

Microhabitat Associations of Three Sympatric Species of Naucoridae (Insecta: Hemiptera)

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ABSTRACT Samples (0.5 m²) were taken from the South Llano River, Kimble County, Tex., to determine inter- and intraspecific differences in microhabitat association for the three most abundant species of Naucoridae. Various aspects of substratum condition, current speed, temperature, depth, as well as complex key hydraulic features, were used to characterize the microhabitat for each sample. Eight species of naucorids occur in the river; however, only *Ambrysus circumcinctus* Montandon, *Cryphocricos hungerfordi* Usinger, and *Limnocoris lutzi* La Rivers occurred with sufficient frequency in our samples to allow statistical analysis. None of the three species exhibited age-related differences in microhabitat association based on multivariate analysis of variance (MANOVA), and none of the examined abiotic variables yielded significant differences between nymphs and adults when analyzed from a univariate perspective except Froude number for *L. lutzi*. Both *A. circumcinctus* and *C. hungerfordi* exhibited highly significant differences (MANOVA) in abiotic characteristics between quadrats of occurrence and nonoccurrence. Results of individual analyses of variance (ANOVAs) indicated that 9 of the 10 abiotic variables were significant for *A. circumcinctus* and 8 for *C. hungerfordi*. In contrast, quadrats where *L. lutzi* occurred could not be distinguished from those in which it was absent based on MANOVA, and only two abiotic variables exhibited significance in the ANOVAs. Associations between age groups (nymphs and adults) within a species and between all possible species pairs (combined age groups) also were evaluated with contingency χ^2 tests using presence-absence data and with Pearson's product-moment correlations using density data. In all cases, significant negative associations were not detected, suggesting that neither age groups nor species exhibit microhabitat segregation. Discriminant function analysis for each species supported MANOVA results on presence-absence data. Separate multiple step-up regressions were used to evaluate which abiotic factors were most related to the density for each species. Significant variables included mean current speed, which accounted for 23.8% of the variation in density of *A. circumcinctus*; rock standard error of the mean, which accounted for 43.1% of the variation in density of *C. hungerfordi*; Froude number and depth range, which together accounted for 39.0% of the variation in density of *L. lutzi*. In summary, each common naucorid clearly shows microhabitat associations, but the evidence of interspecific differences is indirect.

KEY WORDS Insecta, microhabitat association, lotic ecology, Naucoridae

ALTHOUGH MUCH OF CONTEMPORARY ECOLOGY focuses on the factors affecting the composition and structure of communities (see Strong et al. 1984, Kikkawa & Anderson 1986), little empirical work has examined the interactions between abiotic and biotic factors in structuring stream ecosystems. The importance of interspecific interactions often is minimized because regular or episodic changes in hydrological features that promote flooding or desiccation are thought to regulate the density of aquatic organisms and mitigate the effects of competition (see Power et al. 1988, Resh et al. 1988).

The microdistribution of lotic insects often correlates with substratum size (Cummins 1964, Cummins & Lauff 1969) and flow velocity (Stout 1981). Microspatial separation of syntopic benthic invertebrates on the basis of substratum particle size also

has been demonstrated (Ulfstrand 1967). Minshall (1984) concluded that the substratum was the primary determinant of the abundance and distribution of aquatic insects in general, and Cummins (1964) stated that substratum particle size was the "common denominator" in benthic stream ecology. In contrast, Stutzner et al. (1988) considered substratum characteristics to be less important than mean current velocity and other complex hydraulic characteristics in accounting for the distribution of lotic macroinvertebrates.

Members of the family Naucoridae (Insecta: Hemiptera) are one of the most abundant arthropod predators in streams of the southwestern United States. Naucorids are keystone consumers, occupy a central position in trophic webs, and greatly influence other biota (Stout 1981). Nonetheless, little detail is known of their biology (Gonsoulin 1973). Nymphs and adults are continual subsurface inhabitants, and respiration is typically by means of a compressible air bubble, although evidence of

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plastral respiration exists for the genus *Cryphocricos* (Parsons & Hewson 1974). Of the 21 U.S. species, the four species of *Pelocoris* are found in lentic situations and several species of *Ambrysus* occur in isolated desert hot springs (Polhemus & Polhemus 1988). Members of the other genera (i.e., *Cryphocricos*, *Limnocoris*, *Usingerina*) as well as most species of *Ambrysus* primarily are lotic. Of the lotic species, some inhabit vegetated areas, whereas others are associated with rocks and other substratum materials.

