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GENETIC VARIABILITY AND GENE FLOW IN *METEPEIRA VENTURA* (ARANEAE, ARANEIDAE)

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ABSTRACT. Levels of genetic variability and gene flow among three populations of *Metepeira ventura* on Santa Catalina Island, California, were evaluated based on variation at 10 gene loci. Mean heterozygosity (observed) per population was 10.4% and mean polymorphism was 36.7%, consistent with levels of variability in other arthropods. Values of F_{ST} for the five polymorphic loci (mean F_{ST} = 0.009) suggest that gene flow prevents the genetic differentiation of these populations. The average number of migrants per generation (Nm) among these populations is estimated to be 28.6. The lack of inter-population genetic differentiation may result from aerial dispersal and/or crawling along vegetation by *M. ventura*. Such similarity may also be due to the more widespread vegetative cover of Santa Catalina prior to overgrazing, which may have physically united these populations in the recent past, allowing for gene flow among them.

Levi (1973) observed that, in general, smaller spiders have a greater number of species than larger forms. For example, the orb weaver genus *Araneus* in North America has about 20 species in the large-sized *diadematus* group, but over 30 small species (Levi 1971). Levi (1973) suggested that such a pattern might be due to discontinuities in the distribution of small species, permitting geographic speciation, as well as minimal genetic exchange among populations, perhaps related to habitat specialization. While small spiders might be expected to be easily dispersed among populations via ballooning (aerial transport on wind blown silk threads), it appears that ballooning is mainly a means of short-range movement *within* populations (Decae 1987).

The small orb weaver *Metepeira* is found throughout the Americas, including the California Channel Islands (Levi 1977). This spider spins an orb-web in low vegetation with an adjacent barrier web slightly to the side and above. The preferred web site is typically unobstructed, rigid vegetation, such as dead or leafless branches, cactus, signposts or fences (Levi 1977; Uetz & Burgess 1979). Individual *Metepeira* are generally solitary, though members of some species (e. g., *M. datona*, *M. spinipes*) are social (Schoener & Toft 1983; Uetz 1986, 1988). *Metepeira* have an annual life-cycle; spiderlings are born in spring and adults may be collected from summer to early fall (Levi 1977; Spiller 1984). Although other araneid spiderlings commonly balloon (Dean & Sterling 1985; Greenstone et al. 1987), this behavior has not been observed for *Metepeira* (Comstock 1948; Kaston 1948; Levi 1977).

On Santa Catalina Island, California, web sites of *M. ventura* appear to be preferentially located on the prickly-pear cacti *Opuntia littoralis* and *Opuntia oricola* (pers. obs.). *O. littoralis* and *O. oricola* are low, weedy cacti found in discontinuous patches on most parts of the island (Minnich 1980; M. Gay pers. comm.). Their presence appears to be positively correlated with the actions of feral herbivores (goats, pigs, sheep), whose rooting or browsing activities commonly eliminate or reduce most herbivorous vegetation (e. g., Brown 1980; Bennett 1993; Perlmutter 1993) but not the spiny *Opuntia* (Hobbs 1980; Minnich 1980). Given the mosaic distribution of *O. littoralis* and *O. oricola* on Santa Catalina, populations of *M. ventura* appear to be distributed in numerous, spatially isolated patches. In this study, we analyze patterns of genetic variation within and among *M. ventura* populations occupying such patches, as well as estimate levels of inter-population gene flow.

METHODS

Collections.—We collected *Metepeira* from three sites on Santa Catalina Island. The first site

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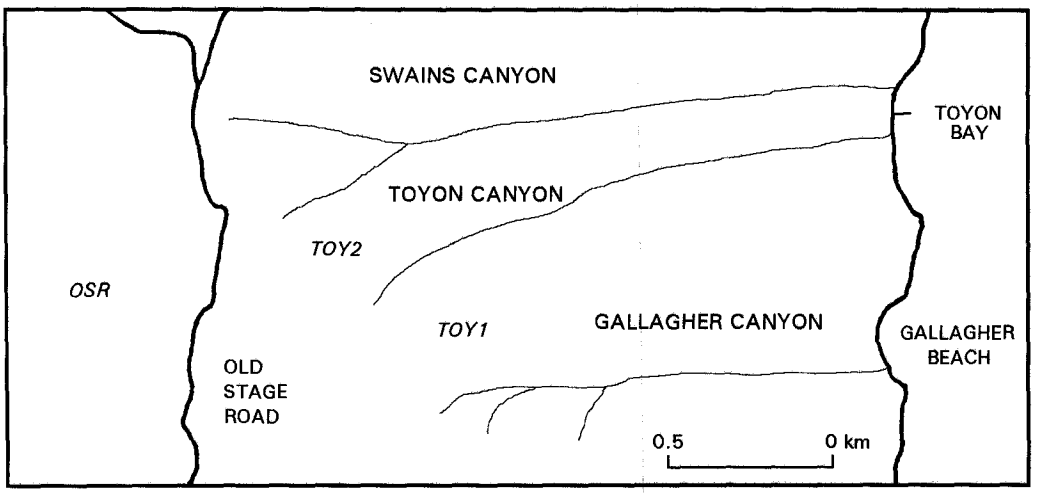

