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Environmental factors affecting the diversity of reptiles in the deep canyon transect of the Colorado Desert, California

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ENVIRONMENTAL FACTORS AFFECTING THE DIVERSITY OF REPTILES IN THE DEEP CANYON TRANSECT OF THE COLORADO DESERT, CALIFORNIA

A Thesis

Presented to the

Faculty of

California State

College, San Bernardino

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

in

Biology

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by

James W. Cornett

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ABSTRACT

Physical and floristic parameters were measured and evaluated in the Deep Canyon Transect, California, to determine their effects on reptile diversity.

Of the 23 environmental measures considered, habitat patchiness, the horizontal dispersion of perennial plants and boulders considered together, was the best predictor of reptile diversity ($r = 0.720$, $p<0.01$). Territorial and thermal diversity may be the niche dimensions which are being exploited.

A secondary factor helping to predict reptile diversity appears to be heat availability. South-facing slopes and large, heat-retaining boulders may promote a diverse reptile fauna through potential lengthening of activity periods and consequent expansion of niche exploitation opportunities.

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INTRODUCTION

Biological communities differ not only in species composition, but in the number of species or "species diversity" they contain. Because species diversity has been thought to promote community stability (MacArthur, 1955; Wilhm, 1967; Barret, 1968; Odum, 1969; Shure, 1971), ecologists have considered it an important topic for decades.

This thesis reports on the results of a 16 month study conducted in the Deep Canyon Transect of the Colorado Desert, California. The general objective was to identify those features of the environment which might be of predictive value in determining the diversity of reptiles both within and between habitat types.

Two hypotheses were the basis for the design of the experiments. First, since reptiles are ectothermic, they might respond to relatively warm environments by an increase in species diversity. The mechanism would operate via a potential extension, both daily and seasonally, in their activity periods due to increased heat availability. This would provide more time in which to subdivide the niche hypervolume and thus allow more species to coexist. This hypothesis is an offshoot of MacArthur and Wilson's (1963) ecological time theory and provides a causal mechanism for Pianka's (1967) quandary as to why reptile faunas are more diverse in regions of warm climatic regimes.

The second hypothesis involves habitat heterogeneity. Species diversity in both birds and mammals has been shown to be positively correlated with components of habitat heterogeneity: birds with foliage height diversity (MacArthur, 1964; Terborgh, 1977), rodents with foliage height diversity (Rosenweig and Winakur, 1969), birds with horizontal habitat patchiness (Roth, 1976), and rodents with a combined index of both vertical and horizontal habitat patchiness (Stinson, 1978). Pianka (1966, 1967) has shown a relationship between lizard species diversity in flatland desert regions and shrub volume diversity. It was thought that these or other aspects of habitat heterogeneity might also predict the diversity of not just lizards, but all reptiles both within and between various types of habitats.

The information obtained from such a study might give some insight into the development of species diversity in biological communities.

This research is unique in that it is the first attempt to examine reptile diversity in conjunction with (1) an elevational gradient, (2) slope aspect, and (3) habitat patchiness. To the best of the author's knowledge this is the only study designed to correlate the diversity of a group of organisms with certain quantitative measures of gross substrate features. A new approach to the measurement of community diversity is also proposed.

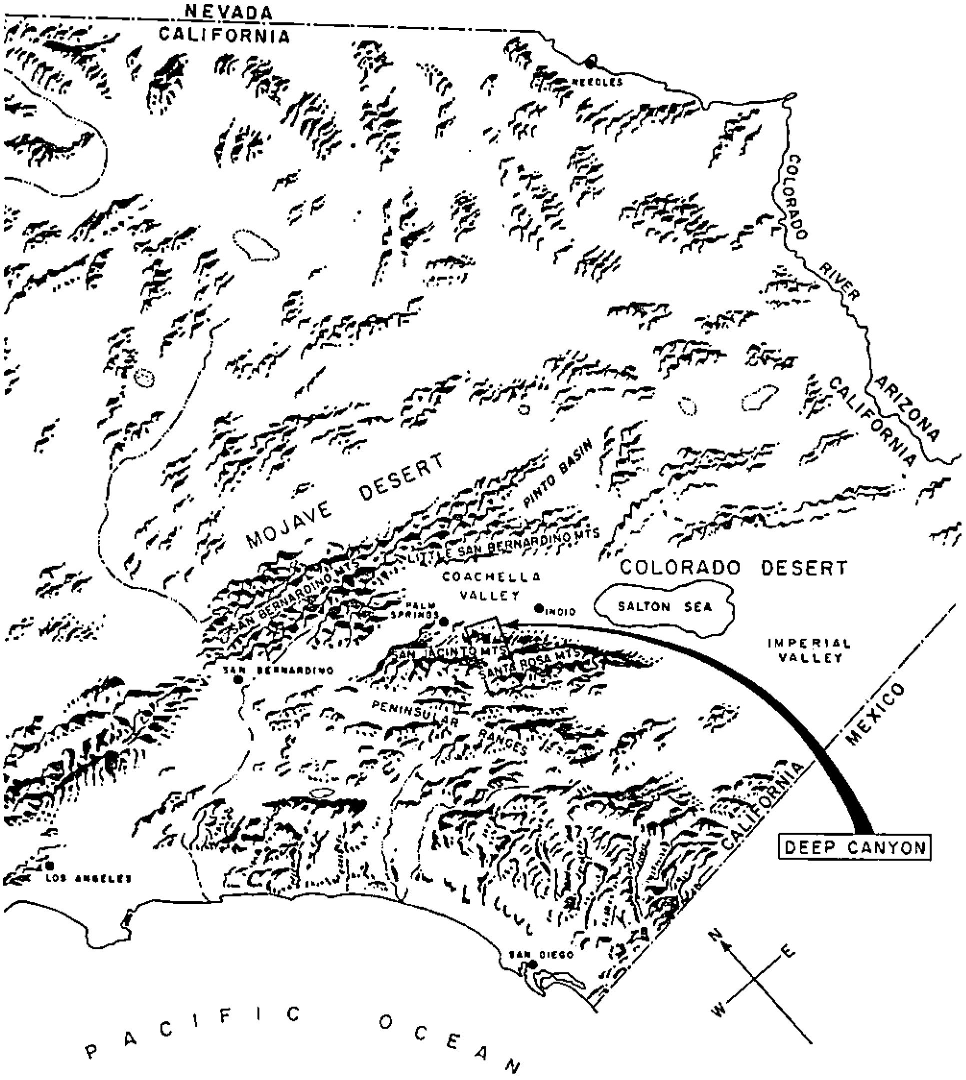
AREA OF STUDY

Quadrats were established in a variety of habitats along the western edge of the Colorado Desert. Specifically, they laid within a belt transect encompassing the Deep Canyon drainage area of the Santa Rosa Mountains and adjacent Coachella Valley (Figure 1). This region was selected because of the large number of reptile species which occupy it (Stebbins, 1966), and the remarkable variety of habitat types.

The transect is composed of arid and semiarid land and stretches from the central floor of the Coachella Valley at an elevation near sea level, to Toro Peak at 2,657 m in the Santa Rosa Mountains. Much of the valley and all of the Santa Rosas are part of what geologists term the Peninsular Ranges province, a primarily north-south trending system running nearly 1,600 km, from the tip of the Baja Peninsula to the San Gorgonio Pass in southern California. The province is of relatively recent geologic origin as it is thought that the Santa Rosa Mountains were uplifted considerably during the late Tertiary and Quaternary, roughly ten to two million years ago (Dibblee, 1954).

The mountains are comprised of highly metamorphosed sedimentary rock further deformed by igneous intrusion. The eroding action of various mechanisms has resulted in

Figure 1. Location of the Deep Canyon Transect along the western edge of the Colorado Desert, California (from Ryan, 1968).


NEVADA
CALIFORNIA
NEEDLES
COLORADO RIVER
ARIZONA
CALIFORNIA
MOJAVE DESERT
PINTO BASIN
LITTLE SAN BERNARDINO MTS
SAN BERNARDINO MTS
COACHELLA VALLEY
PALM SPRINGS
INDIO
COLORADO DESERT
SALTON SEA
IMPERIAL VALLEY
SAN JACINTO MTS
SANTA ROSA MTS
SAN BERNARDINO
PENINSULAR RANGES
MEXICO
CALIFORNIA
DEEP CANYON
LOS ANGELES
SAN DIEGO
N
E
W
PACIFIC OCEAN

these rock types being broken down into ever finer particles as they move down the slopes. Thus fine, wind-blown alluvium blankets the valley floor and the largest boulders and rock outcrops, in general, predominate at higher elevations.

Relatively level terraces are present at a number of intermediate altitudes. They appear as islands among the extremely rocky slopes. All of these lie adjacent arroyos, some of which, like Deep Canyon, run almost the length of the transect and may act as dispersal corridors between the higher and lower elevations.

