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The Gerridae (Hemiptera: Insecta) is a worldwide family whose constituent species exhibit dramatic inter- and intra-specific variation in the degree of winglessness (Brinkhurst, 1960; Vepsäläinen, 1978; Calabrese, 1979). At one extreme, the family contains species which are fully winged in all populations and during all seasons, while several species consist almost exclusively of wingless morphs over large geographical ranges and during all seasons. Many species exhibit the intermediate case of wing-polymorphism: the occurrence of various combinations of fully winged, partially winged and/or wingless morphs in the same population at the same time. Various wing-polymorphic species show differing patterns of spatial and/or temporal changes in morph ratios and patterns may vary both inter- and intraspecifically.

The dramatic differences in frequency of winged morphs pose intriguing questions regarding the evolutionary forces responsible for degree of winglessness and the relationship between degree of winglessness and genetic structure of water-strider species. One might expect genetic structure to be strongly influenced by degree of winglessness via reduction of flight dispersal ability and consequent reduced gene flow. Thus, species composed almost exclusively of wingless individuals should exhibit patterns of marked genetic differentiation and reduced levels of within-population variability typically found in organisms with reduced dispersal (Avise and Selander, 1972; Laing et al., 1976; Selander, 1976). However, additional factors may counteract the effects of reduced dispersal by flight. Gene flow among populations may occur via alternate modes of dispersal, including passive stream drift and overland dispersal (Riley, 1920). Furthermore, marked genetic differentiation among populations is not a necessary consequence of severely reduced dispersal if locality-independent balancing selection is operating (McKechnie et al., 1975).

In this study I compare patterns of spatial variation of polymorphic enzyme-loci and levels of variability in two species of waterstriders (Gerridae: Hemiptera) with differing degrees of winglessness: the nearly wingless *Gerris remigis* and the wing-polymorphic *Limnoporus canaliculatus.*

Species Studied

Gerris remigis is the most widely distributed and the most abundant North American gerrid species (Drake and Harris, 1934), occurring throughout the continental United States, Mexico, south to Guatemala. In the eastern U.S., *G. remigis* occurs principally on flowing water. Calabrese (1979) recorded greater than 99% wingless morphs in museum and field collections of *G. remigis* in Connecticut. *Limnoporus canaliculatus,* which until recently was known as *Gerris canaliculatus* (Anderson, 1975), ranges from Florida to Maine and west to Illinois and Michigan (Calabrese, 1974). The species occurs on ponds, swamps and sluggish streams.

TABLE 1. *Location of sampling sites for* Gerris remigis *and* Limnoporus canaliculatus *and the frequency of wingless morphs found at each site.*

Sampling site	Frequency of wingless morphs*	
	G. remigis	*L. canaliculatus*
Beddington, Maine (BD)	1.00 (44)**	0.03 (30)
Hartland, Vermont (HT)	1.00 (47)	—
Petersham, Mass. (PT)	1.00 (50)	0.29 (49)
Swift River, Mass. (SW)	1.00 (56)	—
Schoolhouse Brook, Conn. (SB)	1.00 (59)	—
Pink Ravine, Conn. (PR)	1.00 (41)	0.15 (39)
Willimantic, Conn. (WI)	—	0.79 (42)
Niantic, Conn. (NI)	1.00 (59)	0.54 (45)
Maplewood, N.J. (MW)	0.94 (107)	—
Bass River State Park, N.J. (BR)	—	0.96 (46)
Shenandoah Nat. Park, Va. (SH)	1.00 (24)	—
Athens, Georgia (AT)	—	0.72 (40)

* Frequency of wingless morphs was recorded in Sept., 1976, for all populations of *L. canaliculatus*, except for the Beddington population which was sampled in August, 1976. Frequency of wingless morphs was recorded at various times from July to October, 1976–1977, for populations of *G. remigis* (see Materials and Methods).
** Numbers in parentheses are the total number of individuals scored for morph type.

