspecific treatment of *E. cahawbensis* (treatment "4A", Fig. 5A), as suggested in the growth rate analysis (Fig. 3A).

Discussion

The results of both field and laboratory experiments provide evidence that *E. cahawbensis* and *E. carinifera* strongly compete both intra- and interspecifically based on reduced growth rates at increased densities. Few previous studies have demonstrated interspecific competition in streams, and to our knowledge, this is the first to show competition between coexisting lotic snail species. These experiments, as well as a separate food limitation experiment, suggest exploitation of a limited food resource as one potential mechanism of competition. The strengths of intra- and interspecific competition were nearly identical which potentially allows these two strong competitors to coexist.

Food limitation

Resource limitation is widely recognized as a necessary condition for demonstrating competition (Birch 1957), but is often overlooked experimentally and assumed to be the case. Results from our food limitation experiment support our hypothesis that growth rates of *E. cahawbensis* and *E. carinifera* are potentially limited by food quantity. Juveniles of both species, as well as large *E. cahawbensis* (sizes III–V), grew significantly faster when fed high biomass periphyton vs typical Hendrick Mill Branch periphyton. Differences between food level treatments were not significant for *E. carinifera*; however, growth rates of *E. carinifera* were lower than those of *E. cahawbensis* and the patterns of response were almost identical. This suggests that the length of the experiment may not have been long enough for significant differences among treatments to be detected. It is likely that species composition of the periphytic assemblage was altered by enrichment, causing a change in food quality as well as food quantity. Regardless of whether increased snail growth rates were caused by an increase in food quantity or quality, our experiment still demonstrates food limitation. These data agree with those of Hill (1992) and Hill et al. (1992b), in which growth of *E. clavaeformis* was consistently higher in food augmented microcosms than in natural food level microcosms.

No differences were found in neutral lipid storage among snails from either treatment. Others have found this to be a valuable measure of snail "health" or reproductive potential (e.g., Hill 1992, Hill et al. 1992b, 1995). The lack of any discernible pattern in this study suggests that most energy was directed towards growth, and that snails did not differentially store neutral lipids. Snails may have also stored excess carbon as glycogen which was not measured in this study.

Table 4. The relative strengths of intra- and interspecific competition. Values represent the growth obtained by individuals in treatments 2A, 2B, or A + B divided by mean growth rates of conspecifics in control treatments (A or B). * indicates a significant difference between proportions (Student-Newman-Keuls comparison, $P < 0.05$).

		Proportion of maximum growth		
	Species	Intraspecific		Interspecific
Field (4 weeks)	*E. cahawbensis*	0.81	ns	0.72
		ns		ns
	E. carinifera	0.69	ns	0.87
Field (7 weeks)	*E. cahawbensis*	0.78	ns	0.71
		ns		ns
	E. carinifera	0.70	ns	0.81
Laboratory (4 weeks)	*E. cahawbensis*	0.57	*	0.90
		ns		ns
	E. carinifera	0.73	ns	0.98
Laboratory (7 weeks)	*E. cahawbensis*	0.65	ns	0.80
		ns		ns
	E. carinifera	0.77	ns	0.88

Intra- versus interspecific competition

The experimental design used in this study allowed the simultaneous assessment of the existence and relative strengths of both intra- and interspecific competition. Their relative strengths are critical in assessing whether interspecific interactions are important in determining the distribution and abundance of populations (e.g., Connell 1983, Underwood 1986). For example, if intraspecific competition is stronger than interspecific competition, populations may be regulated by conspecifics to levels below that necessary for the effects of interspecific interactions to be realized (e.g., Underwood 1978, Creese and Underwood 1982). Nonetheless, in Connell's review (1983) only 14 out of 72 studies of competition examined both intra- and interspecific competition.

Both *E. cahawbensis* and *E. carinifera* were affected by the density of conspecifics and congeners. In every case, the high density treatments (4A, 4B, A + 3B, B + 3A) significantly reduced growth rates below those of the average field density (A + B), and well below the low density treatments (A or B). Growth rates of snails in the low density treatments (representing a "release" from the average condition because the congener was removed) were generally higher than the average natural condition. This range of responses is likely to occur throughout the stream because treatment densities were well within the range of the naturally occurring densities. In fact, even the highest density treatment used in this study is often exceeded in areas of Hendrick Mill Branch (Huryn et al. 1994). A comparison of ambient growth rates in field enclosures (A + B and B + A, range of 1 SD: 0.83–1.44%/d) and laboratory enclosures (A + B and B + A, range of 1 SD: 0.38–1.25%/d) with growth rates of free-ranging tagged snails of similar initial size (0.42–1.98%/d, Huryn et al. 1994) supports the notion that snails were not significantly influenced by field enclosures. Thus, our results likely represent growth responses in natural populations at Hendrick Mill Branch.