Figure 1.—Toyon Canyon region of Santa Catalina Island, California, showing *Metepeira ventura* sample sites. Population abbreviations follow Table 1.

(TOY1) was a 123 × 31 m area on a ridge between Gallagher Canyon and Toyon Canyon; the second site (TOY2) was a 92 × 31 m area on a ridge between Toyon Canyon and Swains Canyon, parallel to and north-west of the first site; and the third site (OSR) was a 80 × 31 m area west of the first two sites along Old Stage Road (Fig. 1). The vegetation at all sites primarily consisted of many small patches of *Opuntia*, intermixed with the bush *Rhus*, and all sites were bordered by more obstructed and/or less rigid vegetation (e. g., grasses), where *Metepeira* could seldom be found. Spiders were collected from *Opuntia* and from intermixed vegetation at the three sites. Sampling areas were not uniform because of the varying shapes and sizes of the vegetative patches at each site. Sample sizes were 42–43 spiders from each population (Table 1). In the laboratory, spiders were starved for at least a week and then frozen at −75 °C until they were prepared for electrophoresis.

Table 1.—Summary of collections of *Metepeira ventura* on Santa Catalina Island, California. Samples include spiders of all instars.

Locality (abbreviation)	Sample size	Dates of sampling
Toyon Canyon, S ridge (TOY1)	43	30 January, 1993
Toyon Canyon, N ridge (TOY2)	42	31 January, 1993
Old Stage Road (OSR)	43	6 February, 1993

Of the 11 species of *Metepeira* in California, four are known from the California Channel Islands: *M. crassipes*, *M. foxi*, *M. grinnelli* and *M. ventura* (Levi 1977). To ensure that we had pure samples, 68 adult male and female specimens collected at the three sites were examined by W. Icenogle and H. Levi and identified as *M. ventura*. Since the female epigynum and male palpus of juvenile *Metepeira* are undeveloped, immatures of this genus cannot be as readily identified to species (Levi 1977). To solve this problem, all spiders collected were examined under a Wild M3 microscope for the presence/absence of a white stripe on the sternum. A black sternum with no longitudinal stripe is a characteristic of *M. foxi* but not of *M. crassipes*, *M. grinnelli* or *M. ventura* (Levi 1977). All spiders collected had white stripes on their sternums, ruling out the presence of *M. foxi* in our samples. The stripes of very young juveniles and sub-adult males tended to be less distinct and appeared off-white in some individuals. The identification numbers of these spiders were recorded along with remarks about their appearance. This precaution was taken to determine later whether these individuals might exhibit unusual electrophoretic banding patterns, perhaps indicating their assignment to *M. crassipes* or *M. grinnelli*. No such electrophoretic differences were found, so we are confident our samples were pure *M. ventura*.

Electrophoresis.—A survey of 19 enzymes on up to two buffer systems (Appendix 1) revealed

Table 2.—Enzyme/buffer combinations for starch gel electrophoresis. E.C. number denotes Enzyme Commission identification number (Commission on Biochemical Nomenclature 1979). Buffer abbreviations follow Appendix 1.