Populations of L. *canaliculatus* consist of various proportions of fully-winged, wingless, and (very rarely) short-winged individuals. The frequency of fully-winged individuals varies seasonally, the highest frequency occurring from September to November in Connecticut and Virginia populations (Bobb, 1951; Calabrese, 1979). Calabrese (1979) reported that Connecticut populations contained greater than 25% winged individuals during all seasons. However, I have found Connecticut and Massachusetts populations to consist almost exclusively of wingless individuals from July through early August (Zera, unpubl.). This observation is similar to the data of Bobb (1951) for Virginia populations.

Both *G. remigis* and *L. canaliculatus* are at least bivoltine in Connecticut (Zera and Saks, unpubl.), while in Florida, *L. canaliculatus* breeds throughout the year (Penn and Goldsmith, 1950). In Connecticut, both species overwinter as adults. Individuals emerge the following April-May and mate throughout this time. Adults of the subsequent summer generation begin to emerge in late June, and adults of both species can be seen continuously from this time through late October. Mating pairs are commonly seen from July through August.

There are no published data for dispersal in either species. However, it is likely that population mixing occurs in *L. canaliculatus* as a result of dispersal of winged individuals to and from overwintering sites, as has been reported for several European gerrid species (see Discussion).

Sampling and Electrophoresis

Samples were taken from eight populations of *Gerris remigis* ranging from Maine to Virginia and seven populations of *Limnoporus canaliculatus* ranging from Maine to Georgia during July–October of 1976 (Table 1). No sampling sites were directly connected by water. All sites contained water throughout the year.

The number of winged and wingless morphs was recorded in each fall (Sept.) population sample of *L. canaliculatus*. The frequency of morphs was recorded in each population of *G. remigis* in both summer and fall since there is no evidence for seasonal change in the near unitary frequency of wingless morphs (Calabrese, 1979).

The following enzymes were studied in the two species: α-Glycerophosphate dehydrogenase (α-Gpdh, E.C. 1.1.1.8); Malate dehydro-

genase (Mdh, E.C. 1.1.1.37), anodal Mdh-1 and cathodal Mdh-2; Isocitrate dehydrogenase (Idh-1, E.C. 1.1.1.42); Malic enzyme (Me, E.C. 1.1.1.40); and Esterase (Est, E.C. 3.1.1.1), Est-3 and Est-4.

In order to obtain a larger sample of loci for heterozygosity estimates, three populations of *L. canaliculatus* (Petersham, Pink Ravine and Niantic) and two populations of *G. remigis* (Pink Ravine and Niantic) were resampled in 1977 for variation in the following additional enzymes: Glutamate-oxaloacetate transaminase (GOT, E.C. 2.6.1. 1), GOT-1 and GOT- 2; 6-Phosphogluconate dehydrogenase (6- PGDH, E. C. 1.1.1.43); Phosphoglucose isomerase (PGI, E. C. 5.3.1.9); Glucose-6- phosphate dehydrogenase (G-6-PDH, E.C. 1.1.1.49); Leucine napthylamidase (NAP, E.C. 3.4.—.—); Acid phosphatase (ACPH, E.C. 3.1.3.2); Fumarase (FUM, E.C. 4.2. 1.2); Xanthine dehydrogenase (XDH, E.C. 1.2.3.2); Phosphoglucomutase (PGM, E.C. 2.7.5.1); Peptidase (PEP, E.C. 3.4.1.—); and an additional Isocitrate dehydrogenase locus (IDH-2, E.C. 1.1.1.42). In total, 18 loci were examined in *G. remigis* and 16 loci in *L. canaliculatus.*

In addition to the populations listed above, a new population (Swift) of G. remigis was sampled during 1977 for variation at the 18 loci surveyed in the other populations of this species.

Gerrids were homogenized in 0.1 ml (*G. remigis*) or 0.05 ml (*L. canaliculatus*) of 0.05 M Tris-HCl buffer, pH 7.0, containing 0.01 M mercaptoethanol. Crude homogenates were absorbed onto paper wicks and applied to horizontal starch gels prepared with Electrostarch (lots 307 or 371; Otto Hiller, Madison, Wisconsin) at a concentration of 12% (w/v).

