Cascading Chromosomal Speciation in Lizards: A Second Look[1]

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ABSTRACT: The extent of Robertsonian chromosomal variation in the iguanid lizard *Sceloporus grammicus* of Mexico is exceptional among lower vertebrates, and this case has been the basis for the cascading chromosomal speciation hypothesis. This paper examines some of the population genetic assumptions of this model by comparing allozyme variability within and among 13 samples of *S. grammicus* with an equal number of samples of the chromosomally monotypic congener *S. graciosus*. Only homologous enzyme loci resolved in both species are used in the comparison. Estimates of such parameters as mean levels of heterozygosity, average number of alleles per locus, genetic distances, and *F* statistics are generally inconsistent with assumptions of strong population subdivision and/or recent bottlenecks associated with extinction–colonization events in *S. grammicus*.. We tentatively conclude that the population structure of at least some chromosome races in this complex is sufficiently panmictic to retard the fixation of electromorphic variants. Problems of making inferences about speciation mechanisms from population genetic correlates are discussed.

THE IGUANID LIZARD *Sceloporus grammicus* of Mexico previously has been shown to be one of the most chromosomally polytypic of all nonmammalian vertebrates. The cytogenetic studies of W. P. Hall (1973, 1980) have revealed a complex of seven distinct chromosome races (hereafter referred to as cytotypes) in what has been taxonomically recognized as a single morphological species (Smith 1939, Smith and Taylor 1950). Some of these cytotypes seem to be distributed parapatrically, and at least three narrow hybrid zones have been located between

different cytotypes (Hall 1973, Hall and Selander 1973). The taxonomic status of these populations is largely unknown. Some studies suggest that at least some of the cytotypes are morphologically inseparable (Sites 1982, Sites and Dixon 1981), while others suggest that a small amount of phenotypic divergence has accompanied the chromosomal differentiation (Lara-Gongora 1983). Hall (1973, 1980, 1983) has proposed a model of "cascading chromosomal speciation" to explain the karyotypic variability in the *S. grammicus* complex, and to account for the geologically recent and rapid speciation in *Sceloporus* relative to other sceloporine lizard genera, all of which are species-depauperate and apparently chromosomally monotypic (see also, Paull et al. 1976). Some implications of this model are discussed below, but it will be instructive to review briefly chromosomal variation in *S. grammicus* here.

CHROMOSOMAL VARIATION IN
Sceloporus grammicus

The probable ancestral karyotype in the *Sceloporus grammicus* complex (cladistic

arguments presented in Paull et al. 1976) was originally designated by Hall (1973) as the "standard," or "S," race, and is characterized by a diploid number of 32 chromosomes (females only; males in this and all other cytotypes normally possess one less chromosome than females due to an X_1X_2Y sex chromosome system; see Cole et al. 1967). The complement is comprised of six pairs of meta- or submetacentric macrochromosomes and either 19 (male) or 20 (female) microchromosomes. A diagrammatic karyotype of S is given in Figure 1, and its known distribution is plotted in Figure 2.

Derived cytotypes include P1, polymorphic for a presumed fission of macrochromosome pair 1 (Figure 1), which is confined to pine forests above 3200 m on three volcanic mountains that form the eastern divide of the Valley of Mexico. Roughly 10% of all individuals are heterozygous for this fission. The P1 cytotype is regarded by Porter and Sites (1986) as part of the S race, and this has been confirmed genetically (Sites et al., 1988a). Five other cytotypes are fixed for presumed fissions in various pairs of macrochromosomes; the configurations of these are shown in Figure 1, and their ranges plotted in Figure 2. The F5 cytotype ($2n = 33\male$, $34\female$), fixed for a fission of macrochromosome pair 5, is known only from ten individuals at two localities in the northern reaches of the Sierra Madre Occidental in Chihuahua, Mexico (Figure 2). An F6 race (also $2n = 33\male$, $34\female$, but fixed for a macrochromosome pair 6 fission) is widely distributed through central parts of the Sierra Volcanica Transversal, and north through parts of the Sierra Madre Oriental. Apparently, there are also three disjunct populations in north-central Nuevo Leon (Figure 2). Another widespread derivative is F5 + 6 ($2n = 35\male$, $36\female$), which occupies southern parts of the Chihuahuan desert and the coastal plains bordering the lower Rio Grande River Valley (Figure 2).

Hall (1973) also recognized two distinct, highly derived "multiple fission," or "FM," cytotypes that appear to be confined to a small region of central Mexico (Figure 2). An FM1 race is fixed for fissions of macro-chromosome pairs 2, 3, 5, and 6, and polymorphic for fissions of pairs 1 and 4 at frequencies of about 40% and 15%, respectively. The most derived race is FM2, which is fixed for fissions of all macrochromosome pairs except possibly pair 4 (approx. 50% frequency) and has an extra pair of microchromosomes. These karyotypes are illustrated schematically in Figure 1. Original karyotypes are illustrated in Hall (1973) and Sites (1983), and additional variation is described by Porter and Sites (1986).

CASCADING CHROMOSOMAL SPECIATION AND ITS IMPLICATIONS

Hall's (1983) cascade model was proposed to explain the correlation between rapid speciation and extensive chromosomal evolution in *Sceloporus*, and incorporates three basic sets of assumed or demonstrated circumstances. First, chromosomally differentiated species originate as very small founder populations. Second, the probability that chromosomal differentiation will occur at all is profoundly affected by: (*a*) rates of chromosomal mutation; (*b*) behavior of the chromosomes in meiosis and the genetic consequences of any meiotic errors; (*c*) details of the species' mating system; and (*d*) details of its population structure [see also Lande (1979) and Hedrick (1981) on this point]. A third important feature includes the aspects of a species' genetic system listed above that are genetically controlled (for more detail, see Hall 1983:667–670). Chromosomal polytypy in *S. grammicus* is taken by Hall to exemplify the cascade mechanism in progress.