The relative strengths of intra- and interspecific competition among *E. cahawbensis* and *E. carinifera* were almost identical in the field and laboratory competition experiments (Table 4). The identity of the competitor generally had no bearing on the ultimate growth response of snails, suggesting that neither *E. cahawbensis* nor *E. carinifera* can be considered a superior competitor at Hendrick Mill Branch.

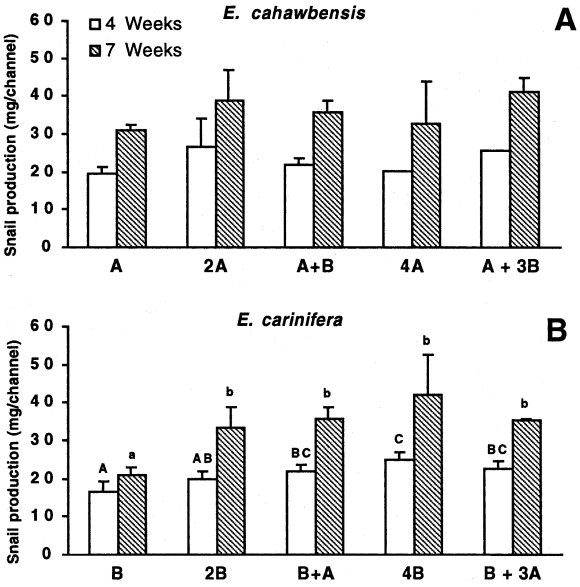

Fig. 4. Mean secondary production (mg/channel) + 1 SD ($n = 3$) of *Elimia cahawbensis* (A) and *Elimia carinifera* (B) at 4 and 7 weeks in the field competition experiment. Treatments correspond to those described in Table 2. Significant differences were determined using SNK multiple comparisons; different letters indicate significant differences among treatments (capital letters – 4 weeks, lower-case letters – 7 weeks). Absence of letters (as in *E. cahawbensis*) indicates that there were no statistical differences among treatments.

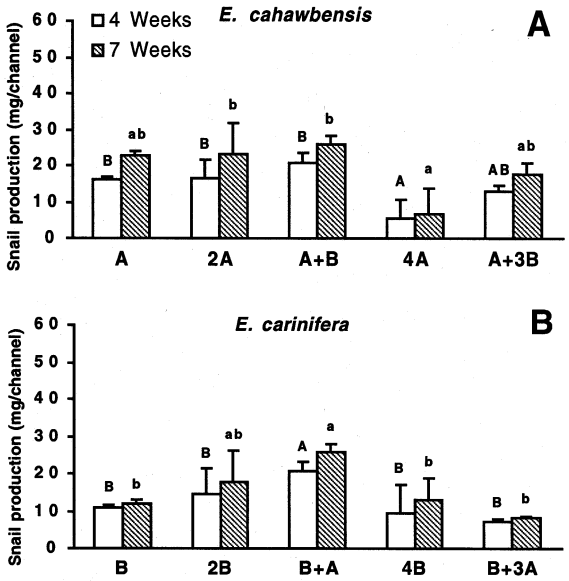

Fig. 5. Mean secondary production (mg/channel) + 1 SD ($n = 3$) of *Elimia cahawbensis* (A) and *Elimia carinifera* (B) at 4 and 7 weeks in the laboratory competition experiment. Treatments correspond to those described in Table 2. Significant differences were determined using SNK multiple comparisons; different letters indicate significant differences among treatments (capital letters – 4 weeks, lower-case letters – 7 weeks).

Throughout the competition experiments, snails usually depressed periphyton biomass. The largest differences found were between channels with snails and those without snails, with very similar levels of periphyton AFDM and chlorophyll *a* among density treatments. This suggests that low snail densities were capable of reducing periphyton biomass to a similar level as high snail densities. At this low periphyton biomass level, snail growth was likely limited by biomass-specific periphyton production.

Estimates of total snail production for each treatment enabled us to assess the relative amount of grazing pressure on algae, regardless of density, and these results were consistent with no differences in periphyton biomass across snail densities. For example, 18 snails in treatment "A" or "B" accumulated the same amount of biomass as 72 snails in the "4A" or "4B" treatments. The density-dependent response in growth rate resulted in similar snail production among treatments, and indicated that snails compensated for the absence of other individuals by increasing their consumption and growth. Thus, the overall impact of snails (i.e., grazing pressure as reflected by total secondary production, and amount of energy contributed to the system by snails) remained relatively constant regardless of density or species present. This result demonstrates the value of estimating secondary production versus static measures such as abundance or biomass. To some extent, *E. cahawbensis* and *E. carinifera* may be considered functionally redundant species in this system (sensu Walker 1992, 1995, Lawton and Brown 1993).