Relatively detailed weather records were available for most of the quadrats. Unless otherwise stated, the climatic data presented represents the mean value for the years 1976, 1977, and 1978 inclusive.

The Deep Canyon Transect lies within the rain shadow of the Santa Rosa and nearby San Jacinto Mountains. These ranges tend to shield the region from storms originating over the Pacific Ocean. Summer storms, arriving in the opposite direction from the Gulf of Mexico, are sufficiently infrequent so that the lower elevations are subjected to true desert conditions, receiving less than 25 cm of precipitation annually.

As can be seen from Table 1, precipitation generally increases with elevation. The Asbestos Mountain shelter

TABLE 1. Mean precipitation, in millimeters, at the six weather shelters in the Deep Canyon Transect. Shelter elevations, in meters, listed below shelter name. Means computed from three years of measurement, 1976-78 inclusive (Boyd Deep Canyon Desert Research Center).

Shelter Site	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Living Desert Reserve 122 m	429	274	214	017	116	001	006	325	531	079	158	217	2,367
Boyd Center 294 m	462	295	230	019	125	001	006	351	572	085	170	234	2,550
1650 Site[a] 486 m	377	244	268	020	088	002	005	299	560	054	176	271	2,364
Agave Hill 836 m	559	361	302	032	130	002	020	455	817	082	224	348	3,332
Taylor Site 1,094 m	589	544	433	091	153	005	444	406	861	124	294	459	4,403
Asbestos Mtn.[b] 1,337 m	708	738	632	128	211	008	099	541	856	070	304	547	4,842

[a] Mean for entire three year period extrapolated from the only year of measurement, 1978.

[b] Climatic data from University of California Pinyon Flat Geophysical Observatory.

(1345 m), for example, receives over twice the precipitation of the Boyd Center station (294 m).

Precipitation is variable from year to year though there is a high probability of winter and late summer rain. In 1978 at the Boyd Center precipitation totaled 29.08 cm, over two and a half times the mean as determined for an 18 year period (Table 2).

In general there is a moderate decrease in mean temperature with an increase in elevation (Table 3). The only exception is the Living Desert Reserve station which, although lower in elevation, has a lower mean temperature. This apparently is a result of cold air flowing to the valley floor at night which sharply reduces the annual mean minimum temperature (Jan Zabriskie, Boyd Deep Canyon Desert Research Center, personal communication). If only mean maximum temperatures are compared then an actual temperature gradient exists.

Hot summers and mild winters prevail at the lower elevations while the three highest stations (Agave Hill, Taylor Site, and Asbestos Mountain) experience warm summers and cool winters (Table 3).

There seems no obvious correlation between elevation and degree of temperature flucuation over a 24 hour period. Each station cools off at a somewhat different rate, but

TABLE 2. (A) Previous years' (1961-78) precipitation at Boyd Center in millimeters. (B) Eighteen year mean precipitation (calculated from A) at Boyd Center in millimeters. (Boyd Deep Canyon Desert Research Center).

A

1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973
343	450	1514	734	2045	1057	1011	638	1057	1029	348	869	709
1975	1976	1977	1978									
597	3061	1681	2908									

B

Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual Mean
157	102	122	046	030	005	051	137	147	071	152	157	1,179

TABLE 3. Mean monthly and annual temperatures at the six weather shelters in the Deep Canyon Transect. Means, in degrees centigrade, computed from three years of measurement, 1976-78 inclusive (Boyd Deep Canyon Desert Research Center).

Shelter Site		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	$\bar{X}$	$\bar{X}$ Annual
Living Desert	Max	20	22	24	29	32	40	41	39	36	33	26	19	30	22
Reserve 122 m	Min	7	9	9	11	16	20	24	22	20	17	10	6	14	
Boyd Center	Max	19	22	22	27	31	39	40	39	33	31	25	19	29	23.5
294 m	Min	10	13	12	15	18	24	27	26	23	21	15	10	18	
1650 Site[a]	Max	19	21	22	27	31	38	39	37	33	32	24	18	28	23
486 m	Min	10	13	13	15	19	25	28	26	23	23	15	10	18	
Agave Hill	Max	15	17	19	23	27	34	35	34	29	28	20	16	25	20.5
836 m	Min	8	10	10	12	17	23	26	24	20	20	12	8	16	
Taylor Site	Max	14	16	15	20	25	32	34	33	28	26	21	15	23	17.5
1,094 m	Min	4	6	5	9	13	21	23	21	17	15	9	3	12	
Asbestos Mtn.[b]	Max	13	15	14	19	23	31	26	32	27	25	18	14	22	15
1,337 m	Min	0	2	1	4	9	17	19	18	13	10	3	0	8	

[a] Mean for entire three year period extrapolated from the only year of measurement, 1978.

[b] Climatic data from University of California Pinyon Flat Geophysical Observatory.

this seems more a result of local physiography than altitude.

Temperatures are fairly predictable from year to year. For example, the mean maximum temperature for 1978 at the Boyd Center was 29 degrees C or just one degree above the 18 year mean of 28 degrees C (Table 4).

Xerophilic vegetation dominates the landscape of the Deep Canyon Transect. Cacti and perennial shrubs are the most abundant plant forms though trees may be locally common along dry washes (_Cercidium floridum_) and at intermediate or higher elevations (_Pinus monophylla_). In general, perennial vegetation is sparse and widely spaced below 1000 m (Taylor Site).

TABLE 4. Eighteen year temperature means (1961-78) at the Boyd Center, in degrees centigrade (Boyd Deep Canyon Desert Research Center).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	$\bar{X}$	$\bar{X}$ Annual
Max	18	21	22	26	30	36	39	38	34	30	23	18	28	23
Min	9	12	13	15	18	23	27	27	24	21	14	10	18	

METHODS AND MATERIALS

Thirteen one quarter hectare quadrats were established in which reptile populations were sampled (Figure 2). Each quadrat was square with 50 m sides. Site selection was dependent upon seven factors: elevation, accessibility, vegetation, substrate features, degree of slope, slope aspect, and proximity to standard U.S. Weather Bureau shelters maintained by the Boyd Deep Canyon Desert Research Center staff (Table 5).

Six quadrats--G, A, F, H, I, and L--were set up along an elevational gradient primarily to test the effect of various thermal environments on reptile diversity. Each quadrat was south facing and rocky (Figures 3, 4, 5, 6, 7, and 8).

Two quadrats, B and J, were plotted on rocky, north-facing slopes to test the effect of slope aspect on reptile diversity. These were compared to quadrats A and I respectively, which were situated at the same elevations but on south-facing slopes (Figures 9 and 10).

Quadrats C and K were established in areas of relatively dense vegetation including trees. Quadrat C lay along the border of a wash and quadrat K was in the midst of a pinyon forest at an altitude of 1250 m. Quadrats D and M respectively, lay at the same elevations as C and K

Figure 2. The Deep Canyon Transect, Colorado Desert, California, showing relative locations of study quadrats (large letters).