Although the natural history of other aquatic insect taxa, such as caddisflies (Cummins 1964), stoneflies, mayflies, and riffle beetles (Cummins & Lauff 1969), is well known, microhabitat associations of temperate North American naucorids are undocumented and poorly understood at best. Much of the literature dealing with New World naucorids has concerned species descriptions, taxonomic revisions, and faunal lists or catalogs (e.g., Polhemus & Polhemus 1988). The modest body of literature considering naucorid biology has been reviewed by Polhemus (1979). Only a few papers (Stout 1978, 1981; Sites & Nichols 1990) have dealt with ecological considerations of New World naucorids. In each paper by Stout, the data relate to tropical species in Costa Rica: Migratory dynamics were shown to affect the spatial distribution of *Limnocoris insularis* Champion (Stout 1978), whereas abiotic parameters affected the distribution of *L. insularis* and *Cryphocricos latus* Usinger (Stout 1981). Stutzner et al. (1988) discussed the importance of several abiotic characteristics that affect the distribution of *Aphelocheirus aestivalis* (F.) in European streams. Although it is common for one or two species to be present in a temperate stream (Usinger 1974), speciose assemblages are uncommon to the point that La Rivers (1951) expressed surprise that four species coexisted in one body of water. Preliminary research revealed the coexistence of eight species, representing four genera, in the South Llano River (Texas). Presented here are data on microhabitat associations of the three most common species of naucorids in the South Llano River of central Texas.

Materials and Methods

The South Llano River, located on the Edwards Plateau in central Texas, originates in Edwards County and meanders 175 km to its confluence with the North Llano River in Kimble County. The South Llano River is spring-fed, and its watershed receives large amounts of precipitation from convective thunderstorms in the spring, and from the movement of moisture-laden air along the tropical Gulf storm tract (Baker 1977). Extensive siltation occurs during periods of flooding in part because the surrounding habitats have been modified as rangeland. The South Llano River is typical of streams that originate on the Edwards Plateau. Regional bedrock is of the Edwards Group of Cre-

taceous Limestones (Sorenson & Allen 1979); stream channels are bedrock and alluvium, whereas the associated floodplain and terraces are composed of alluvium (B. L. Allen, Texas Tech University, personal communication). Emergent vegetation is common along the margins of the South Llano River, and the flora is dominated by water willow, *Justicia americana* (L.).

Sampling Regime. Data were obtained on 14 and 15 May 1988 from the South Llano River on the Texas Tech University Center campus, Junction, Kimble County. Fifty randomly selected sites were chosen to represent the range of current speed, depth, and substratum particle size present in the South Llano River. Based on previous research (Sites 1990, Sites & Nichols 1990), sampling was stratified by placing ≈ 10 quadrats in each of the five major microhabitats: (1) fast current and large rocks, (2) fast current and vegetation, (3) intermediate current and midsized rocks, (4) slow current and small rocks, and (5) slow current and vegetation. Before sampling, a 0.5-m² brass frame (0.32 by 1.36 m) was placed on the river substratum, and abiotic characters were quantified by taking three measurements each of current speed, using a hand-held current meter (model 2030R; General Oceanics, Miami), depth, and temperature. The length and width of 10 rocks that occurred under each of 10 marks on the brass frame were measured to characterize the substratum. Rock size was calculated from length and width measurements as the surface area of an oval. Because substratum roughness and slope were not measured, the only complex hydraulic key characteristics that could be calculated were Reynolds number and Froude number. Reynolds number is given by the ratio of the product of mean current speed and mean depth to kinematic water viscosity, whereas Froude number was measured as the ratio of mean current speed to the square root of the product of mean current depth and the acceleration due to gravity (Stutzner et al. 1988).

After abiotic parameters were measured, the substratum was kick-sampled within the brass frame. An aquatic D-net (width, 0.32 m) was held ≈ 25 cm downstream from the sampled substratum. Net contents were emptied into a white plastic pan, and all macroinvertebrates removed and placed in 85% ethyl alcohol. Naucorids were identified, separated, and quantified in the laboratory.