All the above parameters can vary considerably and still have minimal effects on individual fitness. If loci determining these factors are polymorphic, demes small enough for fixing chromosomal rearrangements also may show substantial variation in these parameters due to genetic drift. Thus, over the range of a species with the appropriate population structure, some demes by chance will have a genetic background more favorable to the generation and fixation of chromosomal rearrangements than will others.

It follows that chromosomal speciation will more likely begin in these "favorable demes" than in others. Founder populations that survive as new species will tend to perpetuate the favorable genetic backgrounds, so chromosomally derived species will, on average, offer more favorable circumstances for further chromosomal speciation than will ancestral species (Hall 1983:667). This is essentially a positive feedback amplification
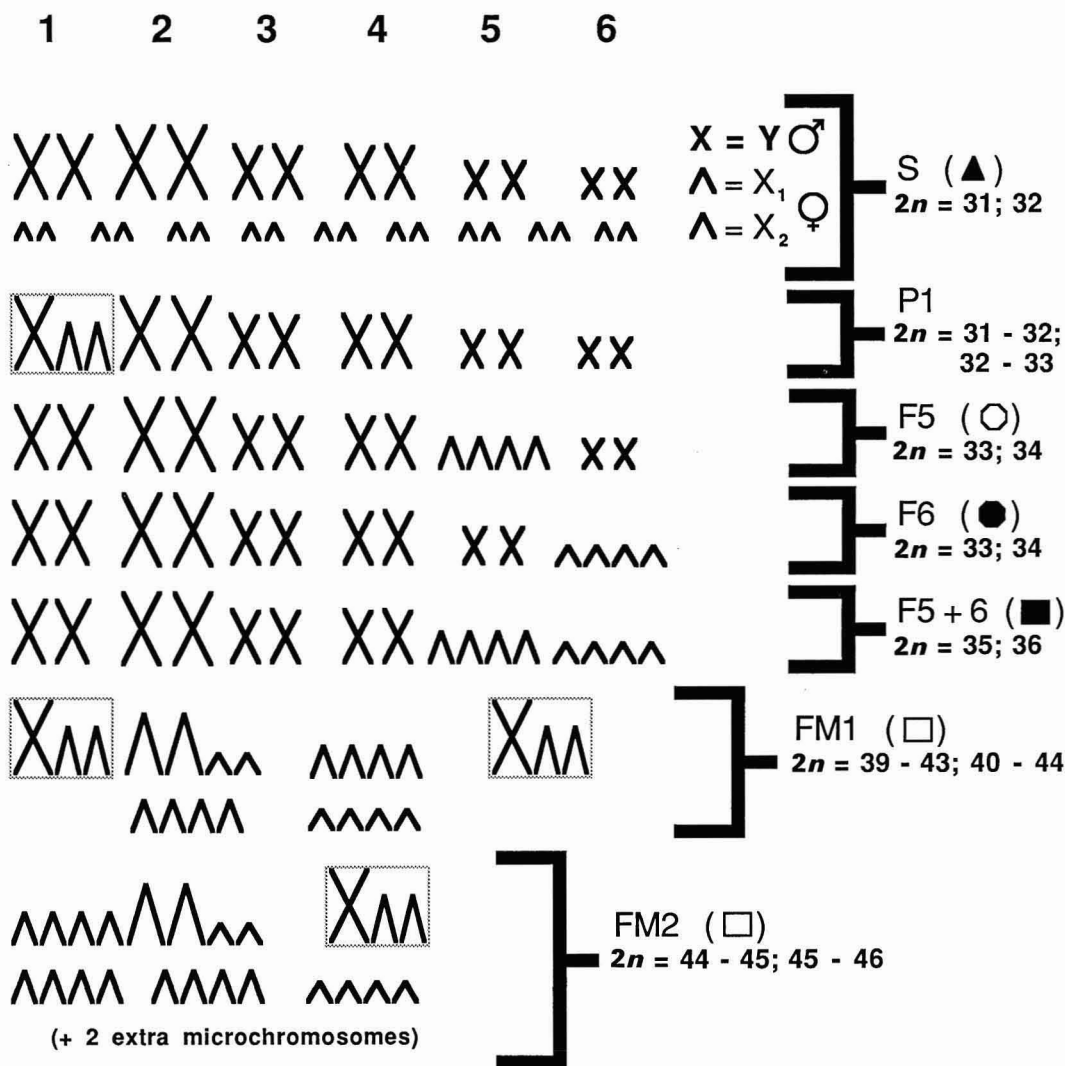
FIGURE 1. Seven chromosome races (cytotypes) originally described by Hall (1973) in *Sceloporus grammicus*. The standard, or S, race is presumed ancestral to all others, and is characterized by six pairs of biarmed macrochromosomes and nine pairs of microchromosomes plus a single biarmed Y chromosome (in males) or an extra pair of acrocentric elements (X_1 and X_2 in females). The inferred rearrangements characteristic of each race and its designation (S, P1, F5, etc.) are described in the text, and the symbols in parentheses are those used on the range map (Figure 2). Diploid numbers to the left of the semicolon are those of males, with females to the right. Macrochromosome pairs known to be polymorphic in all known populations of a cytotype are enclosed by dashed lines. Microchromosome arrangements are shown only for S, but appear to be identical in all other cytotypes except FM2, which has an additional pair.