DEEP CANYON TRANSECT

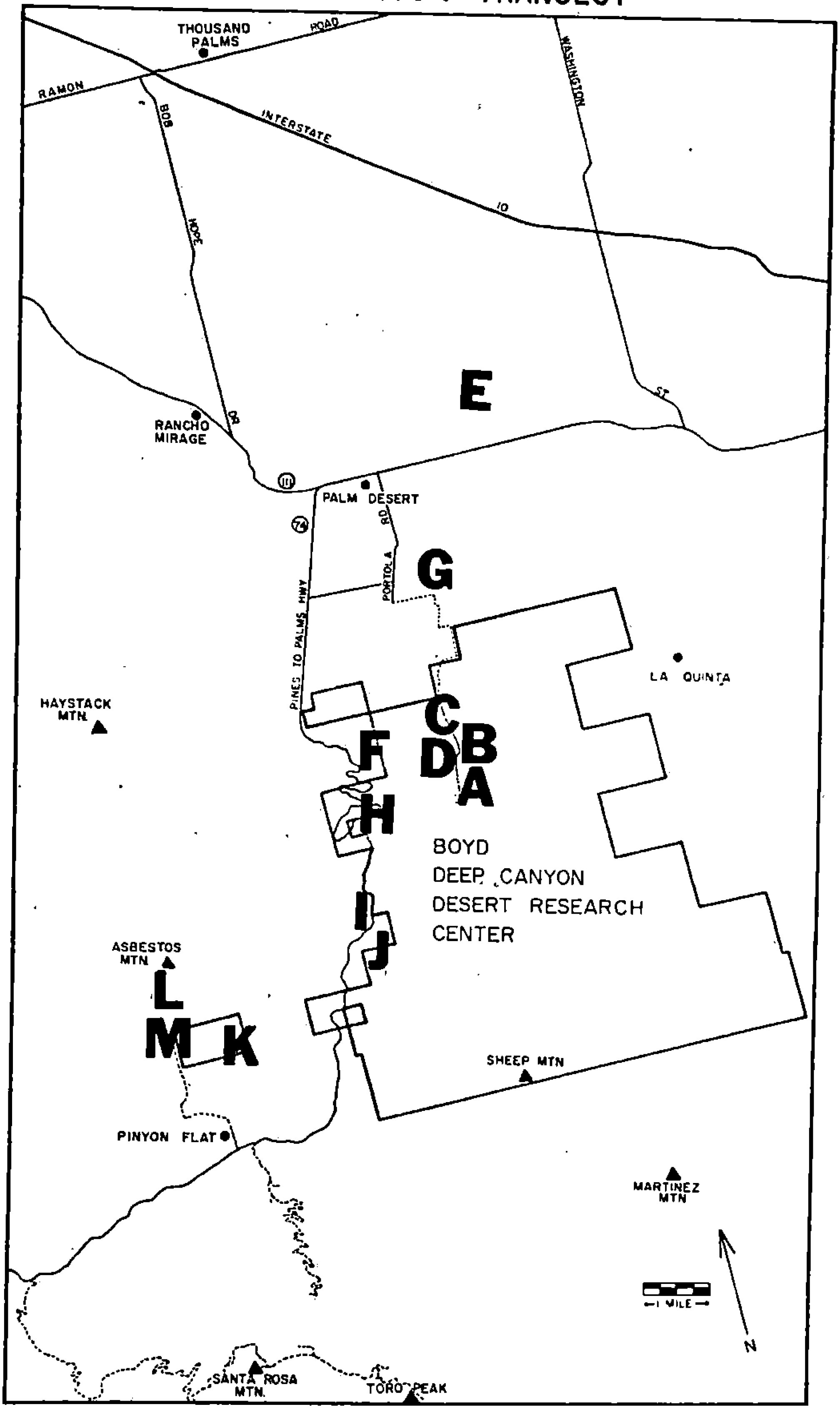


TABLE 5. Elevations (in meters) and weather shelter locations for 13 study quadrats located in the Deep Canyon Transect, California. Quadrats are grouped according to their primary experimental function (PEF). Letters in parentheses refer to control quadrats used for comparative purposes.

Quadrat	Elev.	Weather Shelter Location	PEF
G	162	Living Desert Reserve	elev.-temp.
A	310	Boyd Center	elev.-temp.
F	489	1650 Site	elev.-temp.
H	840	Agave Hill	elev.-temp.
I	1085	Taylor Site	elev.-temp.
L	1345	Asbestos Mtn.	elev.-temp.
B (A)	306	Boyd Center	slope aspect
J (I)	1095	Taylor Site	slope aspect
C (D)	244	Boyd Center	veg. het.
K (M)	1250	Asbestos Mtn.	veg. het.
D (C)	249	Boyd Center	veg. het.
M (K)	1311	Asbestos Mtn.	veg. het.
E	52	No data	substrate het.

Figure 3. Quadrat G was located on a rocky, south-facing hillside with a 35 degree slope. Sparse vegetation characterized this quadrat situated at an elevation of 162 m in the Deep Canyon Transect, California.

Figure 4. Quadrat A was located on a rocky, south-facing hillside with a 30 degree slope. It was situated at an elevation of 310 m in the Deep Canyon Transect, California.

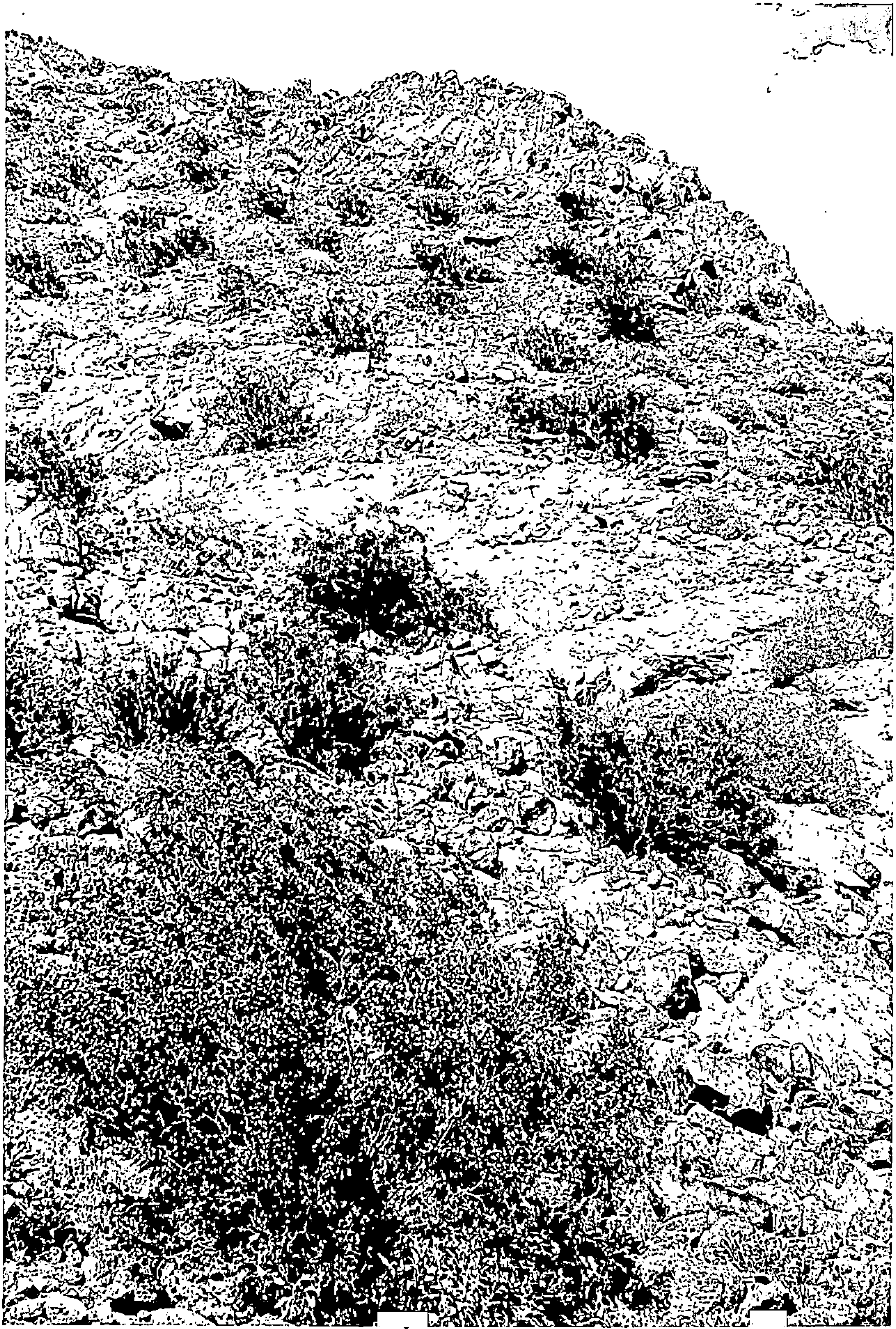


Figure 5. Quadrat F was located on a rocky, south-facing hillside with a 25 degree slope. It was situated at an elevation of 489 m in the Deep Canyon Transect, California.

Figure 6. Quadrat H was located on a rocky, south-facing hillside with a 15 degree slope. Large desert agave (*Agave deserti*) clumps characterized this quadrat situated at an elevation of 840 m in the Deep Canyon Transect, California.

Figure 7. Quadrat I was located on a rocky, south-facing hillside with a 23 degree slope. Massive boulders characterized this quadrat situated at an elevation of 1085 m in the Deep Canyon Transect, California.

Figure 8. Quadrat L was located on a rocky, south-facing hillside with a 24 degree slope. Situated at 1345 m in elevation, it was the highest of the 13 quadrats located in the Deep Canyon Transect, California.

Figure 9. Quadrat B was located on a rocky, north-facing hillside with a 27 degree slope. Situated at an elevation of 306 m in the Deep Canyon Transect, California, this quadrat was compared with quadrat A to test the effects of slope aspect on reptile diversity.

Figure 10. Quadrat J was located on a rocky, north-facing hillside with a 22 degree slope. Situated at 1095 m in elevation in the Deep Canyon Transect, California, this quadrat was compared with quadrat I to test the effects of slope aspect on reptile diversity.

but in areas of scant vegetation without trees. Quadrat E was situated in an area of loose, windblown sand almost totally devoid of surface features of any kind (Figures 11, 12, 13, 14, and 15).