Statistical Analysis. The data were analyzed from both univariate and multivariate perspectives using the SPSS[®] statistical package (SPSS 1986). Chi-square contingency tests (Sokal & Rohlf 1981) were used to evaluate if nymphs and adults of each species were distributed randomly with respect to each other based on frequencies of occurrence. Similarly, Pearson product-moment correlation analyses (Sokal & Rohlf 1981) were used to evaluate if the densities of nymphs and adults of each species were interrelated for sites in which at least one age group was present. Quadrats with high densities (those in

Table 1. Taxa and body measurements^a (mm) of Naucoridae occurring in the South Llano River, Kimble County, Texas

Taxon	Length	Width	Depth
<i>Ambrysus circumcinctus</i> Montandon	7.75 ± 0.06	4.24 ± 0.03	1.12 ± 0.04
<i>A. lunatus</i> Usinger	9.99 ± 0.18	6.68 ± 0.12	1.58 ± 0.08
<i>A. pudicus barberi</i> Usinger	8.16 ± 0.11	5.34 ± 0.07	1.44 ± 0.03
<i>A. pulchellus</i> Montandon	8.72 ± 0.12	5.20 ± 0.09	1.68 ± 0.04
<i>A. puncticolis</i> Stål	14.20 ± 0.21	8.22 ± 0.27	2.00 ± 0.04
<i>Cryphocricos hungerfordi</i> Usinger	8.53 ± 0.14	4.14 ± 0.06	0.98 ± 0.03
<i>Limnocoris lutzi</i> La Rivers	6.52 ± 0.05	4.58 ± 0.02	1.50 ± 0.03
<i>Pelocoris f. femoratus</i> (Palisot de Beauvois)	9.86 ± 0.22	5.72 ± 0.11	2.36 ± 0.06

^a Measurements are $\bar{y} \pm SE$ of total body length (tip of typlus to tip of abdomen), width (widest point), and depth (scutellum to metapleural base) of five male and five female adults.

the top quartile for a particular group) were considered to be preferred sites. Multivariate analysis of variance (MANOVA) was used to evaluate if particular abiotic characteristics (mean, minimum, maximum, range, and standard error of rock surface area; mean and range of current speed; mean temperature; mean and range of depth; Reynolds number; and Froude number) of the preferred sites of adults differed from those of nymphs for each common naucorid species separately (*Ambrysus circumcinctus* Montandon, *Cryphocricos hungerfordi* Usinger, and *Limnocoris lutzi* La Rivers). Discriminant function analysis (DFA) was subsequently used to identify the linear combination of the abiotic variables that best distinguished between the age groups. The position of preferred sites for each age group along the first axis indicates the degree of overlap between groups in terms of microhabitat association; subsequent classification phases provide an evaluation of the efficacy of the DFA in properly associating particular sites as more suitable for nymphs or adults. Separate one-way analyses of variance (ANOVAs) were used to evaluate the potential importance of a particular abiotic variable in distinguishing between the preferred sites of each age group. Because microhabitat associations of adults and nymphs did not differ significantly for each species based on the previous analyses, densities of the age groups within quadrats were combined in all subsequent analyses.

Interspecific comparisons of the frequency of occurrence of all possible pairs of the three dominant species were estimated by coefficients of association (Cole 1949, Hurlbert 1969) and evaluated by χ^2 contingency tests. Similarly, density relationships between each pair of species for sites in which at least one of the two taxa is present were estimated by Pearson product-moment correlations. Microhabitat association for each species was evaluated based on presence-absence data, as well as on density data. In the first approach, we compared abiotic characteristics of quadrats in which a species was absent with those in which it was present using MANOVA, followed by ANOVAs for each dependent variable. Again, DFA was used to characterize differences between quadrats in which a species was present from those in which it was absent. The results of the classification phase of the

DFA were used to assess the utility of the suite of microhabitat variables in distinguishing between sites with and without a particular species of naucorid. In the second approach, multiple step-up regression was used in which total density was the dependent variable and the suite of abiotic characteristics constituted the independent variables. A separate analysis was conducted for each species, and those quadrats in which a species did not occur were excluded from the analysis for that species. Finally, MANOVA and DFA were used to evaluate if any of the species differed with respect to the microhabitat characteristics of their preferred sites (those in the top quartile of densities for age groups combined).