FIGURE 2. Approximate distribution throughout Mexico of all *Sceloporus grammicus* cytotypes except P1, which is confined to thre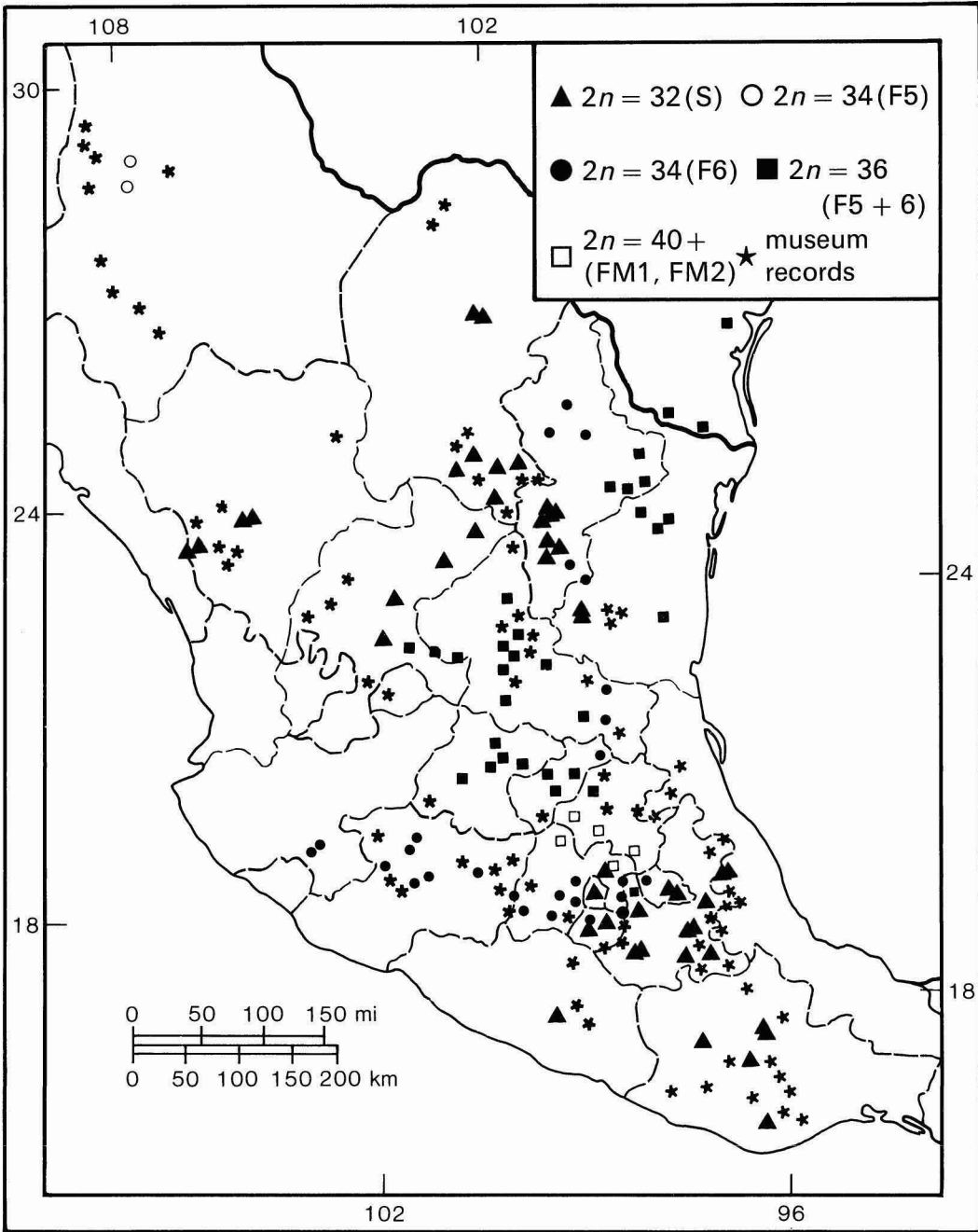e mountain peaks (above 3200 m) forming the eastern divide of the Valley of Mexico. Symbols and abbreviations are as in Figure 1. Modified from Hall and Selander (1973).

process that would work in each speciation event to produce a predominantly linear and increasingly rapid "cascade" of speciations ($S \rightarrow F6 \rightarrow F5 + 6 \rightarrow$ etc.). The chain would be terminated by either saturation of niches by derived species, or exhaustion of the chromosomal substrate available for a particular type of rearrangement (i.e., fissioning of all biarmed macrochromosomes in the original *Sceloporus grammicus* karyotype).

Hall's (1983:671) major assumptions are: (1) that a chromosomal rearrangement is initially deleterious and can function as a postmating isolating mechanism in a zone of parapatric hybridization by causing a high frequency of aneuploidy in chromosomal heterozygotes; and (2) *Sceloporus grammicus* is characterized by very small effective population sizes and very low levels of between-population gene flow. Hall (1983:669) further predicts that the founder population required for the chance fixation of a negatively heterotic chromosomal rearrangement is ideal for other stochastic phenomena such as the random fixation or drift of alleles at a variety of polymorphic gene loci. We have further made the inference that fixation and spread of new arrangements would be expedited by repeated extinction–colonization events in a manner envisioned by Lande (1979, 1985).

We have approached the cascade hypothesis and the study of chromosomal variation in the *Sceloporus grammicus* complex from theoretical, cytogenetic, and population genetic perspectives, and report on an extension of the third perspective here. Thirteen populations representing three cytotypes of *S. grammicus* were studied electrophoretically by Sites and Greenbaum (1983), but they had no equivalent data base against which to evaluate the genetic structure of the *S. grammicus* populations. Thompson and Sites (1986) attempted to overcome this problem by generating an equivalent allozyme data set for the chromosomally monotypic congener *S. graciosus*, and then reanalyzing the raw data from the original *S. grammicus* study with the same statistical packages as those used for *S. graciosus*. The two data sets were then evaluated within the conceptual

framework of the "genetic architecture" of various speciation mechanisms (Templeton 1980a, 1980b, 1981, 1982), as well as expected consequences of Hall's cascade model. For both *S. grammicus* and *S. graciosus*, 13 populations were sampled from roughly equivalent geographic areas in north-central Mexico (Sites and Greenbaum 1983, Figure 1) and the western United States (Thompson and Sites 1986, Figure 1). The two species were then statistically compared for several population genetic parameters calculated from allozyme surveys of 19 enzyme products screened in each species. When compared to theoretical expectations (see below), results were inconsistent with models of extreme population subdivision and/or frequent bottlenecks and extinction–colonization events in *S. grammicus*.

Although Thompson and Sites (1986) tried to make the data sets for both species of *Sceloporus* as equivalent as possible, an important source of bias may have been introduced by the subsets of enzyme loci sampled from each species. A total of 19 loci was used for each species, and this total included a roughly equivalent proportion of monomeric, dimeric, and tetrameric proteins in both (for details, see Thompson and Sites 1986). However, a few enzymes were sampled for each species that were not resolved in the other, and Simon and Archie (1985) have shown that choice of enzyme loci can influence dramatically estimates of allozyme heterozygosity. These results logically could be extended to related parameters such as mean number of alleles per locus, proportion of polymorphic loci, and probably even genetic distances.