The 0.135 M Tris-citrate buffer of Shaw and Prasad (1970) was adjusted to different pH's by varying the concentration of citric acid. MDH, ME, IDH, GOT, *a*-GPDH, FUM, ACPH in *L. canaliculatus* only, and PGI were resolved at pH 7.3. G-6-PDH and 6-PGDH were resolved at pH 8.0 and ACPH in *G. remigis* was resolved at pH 6.8. Phosphoglucomutase was resolved using the Tris-maleate-EDTA buffer of Shaw and Prasad (1970) and XDH was resolved using buffer "B" of Ayala (1972). Peptidase, NAP, and Esterases were resolved using the LiOH buffer of Selander et al. (1971).

Gels were stained for the appropriate enzymes as in Shaw and Prasad (1970). For ACPH, gels were soaked in 0.25 M Na-acetate buffer, pH 4.5, for 30 min prior to staining.

Observed genotypic numbers were compared with their Hardy-Weinberg expectations by the χ^2-test (Sokal and Rohlf, 1969). Geographic variation of polymorphic loci was analyzed using R × C tests of homogeneity of genotypic numbers (Workman and Niswander, 1970). Polymorphic loci surveyed during 1976 as well as additional polymorphic loci discovered during the 1977 sampling were analyzed. Rare genotypic classes were pooled with their most electrophoretically similar class until not more than 20% of the cells of the R × C table contained expected values less than five and no cell contained an expected value less than one (Conover, 1971). These criteria could not be met for the weakly polymorphic *Idh-1* and *Me* loci of *L. canaliculatus*. R × C tests of homogeneity were still performed on these loci, since they conform to less stringent criteria (i.e., no cell of an R × C table with an expected value less than one, Lewontin and Felsenstein, 1965). A posteriori STP tests (Sokal and Rohlf, 1969) were; done on all R × C tests of homogeneity. The *Mdh-2* and *Est-4* loci of *G. remigis* were not analyzed statistically for geographical variation, since it is obvious by inspection that marked geographical variation is present.

Two values of average heterozygosity per individual (H) were calculated. One value, H_t, was calculated using all loci surveyed in each species, while a second value, H_h, was calculated using only the 15 presumed homologous loci surveyed in both species. The calculation of average heterozygosity using only homologous loci was done since this eliminates the confounding effects of interlocus variation in interspecific comparisons of average heterozygosity (Selander, 1976). For this reason, only H_h, was used in the comparison of heterozygosity between the two species.

TABLE 2. *Allele frequencies for polymorphic loci surveyed in populations of* Gerris remigis *(*n = *number of individuals surveyed; alleles with frequencies less than 0.05 in all populations are not shown).*

Enzyme	Allele and sample size	Locality								
		BD	HT	PT	SW	SB	PR	NI	MW	SH
MDH-1	*n*	44	46	70	44	48	67	70	60	24
	a	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.979
	b	1.000	0.945	0.850	0.943	0.990	0.992	0.939	1.000	0.021
	c	0.000	0.055	0.150	0.057	0.010	0.008	0.061	0.000	0.000
MDH-2	*n*	40	47	67	41	97	112	88	50	19
	a	0.000	0.000	0.000	0.231	0.887	0.969	0.989	1.000	0.000
	b	0.057	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	c	0.943	1.000	1.000	0.769	0.113	0.031	0.011	0.000	1.000
IDH-1	*n*	41	39	76	44	23	44	58	44	6
	a	0.929	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	b	0.071	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
EST-3	*n*	—	—	—	52	55	56	54	—	—
	a	—	—	—	0.000	0.000	0.000	0.075	—	—
	b	—	—	—	0.192	0.109	0.170	0.270	—	—
	c	—	—	—	0.808	0.891	0.830	0.575	—	—
	d	—	—	—	0.000	0.000	0.000	0.085	—	—
EST-4	*n*	—	—	—	—	—	—	—	29	21
	a	—	—	—	—	—	—	—	0.000	0.977
	b	—	—	—	—	—	—	—	0.206	0.023
	c	—	—	—	—	—	—	—	0.794	0.000
ACPH	*n*	—	—	—	16	43	52	—	—	—
	a	—	—	—	0.000	0.094	0.115	—	—	—
	b	—	—	—	0.906	0.872	0.866	—	—	—
	c	—	—	—	0.094	0.034	0.019	—	—	—
PGM	*n*	—	—	—	52	41	52	—	—	—
	a	—	—	—	0.885	0.988	0.981	—	—	—
	b	—	—	—	0.115	0.012	0.019	—	—	—

