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Effects of habitat fragmentation and differing mobility on the population structures of a Great Basin dragonfly (*Sympetrum corruptum*) and damselfly (*Enallagma carunculatum*)

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EFFECTS OF HABITAT FRAGMENTATION AND DIFFERING MOBILITY ON THE POPULATION STRUCTURES OF A GREAT BASIN DRAGONFLY (*SYMPETRUM CORRUPTUM*) AND DAMSELFLY (*ENALLAGMA CARUNCULATUM*)

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ABSTRACT.—The population structure of 2 Great Basin odonate species was assessed using protein electrophoresis. Analyses included 7 populations of *Sympetrum corruptum* (suborder Anisoptera), a migratory and highly mobile dragonfly, and 8 populations of *Enallagma carunculatum* (suborder Zygoptera), a weak flier that is not known to migrate far from natal water sources. Though we expected the damselfly (*E. carunculatum*) to show greater genetic isolation than the dragonfly (*S. corruptum*), both species apparently had high levels of gene flow (theta = 0.0604 for *S. corruptum*, theta = 0.0485 for *E. carunculatum*) and showed no evidence for isolation by distance. These results suggest that both species are highly vagile and that the most important factors affecting population structure of these odonates may be ecological conditions such as habitat patchiness and the ephemerality of water sources.

Key words: Odonata, protein electrophoresis, isolation by distance, Great Basin, gene flow.

Dispersal and associated gene flow affect the long-term survival and evolution of species. These aspects of population structure are particularly important in fragmented habitats where movement between suitable sites may be difficult. Several factors can affect dispersal, including geographic barriers, species mobility, and ecological limitations (e.g., availability of food or breeding sites). The Great Basin's isolated habitat islands make it a classic region for studying the effects of insularization on community distributions (e.g., Brown 1971, 1978, Johnson 1975, but see Lawlor 1998). Generally, boreal mammals are isolated on mountaintops, while birds are much less isolated. Both Brown and Johnson attributed this to the very different dispersal capabilities of the 2 taxa. Butterflies are also distributed according to their vagility, or genetically effective dispersal. Vagile species occurrences are significantly less correlated with habitat area than are sedentary species (Wilcox et al. 1986). Population genetic structure, like community structure, is strongly dependent on movement. Genetic variability among populations should be correlated with vagility since gene flow is the result of individuals moving between populations. Geographic isolation can restrict gene flow, producing an isolation by distance pattern (Wright 1943) that is usually most pronounced in sedentary species. Several studies of Great Basin organisms have shown some level of genetic isolation that could be attributed to geographic, ecological, or mobility factors (Yandell 1993, Britten et al. 1994, 1995, Britten and Rust 1996, Porter and Rust 1996, Epps et al. 1998).

Typically, Great Basin species have exhibited genetic differentiation at various spatial scales. Dune beetles in the genus *Agaelia* (Porter and Rust 1996) and *Eusattis muricatus* (Britten and Rust 1996, Epps et al. 1998) have low levels of gene flow and significant isolation by distance at large scales, but not within single dune complexes. Whitebark pine (*Pinus albicaulis*) also shows genetic divergence between populations, probably due largely to genetic drift (Yandell 1993). Similar differentiation attributable to drift occurs in the butterfly *Euphydryas editha* (Britten et al. 1995).

During the Pleistocene, Lake Lahontan covered much of the northwestern Great Basin. With a maximum size of 22,400 km^2, it provided large, continuous habitat for aquatic organisms. The lake level rose and fell intermittently throughout the Pleistocene. Portions

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of the lake were isolated periodically by several high physiographic separations, or sills. These sills divided the Lahontan Basin into 7 subbasins (Benson and Thompson 1987). This physical separation also may have impacted the lake's aquatic fauna. Organisms that once existed in a continuous water body were isolated in remaining lake fragments (Hubbs et al. 1974, Sigler and Sigler 1987) in much the same way that boreal mammals were at least partially isolated on mountaintops as the climate warmed at the end of the Pleistocene (Brown 1971, 1978). Eventually, xeric conditions predominated in the Great Basin, leaving little surface water. The aquatic habitats that exist today are not only discontinuous, but many are ephemeral, providing highly variable conditions for the species occupying them.

Dragonflies and damselflies (order Odonata) are ancient insects that undoubtedly occurred at Lake Lahontan throughout its existence. Many species are still present at isolated water sources that remain within subbasins. Odonates are highly visible insects with differing mobilities. They have complex life cycles in which the larval stage is completely aquatic while adults are terrestrial and can fly. Adults are long-lived and frequently able to move great distances (Corbet 1963). Generally, dragonflies (suborder Anisoptera) are stronger fliers than damselflies (suborder Zygoptera). Given this, one would expect the more mobile dragonflies to have greater gene flow between populations in patchy habitat than damselflies. In this study, we selected 1 species from each suborder to compare the effects of differing mobility on gene flow. The dragonfly *Sympetrum corruptum* Hagen (Libellulidae) is migratory and therefore highly mobile (Walker 1953). The damselfly *Enallagma carunculatum* Morse (Coenagrionidae) does move away from water, but it is not known to be migratory (Walker 1953). McPeek (1989) found that other *Enallagma* species are extremely philopatric, suggesting that these damselflies may be much more genetically isolated than dragonflies. Both species are widespread and abundant in the Great Basin. Very few studies have addressed the genetic structure of odonate populations (but see Chung et al. 1997); we know of no studies that have analyzed Great Basin species.

Based upon their natural history, we expected to find greater gene flow in *Sympetrum corruptum* than in *Enallagma carunculatum*. We collected samples of both species from sites in subbasins of Lake Lahontan, expecting that the odonate groups living within them had been separated since water receded and isolated the subbasins more than 10,000 YBP. Thus, each subbasin should contain genetically distinct populations. Other studies of insects have shown reasonably high levels of genetic differentiation among populations at scales similar to those examined in this study (caddisflies: Jackson and Resh 1992; aquatic invertebrates: Boileau et al. 1992; butterflies: Britten et al. 1994, 1995; dune beetles: Porter and Rust 1996, Britten and Rust 1996). We estimated isozyme variability in both species using protein electrophoresis, a technique used widely during the past 30 yr to measure genetic variability within and among populations. Ultimately, information about odonate population genetics will allow assessments of their responses to habitat fragmentation and variable environments.