Enzyme	# Loci	Abbrev.	E.C. number	Buffer
Adenylate kinase	1	ADKIN	2.7.4.3	TMA
Arginine phosphokinase	2	APK	2.7.3.3	REG
Fumarase	1	FUM	4.2.1.2	TMA
Glucosephosphate isomerase	1	GPI	5.3.1.9	REG
Glyceraldehyde-3-phosphate dehydrogenase	1	G-3-PDH	1.2.1.12	TC1
Isocitrate dehydrogenase	1	IDH	1.1.1.42	TMA
Phosphoglucomutase	2	PGM	2.7.5.1	TC1
Superoxide dismutase	1	SOD	1.15.1.1	REG

consistently scorable activity for 10 loci (Table 2); electrophoretic techniques and staining protocols are described in Ramirez (1990). Gels were 12.5% hydrolyzed starch (StarchArt Corporation). No significant differences in the banding patterns of spiders of different age or sex were ever detected, making it possible to examine spiders of all instars. All genotypes were inferred from the appearance of the staining patterns and the known subunit structure of the enzymes (Harris & Hopkinson 1976; Richardson et al. 1986).

Data analysis.—We used the BIOSYS-1 (version 1.7; Swofford & Selander 1981, 1989) computer package to analyze the electrophoretic data. Agreement between observed population genotypic ratios and Hardy-Weinberg expectations was evaluated by Chi-square tests for goodness of fit (Sokal & Rohlf 1981); Levene's (1949) correction for small sample size was applied to the expected frequencies. To test the null hypothesis that allele frequencies in the three populations are not significantly different, contingency table Chi-square analysis (Brower & Zar 1984) was performed. To determine the extent of heterozygote deficiency or excess in a population, Wright's (1969) fixation index was calculated for all polymorphic loci.

The apportionment of genetic differentiation among populations was analyzed by use of Wright's (1965) F_{ST} statistic as modified by Nei (1977). All F_{ST} values were calculated using means and variances of allele frequencies weighted by sample sizes. Gene flow (Nm) was estimated from the F_{ST} values, using the equation $Nm = (1 - F_{ST})/4F_{ST}$ (Wright 1951). The mathematical definitions of the population genetic parameters reported here can be found in standard population genetics textbooks (e. g., Hedrick 1985; Hartl & Clark 1989).

Table 3.—Allele frequencies in populations of *Metepeira ventura*. Population abbreviations follow Table 1, locus abbreviations follow Table 2, and sample sizes are in parentheses.

	Population		
Locus/allele	TOY1	TOY2	OSR
ADKIN	(43)	(42)	(41)
A	1.000	0.988	1.000
B	0.000	0.012	0.000
APK-1	(43)	(42)	(43)
A	1.000	1.000	1.000
APK-2	(43)	(42)	(43)
A	1.000	1.000	1.000
FUM	(43)	(42)	(43)
A	1.000	1.000	0.977
B	0.000	0.000	0.023
GPI	(43)	(42)	(43)
A	0.035	0.036	0.035
B	0.105	0.036	0.035
C	0.791	0.869	0.849
D	0.058	0.024	0.058
E	0.012	0.036	0.023
G-3-PDH	(43)	(42)	(43)
A	1.000	1.000	1.000
IDH	(43)	(42)	(43)
A	0.000	0.012	0.000
B	0.930	0.964	0.953
C	0.070	0.024	0.047
PGM-1	(43)	(42)	(41)
A	0.523	0.488	0.549
B	0.140	0.155	0.232
C	0.302	0.345	0.207
D	0.035	0.012	0.012
PGM-2	(43)	(42)	(41)
A	1.000	1.000	1.000
SOD	(43)	(42)	(43)
A	1.000	1.000	1.000

Table 4.—Genetic variability measures for the three study populations (± SE). n = mean sample size per locus; A = mean number of alleles per locus; P = % of loci polymorphic (a locus is considered polymorphic if the frequency of the most common allele does not exceed 0.99); H_o = observed heterozygosity; H_e = expected mean heterozygosity calculated using the unbiased estimate of Nei (1978). Population abbreviations follow Table 1.

Population	n	A	P	H_o	H_e
TOY1	43.0	1.8 ± 0.5	30.0	0.109 ± 0.064	0.112 ± 0.068
TOY2	42.0	2.0 ± 0.5	40.0	0.095 ± 0.063	0.096 ± 0.064
OSR	42.4	1.9 ± 0.5	40.0	0.108 ± 0.071	0.102 ± 0.063

RESULTS

There were 21 alleles identified at the 10 genetic loci (Table 3); five loci (APK-1, APK-2, G-3-PDH, PGM-2, SOD) were monomorphic across all three populations. The five remaining loci (ADKIN, FUM, GPI, IDH, PGM-l) were polymorphic for two or more alleles in at least one of the three sites. Alleles unique to particular sites (private alleles) were nonexistent (TOY1) or rare (OSR, TOY2) (Table 3).