RESULTS

Eleven of 18 loci surveyed in *G. remigis* were monomorphic (*a-Gpdh, Me, Got-1, Got-2, 6-Pgdh, Fum, Pgi, G-6-pdh, Nap, Pep,* and *Xdh*), while 8 of 16 loci in *L. canaliculatus* were monomorphic (*Got-1, Got-2, Fum, Nap, G-6-pdh, Mdh-1, Idh-2,* and *Xdh*). A monomorphic locus is defined as a locus containing one and the same allele with a frequency greater than 0.95 in all sampled populations.

Allele frequencies of polymorphic loci are given in Tables 2 and 3. No significant deviations from Hardy-Weinberg expectations were observed, except at the *6-Pgdh* locus in the Niantic population of L. *canaliculatus.* No biological significance is attributed to this single deviation.

Frequency of Wingless Morphs

All sampled *G. remigis* were wingless, except for six individuals from the Maplewood population (Table 1). In contrast, the frequency of wingless individuals varied considerably among populations of *L. canaliculatus* in the Beddington and Bass River populations, respectively (Table 1).

Geographical Variation

Five of six polymorphic loci in *G. remigis* exhibited significant among-population heterogeneity *(Mdh-1,* $G_{(8)} = 243.72$, $P < .005$; *Mdh-2,* heterogeneous by inspection; *Est-3,* $G_{(3)} = 14.35$, $P < .005$; *Est-4,* heterogeneous by inspection; *Pgm,* $G_{(2)} = 13.81$, $P < .005$). Acid

TABLE 3. *Allele frequencies for polymorphic loci surveyed in populations of* Limnoporus canaliculatus *(*n = *number of individuals surveyed; alleles with frequencies less than 0.05 in all populations are not shown).*

Enzyme	Allele and sample size	Locality						
		BD	PT	PR	WI	NI	BR	AT
α-GPDH	*n*	29	101	97	44	66	44	45
	a	0.068	0.045	0.021	0.092	0.062	0.000	0.000
	b	0.743	0.782	0.820	0.805	0.744	0.771	0.767
	c	0.189	0.173	0.159	0.103	0.194	0.229	0.233
EST-3	*n*	—	57	48	41	45	42	39
	a	—	0.027	0.052	0.037	0.122	0.047	0.025
	b	—	0.561	0.407	0.549	0.457	0.120	0.334
	c	—	0.263	0.468	0.317	0.355	0.130	0.602
	d	—	0.149	0.073	0.073	0.055	0.607	0.039
	e	—	0.000	0.000	0.024	0.011	0.096	0.000
IDH-1	*n*	30	49	72	55	64	35	62
	a	0.000	0.000	0.048	0.000	0.015	0.086	0.032
	b	1.000	1.000	0.952	1.000	0.985	0.914	0.968
ME	*n*	27	52	40	36	50	35	24
	a	0.000	0.038	0.000	0.042	0.010	0.271	0.000
	b	1.000	0.962	1.000	0.958	0.990	0.729	1.000
PGM	*n*	—	51	52	—	48	—	—
	a	—	0.271	0.295	—	0.317	—	—
	b	—	0.729	0.705	—	0.683	—	—
PGI	*n*	—	45	72	—	32	—	—
	a	—	0.366	0.417	—	0.579	—	—
	b	—	0.634	0.583	—	0.421	—	—
ACPH	*n*	—	33	42	—	30	—	—
	a	—	0.000	0.072	—	0.000	—	—
	b	—	0.318	0.297	—	0.283	—	—
	c	—	0.213	0.072	—	0.166	—	—
	d	—	0.363	0.452	—	0.467	—	—
	e	—	0.106	0.107	—	0.084	—	—
6-PGDH	*n*	—	—	—	—	32	—	—
	a	—	—	—	—	0.281	—	—
	b	—	—	—	—	0.360	—	—
	c	—	—	—	—	0.124	—	—
	d	—	—	—	—	0.235	—	—