Results

Eight naucorid species coexist in the South Llano River (Table 1); voucher specimens are deposited in the Texas Tech University Entomological Collection. Of these, only *A. circumcinctus*, *C. hungerfordi*, and *L. lutzi* occurred with sufficient frequency or density (Table 2) in our samples to allow statistical analysis. A variety of criteria (e.g., those of Pillai, Hotelling, Wilks) exist for calculating *F* statistics for MANOVA (Morrison 1976). Consideration of sample size, underlying assumptions, and power should be involved in selection of the appropriate statistics; however, all three criteria produced identical *F* and *P* values (to four significant digits) for intraspecific comparisons, and in the case of interspecific comparisons produced *P* values of only slightly different magnitude but which were in accord with respect to statistical conclusion. Thus, statistics herein are those based upon Wilks Lambda, which gives rise to exact *P* values.

Intraspecific Differences in Microhabitat Association. None of the three common naucorid species exhibited age-related differences in microhabitat association based on MANOVA (*A. circumcinctus*: $F = 0.203$; $df = 12, 12$; $P = 0.995$. *C. hungerfordi*: $F = 0.689$; $df = 12, 12$; $P = 0.737$. *L. lutzi*: $F = 0.419$; $df = 12, 12$; $P = 0.927$). Moreover, none of the 12 abiotic variables yielded significant differences between nymphs and adults in the ANOVAs for any of the three species with the exception of Froude number for *L. lutzi* ($P = 0.048$).

Table 2. Frequency and density of nymphs and adults of three naucorid species in 50 quadrats (0.5 m²) in the South Llano River

Estimate	<i>Ambrysus circumcinctus</i>			<i>Cryphocricos hungerfordi</i>			<i>Limnocoris lutzi</i>		
	Nymphs	Adults	Total	Nymphs	Adults	Total	Nymphs	Adults	Total
Frequency ^a	30	29	34	21	21	30	12	34	35
Mean density	2.4	2.9	5.3	0.8	1.6	2.4	0.4	5.4	5.8
Standard error	0.43	0.56	0.94	0.17	0.44	0.48	0.14	1.34	1.39

^a Number of quadrats within which each group occurs.

The degree to which the microhabitat associations of adults and immatures overlap is illustrated graphically for each species by the frequency distributions of the preferred sites of adults and immatures along the canonical axis from the DFA (Fig. 1). Considerable overlap between nymphs and adults is indicated for each of the three species of naucorids. Only 58.3 and 61.5% of the preferred sites of nymphs and adults, respectively, were correctly ascertained by DFA for *A. circumcinctus* (overall classification error rate of 40.0%). For *C. hungerfordi* and *L. lutzi*, the classification was only slightly improved compared with that for *A. circumcinctus*. More specifically, 76.9% (nymphs) and 69.2% (adults) of the preferred sites for *C. hungerfordi* and 66.7% (nymphs) and 76.9% (adults) of the preferred sites for *L. lutzi* were correctly identified by DFA, resulting in an overall classification error rate of 27.0% for *C. hungerfordi* and 28.0% for *L. lutzi*. In combination, MANOVA and DFA unequivocally indicate the absence of significant mean microhabitat differences between nymphs and adults, with many of the preferred sites of nymphs indistinguishable from those of adults.

The parametric results based on microhabitat characteristics are further supported by the non-parametric and correlation analyses (Table 3). A significant contingency χ^2 analysis coupled with a negative association index (c) is evidence for spatial separation of nymphs and adults. The significant χ^2 analyses and positive association indices (c) between nymphs and adults for *A. circumcinctus* and *L. lutzi* indicate that for each species, the age groups tend to occur or avoid particular sites jointly. The nonsignificant χ^2 test for *C. hungerfordi* indicates that nymphs and adults are distributed at random with respect to each other (nonetheless, this comparison approaches significance [$0.10 > P > 0.05$] and has a positive association index, as do the other two species). Age-specific segregation by microhabitat is not evidenced by any of the three naucorids; in fact, nymphs and adults tend to occur in or be absent from the same sites. The χ^2 analyses would not detect spatial separation in situations where both nymphs and adults frequently cooccur but with inversely related densities. More particularly, significant and negative correlation based on density is evidence of age-specific segregation of nymphs and adults within sites where either occurs. This does not occur for any of the three