Population variability.—In general, the variability of individual *Metepeira* populations was high (Table 4). The mean number of alleles per locus was 1.9 (range = 1.8–2.0), mean heterozygosity (observed) was 0.104 (range = 0.095–0.109), and mean polymorphism was 36.7% (range = 30.0–40.0%).

Gene frequencies in population subsamples deviated significantly from Hardy-Weinberg expectations in only one of the 11 cases with polymorphic loci (Table 5). Values of Wright's (1969) fixation index for each polymorphic locus ranged from −0.134 to +1.00 (Table 5), with the largest positive value (1.00; indicative of heterozygote deficiency) being found for the single case (FUM) which deviated significantly from Hardy-Weinberg equilibrium. Thus, individual populations were essentially in conformance with Hardy-Weinberg equilibrium and in the one case where significant deviation was indicated, it was in the form of heterozygote deficiency.

Interpopulation differentiation and gene flow.—Allele frequencies for polymorphic loci were not significantly different among the three populations (Table 6). Populations were also minimally structured as indicated by Wright's F_{ST} statistic (Wright 1965; Nei 1977) (Table 7). On average, approximately 0.9% of the total variance in allele frequencies in *M. ventura* was due to genetic differences among populations, with the remainder of the total gene diversity (99.1%) being found among spiders within any given population ($1 - F_{ST}$). Using the F_{ST} values to estimate gene flow, the mean number of migrants per generation (Nm) among these populations is 28.6 (Table 7). This value, as well as all Nm values in Table 7, are well above the theoretical threshold level at which gene flow is sufficient to homogenize populations genetically in the absence of selection (Nm = 1; Slatkin 1987). Hence, these spatially separate populations are statistically part of a single, minimally-structured unit with an undifferentiated gene pool, presumably maintained by significant gene flow.

DISCUSSION

Population variability.—*Metepeira ventura* populations on Santa Catalina Island are highly variable and in Hardy-Weinberg equilibrium. In their review of allozyme variation, Nevo et al. (1984) reported the following values of mean observed heterozygosity (H_o) and polymorphism

Table 5.—Fixation index values for each polymorphic locus in each population. Missing values indicate a locus not polymorhpic in that population. Significance levels indicate the results of Chi-square tests for deviation from Hardy-Weinberg equilibrium at polymorphic loci in each population. Population abbreviations follow Table 1. * $P < 0.001$.

	Locus				
Population	ADKIN	FUM	GPI	IDH	PGM-1
TOY1	—	—	−0.101	−0.075	0.091
TOY2	−0.012	—	0.009	−0.029	−0.001
OSR	—	1.00*	−0.107	−0.049	−0.134

Table 6.—Results of contingency Chi-square analysis of polymorphic loci. The null hypothesis is that there is no significant variation in allele frequencies among populations. Locus abbreviations follow Table 2.

Locus	Number of alleles	χ^2	df	*P*
ADKIN	2	2.008	2	0.36642
FUM	2	3.985	2	0.13638
GPI	5	7.499	8	0.48387
IDH	3	4.017	4	0.40369
PGM-1	4	7.001	6	0.32074
	(Totals)	24.510	22	0.32108

Table 7.—Values of F_{ST} and Nm for each variable locus. The F_{ST} values are the averages for a locus of the values computed for each allele. The estimates of Nm are based on Wright's (1951) formula: $Nm = (1 - F_{ST})/4F_{ST}$. Locus abbreviations follow Table 2.

Locus	F_{ST}	Nm
ADKIN	0.008	31.0
FUM	0.016	15.4
GPI	0.009	27.5
IDH	0.006	41.4
PGM-1	0.009	27.5
Mean	0.009	28.6

(P, % of loci polymorphic) for invertebrates: invertebrates in general, $H_o = 10.0\%$ and $P = 37.5\%$; *Drosophila* species, $H_o = 12.3\%$, $P = 48.0\%$; other insects, $H_o = 8.9\%$, $P = 35.1\%$; and chelicerates (including spiders), $H_o = 8.0\%$, $P = 26.9\%$. Among spiders, variability levels have been reported for three araneids: *Araneus ventricosus* ($H_o = 9.4$, $P = 20.0\%$) (Manchenko 1981); *Meta menardi* ($H_o = 2.7\%$, $P = 9.6\%$) (Laing et al. 1976); and *Metepeira spinipes* ($H_o = 17.2\%$, P not reported) (Uetz et al. 1986). The lower values for *Meta menardi* may be related to its cave-dwelling existence (Culver 1982). Thus, levels of variability in *M. ventura* ($H_o = 10.4\%$, $P = 36.7\%$) are consistent with those for invertebrates and other araneids (save for *Meta menardi*).

