

Variation in Populations of Yarrow's Spiny Lizard, *Sceloporus jarrovi*, in the Northern Madrean Archipelago Region

George Middendorf and Jack Frankel
Department of Biology, Howard University, Washington, DC

Douglas Ruby
Department of Natural Science, University of Maryland Eastern Shore, Princess Anne, MD

Abstract—Population genetic analysis of Yarrow's spiny lizard, *Sceloporus jarrovi*, suggests a meta-population distribution pattern with potential divergence of genetically based traits. Comparing male pushup displays revealed populations east and west of the San Pedro River valley to be more similar among themselves than to those on the other side. Intensive studies of a single population revealed high site fidelity and movement constrained by the availability of crevices suitable for over-wintering and habitat with suitable thermal and humidity ranges. Observations suggest a species that does not disperse over large distances, and that current distribution patterns arose during extended Pleistocene pluvial periods.

Introduction

Because understanding population structure is a major concern for ecologists, the use of electrophoretic and molecular techniques to traditional approaches has been of great benefit. However, they have been viewed skeptically rather than as supportive (Avice 1994). Patterns of dispersal, mating systems, migrations and genetic drift due to isolation influence population gene flow and genetic integrity. If barriers reduce dispersal and isolate populations, divergence among populations may occur. Suites of characteristics can be compared to identify selection pressures (whether environmental change or due to drift and stochastic forces) and the strength of genetic change. Fragmented populations can provide natural experiments of evolution in parallel, and comparison among isolated populations can provide important information concerning historical dispersal events (Foster and Endler 1999). In a series of studies over the past 30 years, we collected data on population structure and dispersal in a geographically fragmented montane lizard. Together, these data provide a more complete understanding of factors influencing current populations and historical movement patterns.

Whether some classes of traits evolve faster than other categories has been controversial in evolutionary studies, but the issue has intensified with new molecular techniques (Flores-Villela et al. 2000). Behavioral traits might be considered more conservative, that is, more resistant to change in gene frequency, than either molecular or morphological traits because behaviors, particularly reproductive behaviors, should be subject to strong stabilizing selection where species identification, fitness cues, and mate choice are important. If unusual or novel displays are selected against, stabilizing selection may constrain variation. Conversely, sexual selection

may force rapid change if specific display patterns are favored (Masta and Maddison 2002). Thus, among-population variation in reproductive display patterns is biologically interesting (Foster and Cameron 1996).

Because lizards use pushup displays in territorial displays and courtship (Carpenter and Ferguson 1977), they play an important communication role and should be subject to strong selection pressures. Whether the selection is stabilizing or directional has not been well investigated. Carpenter (1978) analyzed displays in many iguanid lizards for a phylogenetic analysis and treated each species as independent units, ignoring population and individual level variation. His analysis revealed enormous variation, even among related species, and phylogenetic relationships were not clearly delineated. More recently, Martins' (1993) reanalysis of these data revealed low predictability of display pattern to either body size or habitat. Although geographic variation in pushup displays in *Uta* and *Sceloporus* was examined by Ferguson (1971, 1973), such an approach has been poorly appreciated as an evolutionary tool for understanding population structure. Comparisons of electrophoretic and behavioral variation would be useful in testing hypotheses about congruent changes in characters.

The montane lizard *Sceloporus jarrovi* occurs in a disjunct geographic distribution in the island mountains of southern Arizona and New Mexico (Chaplin 1964). Most of its biology is known from work in the Chiricahuas (Ballinger 1973; 1979 Duncan et al. 2003; Middendorf 1984; Middendorf and Simon 1988; Simon 1975; Simon and Middendorf 1976, 1980), the Pinalenos (Ruby 1977, 1978, 1981, 1986; Ruby and Baird 1993, 1994), and the Quinlan Mountains (Goldberg 1971). However, genetic, morphological, and behavioral variation, which might result from the current fragmented geographic distribution, has not been fully examined.

The goal of this study is to discuss electrophoretic variation among populations, to characterize behavioral displays in ten mountain ranges within Arizona and New Mexico, with emphasis on five major mountains, and to document patterns of dispersal of individual lizards. Together, the results may infer constraints on history of these populations, suggest selective factors affecting displays, and allow testing of hypotheses about display evolution by treating each population as a phylogenetic unit (Foster and Cameron 1996).