All perennial plant species found in each quadrat were identified. Taxonomic nomenclature follows Munz (1974). Species densities were determined by counting all individuals within a 10 m wide belt transect through the center of each quadrat and parallel to the countour of any slope.

Plant coverage was determined, as described by Smith (1974), by running three equally spaced line transects across the width of the quadrats, again parallel with any slope contour.

Plant heights and widths were measured for all perennials encountered along the three line transects mentioned above. Plant volumes were calculated using the formula for an oblate spheroid: $V = 4/3 \pi ab^2$, where "a" is the linear dimension of the major axis or width, and "b" the linear dimension of the minor axis or height (Pianka, 1967).

Plant species diversity was calculated for each quadrat using Shannon's diversity index, $H = -\Sigma p_i \log p_i$ (1948). In this case, "H" is calculated using "p_i" equal to the proportion of coverage of the "i"th species along a line transect.

Plant height diversity and plant volume diversity were

Figure 11. Quadrat C was located in a level, tree-lined wash. Situated at an elevation of 244 m in the Deep Canyon Transect, California, this quadrat was compared to quadrat D to test the effects of certain vegetation parameters upon reptile diversity.

Figure 12. Quadrat K was located at an elevation of 1250 m in the Deep Canyon Transect, California. Level terrain, sandy but compacted soil, and trees characterized this quadrat

Figure 13. Quadrat D was located on an alluvial fan at an elevation of 249 m in the Deep Canyon Transect, California. Scant vegetation and relatively level terrain characterized this quadrat.

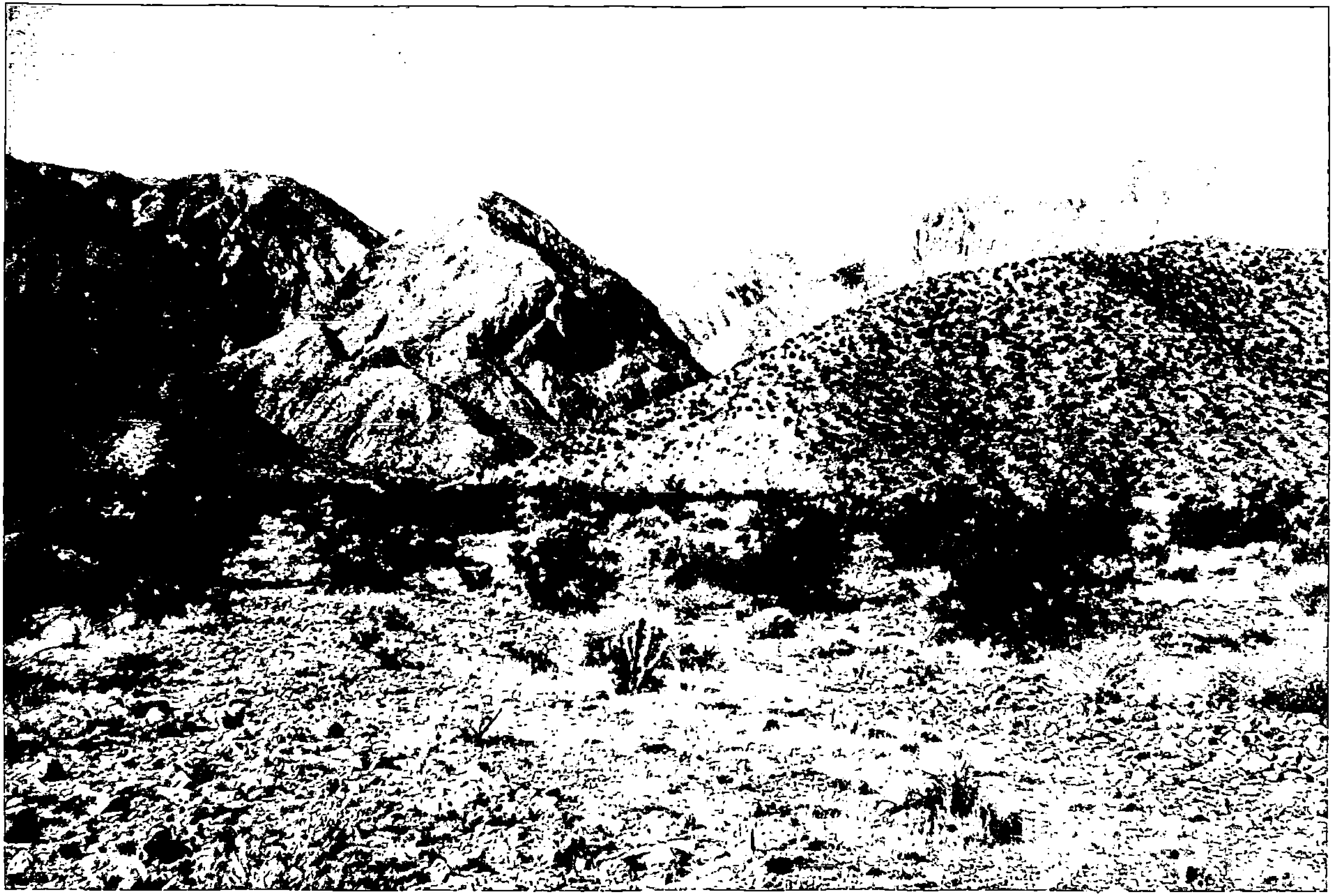


Figure 14. Quadrat M was located on level terrain at an elevation of 1311 m in the Deep Canyon Transect, California. A lack of trees and rocks characterized this quadrat.

Figure 15. Quadrat E was located at an elevation of 52 m in the Deep Canyon Transect, California. A substrate of fine, windblown sand and extremely sparse perennial vegetation characterized this quadrat.

calculated for each quadrat, once again using Shannon's formula. A logarithmic series of height and volume categories was devised which gave more emphasis to the smaller sizes. The assumption was that these variances would be more important to the relatively small and primarily terrestrial reptiles which were thought to occupy this region. Plant height categories in meters are as follows:

0 to 0.20
0.21 to 0.40
0.41 to 0.80
0.81 to 1.60
1.61 to 3.20
3.21 to 6.40
> 6.40

Plant volume categories in cubic meters are as follows:

0 to 0.05
0.051 to 0.20
0.21 to 0.80
0.81 to 3.20
3.21 to 12.80
12.81 to 50.00
50.01 to 200.00
200.01 to 800.00
> 800.00

The size categories are equivalent to species ("i") when calculating the diversity values.

A variety of plant forms grow in the Deep Canyon Transect. Six distinctive forms were noted: galleta grass tufts (Hilaria rigida), subshrubs (less than 0.80 m^3), shrubs, trees, cacti, and desert agave clumps (Agave deserti). Plant form categories were equivalent to species ("i") when calculating the diversity values.

Taken as a group, perennials may be distributed after one of three patterns: random, evenly spaced, and clumped. The point-centered quarter technique was used to measure the variation in distances between plants and thus provide an indication of their distributional pattern (Roth, 1976). The technique involves measuring the distance from a central point to the nearest plant in each quarter of a circle. A collection of distances from a quadrat with regularly distributed vegetation should have less variation than ones collected from quadrats with random or clumped distributions of vegetation. The coefficient of variation of the distances is calculated by: $CV = SD/\bar{X}$, where SD is the standard deviation and $\bar{X}$ is the mean of the point-to-point distances. This value indicates the degree of variation among a collection of distances and can be used to indicate distributional patterns of plants in a given quadrat. A large CV suggests a clumped or random pattern, spatially heterogeneous or "patchy" in character. A small CV suggests an evenly spaced distribution, spatially homogeneous in character.

The degree of slope of each quadrat was determined through use of a clinometer.

An attempt was made to quantify gross substrate features, namely rocks and boulders. Three aspects of "rockiness" were assumed for any given habitat and they followed closely the techniques used to measure certain plant parameters. (In this study only rocks 20 cm or larger in their greatest dimension were considered. This seemed the minimum size that could be of utility in terms of providing shelter, aiding in thermoregulation, or facilitating display behavior.)

Rock coverage, the ground area covered by rocks 20 cm or larger, was determined by running two equally spaced line transects across the width of the quadrats and parallel with any slope contour. Only the intercept distance of rocks in the above size category was considered.

Rock volume was a second aspect of rockiness. This was calculated as with plants, using the formula for an oblate spheroid: $V = 4/3 \pi ab^2$. This seemed the most appropriate generalized shape for rocks as they normally rest on their widest dimension.