METHODS

We collected adults of both the dragonfly *Sympetrum corruptum* and the damselfly *Enallagma carunculatum* from most subbasins of Pleistocene Lake Lahontan and several sites outside the Lahontan Basin during the summers of 1995–96 (Fig. 1). Both years had above-average precipitation, while the preceding 8 yr had been very dry. However, it is unlikely that any of the sampling sites except Artesia Lake had dried up entirely during the drought. The Lahontan Basin is defined as the area submerged during the lake's high-stand elevation of 1330 m, which occurred approximately 13,800 YBP (Fig.1; Grayson 1993). Since 2 rivers flow through the Carson/Humboldt subbasin, we collected samples from sites on each river. Pine Reservoir is in the Carson River portion of the subbasin, while Rye Patch Reservoir and Taylor Ditch are in the Humboldt River portion. Only 1 site was sampled in each of the remaining subbasins: Sutcliffe Pond in Pyramid subbasin, Mason Valley in Walker subbasin, Fleming Management Area in Honey subbasin, and Guru Pond in Quinn subbasin. Artesia Lake, Little Washoe Lake, and Oxbow Pond are found in pluvial basins outside the Lahontan Basin. All sites except Taylor Ditch and Artesia Lake are ponds, either natural or

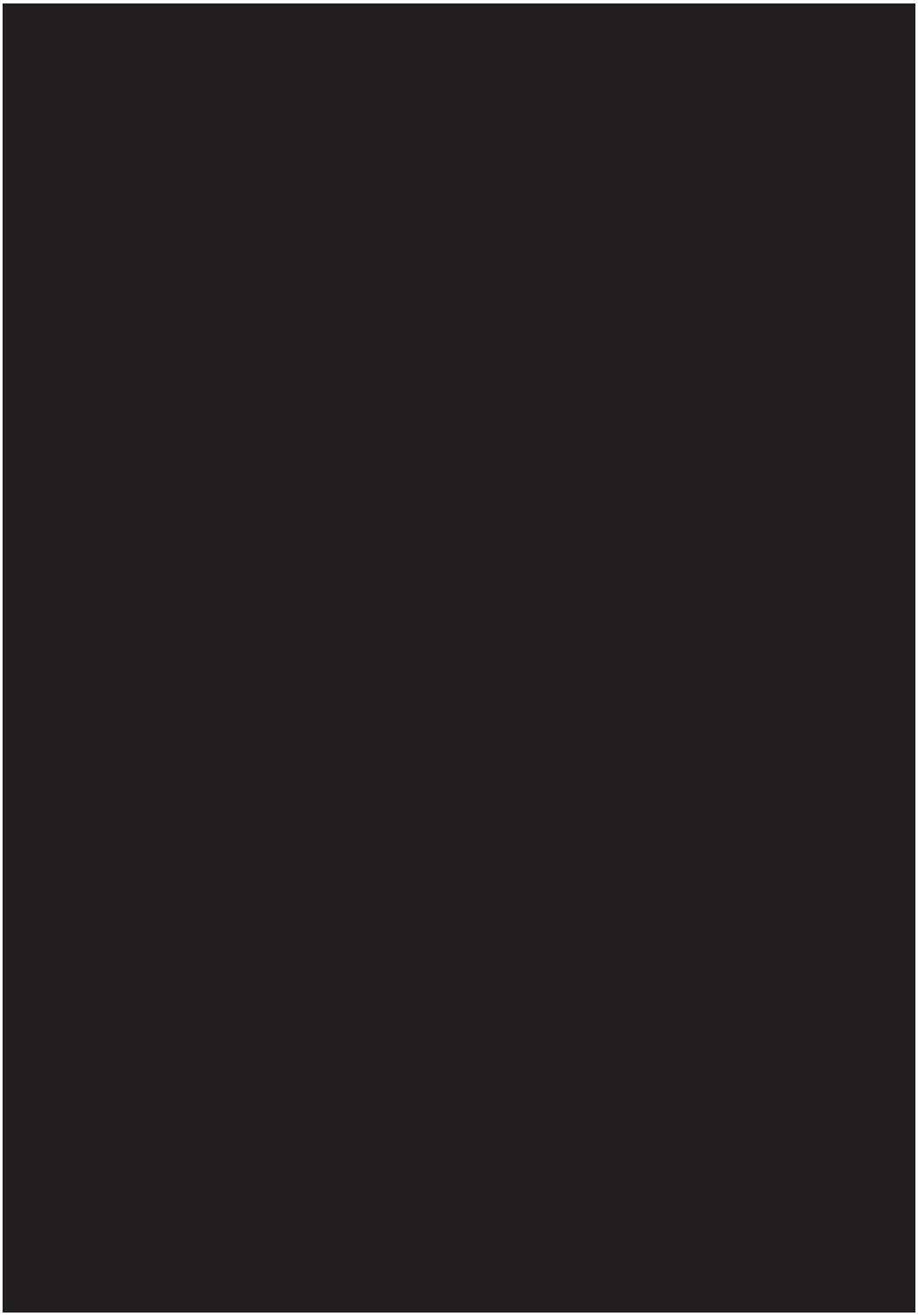

Fig. 1. Subbasins of Lake Lahontan (from Benson 1987) with collection sites for this study: (1) Artesia Lake, (2) Pine Reservoir, (3) Little Washoe Lake, (4) Rye Patch Reservoir, (5) Sutcliffe Pond, (6) Mason Valley, (7) Fleming Management Area, (8) Taylor Ditch, (9) Guru Pond, (10) Oxbow Pond.

human-made. Taylor Ditch and Artesia Lake contain areas of standing or slow-moving open water. No samples were collected in Buena Vista or Winnemucca subbasins because neither had enough surface water to support sufficiently large populations for collecting. Both species were found in these subbasins, however. Though individuals were present, we did not collect *S. corruptum* in Quinn subbasin because we could not find sufficient numbers of specimens at potential sampling sites.