Methods

Genetics

The genetic differences within and among populations of *S. jarrovi* in the southeastern Arizona region were investigated by examining the electrophoretic profiles of soluble esterase isozymes. Tissue samples were obtained from the tail muscle of 313 individuals sampled from 37 locations in southeastern Arizona. Lizards were collected at study sites in the Chiricahua, Huachuca, Pinaleno, and Santa Rita Mountains. In the Chiricahua Mountains, lizards were obtained from a total of 17 collection sites; four locations in Pinery Canyon (30 females, 24 males), five in Turkey Creek (33 females, 29 males), three in Cave Creek Canyon (20 females, 34 males), one in Tex Canyon (7 females, 0 males), and four in Rucker Canyon (25 females, 30 males). In the Huachuca Mountains, lizards were sampled from multiple locations in Ramsey Canyon (15 females, 6 males) and from a single study site in Carr Canyon (3 females, 0 males). In the Pinaleno Mountains, lizards were sampled from four locations on Mount Graham (30 females, 8 males). In the Santa Rita Mountains, lizards were obtained from study sites in Madera Canyon (12 females, 7 males). Protein samples were obtained from each tail by removing the skin and vertebrae, and homogenizing the muscle with a glass tissue grinder in an equal volume of 2% 2-phenoxyethanol (Spohn and Guttman 1976). Homogenates were centrifuged at 4 °C, and 40 µl aliquots of supernatant were subjected to electrophoretic analysis.

Electrophoresis was conducted using an acrylamide vertical slab system, maintained at 4 °C. Samples were run on 6% gels containing a 0.375 M Tris-HCl buffer at pH 8.9 at 300 V for 3 hr. The electrode buffer was 0.3 M sodium borate at pH 8.0. The gels were incubated in solutions containing alpha-naphthyl acetate, beta-naphthyl acetate, or alpha-naphthyl propionate.

Esterases were classified by their relative susceptibility to various sulfhydryl and organophosphorus inhibitors (Tashian 1965; Holmes and Whitt 1970; Frankel 1982). These included eserine sulfate (ES), diisopropylfluorophosphate (DFP), parahydroxymercuribenzoate (PHMB), and parachloromercuribenzoate (PCBM). Esterases inhibited by ES and DFP are classified as cholinesterase, those by DFP alone as carboxylesterase, and those by PHMB and/or PCBM as arylesterase. Isozymes resistant to all inhibitors are designated as esterase resistant (ER), and those resistant to inhibition but preferentially hydrolyzing acetate substrate as acetylcholinesterase.

Display Analyses

Animals were extensively filmed at sites in five mountain ranges in southeastern Arizona: the Chiricahuas (Cave Creek Canyon), Pinalenos (Wet Canyon), Dragoons, Huachucas (Miller Canyon), and Santa Ritas (Madera Canyon). In each range, displays of eight to ten resident males were filmed by staging aggressive encounters with a tethered intruder male of similar size. Fewer displays were filmed in five other ranges: the Dos Cabezas, Galiuro, Animas, Peloncillo, and Mule Mountains. Filming was done during summers of 1973-1974 and 1995-1997. Movies were taken with a Bolex H16 movie camera with 80 mm zoom lens or a Sony videocam with zoom lens. Films were analyzed frame by frame on a Vanguard motion analyzer (24 f/s) or measured on a video monitor screen (30 f/s).

For the five major ranges, the timing of specific units of the display and the relative height of display units (H1, H2, etc., depending on their position in the display sequence) were measured, ratios were calculated, and average values were computed for each mountain range. Relative heights of displays were used because of variation in the field condition, such as the size of lizards, the distance between animal and camera, and the amount of zoom. The unit 1 in each display set served as an arbitrary standard of relative height. Differences between mountain ranges were examined through a comparison of typical patterns. Because homologies among display elements remain presumptive at this time, statistical analyses were not conducted. Variation between individuals within a population may occur but is not reported here.

Dispersal

Patterns of movement by individual lizards were examined through mark-recapture studies of *Sceloporus jarrovi* in Crystal Creek Canyon in the Chiricahua Mountains. During six study periods from March 2001 through July 2003, 460 lizards were noosed along a 0.5 km transect. Animals were captured during a 1-2 week period in March when in their winter hibernacula locations and during a 3-4 week period in July on their summer territories. For each capture, we recorded location in the canyon, size (snout-vent and tail length), weight, and sex. All animals were individually identified by toe-clipping and paint-marked. Data were analyzed to determine distances moved by individuals on seasonal (between hibernacular and territorial sites) and annual (between hibernacular sites and between territorial sites) bases.