Our purpose in this paper is to reassess the population genetic parameters in *Sceloporus grammicus* and *S. graciosus* by calculating several estimates of genetic variability and distance based only on those loci common to both species. Our specific objective is to determine whether the former has a more "Wrightian" population structure that would be conducive to a "chromosomal transilience" (both terms are used as defined by Templeton 1980a) relative to a chromosomally monotypic congener. Given an

adequate level of genetic variability in the ancestral population, the type of structuring required by the cascade hypothesis should maximize the degree of interdemic divergence, because individual founders are being drawn from the same ancestral population (Slatkin 1977). Further, the frequent small bottlenecks required to fix new chromosomal mutations (see Chesser and Baker 1986) also would be expected to reduce within-sample levels of variability (Nei et al. 1975, Sirkkomaa 1983). Demonstrations of significantly higher levels of population substructuring and higher between-sample D values, coupled with lower within-sample variability estimates, would suggest that *S. grammicus* does have a population structure that would permit a reasonable chance for fixation of strongly negative heterotic rearrangements. The opposite results would be inconsistent with most chromosomal transilience hypotheses. It is important to note that our results cannot resolve questions of other modes of chromosome evolution in *S. grammicus*, such as the primary chromosomal allopatry associated with colonizing radiations (King 1981, 1984), or the sequential establishment of multiple chromosomal rearrangements, each with small individual meiotic effects (Walsh 1982, White 1978a). We also cannot address the possibility of differential chromosomal mutation rates between *S. grammicus* and *S. graciosus*.

MATERIALS AND METHODS

Thirteen natural populations were sampled for both species from roughly equivalent areas in portions of their respective ranges (for range maps, see Sites and Greenbaum 1983, Figure 1; Thompson and Sites 1986, Figure 1). In both cases, 12 samples were taken from within a geographically contiguous part of the range and one from a geographically isolated population. Lizards were captured by noosing or by stunning with rubber bands, and voucher specimens are deposited in either the Texas Cooperative Wildlife Collection (TCWC) at Texas A&M University, or the Monte L. Bean Life Science Museum at Brigham

Young University (BYU). Geographic localities sampled for each species are summarized by Thompson and Sites (1986, Table 2).

Details of the karyotypic methods are given by Sites (1983), and involve a modification of the yeast treatment technique described by Cole and Leavens (1971). Descriptions of the electrophoretic protocols are given by Sites and Greenbaum (1983) and Thompson and Sites (1986). The 13 homologous gene loci resolved for both species included the following enzyme products: aminopeptidase (Ap-A, EC 3.4.11.1), aspartate aminotransferase (M-Aat-A, EC 2.6.1.1), glucose-6-phosphate isomerase (Gpi-A, EC 5.3.1.9), glycerol-3-phosphate dehydrogenase (G3 pdh-B, EC 1.1.1.8), isocitrate dehydrogenase (S-Icdh-A, EC 1.1.1.42), lactate dehydrogenase (Ldh-A, -B, EC 1.1.1.27), malate dehydrogenase (M-Mdh-A, S-Mdh-A, EC 1.1.1.37), phosphogluconate dehydrogenase (Pgdh-A, EC 1.1.1.44), phosphoglucomutase (Pgm-A, EC 5.4.2.2), and superoxide dismutase (S-Sod-A^1, -A^2, EC 1.15.1.1). Enzyme nomenclature follows recommendations of the Nomenclature Committee of the International Union of Biochemistry (1984), locus abbreviations follow Murphy and Crabtree (1985), and stains were taken either from Harris and Hopkinson (1976) or from Selander et al. (1971).

Allozyme data from both species were analyzed using the BIOSYS-1 program of Swofford and Selander (1981), so that both sets of statistics are directly comparable. Measures of genetic variability computed for each population include average locus heterozygosity by direct count ($\bar{H}_{DC}$), the mean number of alleles per locus ($\bar{A}$), and the genetic distance coefficients (D) of Nei (1978). Wright's (1965, 1978) hierarchial F statistics, F_{IS}, F_{ST}, and F_{IT}, were calculated for all samples within each species, and intersample allele frequency heterogeneity was evaluated by the methods of Workman and Niswander (1970).

RESULTS

Of the 13 homologous loci examined in both species, S-Sod-A^2 was monomorphic in

Sceloporus grammicus, and Ap-A, Ldh-B, M-Mdh-A, and S-Sod-A[1] were monomorphic in *S. graciosus*. Electromorph frequencies for the remaining polymorphic loci are summarized in Table 1. The alphabetical designation of electromorphs follows Thompson and Sites (1986).

Table 2 summarizes the mean number of alleles per locus ($\bar{A}$) and the mean locus heterozygosity (by direct count, $\bar{H}_{DC}$) for both *Sceloporus grammicus* and *S. graciosus*. A two-tailed Mann–Whitney test for overall median differences showed that *S. graciosus* (median $\bar{A} = 1.16$) had significantly fewer alleles per locus than did *S. grammicus* (median $\bar{A} = 1.53$, $W = 251.0$, $P < 0.0001$). By the same test, *S. graciosus* also had significantly less heterozygosity (median $\bar{H}_{DC} = 0.017$) than did *S. grammicus* (median $\bar{H}_{DC} = 0.089$, $W = 260.0$, $P < 0.0000$).

Nei's (1978) genetic distance coefficients were calculated for all pairwise comparisons of each species and are summarized in Table 3. The range of D values for *Sceloporus grammicus* is from 0.00 to 0.108 ($\bar{X} = 0.028 \pm 0.025$, median $= 0.022$; the "$\pm$" here and elsewhere in the text refers to one standard deviation), and for *S. graciosus* is from 0.00 to 0.164 ($\bar{X} = 0.055 \pm 0.045$, median $= 0.063$). The median D values are significantly higher in *S. graciosus* (two-tailed Mann–Whitney $W = 6869.5$, $P = 0.0082$).