We collected approximately 30 adults of each species at each site (Table 2). Only male *E. carunculatum* were used for genetic analyses because females are difficult to distinguish from other *Enallagma.* Most specimens were captured with an aerial insect net. *Sympetrum corruptum* were also collected using a .22-caliber rifle loaded with dust shot. Aerial-net captures were transported live to the lab and then frozen at –80°C. Shot individuals were placed on dry ice until they could be transferred to the –80°C freezer.

Samples were prepared for horizontal starch gel electrophoresis according to methods outlined by Selander et al. (1971) and May (1992). Allozyme variation was analyzed at 28 presumptive loci for *S. corruptum* and 19 presumptive loci for *E. carunculatum* (Table 1).

Mean heterozygosity, deviations from Hardy-Weinberg equilibrium, heterogeneity among populations, *F* statistics (Wright 1978), and Nei's genetic distances (Nei 1978) were calculated with BIOSYS-1 (Swofford and Selander 1981). We estimated thetas for each species and the 95% confidence intervals around them with 10,000 bootstrap iterations using a program developed by Miller (1997). Theta corresponds to F_{st} and provides a means of estimating among-population variances in allele frequencies (Weir 1990). Using a program developed by Slatkin (1993), we also assessed gene flow among populations for each species in relation to geographic distance (isolation by distance, Wright 1943). This method calculates G_{st}, which is the multiallelic form of F_{st} (Hartl and Clark 1989). From this, the log number of effective migrants (Nm) per generation was calculated and regressed against the log geographic distances between all pairs of collection sites for each species. The simultaneous test procedure (Sokal and Rohlf 1981) was used to assess homogeneity among populations for *E. carunculatum*. The most variable loci were used in this analysis. A constant critical value of $\chi^2_{0.05[5]} = 11.070$ was used for these heterogeneity tests (Sokal and Rohlf 1981). A sequential Bonferroni analysis was used as a control for type I error (Rice 1989).

TABLE 1. Loci, enzymes, enzyme commission numbers, and electrophoretic buffers used to assay *Sympetrum corruptum* and *Enallagma carunculatum.*

Loci	Enzyme	E.C. number	Buffers[3]
AAT[2]	Aspartate aminotransferase	2.6.1.1	C
AK[2]	Adenylate kinase	2.7.4.3	C
DIA[1,2]	NADH diaphorase	1.8.1.-	C,R
ESTF[1,2]	Fluorescent esterase	3.1.1.-	R, 4
G3P[1,2]	Glycerol-3-phosphate dehydrogenase	1.1.1.8	C, 4
GAM[1]	Fluorescent galactosaminidase	3.2.1.23	R
GAPDH[1,2]	Glyceraldehyde-3-phosphate dehydrogenase	1.2.1.12	C
GP[2]	General protein	-.-.-.-	4, R
GPI[1,2]	Glucosephosphate isomerase	5.3.1.9	4
HA[1]	Fluorescent hexosaminase	3.2.1.52	R
HBDH[1,2]	Hydroxybuterate dehydrogenase	1.1.1.30	TC-1, R
IDH[1]	Isocitrate dehydrogenase-NAD	1.1.1.42	TC-1
LAP[2]	Leucine aminopeptidase	3.4.11.1	R
LDH[2]	Lactate dehydrogenase	1.1.1.27	R
MDH[2]	Malate dehydrogenase	1.1.1.37	4
MPI[1,2]	Mannosephosphate isomerase	5.3.1.8	TC-1, 4
PEP[1,2]	Peptidase-leu-gly-gly	3.4.-.-	4, R
PGD[1]	Phosphogluconate dehydrogenase	1.1.1.43	4, C
PGM[1,2]	Phosphoglucomutase	5.4.2.2	TC-1, 4
SOD[2]	Superoxide dismutase	1.1.15.1	4

[1]*Enallagma carunculatum*
[2]*Sympetrum corruptum*
[3]Selander et al. (1971) and May (1992)

RESULTS

Sympetrum corruptum

Twenty-eight loci were resolved for *Sympetrum corruptum.* Frequency of polymorphic loci was high. Using the 99% criterion (frequency of the most common allele does not exceed 99%), we found the mean percentage of polymorphic loci to be 24.5% (range 14.3–35.7%). Using the 95% criterion resulted in a mean percent polymorphism of 7.1%. Mean number of alleles per locus was 1.32, and mean heterozygosity was 2.3% (range 2.0–2.7%; Table 2).

Mean heterozygosity was used to determine deviations from expected Hardy-Weinberg values in a contingency table. Of 48 tests for conformity to Hardy-Weinberg expectations, 12 (25%) significant departures were found using Levene's test (1949). All deviations were heterozygote deficiencies. We detected no apparent trends for specific loci or specific populations with high numbers of deficient loci.

After using a sequential Bonferroni to control type I error, we found no significant heterogeneity in allele frequencies among locations for any loci.

Fixation indices were low, suggesting high levels of gene flow. Theta was estimated at 0.0485 with a 95% confidence interval of 0.0028–0.0698. F_{it} was 0.259. Nei's genetic distances (Table 4) were extremely low, with some populations showing no differentiation.

An analysis for isolation by distance (Wright 1943) was conducted using an approach introduced by Slatkin (1993). The slope of the regression was nearly zero (–0.013; Fig. 2A), showing very little evidence for isolation by distance. Additionally, Nm values were very high (Table 5), indicating very high levels of gene flow, or effective panmixia (Slatkin 1993).

The simultaneous test procedure (Sokal and Rohlf 1981) grouped all populations from all Lahontan subbasins and outside basins into 1 homogeneous group ($G = 11.08$, df = 4, $P = 0.103$). This analysis was based on the ESTF-2 locus.