phosphatase, the only polymorphic locus which did not exhibit significant among-population heterogeneity, approached statistical significance ($G_{(2)} = 5.88$, $.1 > P > .05$). In contrast, five of seven polymorphic loci surveyed in *L. canaliculatus* exhibited *no* significant among-population heterogeneity *(α-Gpdh,* $G_{(6)} = 7.54$, $P > .1$, *Idh-1,* $G_{(6)} = 10.99$, $.1 > P > .05$; *Pgm,* $G_{(4)} = 1.57$, $P > .1$; *Pgi,* $G_{(4)} = 7.48$, $P > .1$; *Acph,* $G_{(6)} = 4.34$, $P > .1$). Of the two loci which were significantly heterogeneous *(Est-3,* $G_{(20)} = 133.65$, $P < .005$ and *Me,* $G_{(6)} = 53.93$, $P < .005$), significant heterogeneity at the *Me* locus was due to the Bass River population. The subset of samples excluding the Bass River population was statistically homogeneous. Similarly, the majority (but not all) of the heterogeneity at the *Est-3* locus was due to the Bass River population. This population was the only population to form a unique subset in the STP analysis.

The pattern of variation was very different for polymorphic loci of the two species. Four of six polymorphic loci of *G. remigis (Mdh-1, Mdh-2, Est-3, Est-4)* exhibited sharp disconti-

nuities in allele frequencies with different alleles fixed in some populations at the *Mdh-2* locus and nearly fixed at the *Mdh-1* locus (Table 2). At the *Est-4* locus, an allele which was nearly fixed in the Shenandoah population was absent from the Maplewood population. However, at each locus in *L. canaliculatus,* the same allele (or pair of alleles at the *Est-3* locus) predominated in all populations, with the exception of the *Est-3* locus in the Bass River population (Table 3).

Local differentiation among populations of *G. remigis* was marked. For example, the STP analysis of the *Est-3* locus showed significant among-population heterogeneity for the Connecticut samples. Different alleles predominated at the *Mdh-2* locus in the Swift and Pink Ravine populations. These were also significantly different at the *Pgm* locus. Populations separated by five miles or less were significantly different at the *Mdh-2* locus (Pink Ravine and Schoolhouse Brook, $G_{(1)} = 4.77$, $P < .05$; Swift and Petersham, $G_{(1)} = 15.17$, $P < .005$). No local differentiation was observed at polymorphic loci in *L. canaliculatus*. Esterase-3, although exhibiting significant heterogeneity for the total sample of all populations, exhibited no significant among-population heterogeneity for the subset of samples north of Bass River.

Average Heterozygosity

Since H_h and H_t (see Materials and Methods) were essentially identical in each species, only H_h values will be reported. Average heterozygosity for *G. remigis (*$H = 0.058 \pm 0.026$) was significantly lower than for *L. canaliculatus (*$H = 0.234 \pm 0.072$), as tested by Wilcoxon's signed ranks test *(*$Ts = 13$, $P < ,025$; two tailed test).

Discussion

Gerris remigis and *Limnoporus canaliculatus* differ markedly, both in degree of population differentiation at polymorphic loci and in amounts of variability within populations. *L. canaliculatus* exhibits the pattern of geographical variation and levels of variability typically found in continental insect species (Ayala, 1972; Lewontin, 1974) and other winged gerrid species (Varvio-Aho et al., 1978; Varvio-Aho and Pamilo, 1979). In these species (as in *L. canaliculatus)* allele frequencies of polymorphic loci are often homogeneous over large distances. Average heterozygosity for *L. canaliculatus* (0.234 ± 0.072) is within the range for "typical" insects or invertebrates (Powell, 1975; Selander, 1976).

In contrast to *L. canaliculatus,* polymorphic loci of *G. remigis* typically exhibit marked spatial variation of allele frequencies, sometimes over short distances. Average heterozygosity in *G. remigis* ($H = 0.058 \pm 0.026$) is well below the value for "typical" insects or invertebrates (Powell, 1975; Selander, 1976). Allozyme data for *G. remigis* are similar to data obtained for species inhabiting geographical or ecological islands (Avise and Selander, 1972; Saura et al., 1973; Laing et al., 1976; Selander, 1976). For example, in six cave populations of troglobite beetle, *Ptomaphagus hirtus,* amounts of genetic variability were about one-third that of "typical" invertebrates. Of six polymorphic loci studied, different alleles were fixed at three loci, while large spatial differences in allele frequencies were observed at the other three polymorphic loci (Laing et al., 1976).