Gene flow.—The patchy distribution of *Opuntia* on Santa Catalina Island organizes *M. ventura* into numerous local populations. The low values of F_{ST} and large values of Nm indicate that gene flow is sufficiently strong that it prevents genetic drift from causing local genetic differentiation. Clearly, Levi's (1973) suggestion that populations of small spider species experience minimal genetic exchange does not apply to these populations of *M. ventura*. However, these populations are fairly close together and a study of more widely spaced samples may show that gene flow drops off considerably beyond a particular interpopulation distance, consistent with Levi's hypothesis.

Since Nm estimates derived from allele frequency data may be due to both *contemporary* and *historic* opportunities for gene flow (Slatkin 1987), it is important to consider such possibilities for *M. ventura*. While no *Metepeira* have been reported to balloon, little is known of the biology of many species (Levi 1977) and so it is possible that *M. ventura* may be capable of aerial dispersal. If so, interpopulation movement could be via ballooning and/or crawling along vegetation. Uetz et al. (1982) marked adults and juveniles of the social *M. spinipes* from various local colonies in central Mexico and noted little change during several months in colony membership. While this study would seem to indicate that *Metepeira* have limited dispersal tendencies, it may be unwise to generalize from the social *M. spinipes* to solitary species like *M. ventura*, since sociality may select for colony fidelity (Uetz et al. 1982; Uetz 1986). On the other hand, Uetz et al. (1982) also found that optimal web sites for *M. spinipes* were in *Agave* and *Opuntia* and since such cacti were patchily distributed in their study area, they suggested that selection might favor individuals which stayed in their respective patches. While the same reasoning would seem to hold for *M. ventura* and *Opuntia* on Santa Catalina, only a long-term study of the movements of marked individuals can determine contemporary levels of migration and, thus, of gene flow.

Historically, interpopulation gene flow would presumably have been facilitated by the more widespread vegetative cover of Santa Catalina prior to human-caused alterations. The island has been severely overgrazed for over a century by introduced bison, deer, goats, pigs and other livestock, significantly reducing the amount of chaparral and coastal sage scrub habitat (Minnich 1980). This enabled the normally coastal *Opuntia littoralis* and *O. oricola* to spread into bare inland areas (Sauer 1988; M. Gay pers. comm.). In contrast, near the city of Avalon and other areas of decreased grazing, contiguous stands of native vegetation are extensive (cover can exceed 70%) (Coblentz 1980; Minnich 1980). Thus, the high Nm value for *M. ventura* is likely

due at least in part to the less open landscape of pre-human Santa Catalina. In the future, we plan to use both direct (marking) and indirect (genetic) means to determine movement among web sites at varying inter-population distances in both heavily grazed and more natural areas to clarify the exact relationship between distance, the vegetative matrix and gene flow in *M. ventura*.

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Appendix 1.—List of enzymes screened, standard abbreviations and buffer systems with which enzymatic activity was assayed in *Metepeira ventura*. X = good results; 0 = no activity or poor results. Buffer abbreviations: REG—Discontinuous Tris-citrate (Poulik 1957); TC1—Continuous Tris-citrate I (Selander et al. 1971); TMA—Tris-maleate (Selander et al. 1971).

Enzyme	Abbrev.	Buffer		
		REG	TC1	TMA
Adenylate kinase	ADKIN			X
Alcohol dehydrogenase	ADH	0		
Arginine phosphokinase	APK	X		
Asparate aminotransferase	AAT		0	
Fumarase	FUM			X
Glucosephosphate isomerase	GPI	X	0	
Glyceraldehyde-3-phosphate dehydrogenase	G-3-PDH		X	
α-Glycerophosphate dehydrogenase	α-GPDH		0	
Hexokinase	HK	0		
Isocitrate dehydrogenase	IDH			X
Lactate dehydrogenase	LDH	0		
Malate dehydrogenase	MDH			0
Malic enzyme	ME			0
Nucleoside phosphorylase	NP			0
Peptidase with leucyl-alanine	PEP(LA)	0		
Phosphoglucomutase	PGM	0	X	
Phosphomannose isomerase	PMI			0
Superoxide dismutase	SOD	X		
Triosephosphate isomerase	TPI			0