Enallagma carunculatum

Nineteen loci were resolved for *Enallagma carunculatum.* Frequency of polymorphic loci was higher than *Sympetrum corruptum*. Using the 99% criterion, mean percentage of polymorphic loci was 68.5% (range 57.9–78.9%). Using the 95% criterion, mean percentage of

TABLE 2. Mean sample sizes, mean number of alleles per locus, percentages of polymorphic loci, mean heterozygosity (direct count), and expected Hardy-Weinberg heterozygosity for *Sympetrum corruptum* and *Enallagma carunculatum.*

Population	Mean sample size per locus	Mean no. of alleles per locus	Percentage of loci polymorphic (99% criterion)	Mean heterozygosity (direct count)	Hardy-Weinberg expected heterozygosity
Sympetrum corruptum					
Artesia Lake	26.4 ± 1.1	1.2 ± 0.1	14.3	0.021 ± 0.014	0.029 ± 0.016
Pine Reservoir	43.5 ± 0.5	1.4 ± 0.1	28.6	0.025 ± 0.014	0.030 ± 0.017
Washoe Lake	22.0 ± 0.8	1.3 ± 0.1	28.6	0.024 ± 0.014	0.031 ± 0.015
Rye Patch Reservoir	32.3 ± 0.6	1.4 ± 0.1	35.7	0.021 ± 0.010	0.022 ± 0.011
Sutcliffe Pond	31.8 ± 0.1	1.3 ± 0.1	21.4	0.020 ± 0.012	0.023 ± 0.011
Mason Valley	31.6 ± 0.2	1.3 ± 0.1	17.9	0.027 ± 0.020	0.026 ± 0.017
Fleming Management Area	26.6 ± 1.5	1.3 ± 0.1	25.0	0.021 ± 0.016	0.048 ± 0.025
OVERALL MEANS		1.32	24.8	0.023	0.030
Enallagma carunculatum					
Sutcliffe Pond	26.4 ± 1.4	1.9 ± 0.2	57.9	0.101 ± 0.033	0.108 ± 0.033
Pine Reservoir	31.8 ± 0.9	2.4 ± 0.2	78.9	0.092 ± 0.024	0.116 ± 0.028
Taylor Ditch	38.2 ± 0.7	2.1 ± 0.2	68.4	0.077 ± 0.022	0.092 ± 0.025
Guru Pond	29.3 ± 0.3	2.1 ± 0.2	68.4	0.076 ± 0.028	0.105 ± 0.028
Fleming Management Area	28.0 ± 0.5	2.5 ± 0.3	78.9	0.114 ± 0.034	0.144 ± 0.034
Oxbow Pond	19.4 ± 0.5	1.8 ± 0.2	57.9	0.106 ± 0.029	0.135 ± 0.035
Little Washoe	28.9 ± 0.7	2.0 ± 0.2	68.4	0.121 ± 0.037	0.152 ± 0.038
Mason Valley	23.0 ± 2.3	1.9 ± 0.2	63.2	0.082 ± 0.027	0.124 ± 0.032
OVERALL MEANS		2.11	68.5	0.095	0.122

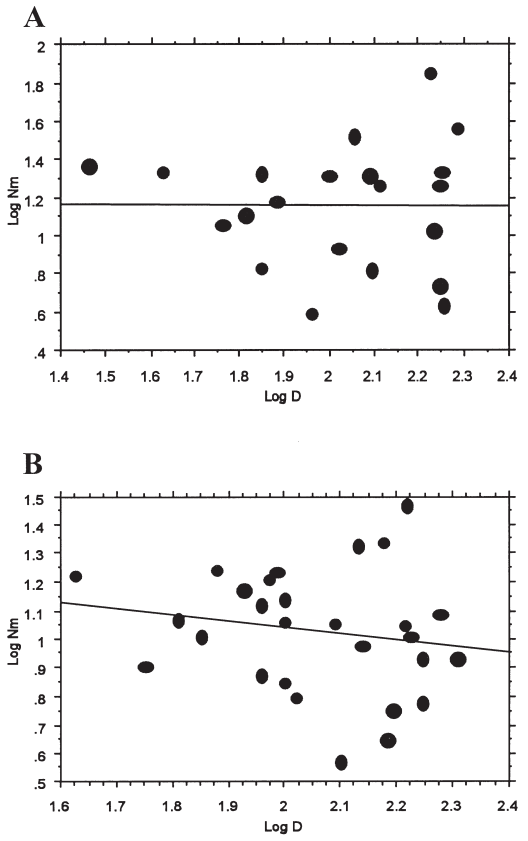

Fig. 2: A, Regression of log pairwise estimates of dispersal (Nm) against log pairwise geographic distances for *Sympetrum corruptum* in the Lahontan Basin, NV. Regression equation: Y = 1.184 * X – 0.013. B, Regression of log pairwise estimates of dispersal (Nm) against log pairwise geographic distances for *Enallagma carunculatum* in the Lahontan Basin, NV. Regression equation: Y = 1.481 * X – 0.220.

polymorphic loci was 44.9%. Mean number of alleles per locus was 2.11. Mean heterozygosity was 9.5% (range 7.6–12.1%; Table 2).

Mean heterozygosity was used to determine deviations from expected Hardy-Weinberg values in a contingency table. Of 103 tests for conformity to Hardy-Weinberg expectations, 24 (23.3%) significant departures were found using Levene's test (1949). All deviations were heterozygote deficiencies. No apparent trends were detected for specific loci or specific populations with high numbers of deficient loci.

After using sequential Bonferroni tests to correct for type I error (Rice 1989), we used contingency chi-square tests for heterogeneity among locations. These tests showed that allele frequencies from at least 1 site differed significantly from the others at 3 of 18 polymorphic loci (Table 3).