naucorid species. In all cases, the correlation coefficient is positive, and for *A. circumcinctus*, the relationship is significant. Densities are either uncorrelated (*L. lutzi* and *C. hungerfordi*) or indicate nymphs and adults occur at highest densities within the same quadrats (*A. circumcinctus*).

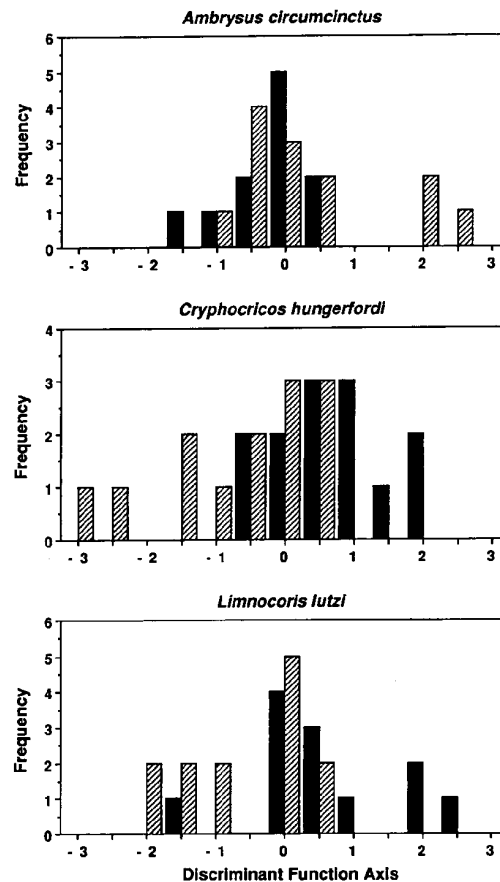


Fig. 1. Microhabitat separation between nymphs and adults for each of the three common species of Naucoridae as revealed by discriminant function analysis (DFA). In each case, the DFA as well as the corresponding MANOVA are nonsignificant, indicating significant overlap in the microhabitat characteristics of age groups within species. ■, nymphs; ▨, adults.

Table 3. Age-specific (nymph versus adult) and interspecific comparisons of frequency of occurrence (contingency χ^2 tests) and density (Pearson's product moment correlation coefficient) of naucorids

	Interspecific comparisons					
	Age-specific comparisons			Interspecific comparisons		
	A. <i>C. circumcinctus</i>	C. <i>hungerfordi</i>	L. <i>lutzi</i>	A. <i>C. circumcinctus</i> L. <i>lutzi</i>	A. <i>C. circumcinctus</i> C. <i>hungerfordi</i>	L. <i>lutzi</i> C. <i>hungerfordi</i>
Frequency						
χ^2	0.655	0.261	0.740	0.41	0.69	0.44
P	19.76	3.41	4.06	6.32	16.68	6.35
P	***	*	NS	*	***	*
df	1	1	1	1	1	1
Density ^b						
r	0.704	0.281	0.217	0.015	0.172	0.138
P	**	NS	NS	NS	NS	NS
df	32	28	33	39	35	38

Asterisks denote level of significance. * $0.05 \geq P > 0.01$; ** $0.01 \geq P > 0.001$; *** $0.001 \geq P$; NS not significant.

^a Coefficient of association.

^b Correlations do not consider quadrats in which both groups are absent.

