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A TEST OF THE CENTRAL-MARGINAL MODEL USING SAND SCORPION POPULATIONS (*PARUROCTONUS MESAENSIS*, VAEJOVIDAE)

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ABSTRACT. The central-marginal model proposes marginal populations contain a lower density of individuals, lower levels of genetic variation, and are more isolated than populations in the center of a species range. Previous tests of the model used *Drosophila,* organisms capable of extended dispersal. We test the central-marginal model with scorpions, organisms with restricted dispersal abilities. We measured genetic variation through allozyme analysis of eight loci (five polymorphic, three monomorphic) to obtain estimates of heterozygosity. We compared differences between the two types of populations with a split-plot ANOVA. We also compared central and marginal populations using standard parametric tests. We found marginal populations contain lower genetic variation than central populations. These populations may be important as models in conservation to study the effects of fragmentation.

Peripheral or marginal populations are those on the boundaries of a species' geographic range. They exhibit unique properties not evident in populations in the center (Brussard 1984). Generally, as one moves outward from the center of a species' range, populations are hypothesized to become less dense, more isolated, and less variable genetically within populations (da Cunha et al. 1959; da Cunha & Dobzhansky 1954; Carson 1959; Soule 1973; Brussard 1984). These trends are embodied in the central-marginal model (Lewontin 1974). Several explanations exist. One hypothesis (da Cunha & Dobzhansky 1954) states genetic polymorphism is positively correlated with the number of niches an organism occupies – more niches are available at the center of a species range. Yet Brussard's (1984) free recombination hypothesis proposes linkage disequilibrium is favored in central populations because extreme phenotypes are selected against, i. e., stabilizing selection occurs. Here, favored genes are linked together to create a stable phenotype with maximal fitness. In theory, at the range margins, linkage equilibrium is selected in stressful environments to create novel phenotypes better able to survive sub-optimal conditions (Brussard 1984).

Research with *Drosophila* suggests the prediction that allozyme heterozygosity is reduced at range margins is not valid (Brussard 1984). However, *Drosophila* probably disperse relatively great distances compared to most non-flying taxa. Non-flying taxa (vertebrates) show a decline in allelic diversity in marginal populations (Soule' 1973). We propose scorpions, unable to disperse great distances, also may illustrate the predictions of Lewontin's (1974) central-marginal model.

METHODS

Relevant scorpion biology.—The scorpion *Paruroctonus mesaensis* Stahnke is restricted to sand dunes and sandy substrates scattered throughout the southwestern United States and northern Mexico. It occurs in dense populations (range = 1600–5000/ha) (Polis & Yamashita 1991) and it is an ecologically important species, as a generalist predator in desert food webs (Polis 1979; Polis & McCormick 1986, 1987). This scorpion is dispersal limited because specialized morphological features adapt and restrict it to sand. The species possess numerous modified setae on their tarsi (sand shoes) to facilitate sand movement and burrow construction (Polis et al. 1986). Further, their ability to detect substrate vibrations to localize prey only functions well on sand (Brownell & Farley 1979). These specializations reduce the likelihood of extended migration. However, reproductive males move extensively when searching for mates (Polis & Farley 1979, 1980).