Results

Genetics

Electrophoretic differences exist both within and between populations of *S. jarrovi*. A total of three soluble esterase phenotypes were exhibited by *S. jarrovi* from the 37 collection sites. Electropherograms of all lizards expressed a highly anodal zone of esterolytic activity (isozyme a), probably

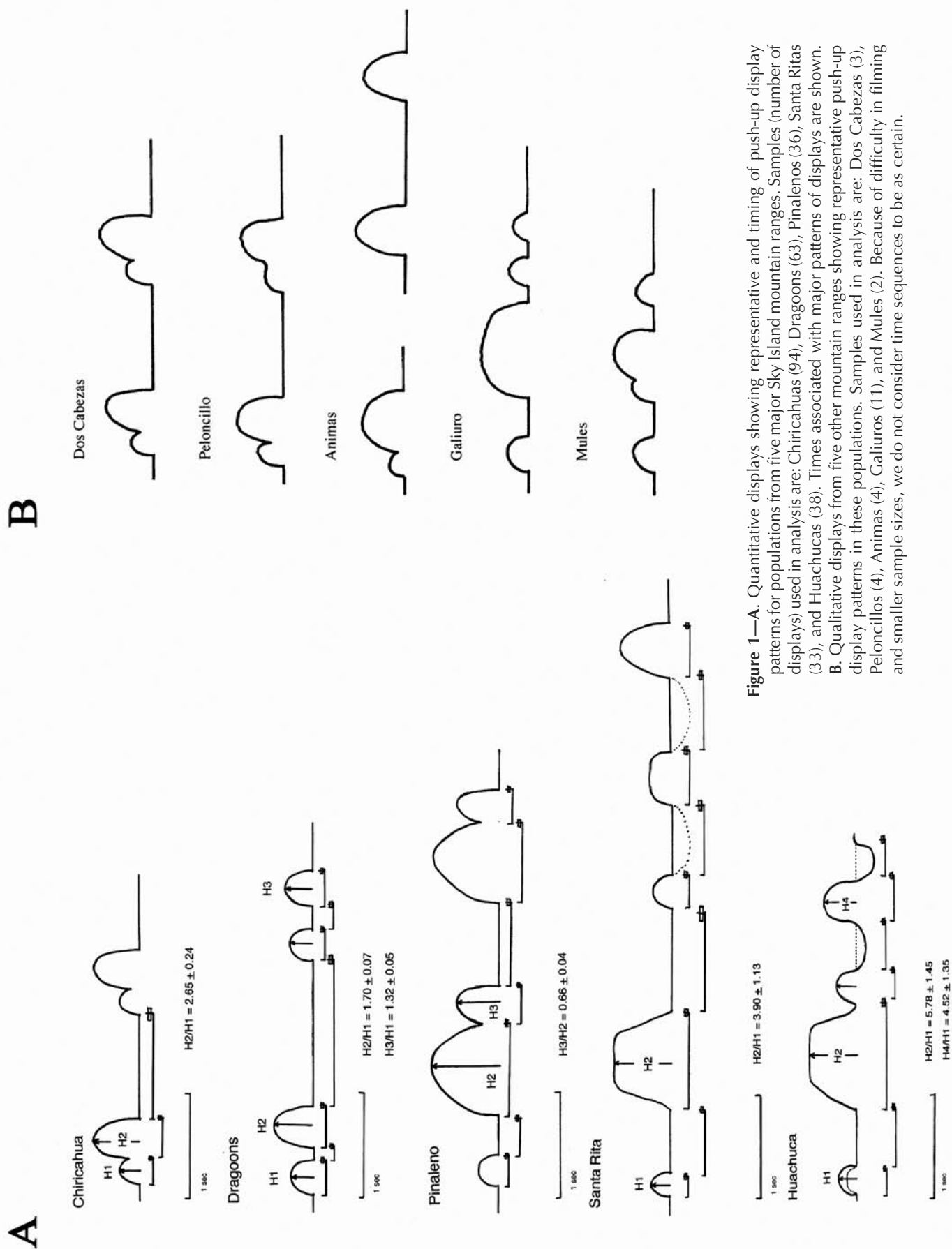


Figure 1—A. Quantitative displays showing representative and timing of push-up display patterns for populations from five major Sky Island mountain ranges. Samples (number of displays) used in analysis are: Chiricahua (94), Dragoons (63), Pinalenos (36), Santa Rita (33), and Huachuca (38). Times associated with major patterns of displays are shown. **B.** Qualitative displays from five other mountain ranges showing representative push-up display patterns in these populations. Samples used in analysis are: Dos Cabezas (3), Peloncillos (4), Animas (4), Galiuros (11), and Mules (2). Because of difficulty in filming and smaller sample sizes, we do not consider time sequences to be as certain.