Population structure was examined in two ways. First, all variable loci in each species were tested for conformation to Hardy–Weinberg expectations. *Sceloporus grammicus* showed a deficiency of heterozygotes at two loci: Pgdh-A at locality 1 ($X^2 = 10.67$, df = 3, $P < 0.05$) and Pgm-A at locality 8 ($X^2 = 13.66$, df = 1, $P < 0.001$). *Sceloporus graciosus* also showed heterozygote deficiency at two loci: Pgdh-A at locality 4 ($X^2 = 14.33$, df = 1, $P < 0.001$) and S-Icdh-A at locality 6 ($X^2 = 53.02$, df = 3, $P < 0.001$).

Second, we calculated F_{IS}, F_{IT}, and F_{ST} values for all variable loci in both species; these are presented in Table 4. Values for F_{IS} give the average deviation of sample genotype proportions from Hardy–Weinberg expectations; F_{IT}, the overall inbreeding coefficients; and F_{ST}, the level of substructuring within the total population. The median values of all F statistics for both *Sceloporus grammicus* and *S. graciosus*, respectively, are as follows: $F_{IS} = -0.042$ and -0.027; $F_{IT} = -0.002$ and -0.002; $F_{ST} = 0.075$ and 0.033. Two-tailed Mann–Whitney tests between species medians showed no significant differences for F_{IS}, F_{IT}, and F_{ST} ($W = 109.0$, $P = 0.6485$; $W = 101.5$, $P = 0.3051$; and $W = 116.0$, $P = 1.000$, respectively).

DISCUSSION

I. Population Structure in Sceloporus grammicus

Results of this study largely corroborate those of the earlier study of Thompson and Sites (1986) in suggesting that, at least over a considerable part of its range, *Sceloporus grammicus* does not have an extremely Wrightian population structure relative to a chromosomally monotypic congener and to other small vertebrates (see also Sites and Greenbaum 1983). In the study by Thompson and Sites, 19 loci were resolved in each species, but a different combination of loci was used to comprise the total in each. Some of the variable enzymes resolved for *S. graciosus*, such as purine nucleoside phosphorylase (Pnp-A, EC 2.4.2.1) or mannose-6-phosphate isomerase (Mpi-A, EC 5.3.1.8), were not part of the standard vertebrate electrophoresis protocol when the original work on *S. grammicus* was done in 1979. Thus, the interspecies comparison made by Thompson and Sites (1986) is valid to the extent that the loci sampled from each species can be considered independent of each other (Archie 1985), but it is potentially biased because the choice of loci can dramatically affect heterozygosity estimates (Simon and Archie 1985). Because the present comparison is based only on individual homologous loci, the source of bias introduced by different combinations of loci can be eliminated as one explanation for the statistically different population genetic parameters estimated in this study.

One factor not considered by Thompson and Sites (1986) that could account for the different levels of variability maintained in these two *Sceloporus* is the possibility of in-

TABLE 1

ELECTROMORPH FREQUENCIES FOR POLYMORPHIC LOCI IN 13 SAMPLES OF *Sceloporus grammicus* AND *S. graciosus*

LOCUS	ELECTROMORPH	1 (17)	2 (35)	3 (26)	4 (28)	5 (23)	6 (20)	7 (28)	8 (22)	9 (23)	10 (16)	11 (19)	12 (30)	13 (10)
S. grammicus														
Ap-A	A	0.941	0.829	0.769	0.929	0.978	0.975	0.893	0.864	0.957	1.000	0.868	0.950	1.000
	B	—	—	0.019	—	—	—	—	—	—	—	0.026	0.017	—
	C	—	—	0.019	—	—	—	—	—	—	—	—	0.017	—
	D	0.059	0.086	0.135	—	0.022	—	0.107	0.114	0.043	—	0.105	0.017	—
	E	—	0.014	—	—	—	—	—	—	—	—	—	—	—
	F	—	0.071	0.058	0.071	—	0.025	—	0.023	—	—	—	—	—
M-Aat-A	A	1.000	1.000	0.980	1.000	1.000	1.000	0.982	0.952	1.000	1.000	1.000	1.000	0.950
	B	—	—	—	—	—	—	0.018	—	—	—	—	—	—
	C	—	—	0.020	—	—	—	—	0.048	—	—	—	—	0.050
Gpi-A	A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.978	1.000	1.000	1.000	1.000
	B	—	—	—	—	—	—	—	—	0.022	—	—	—	—
G3pdh-B	A	1.000	0.912	0.940	1.000	0.957	0.975	0.964	0.977	1.000	1.000	0.553	1.000	0.938
	B	—	—	—	—	—	—	—	0.023	—	—	—	—	—
	C	—	0.044	0.020	—	0.022	—	—	—	—	—	0.447	—	0.062
	D	—	0.044	0.040	—	0.022	0.025	0.036	—	—	—	—	—	—
S-Icdh-A	A	1.000	0.986	0.981	1.000	1.000	0.750	1.000	1.000	1.000	1.000	1.000	0.983	0.950
	B	—	0.014	—	—	—	0.250	—	—	—	—	—	0.017	—
	C	—	—	—	—	—	—	—	—	—	—	—	—	0.050
	D	—	—	0.019	—	—	—	—	—	—	—	—	—	—
Ldh-A	A	1.000	1.000	1.000	1.000	1.000	0.975	1.000	0.881	1.000	1.000	1.000	1.000	0.950
	B	—	—	—	—	—	0.025	—	0.119	—	—	—	—	0.050
Ldh-B	A	0.882	0.414	0.846	0.214	0.261	—	0.852	1.000	—	0.375	—	0.367	0.300
	B	0.118	0.586	0.154	0.786	0.739	0.875	0.148	—	1.000	0.625	1.000	0.633	0.700
	C	—	—	—	—	0.125	—	—	—	—	—	—	—	—
M-Mdh-A	A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.947	0.950	1.000
	B	—	—	—	—	—	—	—	—	—	—	0.053	0.033	—
	C	—	—	—	—	—	—	—	—	—	—	—	0.017	—
S-Mdh-A	A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.983	1.000
	B	—	—	—	—	—	—	—	—	—	—	—	0.017	—
Pgdh-A	A	0.794	0.714	0.577	0.889	0.587	0.800	0.786	0.690	0.587	0.688	0.789	0.650	0.450
	B	0.118	0.129	0.192	0.111	0.413	0.200	0.071	0.119	0.022	—	0.184	0.233	0.150
	C	0.088	0.157	0.231	—	—	—	0.143	0.190	0.391	0.313	0.026	0.117	0.400
Pgm-A	A	1.000	0.986	0.885	0.982	0.978	0.775	0.964	0.932	0.913	1.000	1.000	0.983	1.000
	B	—	0.014	0.115	—	0.022	0.225	0.036	0.068	—	—	—	0.017	—
	C	—	—	—	0.018	—	—	—	—	—	—	—	—	—
	D	—	—	—	—	—	—	—	—	0.087	—	—	—	—