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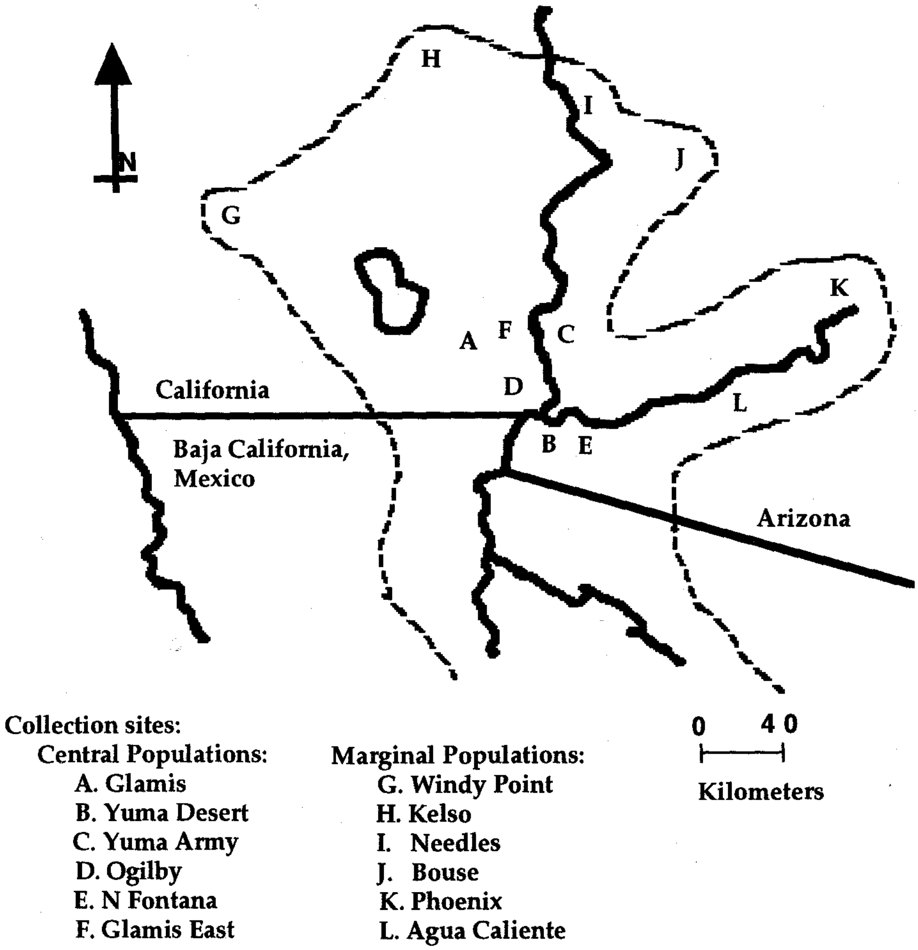

Figure 1.—A partial map of the desert areas of California, Arizona, and Baja California Norte where populations of *Paruroctonus mesaensis* were collected. A proposed range of *P. mesaensis* is indicated by the dashed line.

Collection and electrophoresis procedures.—We collected the scorpions over three years, 1989–1991. *Paruroctonus mesaensis* is easy to collect as it (and all scorpions) fluoresces when illuminated with a ultraviolet light (Sylvania F8T5/BLB). We transported the scorpions alive to the laboratory, froze them with liquid nitrogen, and stored them at −70 °C until electrophoretic analysis.

We electrophoresed five polymorphic and three monomorphic loci from 28 populations. This research was the first allozyme analysis of any scorpion populations, and these eight loci were the only resolvable loci from a screening of 25 enzyme loci on 11 different buffer systems. We assayed a mean of 29 individuals (± 5.7) from each population for each locus. The specific protocols and other pertinent methodology are described in Yamashita (1993).

Central and marginal population determination.—We determined the geographical center of *P. mesaensis* populations from collection data (Haradon 1983; D. Gaffin pers. comm.; Yamashita 1993) (Fig. 1). We determined the following range extremes: in the north (Death Valley, California); in the south, Cabo Lobos (Sonora, Mexico); in the east (Phoenix, Arizona); and in the west (Windy Point in the Coachella Valley, California). We determined the range center to be located 65 km north of Yuma, Arizona by locating the midpoint between the extreme northern and southern and the western and eastern populations. We designated six populations within a 32 km radius of the range center as

Central populations: Glamis, Yuma desert, Yuma Army, Ogilby, N. Fontana, and Glamis East. We delineated peripheral populations as those nearest to edges of the range. These include Windy Point, Kelso, Needles, Bouse, Phoenix, and Agua Caliente.