Rock volume diversities were also calculated for each quadrat. Shannon's (1948) formula was used for this purpose. Volume categories were established in a logarithmic series giving weight to the smaller sized rocks. Each volume category was the equivalent of a species ("i") in computing the diversity value. The seven volume categories, in m^3, were as follows:

< 0.0500

0.0501 to 0.2000

0.2001 to 0.8000

0.8001 to 3.2000

3.2001 to 12.8000

12.8001 to 50.0000

> 50.0000

A third aspect of rockiness is the dispersion or patchiness of rocks within each study quadrat. This was determined, as with plants, by using the point-centered-quarter technique and calculating the CV of the distances from 50 randomly selected points to 200 rocks (Roth, 1976).

A combined index of habitat patchiness was calculated for each quadrat by computing the mean of the CVs for both plant and boulder distances.

Reptiles were captured by hand, noose, or through use of pitfall traps. Five traps, each 45 cm deep and 30 cm wide, were imbedded in the substrate of each quadrat, the top flush with ground level. One trap was placed in the center and the remaining four were placed in the corners of the thirteen quadrats. Each trap was open for 16 months, from April 1, 1978, until July 30, 1979, for a total of 57,600 trapping hours per quadrat. Traps were checked approximately every ten days though more frequently during the summer months. A total of 48 hours was spent in each quadrat capturing reptiles by hand or noose.

Captured reptiles were identified, measured, weighed, marked, and released. Lizards were marked by toe clipping; snakes by removing at least two ventral scales. Marking prevented individuals from being considered more than once in the data.

Reptile diversity was calculated using Shannon's index (1948). However, rather than using individuals of a species as the units of each category ("i"), the number of grams or total biomass was used. This modification was deemed necessary because the abundance of an organism was not felt to be the most satisfactory quantity with which to calculate community diversity. This point has been emphasized by Hurlbert (1971). Most ecologists would probably agree, for example, that ten buffalo would have a more profound impact on one hectare of American prairie than ten cricetine mice, yet their importance would appear the same if Shannon's index were used in the traditional manner. In short, biomass is considered to be of greater importance to a community than numbers of individuals.

RESULTS

In general, perennial plants were more abundant, displayed greater diversity, and covered more ground at higher elevations. Results of the vegetation surveys are presented in Tables 6 through 10.

Gross substrate features (boulders) varied tremendously from one quadrat to the next showing no trends in terms of rock coverage, rock volume, or size diversity (Table 11).

The dispersion or patchiness of rocks and perennials varied widely between quadrats and showed no obvious trend. However, there was a moderately strong correlation between the combined index of habitat patchiness and elevation ($r = 0.748$, $p<0.05$); as elevation increased rocks and perennials became more clumped in their distribution (Table 12).

A total of 643 reptiles, representing 32 species, were captured during the term of this study. Number, biomass, total species, and diversity values for each quadrat or species are presented in Tables 13 and 14.

As mentioned previously, quadrats G, A, H, F, I, and L were established to determine the effect of elevation and temperature on reptile diversity. Though the correlation between elevation and reptile diversity is moderately strong

TABLE 6. Number of individual perennial species per hectare in 13 sample quadrats from the Deep Canyon Transect, California. Quadrats listed in order of increasing elevation (in meters).

Species	Sample Quadrat Letter												
	E 52	G 162	C 244	D 249	B 306	A 310	F 489	H 840	I 1085	J 1095	K 1250	M 1311	L 1345
Acacia greggii			20		20			20	80				40
Agave deserti							4	720		4	60		4
Ambrosia dumosa			4	180	560	4	40	1520					
Arctostaphylos glauca													36
Asclepias albicans				4									
Baccharis brachyphylla									60				
Bebbia juncea			140	560	120			120					
Beloperone californica			180										
Brandegia bigelovii			180										
Cercidium floridum			120	4									
Dalea schottii		4			80	60		80					

TABLE 6. continued

Species	Sample Quadrat Letter												
	E	G	C	D	B	A	F	H	I	J	K	M	L
	52	162	244	249	306	310	489	840	1085	1095	1250	1311	1345
Dalea spinosa			4										
Dudleya saxosa										4			
Echinocactus acanthodes					20	120	20	120					
Echinocereus engelmannii					20			80			60		60
Encelia farinosa		160	4		540	480	1000	1140					
Ephedra aspiris								60					
Ephedra nevadensis									360	4	60		
Eriogonum fasciculatum									1820	60	200	480	720
Eriogonum inflatum					160			80					
Eriogonum wrightii								140	280				
Fagonia laevis				4			460						

TABLE 6. continued

Species	Sample Quadrat Letter												
	E 52	G 162	C 244	D 249	B 306	A 310	F 489	H 840	I 1085	J 1095	K 1250	M 1311	L 1345
Fouquieria splendens					20	20	20						
Haplopappus linearifolius									4	140	380	320	220
Hilaria rigida								3020	1240	420	860	420	1900
Hoffmannseggia microphylla		20											
Hymenoclea salsola			140	60		20							
Hyptis emoryi			4		40								
Juniperus californica										120	120	4	40
Keckiella antirrhinoides									320	4	240		40
Krameria grayi				4	120	4	4	180		4			4
Larrea tridentata	20	60	20	340	200	120	240	4					
Lotus rigidis									80	4	20	120	720

TABLE 6. continued

Species	Sample Quadrat Letter												
	E 52	G 162	C 244	D 249	B 306	A 310	F 489	H 840	I 1085	J 1095	K 1250	M 1311	L 1345
Mammillaria dioica					4								
Mammillaria tetrancistra				60		4	80						
Mirabilis bigelovii					4			80	60				
Nolina parryi										4		20	4
Opuntia basilaris					60		40	100	60	4	100	4	
Opuntia bigelovii				4			20	80					
Opuntia chlorotica													20
Opuntia echinocarpa			4	220		4	120	700	4	160	160	440	160
Opuntia ramosissima				140									160
Penstemon clevelandii													40
Phoradendron californicum			140										

TABLE 6. continued

Species	Sample Quadrat Letter												
	E 52	G 162	C 244	D 249	B 306	A 310	F 489	H 840	I 1085	J 1095	K 1250	M 1311	L 1345
Phoradendron juniperinum											4		
Pinus monophylla										8	20	20	
Prunas fremontii									60	4	60	60	20
Purshia glandulosa										80	4		
Quercus turbinella										140	40	4	60
Rhus ovata										4	20	120	40
Salvia apiana									40	4			
Simmondsia chinensis								20	220	4	120		
Sphaeralcea ambigua						40		140		40	4	20	40
Stephanomeria pauciflora			20					20					4
Viguiera deltoidea									360	4	320		100

TABLE 6. continued

Species	Sample Quadrat Letter												
	E	G	C	D	B	A	F	H	I	J	K	M	L
	52	162	244	249	306	310	489	840	1085	1095	1250	1311	1345
Yucca schidigera										80	80	160	20
Yucca whipplei													100
Total Species	1	4	14	12	15	11	12	21	16	23	21	14	24
Total Densities	20	244	980	1580	1968	876	2048	8424	5048	1296	2932	2192	4552

TABLE 7. Percentage of ground covered by perennial vegetation and percentage of ground covered by more than one plant (overlap) in each of the 13 quadrats in the Deep Canyon Transect, California. Quadrats listed in order of increasing elevation (in meters).

Quadrat Letter	Elevation	Coverage	Overlap
E	52	1.12	0.00
G	162	7.97	0.00
C	244	28.87	6.72
D	249	11.05	0.11
B	306	24.01	3.14
A	310	22.40	0.00
F	489	16.69	0.33
H	840	37.87	1.80
I	1085	29.92	2.88
J	1095	41.47	1.49
K	1250	37.42	4.04
M	1311	41.14	2.90
L	1345	38.97	3.59

TABLE 8. Relative percent cover for the perennial species in 13 quadrats from the Deep Canyon Transect, California. Quadrats listed in order of increasing elevation (in meters).