TABLE 1 (continued)

LOCUS	ELECTROMORPH	1 (23)	2 (17)	3 (23)	4 (23)	5 (18)	6 (27)	7 (13)	8 (24)	9 (23)	10 (17)	11 (19)	12 (20)	13 (25)
S. graciosus														
M-Aat-A	A	1.000	1.000	1.000	0.978	1.000	1.000	0.958	1.000	1.000	1.000	1.000	1.000	1.000
	B	—	—	—	—	—	—	—	—	—	—	—	—	—
	C	—	—	—	—	—	—	0.042	—	—	—	—	—	—
Gpi-A	A	1.000	—	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.118	1.000	1.000	1.000
	B	—	1.000	—	—	—	—	—	—	—	0.882	—	—	—
G3pdh-B	A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.975	1.000	1.000	1.000	1.000	1.000
	B	—	—	—	—	—	—	—	0.025	—	—	—	—	—
S-Icdh-A	A	1.000	1.000	0.870	0.978	1.000	0.963	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	B	—	—	0.130	0.022	—	0.019	—	—	—	—	—	—	—
	C	—	—	—	—	—	0.019	—	—	—	—	—	—	—
Ldh-A	A	1.000	1.000	0.940	0.978	1.000	1.000	1.000	1.000	0.979	1.000	1.000	1.000	0.980
	B	—	—	—	—	—	—	—	—	0.021	—	—	—	0.020
	C	—	—	0.060	0.022	—	—	—	—	—	—	—	—	—
S-Mdh-A	A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.974	1.000	1.000
	B	—	—	—	—	—	—	—	—	—	—	0.026	—	—
Pgdh-A	A	0.975	1.000	0.980	0.935	1.000	0.962	0.938	0.979	0.891	1.000	—	—	—
	B	—	—	0.020	0.065	—	0.038	0.063	0.021	0.087	—	0.105	0.211	0.060
	C	0.025	—	—	—	—	—	—	—	0.022	—	—	—	—
	D	—	—	—	—	—	—	—	—	—	—	0.895	0.789	0.940
Pgm-A	A	1.000	1.000	1.000	1.000	1.000	1.000	0.250	1.000	1.000	1.000	1.000	1.000	0.940
	B	—	—	—	—	—	—	—	—	—	—	—	—	0.060
	C	—	—	—	—	—	—	0.750	—	—	—	—	—	—
S-Sod-A[2]	A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.979	1.000	1.000	1.000	1.000
	B	—	—	—	—	—	—	—	—	0.021	—	—	—	—

NOTE: Numbers correspond to localities in Table 2; numbers in parentheses indicate sample sizes; alphabetical designation of electromorphs follows Thompson and Sites (1986).

TABLE 2

GENETIC VARIABILITY ESTIMATES ACROSS 13 HOMOLOGOUS LOCI IN ALL SAMPLES OF *Sceloporus grammicus* AND
S. graciosus

	S. grammicus		S. graciosus	
LOCALITY	$\bar{A}$	$\bar{H}_{DC}$	$\bar{A}$	$\bar{H}_{DC}$
1	1.31	0.050	1.08	0.004
2	1.85	0.115	1.00	0.000
3	1.92	0.134	1.23	0.032
4	1.31	0.053	1.31	0.013
5	1.46	0.084	1.00	0.000
6	1.54	0.112	1.23	0.009
7	1.54	0.075	1.23	0.042
8	1.62	0.087	1.15	0.007
9	1.38	0.060	1.31	0.023
10	1.15	0.067	1.08	0.018
11	1.46	0.121	1.15	0.020
12	1.85	0.092	1.08	0.032
13	1.54	0.102	1.23	0.022
$\bar{X}$ (SD)	1.53 (0.231)	0.089 (0.027)	1.16 (0.106)	0.017 (0.01)

NOTE: $\bar{A}$ = mean number of alleles/locus; $\bar{H}_{DC}$ = mean locus heterozygosity, direct count.

TABLE 3

PAIRWISE COMPARISONS OF GENETIC DISTANCES (NEI 1978) FOR *Sceloporus grammicus* (ABOVE DIAGONAL) AND
S. graciosus (BELOW DIAGONAL)