The similarity of the allozyme data between *G. remigis* and other "island" species, where reduced gene flow is either known or strongly inferred, suggests that gene flow is similarly reduced among populations of *G. remigis*. Reduced gene flow would result in a population structure consisting of isolated demes which could differentiate due to selection and/or drift, accounting for both the degree and pattern of spatial differentiation of allele frequencies. Reduced levels of variability could result from either small present population sizes or the founder effect during colonization.

High mortality during the overwintering period was recorded in British populations of the wingless riverine waterstrider, *Gerris najas* (Brinkhurst, 1966). In a six-year study, win-

ter mortality was always greater than 55%, and sometimes exceeded 90%, in each of four populations. Populations of *G. remigis* were much smaller in the spring than in the summer or fall (Zera and Saks, unpubl.), indicating that high winter mortality may also occur in this species. Population bottlenecks resulting from high winter mortality can severely reduce variability (Nei, 1975), and may be an additional factor responsible for the low variability found in populations of *G. remigis.*

Spatially homogeneous allele frequencies among populations of *L. canaliculatus* may be the result of extensive dispersal and gene flow. However, homogeneous allele frequencies do not necessarily imply extensive gene flow since only a small amount of gene flow is needed to swamp out local differentiation due to random drift (Lewontin, 1974). Similar allele frequencies in different populations may also be due to locality-independent balancing selection in the absence of gene flow. Therefore, allozyme data for *L. canaliculatus* cannot decisively separate the relative contributions of dispersal, selection and drift. However, several additional points should be made. Dispersal is reported to commonly occur in many winged gerrid species (Brinkhurst, 1960; Vepsäläinen, 1971; Callahan, 1974; Landin and Vepsäläinen, 1977). Winged adults of *G. lacustrus* have been found hibernating far from water (Douglas, 1882; Brinkhurst, 1960) and winged forms of the continental European species, *G. rufoscutellatus,* have been found in Britain (Brinkhurst, 1960). Winged gerrids have been found in small pools on top of three story buildings (Calabrese, 1974) and in the laboratory winged morphs of

L. canaliculatus commonly fly from containers. Hence, it seems unlikely that dispersal is restricted in *L. canaliculatus.*

The importance of flight dispersal as a factor responsible for the homogeneous allele frequencies in nearly all populations of *L. canaliculatus* may also be inferred by examining allele frequencies in the one population where flight dispersal seems to be severely reduced, the Bass River population. The Bass River population was the only surveyed population of *L. canaliculatus* which was composed almost exclusively of wingless individuals (94% wingless individuals, Table 1). The almost total absence of winged individuals indicates that gene flow via flight *into* Bass River must be severely reduced. Both the *Est-3* and the *Me* loci exhibit highly divergent allele frequencies in this population, compared with other populations of *L. canaliculatus* (Table *3).* Thus, as in *G. remigis,* when dispersal by flight is severely reduced, genetic differentiation may result. The generality of this hypothesis is being tested further by investigations of differences among populations of *L. canaliculatus* composed predominantly of wingless morphs.

SUMMARY

The relationship between degree of winglessness and genetic structure was investigated in two waterstrider species (Gerridae: Hemiptera) with differing degrees of winglessness: the nearly wingless *Gerris remigis* and the wing-polymorphic *Limnoporus canaliculatus.* Five of six polymorphic loci in *G. remigis* exhibited significant spatial variation of allele frequencies. There was fixation or near fixation of different alleles in different populations at three loci. In contrast, five of seven polymorphic loci surveyed in *L. canaliculatus* exhibited geographically homogeneous allele frequencies. Average heterozygosity in *G. remigis (H* $= 0.058 \pm 0.026$) was one-quarter the value of *L. canaliculatus* ($H = 0.234 \pm 0.072$) and was one-third to one-quarter the value for "typical" insects or invertebrates.

These data indicate that differing degrees of winglessness have resulted in very different genetic structures in the two species.

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