resulting from the expression of a monomorphic locus designated as *Est-1*. A second zone of activity (isozymes b, c, and d) for each phenotype probably results from the expression of a polymorphic locus (*Est-2*). Lizards sampled from each of the Chiricahua and Huachuca locations exhibited one of two phenotypes, each showing the single zone of EST-1 activity and two zones of EST-2 activity, i.e., isozymes abc or abd, although the genetic basis for these phenotypes is unclear. Further, lizards sampled from sites in the Pinalenos and Santa Ritas exhibited only a single zone of EST-2 activity, along with the monomorphic expression of the *Est-1* locus (i.e., isozymes ab).

Each of the four esterase isozymes was capable of estero-lytic activity with all substrates. The EST-1 isozyme (a), by virtue of its sensitivity to PHMB and PCBM, was classified as an arylesterase. Isozymes b, c, and d were found to be sensitive to inhibition by DFP and were classified as carboxylesterases. Since no breeding data are available, the genetic basis for the esterase phenotypes is inferred from their electrophoretic and inhibitor profiles. Indeed, our studies support the presence and expression of two esterase loci: *Est-1* encoding an arylesterase (isozyme a) and *Est-2* carboxylesterases b, c, and d.

Display Analyses

Each of five major populations studied (and most others) has distinct pushup patterns noticeable even to human observers and presumably also to lizards (figure 1). Moreover, we recognize a division into eastern and western patterns, where populations are separated by the San Pedro River drainage, which runs north/south through this part of Arizona and joins the Gila River north of Phoenix. The three major populations in the east (Chiricahuas, Pinalenos, and Dragoons) had relatively simple displays of repetitions of two peak units that differ between populations in both comparative height and timing (table 1; figure 1). Three other populations in the east (Dos Cabezas, Peloncillo, and Animas Mountains) have similar displays to the Chiricahuas, probably resulting from their proximity to one another. The Dos Cabezas connects to the Chiricahuas via a series of low hills, while the Animas and Peloncillos are geographically close to the Chiricahuas. Further analysis of these mountains may reveal more subtle population level differences. The western populations (Huachucas and Santa Ritas) displayed longer and more varied sequences, including a dip downward below the starting height. Eastern populations

Table 1—Ratios of display elements in five major populations of *Sceloporus jarrovi* in Arizona.

Mountain range	No. animals	Display elements	Ratio (X ± SD)
Chiricahuas	11	H2/H1	2.65 ± 0.24
Pinaleno	13	H3/H2	0.66 ± 0.04
Dragoons	8	H2/H1	1.70 ± 0.07
Dragoons	8	H3/H1	1.32 ± 0.05
Santa Ritas	9	H2/H1	3.90 ± 1.13
Huachucas	10	H2/H1	5.78 ± 1.45
Huachucas	10	H4/H1	4.52 ± 1.35

were more similar among themselves than any were to the western populations and vice versa.

Dispersal

Total distance moved by individual lizards ranged from 0 to 138 m ($x = 13.7 \pm 22.7$ m; $n = 98$) between first and last capture (range = 107 to 851 days). When adjusted for time, daily movement ranged between 0 and 0.4 m/day ($x = 0.05 \pm 0.09$ m/day; $n = 98$). Daily movement by males (range = 0-0.43; $x = 0.06 \pm 0.09$ m/day; $n = 44$) did not differ greatly from females (range = 0-0.38; $x = 0.05 \pm 0.08$ m/day; $n = 54$). Most lizards did not move all that far between first and last capture sites; 72 of 98 (73%) moved <10 m. However, while a few of these were recaptured close to their original point of capture, they moved considerable distances either seasonally or annually. For instance, one male moved 167 m up canyon between March 2002 and 2003, and by July 2003, 177 m down canyon—returning to within 10 m of the point of original capture.

Seasonal movement (March-July or July-March) ranged from 0 to 177 m ($x = 17.0 \pm 32.8$ m; $n = 43$). Seasonal movement by males (range = 0-177; $x = 24.0 \pm 38.6$ m; $n = 19$) exceeded that of females (range = 0-128; $x = 11.5 \pm 27.0$ m; $n = 24$). Annual movement between hibernacula (March-March) differed from that between territories (July-July). Average hibernacula movement ranged from 0 to 167 m ($x = 20.6 \pm 38.9$ m; $n = 28$), while average territorial movement ranged between 0 and 150 m ($x = 12.4 \pm 21.8$ m; $n = 55$). Note that the vast majority of individuals moved quite limited distances (table 2), and that the dispersal between hibernacula or from one territory to another are not significantly different ($p > 0.05$).