Fixation indices were low, suggesting high levels of gene flow. Theta was estimated at 0.0604 with a 95% confidence interval of 0.0184–0.0977. F_{it} was 0.232. Nei's genetic distances (Table 4) were extremely low, with some populations showing virtually no differentiation.

Isolation by distance analysis (Slatkin 1993) yielded a regression slope of –0.220 (Fig. 2B), again showing little evidence for isolation by distance. Nm values were very high (Table 5), indicating effective panmixia (Slatkin 1993).

The simultaneous test procedure (Sokal and Rohlf 1981) grouped all populations from all Lahontan subbasins and outside basins into 1 homogenous group, based on ESTF-1 locus ($G = 0.94$, df = 5, $P = 0.97$) and the GAM-1 locus ($G = 11.92$, df = 5, $P = 0.18$). Analyses using HA-1 showed homogeneity among all populations within the Lahontan Basin ($G = 13.34$, df = 5, $P = 0.08$), but were significantly heterogeneous ($G = 29.85$, df = 5, $P = 0.001$) compared to populations from other pluvial basins (Little Washoe Lake and Oxbow Geothermal Pond).

DISCUSSION

Overall levels of genetic variation were low for both the dragonfly, *Sympetrum corruptum*, and the damselfly, *Enallagma carunculatum*. Heterozygosity, polymorphism, and theta values were fairly low compared to other insects (Hartl and Clark 1989), although the damselfly showed more variability than the dragonfly. This is in contrast to all other studies of Great Basin insects, which have revealed higher levels of genetic variation (Britten et al. 1994, 1995, Porter and Rust 1996, Epps et al. 1998). Because *S. corruptum* is migratory, we did not expect its populations to be very differentiated. However, *E. carunculatum* is a weak flier, and other species in the genus *Enallagma* are extremely philopatric (McPeek 1989), so it is initially surprising that so little genetic structure was found.

Other studies have shown that size and mobility are not necessarily good predictors of the scale at which organisms' distribution and

TABLE 3. Loci showing significant heterogeneity for *Enallagma carunculatum* populations.

Locus	No. of alleles	Chi-square	df	*P*
HA-01	3	84.826	14	0.00000
HBDH1	4	47.360	21	0.00084
GPI-2	3	50.071	14	0.00001

genetic differentiation occur. Corals differ dramatically in gene flow, depending upon the mode of larval dispersal (Hellberg 1996). Moose (*Alces alces*) are large and wide ranging, yet exhibit very structured genetic differences on the order of a few kilometers (Chesser et al 1981). Salmon (Salmonidae), also very wide ranging, are extremely philopatric and genetically differentiated (Allendorf and Waples 1996). Jackson and Resh (1992) hypothesized that aquatic insects with broad geographic ranges and high local abundances would exhibit high levels of gene flow. However, their data did not support their predictions.

Though there was little difference in genetic structure between the 2 species, we did weakly support the expectation of greater structure in the damselfly than in the dragonfly. *Enallagma carunculatum* showed significant heterogeneity at 3 loci (HA-01, HBDH1, GPI-1). Based upon the simultaneous test procedure, geographic distribution of alleles of the HA-01 locus in *E. carunculatum* was homogeneous among all locations within the Lake Lahontan Basin. However, locations within this basin did differ significantly from locations in other pluvial basins. *Sympetrum corruptum* showed no significant heterogeneity. The damselfly also had a greater regression slope in isolation by distance analyses than *S. corruptum*, though neither slope was significantly different from zero (Figs. 2A, B). In contrast, *E. carunculatum* also had higher heterozygosity levels and greater polymorphism than *S. corruptum* (Table 2). Mean heterozygosity levels for both species were within ranges found for other insects (Nevo 1978, Brussard et al. 1985), though Chung et al. (1997) found much higher heterozygosity for *Sympetrum darwinianum* and *S. eroticum eroticum*.

Both *S. corruptum* and *E. carunculatum* deviated from Hardy-Weinberg expectations at several loci; all departures were caused by heterozygote deficiencies. Other studies have found large heterozygote deficiencies in insect populations both within the Great Basin (Porter and Rust 1996) and elsewhere (Higby et al. 1982, Wellso et al. 1988), so this trend may not be particularly unusual in insects. Still, heterozygote deficiencies may be attributable to the Wahlund effect, undetected null alleles (Hartl and Clark 1989), inbreeding, or scoring error. Because we obtained high band resolution, scoring error is unlikely. We cannot rule out inbreeding. One way to assess this possibility further is to sample at a finer scale, using more variable molecular markers.

Low theta values could indicate high gene flow among populations. The scarcity and ephemerality of much of the aquatic habitat within the Great Basin make this region of comparatively poor quality for aquatic organisms. Dobzhansky et al. (1979) showed that *Drosophila pseudoobscura* living in unfavorable habitat move greater distances than those occurring in favorable areas. In fact, colonization and extinction may be the principal modes of gene flow for some species (Slatkin 1985). *Enallagma carunculatum*, which is an ecological generalist, may be able to move long distances in a "stepping stone" fashion by stopping at intermediate water bodies before reaching its breeding location. These long-distance dispersal capabilities may make odonate movement analogous to bird movement (Johnson 1975) within the Great Basin. Therefore, ecological factors may strongly influence the genetic structure of these species. Britten et al. (1995) also determined that ecological and mobility factors are both important in the distribution of the butterfly *Euphydryas editha* in the Great Basin, though the ecological limits resulted in high genetic differentiation among populations of this species.

An explanation for the lack of population structure, especially in the dragonfly species, may be that neither species' populations have reached equilibrium between genetic drift and gene flow, or that they have gone through one or more bottlenecks. While odonates

TABLE 4. Nei's (1978) genetic distances for *Sympetrum corruptum* and *Enallagma carunculatum*.