Species	Sample Quadrat Letter												
	E 52	G 162	C 244	D 249	B 306	A 310	F 489	H 840	I 1085	J 1095	K 1250	M 1311	L 1345
Acacia greggii			0.89		1.59				0.54				3.29
Agave deserti								38.89		0.35			4.10
Ambrosia dumosa				6.45	4.73			5.54					
Arctostaphylos glauca													3.62
Baccharis brachyphylla									2.61				
Bebbia juncea				9.77	4.89			1.39					
Beloperone californica			47.13										
Cercidium floridum			27.73										
Dalea schottii					5.37	30.31		5.59					
Dalea spinosa			2.27										
Echinocactus acanthodes					0.48	2.50	1.86	0.15					

TABLE 8. continued

Species	Sample Quadrat Letter												
	E 52	G 162	C 244	D 249	B 306	A 310	F 489	H 840	I 1085	J 1095	K 1250	M 1311	L 1345
Encelia farinosa		73.83			32.76	26.47	65.15	16.27					
Ephedra nevadensis									6.04				
Eriogonum fasciculatum									36.47	13.54	1.71	4.47	13.15
Eriogonum inflatum					5.34								
Eriogonum wrightii									1.74				
Fagonia laevis							4.85						
Fouquieria splendens					21.36	19.78							
Haplopappus linearifolius										7.33		0.67	2.49
Hilaria rigida								21.51	13.27	4.28	6.89	1.72	11.49
Hoffmannseggia microphylla		2.42											
Hymenoclea salsola			4.03										

TABLE 8. continued

Species	Sample Quadrat Letter												
	E 52	G 162	C 244	D 249	B 306	A 310	F 489	H 840	I 1085	J 1095	K 1250	M 1311	L 1345
Hyptis emoryi			5.64		4.25								
Juniperus californica										19.36	15.46		3.97
Keckiella antirrhinoides									8.59	5.74			2.88
Krameria grayi					4.38								
Larrea tridentata	100.00	23.75	12.31	76.07	14.32	20.94	22.70						
Lotus rigidis										2.52		0.47	1.04
Mammillaria tetrancistra				1.00									
Mirabilis bigellovii					0.53			0.34	0.44				
Nolina parryi												2.99	0.66
Opuntia basilaris							1.58	1.42					
Opuntia bigelovii				1.13			3.88	2.46					

TABLE 8. continued

Species	Sample Quadrat Letter												
	E 52	G 162	C 244	D 249	B 306	A 310	F 489	H 840	I 1085	J 1095	K 1250	M 1311	L 1345
Opuntia echinocarpa				3.20				5.10		4.18	3.96	13.42	1.68
Opuntia ramosissima				2.38									
Phoradendron juniperinum											0.38		
Pinus monophylla										3.33	19.87		13.00
Prunas fremontii									6.88	11.00		6.36	2.27
Purshia glandulosa											2.32		
Quercus turbinella											36.32	15.08	17.14
Rhus ovata										18.71		29.56	16.71
Simmondsia chinensis									2.77				
Sphaeralcea ambigua								1.33					1.33
Viguiera deltoidea									17.87	0.95			1.19
Yucca schidigera										3.88	4.55	9.45	

TABLE 9. Mean heights, widths, and volumes for perennial plants in each of the 13 quadrats in the Deep Canyon Transect, California. Quadrats listed in order of increasing elevation.

Quadrat	$\bar{X}$ Height (m)	$\bar{X}$ Width (m)	$\bar{X}$ Volume (m^3)
E	2.05	4.71	58.56
G	1.17	1.93	22.90
C	2.35	4.09	263.42
D	1.08	1.79	32.08
B	1.20	1.64	54.43
A	1.38	2.00	58.56
F	0.96	1.26	10.38
H	0.56	0.90	3.77
I	0.66	0.87	5.45
J	1.13	2.09	114.18
K	1.75	2.26	262.46
M	1.26	2.45	160.97
L	1.10	1.77	148.71

TABLE 10. Plant species diversity (PSD), plant coverage diversity (PCD), plant height diversity (PHD), plant volume diversity (PVD), and plant form diversity (PFD), values for 13 quadrats in the Deep Canyon Transect, California. Quadrats listed in order of increasing elevation.

Quadrat	PSD	PCD	PHD	PVD	PFD
E	0.000	0.000	0.000	0.000	0.000
G	1.189	0.946	0.000	1.753	0.000
C	2.845	2.002	1.876	2.211	1.200
D	2.441	1.310	2.058	2.659	1.044
B	2.880	3.105	1.785	2.477	1.306
A	1.989	2.097	2.134	2.502	0.996
F	2.194	1.482	1.938	2.409	1.241
H	3.114	2.546	1.530	2.344	2.015
I	2.803	2.805	1.558	2.099	1.441
J	3.610	3.371	2.095	2.780	2.528
K	3.332	2.607	1.832	2.233	1.443
M	3.056	2.870	1.500	2.276	1.430
L	2.993	3.560	1.933	2.613	1.666

TABLE 11. Rock coverage (RC), mean rock volume (MRV), and rock volume diversity (RVD) for 13 quadrats in the Deep Canyon Transect, California.[a] Quadrats listed in order of increasing elevation.

Quadrat	RC (%)	MRV (m^3)	RVD
E	0.00	0.00	0.000
G	73.18	3.94	2.443
C	1.38	0.06	0.866
D	1.40	0.03	0.592
B	65.57	17.46	2.393
A	49.07	0.26	1.526
F	37.88	0.37	1.977
H	25.52	5.39	1.795
I	67.53	11.93	2.216
J	35.74	5.75	2.478
K	0.00	0.00	0.000
M	0.00	0.00	0.000
L	41.24	13.53	2.432

[a] Only rocks 20 cm or larger in diameter were considered.

TABLE 12. Coefficients of variation of rock distances (CVR), perennial plant distances (CVP), and the mean of these distances or "habitat patchiness" (HP) values for 13 quadrats in the Deep Canyon Transect, California. Quadrats listed in order of increasing elevation.

Quadrat	CVR	CVP	HP
E	0.000	0.582	0.291
G	2.029	0.937	1.367
C	1.776	1.276	1.526
D	1.205	0.882	1.043
B	2.046	1.052	1.549
A	0.117	1.002	0.559
F	1.248	0.937	1.093
H	1.081	1.471	1.278
I	3.029	1.296	2.163
J	1.255	1.270	1.262
K	0.000	2.158	1.079
M	0.000	1.345	0.672
L	1.704	1.486	1.595

TABLE 13. Number of individual reptile species captured in 13 one quarter hectare quadrats in the Deep Canyon Transect, California. Quadrats listed in order of increasing elevation (in meters).

Species	Sample Quadrat Letter												
	E 52	G 162	C 244	D 249	B 306	A 310	F 489	H 840	I 1085	J 1095	K 1250	M 1311	L 1345
Callisaurus draconoides			6	1									
Chionactis occipitalis			7					2					
Cnemidophorus tigris		13	5	5	8	6	12	8	5	3	3	1	1
Coleonyx variegatus		1	15	7	2	2	5	1					
Crotalus cerastes					1								
Crotalus mitchelli						1							
Crotalus ruber			1										
Crotaphytus collaris					1	1							1
Crotaphytus wislizenii				1									
Diadophis punctatus											1		
Dipsosaurus dorsalis	7				1								

TABLE 13. continued

Species	Sample Quadrat Letter												
	E 52	G 162	C 244	D 249	B 306	A 310	F 489	H 840	I 1085	J 1095	K 1250	M 1311	L 1345
Eumeces gilberti												1	1
Eumeces skiltonianus										1			
Hypsiglena torquata								1					
Lampropeltis getulus		1											
Leptotyphlops humilis								1					
Masticophis flagellum				1									
Phyllorhynchus decurtatus			1	1			1		4				
Pituophis melanoleucus													1
Phrynosoma coronatum												1	
Phrynosoma platyrhinos				2		2	1	2					
Sauromelos obesus		2				14	5	2					

TABLE 13. continued

Species	Sample Quadrat Letter												
	E	G	C	D	B	A	F	H	I	J	K	M	L
	52	162	244	249	306	310	489	840	1085	1095	1250	1311	1345
Sceloporus magister		1	8	1					4			3	
Sceloporus occidentalis											10	2	2
Sceloporus orcutti									4	7			4
Streptosaurus mearnsi		1											
Tantilla planiceps								1					
Uma inornata	65												
Uta stansburiana		30	30	20	29	30	35	24	44	35	12	16	28
Xantusia henshawi									7				
Xantusia vigilis								2			1		1
Urosaurus graciosus			5										
Total individuals	72	49	78	39	42	56	59	44	68	46	27	24	39
Total species	2	7	9	9	6	7	6	10	6	4	5	6	8

TABLE 14. Biomass of individual reptile species captured in 13 one quarter hectare quadrats in the Deep Canyon Transect, California. Reptile diversity values, based upon biomass data, are given at the end of table. Quadrats listed in order of increasing elevation (in meters).