Discussion

We found geographic variation in molecular and behavioral traits among montane populations of *S. jarrovi* that can be related to isolation of populations since the Pleistocene and to the annual movement pattern of this territorial species. Animals sampled from the Pinalenos and Santa Ritas exhibited no variation at either the *Est-1* or *Est-2* loci; these individuals are monomorphic at these loci and exhibit the ab phenotype exclusively. Their esterase profile is clearly distinguishable from

Table 2—Numbers of individuals shown by category range for annual movement between winter hibernacula ($n = 28$) and between summer territories ($n = 55$).

Range category (m)	Hibernacula	Territory
0-25	20	47
26-50	5	7
51-75	1	0
76-100	0	0
101-125	0	0
126-150	1	0
151-175	1	1
176-200	0	0

those animals sampled from collecting sites in the Chiricahua and Huachuca Mountains (see also Frankel and Middendorf 1991), and is suggestive of a major barrier to gene flow between populations inhabiting these distinct locales, perhaps in conjunction with historical dispersal events, but this isozyme pattern does not follow the expected split between east and west of the San Pedro River drainage.

Display patterns for different populations follow two general forms. Patterns in the eastern populations show a higher, tighter combination of two initial units (H1 and H2), while the western populations exhibit longer, slower displays, along with dips in the latter portions of the display that heighten following peak(s). Display differences among individual ranges in both the eastern and western groups are distinguishable. While determination of homologies between displays as varied as the ten populations under study is complicated by the east-west differences, the results support the electrophoretic conclusions presented above and elsewhere (Middendorf and Frankel 1992), as well as suggesting that populations have been isolated for a significant evolutionary time (between 8,000-10,000 years) with significant divergence (Van Devender 1995). The similarity in pushup patterns within eastern and within western populations suggests clustering as a result of a major separation event with subsequent fragmentation into individual mountain populations as seen today (figure 1).

The regional differences between populations may represent founder effects or genetic drift after the complete fragmentation occurred. Habitats where *S. jarrovi* is found are similar for all sites. Both thermal and humidity requirements for habitat are indicated because the species is typically associated with rocky outcrops in the oak-juniper community or higher elevations. Because it is restricted to elevations above 1,400 m, acceptable dispersal corridors across the desert seas between mountain islands probably require much more mesic conditions. Currently these Sky Island mountains are separated by inhospitable terrain (Gehlbach 1981). The east-west divide in *S. jarrovi* populations is marked by the San Pedros River drainage, a particularly low elevation zone that may have barred east-west dispersal in the past, even while more localized dispersal occurred between ranges. Regional topography suggests suitable connecting habitat between eastern and western populations would be much further south in Mexico. Our data suggest a pattern comparable to that of jumping spiders in the Arizona Sky Islands, which includes an inverse relationship between display similarity and geographic distance (Maddison and McMahon 2000; Masta and Maddison 2002). Conceptually similar barriers to dispersal have been proposed for tropical species (Janzen 1967) and for *Cnemidophorus tigris* hybridization in lowland, desert habitat (Dessauer et al. 2000).

Movement between hibernacula and territories, site fidelity to both, and over-wintering aggregations occur in *S. jarrovi* (Burns 1970; Ruby 1977) and are known for other reptiles, e.g., lizards (Boykin and Zucker 1993; Weintraub 1968) and snakes (Aleksuik 1976; Parker and Brown 1980). Distribution and dispersal of *S. jarrovi* appears constrained as individuals did not generally move long distances and observed movements were often back and forth, rather than to more distant locations. Given that reproduction takes place in September

and October (Ruby 1981), effective gene flow is likely to be restricted by the distance an individual moves from hibernacula to territory and the spatial distribution of each. When spacing exceeds territorial dispersal distance, gene flow between these isolated populations is reduced to only those few, over-dispersing individuals.

Further research into geographic variation of behavior, morphology, and molecular characters is currently underway. Comparison of the behavioral divergences with molecular (mitochondrial or nuclear DNA) and morphological traits will provide insight into gene flow and population structure within a population as well as, we believe, demonstrate the "phylogeography" (*sensu* Foster and Cameron 1996) of this now disjunctly distributed species.

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