Population	2	3	4	5	6	7
Sympetrum corruptum						
Artesia Lake	0.000	0.000	0.000	0.001	0.000	0.003
Pine Reservoir		0.000	0.000	0.001	0.000	0.001
Little Washoe Lake			0.000	0.000	0.000	0.002
Rye Patch Reservoir				0.000	0.000	0.003
Sutcliffe Pond					0.001	0.004
Mason Valley						0.002
Fleming Management Area						

Population	2	3	4	5	6	7	8
Enallagma carunculatum							
Sutcliffe Pond	0.007	0.001	0.004	0.002	0.008	0.016	0.002
Pine Reservoir		0.004	0.003	0.001	0.000	0.004	0.003
Taylor Ditch			0.001	0.002	0.005	0.013	0.004
Guru Pond				0.001	0.005	0.010	0.006
Fleming Management Area					0.001	0.005	0.001
Oxbow Pond						0.002	0.003
Little Washoe Lake							0.008
Mason Valley							

TABLE 5. Number of effective migrants (Nm) above the diagonal, and linear distance in km below the diagonal for *Sympetrum corruptum* and *Enallagma carunculatum*.

Population	1	2	3	4	5	6	7
Sympetrum corruptum							
Artesia Lake	***	6.74	11.20	36.47	33.21	23.08	21.65
Pine Reservoir	71.0	***	3.81	18.16	20.28	21.42	18.18
Little Washoe Lake	57.8	91.6	***	4.26	21.33	12.77	20.55
Rye Patch Reservoir	194.0	130.9	180.3	***	6.54	71.21	10.51
Sutcliffe Pond	114.7	100.4	71.1	125.3	***	8.35	14.92
Mason Valley	28.9	42.6	64.9	168.9	104.9	***	5.37
Fleming Management Area	178.7	176.3	123.3	171.6	76.1	176.3	***

Population	1	2	3	4	5	6	7	8
Enallagma carunculatum								
Sutcliffe Pond	***	7.00	13.88	16.13	17.37	21.18	10.27	6.16
Pine Reservoir	100.4	***	11.47	10.09	8.53	14.84	13.18	16.55
Taylor Ditch	100.5	100.8	***	17.11	5.63	7.92	21.67	9.39
Guru Pond	94.1	168.2	96.7	***	7.53	4.43	29.58	12.14
Fleming Management Area	76.1	176.3	156.7	91.2	***	8.57	11.25	5.94
Oxbow Pond	136.2	84.6	56.2	152.7	202.8	***	11.14	3.70
Little Washoe Lake	71.1	91.6	151.1	165.4	123.3	164.3	***	11.71
Mason Valley	104.9	42.6	137.9	189.8	176.3	126.8	64.9	***

probably originally colonized Lake Lahontan more than 35,000 yr ago when water was plentiful, the Great Basin has been very arid with largely ephemeral water sources since the end of the Pleistocene (approximately 10,000 YBP). Because their larval stages are completely aquatic, odonate populations probably cannot persist when bodies of water dry up for any length of time. Therefore, many habitats must be recolonized, or "rescued," by immigration (Brown and Kodric-Brown 1977) after periods of drought. This scenario involves frequent founder and rescue events that facilitate gene flow and commonly leave populations in a state of disequilibrium (Slatkin 1987, Boileau et al. 1992).

All deviations from Hardy-Weinberg equilibrium for both species were heterozygote

deficiencies, suggesting within-population inbreeding. The high Nm values for both species and lack of evidence of isolation by distance also suggest that these species are recent colonizers (Slatkin 1993). This further supports the possibility that ephemeral conditions dictate frequent founder events and population bottlenecks. Without knowing the duration of these bottlenecks or the effective population sizes of the founding groups, it is difficult to determine the impact of these events. However, both the lack of allelic diversity and the heterozygote deficiencies seen in the 2 species may indicate that these events occurred.

Differences in heterozygosity and polymorphism levels between the 2 species are difficult to interpret, given what is understood about their natural histories. The migratory dragonfly, which seems to be very vagile, had lower variability than the supposedly sedentary damselfly. The 2 species may be affected by different constraints operating either historically or recently. For example, a severe bottleneck that reduced dragonfly variability in an ancestral population could result in low variability now despite high vagility. It is also possible that the damselfly is much more vagile than we expected, especially in wet conditions. Its natural history in arid regions is not well known; its abundance and occurrence at ecologically diverse habitats suggest that it may be a much better disperser than its weak flight capabilities seem to indicate.

At the onset of this study, we hypothesized that apparently differing mobilities would significantly affect gene flow, and that physiographic sills surrounding isolated basin habitats would act as barriers to odonate dispersal. While there was evidence of greater genetic structure in *Enallagma carunculatum* than in *Sympetrum corruptum,* our results did not overwhelmingly support these hypotheses. With little structure and no evidence for isolation by distance, extinction and recolonization occurring in a variable and often unfavorable habitat seem likely. This would result in a lack of equilibrium between migration and drift. Additionally, high F_{it} and rather low heterozygosity suggest that within-population inbreeding has been occurring. This implies possible bottlenecks or isolation of subpopulations. Further study, perhaps using more sensitive molecular markers, can assess within-population inbreeding more completely.

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APPENDIX. Allele frequencies at polymorphic loci in *Sympetrum corruptum* populations. Sample sizes are in parentheses. Populations are coded as follows: (1) Artesia Lake, (2) Stillwater, (3) Washoe Lake, (4) Rye Patch Reservoir, (5) Sutcliffe Pond, (6) Walker Basin, and (7) Honey Lake.