Species	Sample Quadrat Letter												
	E 52	G 162	C 244	D 249	B 306	A 310	F 489	H 840	I 1085	J 1095	K 1250	M 1311	L 1345
<u>Callisaurus draconoides</u>			41.2	0.9									
<u>Chionactis occipitalis</u>			73.6					15.7					
<u>Cnemidophorus tigris</u>		103.9	30.9	35.1	62.2	66.5	86.5	84.5	43.5	27.0	10.5	14.0	16.0
<u>Coleonyx variegatus</u>		1.2	63.9	21.6	3.9	4.9	19.5	4.7					
<u>Crotalus cerastes</u>					24.0								
<u>Crotalus mitchelli</u>						80.0							
<u>Crotalus ruber</u>			170.0										
<u>Crotaphytus collaris</u>					23.0	38.0							
<u>Crotaphytus wislizenii</u>				3.8									
<u>Diadophis punctatus</u>											9.0		
<u>Dipsosaurus dorsalis</u>	582.4				64.0								

TABLE 14. continued

Species	Sample Quadrat Letter												
	E 52	G 162	C 244	D 249	B 306	A 310	F 489	H 840	I 1085	J 1095	K 1250	M 1311	L 1345
Eumeces gilberti												7.0	6.8
Eumeces skiltonianus										5.4			
Hypsiglena torquata								7.0					
Lampropeltis getulus		100.0											
Leptotyphlops humilis								6.0					
Masticophis flagellum				10.0									
Phrynosoma coronatum												3.7	
Phrynosoma platyrhinos				28.0		19.6	12.0	31.9					
Pituophis melanoleucus													15.0
Phyllorhynchus decurtatus			12.0	22.0			23.0		69.5				
Sauromelos obesus		308.0				1404.0	694.0	166.0					

TABLE 14. continued

Species	Sample Quadrat Letter												
	E 52	G 162	C 244	D 249	B 306	A 310	F 489	H 840	I 1085	J 1095	K 1250	M 1311	L 1345
Sceloporus magister		21.0	278.3	2.2					135.0			116.0	
Sceloporus occidentalis											65.9	9.9	19.0
Sceloporus orcutti									101.2	118.6			21.5
Streptosaurus mearnsi		15.0											
Tantilla planiceps								6.1					
Uma inornata	779.2												
Urosaurus graciosus			19.4										
Uta stansburiana		44.3	54.9	22.3	67.1	60.5	55.0	57.5	93.5	63.0	15.7	25.4	59.0
Xantusia henshawi									19.7				
Xantusia vigilis								0.8			0.8		0.8
Total Biomass	1361.6	593.4	744.2	145.9	244.2	1673.5	890.0	380.2	462.4	214.0	101.9	175.8	178.3
Diversity Values	0.985	1.967	2.584	2.724	2.266	1.004	1.196	2.300	2.390	1.502	1.524	1.622	2.555

(r = 0.748) it is not statistically significant at the 0.05 level of confidence. A higher correlation exists between reptile diversity and mean temperature which is significant (r = -0.830, $p<0.05$). Combined habitat patchiness (r = 0.820, $p<0.05$) and especially mean rock volume (r = 0.894, $p<0.05$) are also good predictors of reptile diversity in the six quadrats along the elevational gradient.

Quadrats A and I were compared with B and J respectively, to determine the effect of slope aspect on reptile diversity. The latter two quadrats were north facing and the former two south facing. The results appear inconclusive (Table 14). At the lower elevation the north-facing slope was more diverse. At the higher elevation the south-facing slope was more diverse.

Habitat heterogeneity was viewed from a variety of perspectives in this study including number of perennial species present, plant coverage diversity, plant form diversity, plant height diversity, the CV of plant distances, and the CV of boulder distances. When all 13 quadrats were considered no correlation could be shown between any of these parameters and reptile diversity.

This situation existed in the six quadrats along the elevational gradient as well but with one exception. A moderate correlation ($r = 0.650$) was computed between the CV of plant distances and reptile diversity. However this measure was not statistically significant at the 0.05 level of confidence.

When all thirteen quadrats were considered, reptile diversity was best predicted by the degree of the combined index of habitat patchiness ($r = 0.720$, $p<0.01$; Figure 16).

Simple correlations between reptile diversity and all 23 environmental measures calculated in this study are presented in Table 15.

Multiple regression analysis was used to determine if several factors, acting simultaneously, could be the best predictors of reptile diversity. However, the best line could explain only 62.4% of the variation in the dependent variable (reptile diversity) when all thirteen quadrats were considered. The line was represented by a three term equation:

$$Y = 0.530 + 1.103X_1 + 0.183X_2 - 0.239X_3$$

with X_1 the degree of habitat patchiness, X_2 the diversity of plant volumes, and X_3 the diversity of boulder volumes.

Figure 16. Reptile diversity plotted against habitat patchiness. Triangles indicate those quadrats lying along the elevational gradient; squares all other quadrats. Solid lines indicate least squares line for all quadrats with its equation in the upper left corner. Broken line is the least squares line for just the six quadrats lying along the elevational gradient. The equation of this line is in the lower right corner.

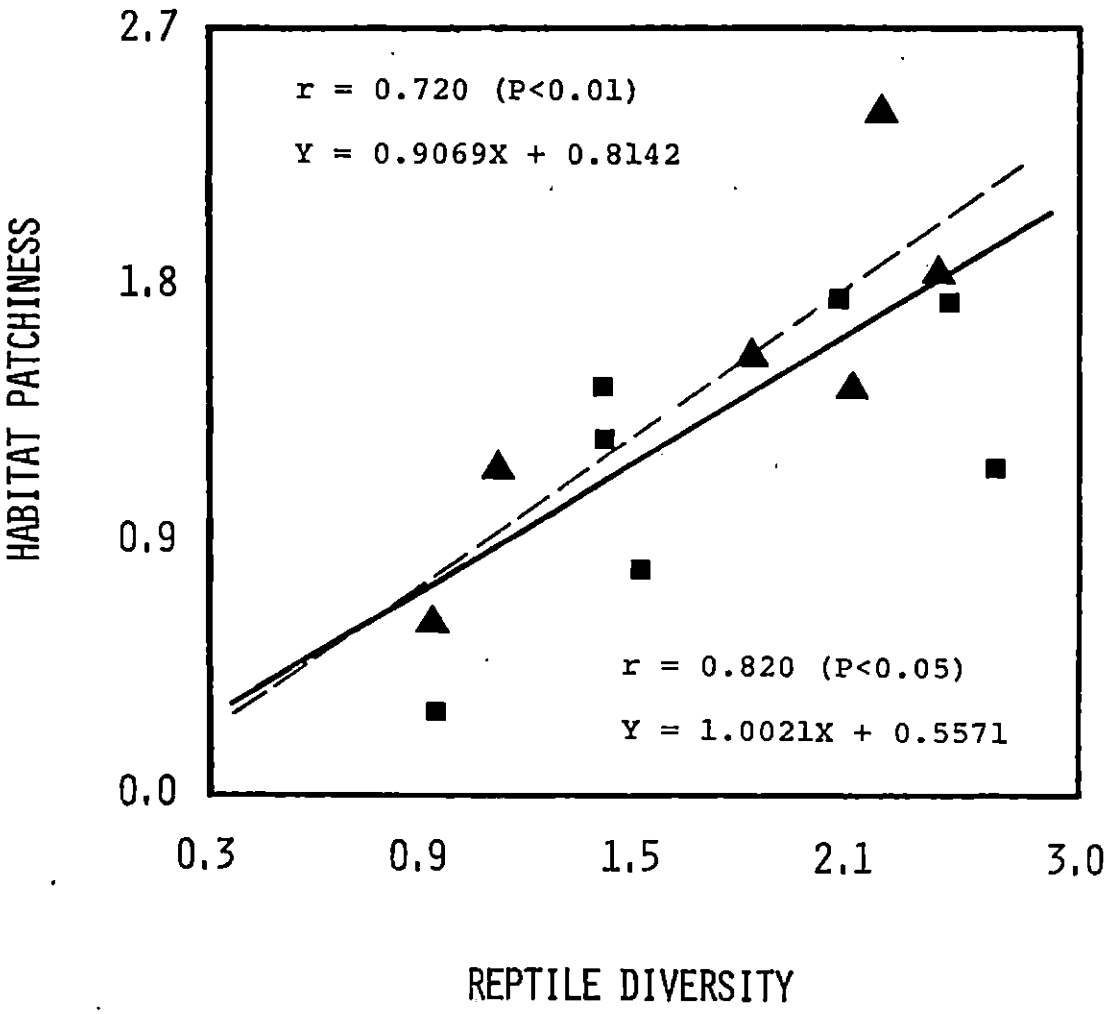

2.7
1.8
0.9
0.0
0.3
0.9
1.5
2.1
3.0
HABITAT PATCHINESS
REPTILE DIVERSITY
r = 0.720 (P<0.01)
Y = 0.9069X + 0.8142
r = 0.820 (P<0.05)
Y = 1.0021X + 0.5571

TABLE 15. Correlations between 23 environmental measures and reptile diversity in (1) all 13 quadrats and (2) the six quadrats along the elevational gradient in the Deep Canyon Transect, California.