Microhabitat Association Based On Presence-Absence Data. Highly significant differences in abiotic characteristics between quadrats of occurrence and absence were exhibited for *A. circumcinctus* and *C. hungerfordi* (Table 4). From the univariate perspective, only three abiotic characteristics (temperature, depth mean, and depth range) were nonsignificant for *A. circumcinctus* and similarly, four abiotic characteristics (current range, temperature, depth range, and Froude number) were nonsignificant for *C. hungerfordi* (Table 4). In contrast, quadrats where *L. lutzi* occurred could not be distinguished from those in which it was absent, based on MANOVA (Table 4), with only two abiotic variables exhibiting significance in the ANOVAs (rock standard error and current mean). The DFA for *A. circumcinctus* (Fig. 2) was significant ($\chi^2 = 39.12$, $df = 12$, $P \ll 0.001$) with current mean ($r = 0.690$) exhibiting the highest correlation with the canonical axis separating the groups. Corresponding classification results correctly distinguished between sites of presence and absence for 88.0% of the cases, with the majority of misclassifications (five of six) occurring when microhabitat characteristics are predicted to be suitable for habitation but the site was uncolonized. A significant DFA ($\chi^2 = 33.11$, $df = 12$, $P < 0.001$) for *C. hungerfordi* (Fig. 2) revealed that Reynolds number ($r = 0.584$) and rock standard error ($r = 0.571$) were most highly correlated with the canonical axis that best distinguished between quadrats of occurrence and non-occurrence. Again, the DFA classification phase correctly distinguished between sites of occurrence and absence for 86.0% of the cases, with more than half of the misclassifications (four of seven) resulting from uncolonized sites exhibiting suitable microhabitat char-

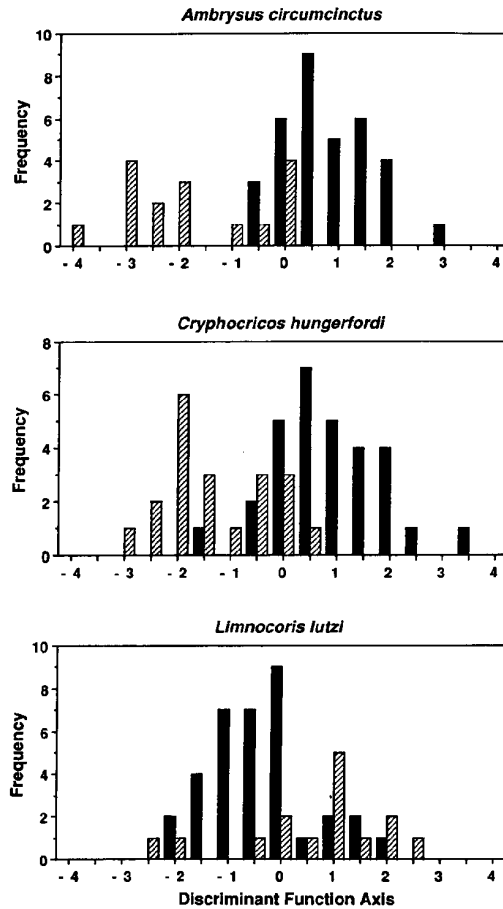


Fig. 2. Microhabitat association as indicated by discriminant function analysis (DFA) separating sites of occurrence from those of absence. *A. circumcinctus* and *C. hungerfordi* show little overlap between sites of occurrence and nonoccurrence and exhibited significant group differences in the DFA, whereas *L. lutzi* did not exhibit a significant DFA and there is correspondingly appreciable overlap between sites of occurrence and non-occurrence. ■, presence; ▨, absence.

acteristics. As expected, given the MANOVA results, the DFA for *L. lutzi* (Fig. 2) was not significant ($\chi^2 = 15.04$, $df = 12$, $P = 0.239$); any abiotic variables correlated with the canonical axis represent spurious information. Nonetheless, the significant interspecific contingency χ^2 analyses with positive association indices (Table 3) for each of the three pairs of species indicate that, in general, some sites are favorable for naucorids whereas, others are unfavorable.

Microhabitat Association Based on Density. Unlike the previous analyses herein, only sites of occurrence were used and the question of microhabitat association becomes: Can we discern a suite of abiotic variables that affect population density?