	Population						
Locus	1	2	3	4	5	6	7
AK-01	(29)	(45)	(24)	(34)	(32)	(32)	(30)
B	0.000	0.000	0.000	0.015	0.031	0.000	0.000
C	1.000	1.000	1.000	0.985	0.953	1.000	1.000
D	0.000	0.000	0.000	0.000	0.016	0.000	0.000
AK-02	(27)	(44)	(9)	(26)	(32)	(32)	(4)
C	1.000	1.000	1.000	0.981	1.000	1.000	1.000
D	0.000	0.000	0.000	0.019	0.000	0.000	0.000
AAT-1	(29)	(45)	(24)	(34)	(32)	(31)	(30)
C	1.000	0.989	0.979	0.985	1.000	0.984	1.000
D	0.000	0.011	0.021	0.015	0.000	0.016	0.000
HBDH1	(29)	(44)	(24)	(34)	(32)	(31)	(30)
B	0.000	0.000	0.021	0.015	0.000	0.000	0.000
C	1.000	0.989	0.979	0.985	1.000	1.000	1.000
D	0.000	0.011	0.000	0.000	0.000	0.000	0.000
LAP-1	(29)	(45)	(23)	(34)	(31)	(31)	(30)
B	0.000	0.000	0.000	0.015	0.000	0.000	0.000
C	1.000	1.000	1.000	0.985	1.000	1.000	1.000
LAP-2	(29)	(42)	(19)	(34)	(30)	(32)	(7)
B	0.000	0.048	0.000	0.000	0.000	0.000	0.143
C	1.000	0.952	1.000	1.000	1.000	1.000	0.857
PGM-3	(26)	(32)	(23)	(34)	(32)	(32)	(30)
B	0.000	0.000	0.000	0.000	0.016	0.000	0.000
C	1.000	1.000	1.000	1.000	0.984	1.000	1.000
PRO-4	(29)	(42)	(22)	(34)	(32)	(32)	(25)
B	0.000	0.000	0.000	0.000	0.000	0.000	0.040
C	1.000	1.000	1.000	1.000	1.000	1.000	0.960
PRO-6	(9)	(40)	(14)	(34)	(32)	(32)	(30)
C	1.000	1.000	1.000	1.000	1.000	0.969	1.000
D	0.000	0.000	0.000	0.000	0.000	0.031	0.000
LDH-1	(23)	(44)	(23)	(34)	(32)	(32)	(30)
B	0.000	0.000	0.043	0.000	0.000	0.000	0.033
C	1.000	1.000	0.957	1.000	1.000	0.984	0.967
D	0.000	0.000	0.000	0.000	0.000	0.016	0.000
EST-1	(29)	(45)	(24)	(34)	(32)	(32)	(30)
C	1.000	1.000	0.958	1.000	1.000	1.000	1.000
D	0.000	0.000	0.042	0.000	0.000	0.000	0.000
EST-2	(29)	(45)	(24)	(34)	(32)	(32)	(30)
A	0.000	0.000	0.000	0.000	0.000	0.016	0.017
B	0.017	0.033	0.083	0.000	0.016	0.031	0.267
C	0.741	0.689	0.750	0.809	0.844	0.672	0.500
D	0.241	0.278	0.167	0.191	0.141	0.281	0.217
EST-3	(29)	(45)	(24)	(34)	(32)	(32)	(30)
B	0.000	0.000	0.021	0.015	0.000	0.000	0.000
C	1.000	1.000	0.979	0.985	1.000	1.000	1.000
GPI-1	(23)	(45)	(24)	(34)	(32)	(32)	(30)
B	0.000	0.011	0.000	0.000	0.000	0.000	0.000
C	1.000	0.933	0.958	0.971	0.922	0.938	0.950
D	0.000	0.056	0.042	0.029	0.078	0.063	0.050
MDH-1	(29)	(45)	(24)	(34)	(32)	(32)	(30)
C	0.966	1.000	1.000	1.000	0.969	1.000	1.000
D	0.034	0.000	0.000	0.000	0.031	0.000	0.000
MDH-2	(29)	(45)	(24)	(34)	(32)	(32)	(30)
C	1.000	1.000	1.000	1.000	1.000	1.000	0.967
D	0.000	0.000	0.000	0.000	0.000	0.000	0.033

APPENDIX. Continued

	Population						
Locus	1	2	3	4	5	6	7
MPI-1	(29)	(45)	(24)	(28)	(32)	(32)	(30)
B	0.000	0.011	0.000	0.000	0.000	0.000	0.000
C	0.914	0.978	0.958	0.982	1.000	1.000	1.000
D	0.086	0.011	0.042	0.018	0.000	0.000	0.000
MPI-2	(29)	(45)	(11)	(24)	(31)	(32)	(30)
B	0.000	0.011	0.000	0.000	0.016	0.000	0.000
C	1.000	0.989	1.000	1.000	0.984	1.000	1.000
DIA-2	(29)	(44)	(24)	(28)	(32)	(31)	(30)
B	0.052	0.000	0.000	0.018	0.000	0.000	0.067
C	0.897	0.966	1.000	0.982	1.000	1.000	0.933
D	0.052	0.023	0.000	0.000	0.000	0.000	0.000
E	0.000	0.011	0.000	0.000	0.000	0.000	0.000

Allele frequencies in polymorphic loci in *Enallagma carunculatum* populations. Sample sizes are in parentheses. Populations are coded as follows: (1) Sutcliffe Pond, (2) Pine Reservoir, (3) Taylor Ditch, (4) Guru Pond, (5) Fleming Management Area, (6) Oxbow Pond, (7) Little Washoe Lake, and (8) Mason Valley.