Environmental Measure	All Quad.	Elev. Grad.
Number of plant species	0.421	0.534
Plant Species Diversity	0.412	0.544
Plant Coverage Diversity	0.325	0.599
Plant Form Diversity	0.224	0.362
Plant Height Diversity	0.290	-0.436
Mean Plant Height	-0.227	-0.566
Mean Plant Width	-0.266	-0.369
Plant Density	0.401	0.661
Plant Volume Diversity	0.392	-0.166
Mean Plant Volume	-0.197	0.233
Plant Coverage	0.206	0.594
CV of Plant Distances	0.180	0.650
Elevation	0.098	0.748
Slope Angle	-0.283	-0.427
Precipitation	0.092	0.674
Mean Temperature	-0.052	-0.830
Mean Maximum Temperature	-0.172	-0.752
Mean Minimum Temperature	0.087	-0.806
Rock Coverage	0.090	0.067
Rock Volume Diversity	0.250	0.645
Mean Rock Volume	0.468	0.894

TABLE 15. continued

Environmental Measure	All Quad.	Elev. Grad.
CV of Rock Distances	0.669	0.677
Habitat Patchiness	0.720	0.817

DISCUSSION

The results of this study suggest that two environmental features best predict local patterns of reptile diversity: habitat patchiness and heat availability

Habitat patchiness was the most statistically significant of all the environmental measures since it was highly correlated with all thirteen quadrats ($r = 0.720$, $p<0.01$). Specifically, it was the within-quadrat horizontal dispersion of both perennial plants and boulders which best predicted reptile diversity.

This suggests that reptiles partition the environment according to the dispersion of gross features rather than in differences between the features themselves. If it were otherwise, a significant correlation would be expected between reptile diversity and the volume, height, form, or species diversity of plants or the volume diversity of rocks. No such correlations were found in this study.

This conclusion differs from that of Pianka (1967) who found lizard diversity to be most highly correlated with plant volume diversity. Pianka, however, did not measure within quadrat habitat patchiness and it is conceivable that his results would have been different had he measured this component of habitat heterogeneity.

The question must now be asked, by what mechanism(s) might habitat patchiness facilitate a greater partitioning of the environment by reptiles? The literature points to several hypotheses, at least two of which involve phenomena of special importance to this vertebrate class.

Many reptiles on which ethological studies have been conducted, are known to be territorial (Brattstrom, 1974). Specific spatial components of territories, a rock, shrub, stream, etc., are often used by individuals to define territorial boundaries (MacKay, 1975). It would seem that a more clumped distribution of spatial components might allow the establishment of a greater variety of territories and thus promote species packing.

Unfortunately, the collection of data on territorial and interspecific behavior, factors which could affect species diversity, was beyond the scope of this study. Future inquiries into this realm may provide interesting information on this hypothesis.

A second hypothesis explaining the relationship between habitat patchiness and reptile diversity involves thermal diversity. Because of the uneven disruption of radiant energy, a patchy environment should provide a greater array of thermal conditions than a uniform one. There is some evidence to suggest that reptiles do partition their environment according to thermal patches (Ruibal, 1960; Willard, 1960). What, then, is the thermal environment like which would allow for the maximum partitioning of a habitat?

Information generated from the present research, and those studies described in the literature, cannot answer this question directly. There is simply not enough known concerning the thermal requirements of the species involved nor the niche space available to reptiles in general. Indirect evidence, however, may elucidate some significant parameters in regard to the more gross aspects of the thermal environment, in this case heat availability, and its relationship to reptile diversity.

The six quadrats lying along the elevational gradient revealed a negative correlation between temperature and reptile diversity as measured in this study. Reptile diversity increased in the face of a decrease in the mean annual temperature. Could it be that the gross thermal regimes of higher elevations promoted reptile diversity? Or was it because habitat patchiness also increased with elevation? Unfortunately habitat patchiness and elevation are strongly correlated ($r = 0.748$, $p<0.05$) making it difficult to assess the contribution of each one seperately. However, since the relationship between habitat patchiness and reptile diversity prevailed when all thirteen quadrats were considered, whereas the annual mean temperature revealed no such relationship, it would appear that habitat patchiness has a greater bearing on reptile diversity than does this facet of the thermal environment. Multiple correlation techniques could not significantly alter this assumption even when habitat patchiness was simultaneously considered with elevation and/or temperature.

Two findings, however, suggest that other factors influencing heat availability may play secondary roles in influencing reptile diversity.

The strongest correlation computed in this study was between mean boulder volume and reptile diversity ($r = 0.894$, $p<0.05$). One possible explanation is that large rocks act as heat reservoirs, i.e., absorbing radiant energy during the daylight hours and radiating heat back into the environment during the late afternoon and early evening hours. This could prolong favorable thermal conditions for reptiles who cling to boulder surfaces. Large rocks are more effective in this capacity since they cool more slowly than small ones. In the six quadrats along the elevational gradient in the Deep Canyon Transect, rock volume tends to increase with elevation. Large boulders may be important at higher elevations by ameliorating relatively cool air temperatures and thus allowing reptiles to be active longer. A longer activity period would increase the opportunity for niche exploitation which could result in the presence of more species.

My personal observations suggest that certain lizards

(*Sceloporus magister*, *Uta stansburiana*) do cling to warm boulders even after sundown, apparently in an effort to maintain an optimal body temperature.

If the presence of large boulders does in fact enable reptiles to prolong their activity periods, then quadrats with similar air temperature regimes but smaller rocks should reveal less diversity.

Quadrats L, M, and K are situated at approximately the same elevations (1,250 to 1,345 m) and presumably have nearly identical mean temperatures. M and K have no boulders and therefore should, if this hypothesis is true, offer less favorable thermal environments than quadrat L. Their reptile diversity, mean rock volume, and habitat patchiness values are as follows:

Quadrat	HP	RD	$\bar{X}$RV
K	1.079	1.524	0
M	0.672	1.622	0
L	1.595	2.555	13.53

Note that RD is greatest when $\bar{X}$RV is largest. On the other hand, HP does not appear to correlate very well with RD in these three quadrats. Obviously the sample is too small to make any but the most tentative conclusions. But it appears that reptile diversity is more closely associated with an increase in mean rock volume than habitat patchiness in these three quadrats.

The hypothesis that reptile diversity may be influenced by heat availability is further enhanced by slope aspect comparisons. South slopes tested in this study possessed more species, more individuals, and in one sense, greater reptile diversity than did north slopes. (The data in Table 14 appears to reveal no pattern. At lower altitudes reptile diversity is greatest on north slopes. Yet at higher altitudes reptile diversity is less on north slopes. This lack of consistency results from the presence in quadrat A of the large herbivorous lizard, *Sauromelos obesus*. If this species were not so massive, or, if it were even eliminated from the computations, the reptile diversity value of quadrat A would exceed that of quadrat B. The unusual mass of *S. obesus* skews the Shannon index--a drawback even of this refinement in measuring species diversity.) It appears that a greater variety of niches are available for exploitation on south slopes.

The most obvious difference between north and south-facing slopes is the amount of radiant energy they receive. No other important parameter, as determined in this study, was consistent with the slope aspect results. This suggests that an increase in radiant energy and temperature, all other things being equal, may result in an increase in reptile diversity. Once again, the relationship might result from an increase in the activity period of reptiles, allowing more time for them to exploit the niche hypervolume.

SUMMARY

This thesis reports on the results of a 16 month study conducted in the Deep Canyon Transect, Colorado Desert, California. The objective was to identify those features of the environment which might be of predictive value in determining the diversity of reptiles in a given locality.

Thirteen one-quarter hectare quadrats were established in which reptile populations were sampled. To test the effect of various thermal environments on reptile diversity, six quadrats were set up on rocky, south-facing hillsides along an elevational gradient. A strong correlation ($r = -0.830$, $p<0.05$) existed between annual mean temperature and reptile diversity, and, between large heat-retaining boulders and reptile diversity ($r = 0.894$, $p<0.05$) in these six quadrats. However, these correlations did not persist when all 13 quadrats were considered.

Two quadrats were established on north-facing hillsides to further test the relationship between thermal environments and reptile diversity. Reptile diversity was found to be less on these slopes than on similar but south-facing slopes.

Five additional quadrats were established which displayed a variety of substrate and vegetation

characteristics. These, along with the other eight quadrats, were evaluated in terms of their habitat heterogeneity. One component of habitat heterogeneity, habitat patchiness (the horizontal dispersion of both plant and rock features), was the best predictor of reptile diversity ($r = 0.720$, $p<0.01$) when all 13 quadrats were considered.

Habitat patchiness was considered a better predictor of reptile diversity than any direct thermal influence since it was strongly correlated with all 13 quadrats. Territorial and thermal diversity may result from habitat patchiness and may be the niche dimensions being exploited by reptiles.

A secondary factor helping to predict reptile diversity appears to be heat availability. South-facing slopes and large, heat-retaining boulders may promote a diverse reptile fauna through potential lengthening of activity periods and consequent expansion of niche exploitation opportunities.

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