Table 4. Microhabitat association by each species (MANOVA) and importance of each abiotic characteristic in defining microhabitat associations (ANOVA)

Statistical test variable	F statistic		
	<i>A. circumcinctus</i>	<i>C. hungerfordi</i>	<i>L. lutzi</i>
MANOVA ^a	4.74***	3.70***	1.33
ANOVA ^b			
Rock mean	12.62***	10.15**	0.97
Rock SE	8.67**	18.75***	4.44*
Rock range	4.82*	6.21*	0.58
Rock minimum	12.93**	10.81**	0.41
Rock maximum	5.92*	7.45**	0.84
Current mean	35.17***	12.59***	8.05**
Current range	5.05*	0.13	3.99
Temperature	1.11	0.64	0.00
Depth mean	4.02	14.00***	0.94
Depth range	1.68	2.59	1.60
Reynolds number	11.88***	19.68***	3.69
Froude number	11.58***	0.58	2.56

Asterisks denote level of significance: * $0.05 \geq P > 0.01$; ** $0.01 \geq P > 0.001$; *** $0.001 \geq P$.

^a $df = 12, 37$.

^b $df = 1, 48$.

The multiple regression analysis for *A. circumcinctus* was highly significant ($P = 0.003$); only mean current speed was included in the final equation ($y = -5.778 + 0.0543x$), and it accounted for 23.8% of the variation in density among quadrats. The analysis for *C. hungerfordi* produced a single variable equation ($P \ll 0.001$) in which rock standard error of the mean accounted for 43.1% of the variation in density ($y = 1.289 + 4.608x$). The analysis for *L. lutzi* produced a significant two variable equation ($P \ll 0.001$) in which Froude number (x_1) and depth range (x_2) together accounted for 39.0% of the variation in density among quadrats ($y = 0.056 + 8.779x_1 - 0.859x_2$).

Interspecific Comparison of Microhabitat Association. The MANOVA on preferred sites (where densities exceeded four individuals) failed to detect differences among species in terms of microhabitat selection ($F = 1.242$; $df = 24, 40$; $P = 0.266$). Of the 12 abiotic variables, only the ANOVA for mean current speed was significant ($P = 0.018$). The non-significant correlation analyses corroborated these results and indicated that naucorid densities vary at random with respect to the suite of abiotic variables within sites where at least one of the species exists. In contrast, classification results of the DFA correctly associated species with preferred sites of occurrence based on microhabitat variables in 73.5% of the cases.

Discussion

Early work in lotic ecology considered benthic macroinvertebrates to be protected from flow by existing at the substratum surface (Ambuhl 1959). As a result, substratum characteristics, rather than flow attributes, were considered the most important habitat variables determining distribution and

abundance patterns, because they directly limited the size of the organism able to colonize an area and indirectly influenced its size via food particle distribution and susceptibility to predation. The more recent attention to hydraulics has been investigated, at least in part, by the discovery that a number of benthic macroinvertebrate taxa (Craig & Chance 1982, Chance & Craig 1986, Dussart 1987) may experience considerable flow forces at the water-substratum interface (for a cogent review see Statzner et al. 1988), including those with conspicuous dorsoventral flattening or streamlining (Smith & Dartnall 1980, Statzner & Holm 1982, McShaffrey & McCafferty 1987). The effect of these flow forces in terms of lift and drag depends on the size, shape, orientation, and behavior of the organism. Adults and first instars frequently differ in size by an order of magnitude. Thus, microhabitat associations are expected to change as an individual matures. In fact, the actual turbulence conditions experienced by young nymphs and adults may differ by four orders of magnitude (Statzner et al. 1988). Similarly, even if substratum characteristics dominate, smaller nymphs would be expected to occupy different substratum conditions than larger adults.

Contrary to these expectations, age-specific differences in microhabitat association were not detected for *A. circumcinctus*, *C. hungerfordi*, or *L. lutzi*. Two factors could contribute to this result. In part, the lack of significance may be a product of combining all nymphal instars into a single age category, although this seems unlikely given the size distribution of nymphs and their ubiquitous association with adults in our samples.

The role of disturbance in structuring communities is a popular paradigm in contemporary ecosystem ecology (see Pickett & White 1985), and the theory of disturbance as it applies to streams is reviewed by Resh et al. (1988). Stream catchment attributes may have contributed to the absence of age-specific microhabitat associations. The South Llano River, as with most rivers on the Edwards Plateau, is subjected to periodic flooding, which may disrupt or diminish site-specific associations between age or size groups and habitat variables. This disruption would occur regardless of whether substratum or hydraulic characteristics are the primary determinants of distribution. However, heavy rainfall with subsequent flooding had not occurred since the previous June (Buckner et al. 1988, 1989; NOAA 1988), which allowed 11 mo for microhabitat associations to stabilize. Therefore, it is unlikely that disturbances in the recent past could have disrupted age-specific microhabitat associations. We conclude that at least during the time of this study, adults and nymphs did not differ in microhabitat association and that this result is not an artifact of our sampling protocol or a product of episodic events.