Statistical analyses.—We performed two types of analyses to determine if differences between central and marginal populations exist. The first, a method outlined by Weir (1990), tested if heterozygosity differences exist between population types. This design, similar to a split-plot ANOVA, considered variation from five sources: populations, individuals within populations, loci, loci by populations, and loci by individuals within populations. Heterozygotes are entered as 1's, homozygotes, as 0's and the data from each central or marginal populations were pooled. We used electrophoretic data from 20 individuals from each of six central and six marginal populations (120 individuals in each population type) and five loci. We used Weir's analysis because estimates of heterozygosity often exhibit large interlocus variances and non-normal distributions; therefore, many standard parametric tests may be inappropriate (Archie 1985).

Second, we performed standard parametric statistics to determine differences between central and marginal populations. The variables examined were observed average heterozygosity, mean allele number, and percent polymorphism of each population. We calculated these variables using BIOSYS-1 (Swofford & Selander 1989). Observed heterozygosity per locus is the fraction of heterozygous individuals from a given sample for a particular locus (Ferguson 1980; Weir 1990). Observed average heterozygosity is the mean value from all loci. Although heterozygosity values commonly undergo an arcsine transformation, our data did not require such a procedure because most heterozygosity values fell between 0.30 and 0.70, a range that does not require transformation (Sokal & Rohlf 1981).

We used two other indices of genetic variability. Percent polymorphism is the mean number of polymorphic loci in a population. Here, a locus is polymorphic if the frequency of the most common allele is 0.95 or less. The mean number of alleles per locus is the number of alleles at each locus averaged across all loci.

RESULTS

The split-plot ANOVA and standard parametric tests showed the mean heterozygosities from the central and marginal populations were significantly different (Tables 1, 2). The results of the split-plot ANOVA (Table 1) show values from all levels of analysis (populations; individuals within populations; loci; population x loci) were significant ($P \leq 0.001$) except individuals within populations ($P \geq 0.437$). These results establish that central populations are significantly different from marginal ones in heterozygosity. Furthermore, the significant among loci effects suggests that each locus expressed a different pattern of heterozygosity from other loci. Loci within marginal populations were significantly different from loci within central populations, which suggests within each population type (central or marginal), the same locus expressed significantly different heterozygosities.

Table 1.—Split plot ANOVA analysis of two population categories (Central and Marginal). This design is taken after Weir 1990.

	df	MS	F-value	P-value
Category	1	3.54	21.60	≤ 0.001
Individuals within categories	222	0.166	1.01	≥ 0.437
Loci	4	4.29	26.17	≤ 0.001
Category × loci	4	1.29	7.86	≤ 0.001
Error	888	0.164		

The mean genetic variability (observed heterozygosity) in marginal populations (0.106 ± 0.025, n = 6) was significantly less than central populations (0.164 ± 0.018, n = 6; t = 3.80, $0.05 \geq P > 0.01$) supporting the central-marginal model. The mean allele number for the central populations (1.73 ± 0.144) was marginally greater (t = 2.21, $0.1 \geq P > 0.05$) than that of marginal populations (1.52 ± 0.095). The mean percent polymorphism for central populations (45.83 ± 6.45) was also marginally greater (35.42 ± 9.41, t = 2.71, $0.05 \geq P > 0.01$).

DISCUSSION

The significant differences between central and marginal populations for allozyme heterozygosity, mean allele number, and percent polymorphism are consistent with the central-marginal model (Brussard 1984). *Paruroctonus mesaensis* is one of the species that fits the predictions of this model; tests of the model using *Drosophila* allozymes failed to exhibit similar patterns (Brussard 1984). In our study, the decrease in genetic variability in marginal populations prob-

Table 2.—A comparison of genetic variability between central and marginal populations. See text for discussion.