	Population							
Locus	1	2	3	4	5	6	7	8
HA-01	(31)	(33)	(39)	(27)	(26)	(24)	(30)	(8)
B	0.000	0.000	0.000	0.056	0.077	0.000	0.000	0.000
C	0.968	0.712	0.962	0.889	0.731	0.708	0.550	0.750
D	0.032	0.288	0.038	0.056	0.192	0.292	0.450	0.250
HA-02	(31)	(34)	(39)	(28)	(25)	(19)	(30)	(8)
B	0.016	0.088	0.000	0.071	0.020	0.079	0.033	0.000
C	0.984	0.912	1.000	0.929	0.980	0.921	0.967	1.000
EST-1	(31)	(34)	(39)	(30)	(30)	(20)	(30)	(29)
A	0.000	0.029	0.000	0.000	0.000	0.000	0.000	0.000
B	0.000	0.029	0.038	0.033	0.017	0.050	0.050	0.017
C	0.952	0.912	0.962	0.933	0.917	0.900	0.933	0.948
D	0.032	0.015	0.000	0.033	0.050	0.025	0.017	0.017
E	0.016	0.015	0.000	0.000	0.017	0.025	0.000	0.017
EST-2	(30)	(34)	(39)	(30)	(29)	(20)	(30)	(30)
B	0.050	0.044	0.013	0.000	0.000	0.075	0.000	0.033
C	0.950	0.956	0.987	1.000	1.000	0.925	0.917	0.967
D	0.000	0.000	0.000	0.000	0.000	0.000	0.083	0.000
GAM-2	(30)	(33)	(39)	(28)	(25)	(20)	(30)	(30)
A	0.033	0.061	0.000	0.018	0.100	0.125	0.033	0.117
B	0.067	0.030	0.077	0.089	0.020	0.100	0.200	0.050
C	0.900	0.909	0.897	0.893	0.860	0.775	0.767	0.833
D	0.000	0.000	0.026	0.000	0.020	0.000	0.000	0.000
IDH-1	(31)	(34)	(39)	(30)	(29)	(20)	(30)	(25)
B	0.000	0.015	0.000	0.000	0.017	0.025	0.033	0.000
C	1.000	0.971	0.987	0.983	0.983	0.950	0.967	0.920
D	0.000	0.015	0.013	0.017	0.000	0.025	0.000	0.080
MPI-1	(31)	(34)	(39)	(30)	(27)	(20)	(29)	(26)
A	0.016	0.015	0.013	0.000	0.000	0.000	0.000	0.000
B	0.032	0.015	0.077	0.000	0.037	0.050	0.052	0.038
C	0.871	0.912	0.859	0.983	0.907	0.875	0.914	0.865
D	0.081	0.059	0.051	0.017	0.037	0.075	0.034	0.096
E	0.000	0.000	0.000	0.000	0.019	0.000	0.000	0.000
MPI-2	(29)	(34)	(39)	(30)	(27)	(20)	(24)	(24)
B	0.000	0.000	0.000	0.000	0.019	0.000	0.021	0.000
C	1.000	0.985	1.000	0.983	0.981	1.000	0.979	1.000
D	0.000	0.015	0.000	0.017	0.000	0.000	0.000	0.000

APPENDIX. Continued

	Population						
Locus	1	2	3	4	5	6	7
PGM-2	(31)	(34)	(39)	(30)	(30)	(20)	(30)	(30)
B	0.000	0.015	0.000	0.000	0.017	0.000	0.000	0.000
C	0.984	0.971	0.962	1.000	0.983	1.000	1.000	1.000
D	0.016	0.015	0.038	0.000	0.000	0.000	0.000	0.000
HBDH1	(31)	(34)	(39)	(30)	(30)	(20)	(30)	(30)
B	0.000	0.029	0.000	0.000	0.000	0.000	0.000	0.033
C	1.000	0.971	1.000	0.917	1.000	1.000	1.000	0.967
D	0.000	0.000	0.000	0.067	0.000	0.000	0.000	0.000
E	0.000	0.000	0.000	0.017	0.000	0.000	0.000	0.000
PGD-2	(10)	(34)	(39)	(30)	(28)	(20)	(30)	(29)
A	0.000	0.015	0.000	0.017	0.036	0.000	0.017	0.000
B	0.250	0.279	0.269	0.300	0.286	0.325	0.300	0.190
C	0.750	0.706	0.731	0.683	0.661	0.675	0.683	0.810
D	0.000	0.000	0.000	0.000	0.018	0.000	0.000	0.000
G3P-1	(31)	(34)	(39)	(30)	(30)	(20)	(30)	(30)
B	0.000	0.000	0.000	0.000	0.017	0.000	0.000	0.050
C	1.000	1.000	1.000	1.000	0.983	1.000	1.000	0.950
GAPDH	(24)	(33)	(39)	(30)	(29)	(20)	(30)	(30)
B	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.033
C	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.967
DIA-1	(24)	(31)	(39)	(29)	(30)	(19)	(29)	(30)
A	0.000	0.000	0.026	0.017	0.000	0.000	0.000	0.000
B	0.063	0.016	0.051	0.021	0.067	0.000	0.121	0.033
C	0.917	0.935	0.885	0.828	0.850	1.000	0.810	0.917
D	0.021	0.048	0.038	0.034	0.067	0.000	0.069	0.050
E	0.000	0.000	0.000	0.000	0.017	0.000	0.000	0.000
DIA-2	(19)	(29)	(38)	(30)	(30)	(19)	(30)	(30)
B	0.000	0.000	0.000	0.000	0.017	0.000	0.000	0.000
C	1.000	0.966	0.974	1.000	0.950	0.868	0.933	1.000
D	0.000	0.034	0.026	0.000	0.033	0.132	0.067	0.000
PGD-1	(21)	(28)	(39)	(27)	(24)	(12)	(29)	(1)
A	0.000	0.036	0.013	0.000	0.042	0.000	0.000	0.000
B	0.000	0.000	0.013	0.074	0.063	0.000	0.017	0.000
C	1.000	0.929	0.974	0.926	0.896	0.917	0.776	1.000
D	0.000	0.036	0.000	0.000	0.000	0.083	0.207	0.000
PEP-1	(27)	(33)	(39)	(27)	(29)	(20)	(30)	(6)
B	0.093	0.000	0.026	0.037	0.000	0.000	0.000	0.000
C	0.852	0.970	0.897	0.944	0.897	1.000	1.000	1.000
D	0.056	0.030	0.077	0.019	0.103	0.000	0.000	0.000
GPI-1	(18)	(20)	(39)	(30)	(28)	(18)	(30)	(29)
A	0.111	0.000	0.000	0.000	0.054	0.000	0.000	0.034
B	0.194	0.000	0.064	0.033	0.107	0.056	0.067	0.224
C	0.694	1.000	0.936	0.967	0.839	0.944	0.933	0.741