We were able to infer differences among species in microhabitat association as revealed by the mul-

Table 5. Means of abiotic variables at sites in which each naucorid species was present or absent

Variable ^a	<i>Ambrysus circumcinctus</i>		<i>Cryphocricos hungerfordi</i>		<i>Limnocoris lutzi</i>	
	Present	Absent	Present	Absent	Present	Absent
Rock mean	184.7	36.3	189.0	59.6	151.2	104.6
Rock SE	48.4	12.9	55.5	9.6	45.2	18.3
Rock range	540.7	195.9	577.5	209.7	468.4	341.8
Rock minimum	32.4	6.0	33.3	9.9	25.5	20.1
Rock maximum	581.2	186.7	621.2	205.7	502.8	343.4
Current mean	37.8	25.2	37.2	28.7	36.1	28.5
Current range	20.9	18.1	20.2	19.8	20.8	18.3
Temperature	24.9	24.7	24.8	24.9	24.8	24.8
Depth mean	33.8	24.2	36.9	21.4	32.2	27.3
Depth range	4.8	3.2	5.0	3.2	4.7	3.2
Reynolds number	9,333.8	3,751.4	10,120.8	3,685.8	8,569.1	5,161.3
Froude number	1.5	0.8	1.4	1.2	1.4	1.1

^a Measurements are expressed as: cm² (rock surface area); cm/s (current); °C (temperature); cm (depth). Reynolds number and Froude number are dimensionless.

multiple regression analyses based on density and the MANOVAs comparing sites of occurrence and non-occurrence for each species. The density of each species was related to a different subset of abiotic variables. However, interspecific differences among naucorid species were not directly detectable in other multivariate or univariate analyses. Microhabitat heterogeneity may contribute to this phenomenon. Although a site in fast current may contain primarily large rocks, small rocks invariably are held in place beneath the large rocks, possibly obscuring the critical microhabitat attribute of the substratum. Based on direct observation, *C. hungerfordi* typically is found among large rocks in fast water, although *L. lutzi* also may be found in these sites among the small rocks and gravel trapped beneath the larger substrata.

The abiotic variables that characterize the microhabitat in which *A. circumcinctus* may be found are large rocks in fast current (Table 5), whereas the density of this species may be predicted by only mean current speed. The abiotic variables that characterize the microhabitat in which *C. hungerfordi* may be found include deep, fast water with no apparent tolerance of variation in current speed (Table 5), whereas the density of this species may be predicted by only a high rock standard error of the mean. Rock standard error probably appears important because *C. hungerfordi* occurs among large rocks beneath which smaller gravel easily lodges. This species typically is found in the fastest, deepest water of the South Llano River. Both high Froude number and small depth range are significant predictors of *L. lutzi* abundance. The lack of distinction between sites of occurrence and nonoccurrence of *L. lutzi* indicates that it may be more of a generalist than the other two species.

Although each species exhibits microhabitat associations to the extent that certain microhabitat conditions favor higher densities than others, we do not have direct evidence that there are interspecific differences. Nevertheless, because different variables are determinants of density for each species, differences undoubtedly exist that are related

to both flow characteristics and substratum attributes. Sufficient microhabitat heterogeneity may exist within certain sites that would enable two species to coexist at moderate to high density because each can subdivide the local resources. This would reduce the power of interspecific tests to detect differences but not affect statistical analyses of species-specific microhabitat association. Larger numbers of samples and greater precision in quantifying the microhabitat, especially substratum particle size and complex key hydraulic characters, may aid in further elucidating intraspecific and interspecific microhabitat differences. Moreover, repeated sampling during the course of the year while collecting concurrent data on river history (flooding levels, etc.) may provide productive avenues of future research and yield insights into the manner in which abiotic variables and episodic events interact to affect naucorid community organization.

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