	Mean heterozygosity	Mean allele number	% Polymorphism
Central populations			
Glamis	0.153	1.75	37.5
Yuma Desert	0.176	2.00	50.0
Yuma Army	0.136	1.63	50.0
Ogilby	0.167	1.63	37.5
N. Fontana	0.166	1.63	50.0
Glamis East	0.187	1.75	50.0
Mean	0.164	1.73	45.8
SD	0.018	0.144	6.5
Marginal populations			
Windy Point	0.103	1.50	25.0
Phoenix	0.078	1.38	25.0
Bouse	0.131	1.63	50.0
Agua Caliente	0.140	1.50	37.5
Kelso	0.084	1.63	37.5
Needles	0.097	1.50	37.5
Mean	0.106	1.52	35.4
SD	0.025	0.095	9.4
Central *vs* marginal *t*-statistic	3.80	2.21	2.71
P values	$0.05 \geq P > 0.01$	$0.1 \geq P > 0.05$	$0.05 \geq P > 0.01$

ably stems from reduced gene flow or smaller overall population size. Because scorpion dispersal is local, populations at the range margin are less likely to receive migrants from other populations compared to more central populations. Central populations exhibit the highest allele number and percent polymorphism. These populations may maintain higher genetic variability because exchange with other nearby populations is more frequent and population size is generally larger in the center of the range. However, models suggest that a very small effective population size ($n_e < 10$ individuals) is required to reduce significantly the number of alleles per locus within a population (Nei et al. 1975; Rice & Mack 1991).

Some marginal populations (Needles, Bouse, and Phoenix) are geographically isolated from other populations. Needles, north of a mountain range present on either side of the Colorado River, is effectively isolated. The Bouse population exists on the eastern edge of the Cactus Plain, a large sandy region in western Arizona. It is surrounded by rocky habitat and isolated from the nearest population by 40 km. Although Bouse is not separated by a large distance, the intermediate rocky substrate effectively curtails dispersal. No *P. mesaensis* were observed in > 30 hours of searching on rocky habitats adjacent to sandy areas (Polis, unpubl. data).

The Phoenix population is the most eastern and one of the most genetically depauperate populations. Emigration into this area probably occurred along the dry river beds of the Salt and Gila rivers. This population relies on unidirectional gene flow since the substrate outside the river bed is a dispersal barrier to the psammophilic scorpion and no populations exist to the east. The low values of genetic variability may be a result of two primary factors: it is a peripheral population with a low population size and receives little gene flow from other populations.

Peripheral isolate formation may have been enhanced by large scale floods in the Holocene (Ely et al. 1993). The Salt and Gila rivers experienced large-scale floods in the last 5600 years (Ely et al. 1993). Periods of minor and major floods were interspersed. These extreme floods may have created expansion corridors for scorpion movement and isolated populations by fragmenting previous habitat.

Although several studies have compared central and marginal populations, a clear trend is not evident (Hoffman & Parsons 1991). Some report no decrease in genetic variability within marginal populations, e. g., Drosophila allozymes (Brussard 1984) and an annual grass (Rice & Mack 1991). Analysis of dispersal limited animals (frogs) report a decrease in genetic variability among marginal populations (Sjögren 1991). Further research into the properties of marginal populations is warranted because marginal populations, with their insular or peninsular properties, are similar to populations fragmented through man's encroachment upon the environment.

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LITERATURE CITED

Archie, J.W. 1985. Statistical analysis of heterozygosity data: Independent sample comparisons. Evolution, 39:623–637.

Brownell, P. H. & R. D. Farley. 1979. Prey-localizing behaviour of the nocturnal desert sand scorpion, *Paruroctonus mesaensis*: Orientation to substrate vibrations. Anim. Behav., 27:185–193.

Brussard, P. F. 1984. Geographic patterns and environmental gradients: The central-marginal model in *Drosophila* revisited. Ann. Rev. Ecol. Syst., 15: 25–64.