LOCALITY	1	2	3	4	5	6	7	8	9	10	11	12	13
1	—	0.018	0.003	0.037	0.037	0.067	0.000	0.002	0.071	0.023	0.083	0.022	0.035
2	0.080	—	0.017	0.005	0.007	0.022	0.016	0.030	0.018	0.002	0.027	0.001	0.005
3	0.001	0.083	—	0.042	0.035	0.067	0.002	0.002	0.066	0.023	0.083	0.022	0.029
4	0.000	0.081	0.001	—	0.007	0.011	0.035	0.057	0.014	0.007	0.020	0.004	0.013
5	0.000	0.080	0.001	0.000	—	0.015	0.036	0.053	0.017	0.011	0.023	0.002	0.007
6	0.000	0.081	0.001	0.000	0.000	—	0.064	0.089	0.017	0.023	0.026	0.017	0.023
7	0.044	0.130	0.047	0.044	0.044	0.044	—	0.002	0.066	0.020	0.079	0.021	0.032
8	0.000	0.080	0.001	0.000	0.000	0.000	0.044	—	0.090	0.035	0.108	0.036	0.046
9	0.000	0.082	0.002	0.000	0.001	0.000	0.045	0.000	—	0.011	0.025	0.016	0.006
10	0.062	0.001	0.064	0.063	0.062	0.062	0.111	0.062	0.063	—	0.033	0.002	0.000
11	0.071	0.160	0.073	0.068	0.073	0.070	0.117	0.070	0.064	0.141	—	0.029	0.029
12	0.065	0.154	0.067	0.061	0.067	0.063	0.110	0.063	0.058	0.135	0.000	—	0.003
13	0.074	0.164	0.077	0.071	0.076	0.073	0.117	0.075	0.068	0.145	0.000	0.002	—

NOTE: Localities are as in Table 1.

tragenic recombination; that is, recombination between alternative nucleotide sequences within a single gene locus. This is also known as the principle that "polymorphism generates more polymorphism" (Ohno 1970:51), and theoretical studies of several possible mechanisms show that, as long as a minimum amount of variability is maintained at a locus, intragenic recombination can produce new alleles at rates several orders of magnitude above normal mutation rates (Morgan and Strobeck 1979, Watt 1972). In other words, such a process will act as a high-frequency, locus-specific mutation process. Without knowing the chromosomal locations of the enzyme loci in both studies, and without breeding studies to confirm this mechanism in *Sceloporus* (for an example, see Ohno et al.

TABLE 4

F_{IS}, F_{IT}, AND F_{ST} VALUES FOR *Sceloporus grammicus* AND *S. graciosus* CALCULATED FROM 11 AND 9 POLYMORPHIC LOCI, RESPECTIVELY

	S. grammicus				S. graciosus		
LOCUS	F_{IS}	F_{IT}	F_{ST}	LOCUS	F_{IS}	F_{IT}	F_{ST}
Ap-A	−0.122	−0.064	0.052	M-Aat-A	−0.036	−0.004	0.031
M-Aat-A	−0.042	−0.009	0.032	Gpi-A	−0.133	0.927	0.936
Gpi-A	−0.022	−0.002	0.020	G3pdh-B	−0.026	−0.022	0.023
G3pdh-B	−0.381	−0.051	0.239	S-Icdh-A	0.000	0.086	0.086
S-Icdh-A	0.120	0.269	0.169	Ldh-B	−0.042	−0.007	0.033
Ldh-A	−0.098	−0.015	0.075	S-Mdh-A	−0.027	−0.002	0.024
Ldh-B	−0.027	0.446	0.461	Pgdh-A	−0.057	0.744	0.758
M-Mdh-A	−0.048	−0.007	0.039	Pgm-A	0.071	0.703	0.680
S-Mdh-A	−0.017	−0.001	0.015	S-Sod-A[2]	−0.021	−0.002	0.019
Pgdh-A	0.098	0.178	0.089				
Pgm-A	−0.064	0.038	0.095				
$\bar{X}$	−0.055	0.071	0.117		−0.030	0.269	0.288
(SD)	(0.130)	(0.160)	(0.133)		(0.053)	(0.397)	(0.384)

1969), we have no way of evaluating its effect. Intragenic recombination may be responsible for generating some of the allozyme variation at some multiallelic loci in *S. grammicus* (Ap-A, G3pdh-B, etc., Table 1), but even then, the fate of the new electromorphs will be largely influenced by population size and breeding system. One could imagine many hypothetical population structures that would either retain or reduce the locus-specific genetic variability generated by recombination within a cistron, but it seems pointless to speculate further until we have the requisite data base.

If we assume that intragenic recombination is not the only factor responsible for the interspecific differences in genetic variability presented in this study, then factors such as population structure and breeding system also must be important. Hall explicitly states (1983:669): "The founder population required for the chance fixation of a negatively heterotic chromosomal rearrangement is ideal for other stochastic phenomena such as the random fixation or drift of alleles at a variety of polymorphic gene loci." This population structure should display relatively large intersample D values, high F_{ST} values (due to random fixation of alternate alleles at polymorphic loci), and presumably low within-

sample heterozygosity due to inbreeding and drift. An additional feature of Hall's cascade model is that it requires a linear series of bottlenecks to initiate the sequence of speciation events, and several theoretical studies predict pronounced reductions in both heterozygosity levels and mean number of alleles per locus under some conditions (Chakraborty and Nei 1977, Motro and Thomson 1982, Nei et al. 1975, Sirkkomaa 1983). The population structure of *Sceloporus grammicus* thus can be evaluated in light of several different variability estimates.

Our estimates of the mean number of alleles per locus and overall heterozygosity levels do not support a recent bottleneck scenario for the three *Sceloporus grammicus* cytotypes examined (Table 2). Results, in fact, suggest the opposite, i.e., that *S. graciosus* populations may have been subject to more recent bottlenecks and/or more intense inbreeding, as on average they have significantly lower levels of heterozygosity and mean number of alleles per locus than *S. grammicus*. It is, of course, possible that *S. grammicus* has undergone recent bottlenecks but has a population growth rate rapid enough to restore initial variability levels. However, populations undergoing cyclic bottlenecks [the type seemingly required for Hall's cascade model and to spread

a new rearrangement after fixation (Lande 1985)] are expected to have an especially long "lag" between the time of restoration to original population size and the time of restoration to original heterozygosity levels (Motro and Thomson 1982). Coyne (1984) showed significant negative rank correlations between mean allozyme heterozygosities and rates of chromosome number evolution for 15 classes and orders of animals, and interpreted these results as evidence for long-term effects of past bottlenecks during which new chromosomal mutations had become fixed. If Coyne's interpretation is correct, then levels of variability almost certainly should be reduced in a very recently evolved group such as the *S. grammicus* complex. Our estimates of $\bar{A}$ and $\bar{H}_{DC}$ do not support the predictions of Hall's (1983) model.