Laboratory versus field experiments

Laboratory and mesocosm experiments are often criticized as not accurately representing dynamics of natural systems (Carpenter 1996, Schindler 1998). Conducting similar experiments in the laboratory and the field is rarely done, yet it is crucial to understanding how accurately results from the laboratory can be extrapolated to natural field conditions (e.g., Kohler and Wiley 1997). Our results from the field and laboratory were almost identical and suggest that realistic results can be obtained in the laboratory if attempts are made to achieve reasonably natural conditions.

One obvious difference between our field and laboratory experiments was the ability of small invertebrates to colonize field enclosures. However, these invertebrates did not appear to influence the interactions between snail species, and, conversely, the different snail treatments had no effect on the small invertebrates (analysis not shown). It is important to note, however, that *Glossosoma nigrior* (Trichoptera: Glossosomatidae), a potential competitor of *Elimia*, exists at Hendrick Mill Branch, and was prevented from colonizing enclosures. Competition between pleurocerid snails and similar taxa (e.g., *Neophylax etnieri*) has been implicated in other studies (e.g., Hill 1992), and warrants further examination.

Competition and coexistence

Studies of competition are inextricably linked to the issue of coexistence. How do *E. cahawbensis* and *E. carinifera* continue to coexist despite strong interspecific competition for the same limited resource? Assuming similar carrying capacities, classic Lotka-Volterra competition theory predicts that stable coexistence should occur only if, for both species, the effects of intraspecific competition are stronger than the effects of interspecific competition. Although our analysis of competition revealed no statistical difference between intra- and interspecific competition (Table 4), intraspecific competition was slightly stronger than interspecific competition (6 out of 8 comparisons, Table 4). Therefore, coexistence may indeed be mediated by slightly stronger competition among conspecifics than congeners. Alternatively, if one species is, in fact, a superior competitor, the competitive advantage may be so slight that exclusion may take an extremely long time, or may not occur at all (Huston 1979). In order for competitive ex-

clusion to take place, asymmetric interactions must persist for a relatively long period of time (i.e., much longer than the generation time of the competitor). It has been shown theoretically, however, that sufficiently similar competitors may coexist indefinitely (Ågren and Fagerström 1984).

Coexistence of competitors also may be mediated by spatial segregation (i.e., non-overlapping distributions). In order to examine this possibility, we analyzed data from a previous study of the invertebrate fauna at Hendrick Mill Branch (40 samples collected on four dates in 1990, Huryn et al. 1994). Correlation analysis did not detect any positive or negative spatial relationship between *E. cahawbensis* and *E. carinifera* on cobble (density: $r = 0.1$, $P = 0.67$; biomass: $r = 0.08$, $P = 0.75$) or bedrock (density: $r = 0.16$, $P = 0.51$; biomass: $r = 0.08$, $P = 0.73$) habitats. Thus, it is unlikely that spatial segregation mediates the coexistence of *E. cahawbensis* and *E. carinifera*.

Other factors such as disturbance and predation may also prevent competitive exclusion. For example, rare floods may occur during the lifespan of individual snails (3+ years), which can act to reduce population densities and "reset" the system. Nonetheless, we have shown that competition can be strong during base flow conditions, which dominate the hydrology at Hendrick Mill Branch for most of the year (G. M. Ward, Univ. of Alabama, unpubl.). Predators may also influence competitive interactions of their prey directly through prey consumption, or indirectly by altering prey feeding behavior or life history (e.g., Paine 1966, Kohler and McPeek 1989, Crowl and Covich 1990, Lodge et al. 1994, Kuhara et al. 1999, Peckarsky et al. 2001). However, at Hendrick Mill Branch, in-stream predators of snails (i.e., crayfish) are relatively inconspicuous, and consistently high snail densities throughout the year suggest that predators are unable to control snail populations.

In conclusion, strong intra- and interspecific competition occurs among *E. cahawbensis* and *E. carinifera*, which together comprise $\approx 75\%$ of the entire invertebrate biomass at Hendrick Mill Branch. Our study suggests that competition between closely related species may be more important in some streams than previously realized. Future studies should attempt to take into account seasonal differences in the strength of competition, as well as the relative importance of competition versus other controlling factors such as disturbance, predation, and parasitism.

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