Carson, H. L. 1959. Genetic conditions that promote or retard the formation of species. Cold Spring Harbor Symp. Quant. Biol., 24:87–103.

da Cunha, A. B., & T. Dobzhansky. 1954. A further study of chromosomal polymorphism in *Drosophila willistoni* in relation to environment. Evolution, 8:119–134.

da Cunha, A. B., T. Dobzhansky, O. Pavlovsky, & B. Spassky. 1959. Genetics of natural populations. XXVIII. Supplementary data on the chromosomal polymorphism in *Drosophila willistoni* in relation to the environment. Evolution, 13:389–404.

Ely, L. L, Y. Enzel, V. R. Baker, & D. R. Cayan. 1993. A 5000-year record of extreme floods and climatic change in the southwestern United States. Science, 262:410–412.

Ferguson, A. 1980. Biochemical Systematics and Evolution. Wiley & Sons, New York, New York.

Haradon, R. M. 1983. *Smeringurus,* a new species of *Paruroctonus* Werner (Scorpionies, Vaejovidae). J. Arachnol., 11:251–270.

Hoffman, A. A. & P. A. Parsons. 1991. Evolutionary Genetics and Environmental Stress. Oxford Univ. Press, Oxford.

Lewontin, R. C. 1974. The genetic basis of evolutionary change. Columbia Univ. Press. New York, New York.

Nei, M, T. Maruyama, & R. Chakraborty. 1975. The bottleneck effect and genetic variability in populations. Evolution, 29:1–10.

Polis, G. A. 1979. Prey and feeding phenology of the desert sand scorpion *Paruroctonus mesaensis* (Scorpionidae, Vaejovidae). J. Zool., London, 188:333–346.

Polis, G. A. & R. D. Farley. 1979. Characteristics and environmental determinants of natality, growth, and maturity in a natural population of the desert scorpion, *Paruroctonus mesaensis* (Scorpionidae: Vaejovidae). J. Zool., London, 187:517–542.

Polis, G. A. & R. D. Farley. 1980. Population biology of a desert sand scorpion: Survivorship, microhabitat, and the evolution of life history strategy. Ecology, 61:620–629.

Polis, G. A. & S. J. McCormick. 1986. Patterns of resource use and age structure among a guild of desert scorpions. J. Animal Ecol., 55:59–73.

Polis, G. A. & S. J. McCormick. 1987. Competition and predation among species of desert scorpions. Ecology, 68:332–343.

Polis, G. A., C. A. Myers & M. A. Quinlan. 1986. Burrowing biology and spatial distribution of desert sand scorpions. J. Arid Environ., 10:137–146.

Polis, G. A. & T. Yamashita. 1991. The ecology and importance of predaceous arthropods in desert communities. Pp. 180–222. *In* The Ecology of Desert Communities. (G.A. Polis, ed.) Univ. of Arizona Press, Tucson, Arizona.

Rice, K. J. & R. N. Mack. 1991. Ecological genetics of *Bromus tectorum.* I. A hierarchical analysis of phenotypic variation. Oecologia, 88:77–83.

Sjögren, P. 1991. Genetic variation in relation to demography of peripheral pool frog populations (*Rana lessonae*). Evol. Ecol., 5:248–271.

Sokal, R. R. & F. J. Rohlf. 1981. Biometry, 2nd ed. W. H. Freeman & Co., San Francisco.

Soule', M. 1973. The epistasis cycle: A theory of marginal populations. Ann. Rev. Ecol. Syst., 4:165–187.

Swofford, D. L. & R. B. Selander. 1989. BIOSYS-1: A computer program for the analysis of allelic variation in population genetics and biochemical systematics. User's Manual. Illinois Nat. Hist. Survey.

Weir, B. S. 1990. Genetic Data Analysis. Sinauer, Sunderland, Massachusetts.

Yamashita, T. 1993. Genetic and Morphological Variation in Scorpion Populations on Habitat Islands. Ph. D. dissertation. Vanderbilt University, Nashville, Tennessee.

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