Estimates of genetic distances (Table 3) also seem inconsistent with cascading speciation expectations. *Sceloporus grammicus* has a significantly smaller median D value than *S. graciosus*, and its D values fall well within the range of those for local populations of a single species (Ayala 1975).

When population structure is examined in light of Wright's F statistics (Table 4), the two species are shown to be statistically equivalent. The locus-specific differences in F_{IS} values and the overall low F_{IS} values for most loci suggest that inbreeding is not a strong factor in either species. Since the exact breeding units are not known in either species (we assumed each sample was part of one deme), some of the positive F_{IS} values may reflect a Wahlund effect, but this would not be an important bias unless breeding units with very different electromorph frequencies were inadvertently lumped into a single sample. The median F_{ST} values are not statistically different, but the estimate for *Sceloporus grammicus*, while relatively high compared to some invertebrates (Wright 1978), is low relative to most other small vertebrates (see Sites and Greenbaum 1983, Table 7).

II. Validity of the Population Genetic Approach

Our ability to make valid inferences about the genetic structure of any species from allozyme frequency data assumes that such data offer enough resolution to make clear distinctions among sometimes only subtly different population structures. There are problems with this approach (see below). Also, in this study, we have ignored the effects of ecological variables and niche parameters on the heterozygosity levels (see Nevo et al. 1984, for review) and the potential influence of selection on individual polymorphic enzymes (reviewed by Watt 1985). Both factors conceivably could be as important as, or more important than, breeding structure and level of population subdivision influencing the frequencies of allozymes. At present, we do not have the information to address either point. We can only recognize these possibilities as potential sources of bias to our interpretations.

A perhaps more important point to address with the data we do have is one regarding the qualitative nature of both Templeton's (1980a) classification of speciation mechanisms and many of the chromosomal speciation models. For example, the distinctions made by Templeton between Wrightian versus panmictic provide clarity, but in reality represent the extremes of a continuum of population structures. Similarly, values of genetic distance (D) can be "large" or "small" or anything in between, and should be inversely correlated with the degree of population subdivision. Obviously, extreme examples of Wrightian or panmictic population genetic architectures will be readily identifiable, but many intermediate cases will not be easily resolved. Further, the degree of electrophoretic differentiation that accompanies a speciation event will be a function not only of population structure and mechanism of speciation but also the level of variability present in the ancestral population (Templeton et al. 1981). Nevo et al. (1984) have reviewed allozyme variation for 1111 species of plants and animals, and found that heterozygosity estimates for individual (bisexual) species ranged from 0.00 to 0.644. Species with intrinsically low levels of heterozygosity will not have the variability present to fix alternate allozymes at polymorphic enzyme loci even with the most extreme Wrightian population structure. To add to

these caveats, there are now so many permutations of White's (1968, 1978b) stasipatric speciation model (including Hall's cascade hypothesis), with often only very general distinctions between them, that some models have very little predictive value. Many of these are summarized by Sites and Moritz (1987).

In an attempt to clarify distinctions among some chromosomal speciation hypotheses, Sites and Moritz (1987) developed a classification scheme on the basis of genetic mechanisms, fitness of individual chromosomal rearrangements, and population structure. With respect to the latter, these authors have extended Templeton's (1980a) original use of D to include four other genetic correlates, including F_{IS}, F_{ST}, $\bar{H}$, and $\bar{A}$. These distinctions are strictly qualitative, but serve to emphasize some major differences between chromosomal speciation categories. Hall's cascade model, for example, is only one of several models that require some degree of underdominance for the initially heterozygous rearrangement [all these would be included in Templeton's (1980a) "chromosomal transilience" category]. These models have population requirements clearly different from other models that allow for fixation of neutral or heterotic rearrangements that can become effective postmating isolating mechanisms only upon secondary contact (see Sites and Moritz 1987, Table 2). Sites et al. (1988b) have attempted to increase the predictability of some chromosomal transilience mechanisms by conducting computer simulation studies of populations fixing rearrangements of varying degrees of underdominance and under varying bottleneck sizes and frequencies. The allozyme data set from Sites and Greenbaum (1983) was input into 20 initial populations, and ten replications of these were allowed to expand and "crash" (decrease in size to simulate a bottleneck) for 100 breeding periods. These simulations showed that under some conditions that maximize the likelihood of fixation, a distinct electrophoretic profile (with respect to D and F_{IS} values) was generated that was clearly more strongly Wrightian than the original empirical data set. The electrophoretic profile became less distinct as bottleneck size was increased, suggesting that some moderately subdivided populations could allow fixation of rearrangements with a wide range of fecundity effects, and that some modes of chromosomal transilience would be indistinguishable given the heterozygosity levels input from *Sceloporus grammicus*. Additional work is in progress to determine the minimum heterozygosity level necessary to influence the population genetic correlates under varying population structures (C. Moritz and S. Easteal, personal communication). Much more work of this nature will be necessary to increase the testability of the plethora of chromosomal speciation hypotheses.

Given the above constraints on our approach, our conclusions in this and earlier studies (Sites and Greenbaum 1983, Thompson and Sites 1986) must be regarded as tentative. *Sceloporus grammicus* in the region sampled seems to have a population structure sufficiently panmictic to retard fixation of electromorphic variants, and as such is not conducive to the fixation of strongly negatively heterotic chromosomal rearrangements. This corroborates population cytogenetic sampling efforts, which show that fission polymorphisms may be maintained at high levels in some populations in Hardy–Weinberg proportions (Porter and Sites 1985, 1986), and that at least males heterozygous for up to two such rearrangements seem to suffer no meiotic effects (Porter and Sites 1985). Such polymorphisms could become established in relatively panmictic populations if the rearrangements were neutral or positively heterotic in the heterozygous state, and thus obviate the need for assuming strong negative heterosis and the concomitant Wrightian population structure. *Sceloporus grammicus* may be chromosomally polytypic because of a high mutation rate for fissions or because of selection for new rearrangements that confer some advantage in new habitats. On-going population sampling in central Mexico should help resolve some of these questions.

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