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Distribution, abundance, and reproduction of selected reptilian species were studied in riparian habitats along the Colorado River in Grand Canyon National Park. Shoreline and near-shore riparian habitats were found to support the highest densities and highest reproductive rates for most lizard species. Rapid recovery to high density in shoreline habitats within one year of the 1983 flood suggests that lizard populations are very resilient to the deleterious effects of high river flow levels. Shoreline lizard densities along the Colorado River were found to be higher than densities in riverine riparian vegetation, which in turn were higher than densities in non-riparian desert scrub. Shoreline densities for the most common species, which are among the most common and widespread lizard species in the Southwest, were higher than any previously reported anywhere else in the Southwest. The reason for high densities observed is probably abundant food availability on riparian plants and among debris along the water's edge.

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LIZARDS ALONG THE COLORADO RIVER IN GRAND CANYON NATIONAL PARK: POSSIBLE EFFECTS OF FLUCTUATING RIVER FLOWS

Distribution, abundance, and reproduction of selected lizard species were studied in riparian habitats along the Colorado River. Shoreline and nearshore riparian habitats were found to support the highest densities and the highest reproductive rates for most lizard species. High lizard density in shoreline habitats within one year of the 1983 flood suggests that lizard populations are very resilient to the deleterious effects of high river flow levels.

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INTRODUCTION

The contribution of riparian habitat to local species density and diversity of birds and mammals has been relatively well-studied. Gallery forests of cottonwood and willow along southwestern rivers have some of the highest densities of nesting birds in North America, much higher than in surrounding semiarid upland sites (Anderson, Higgins, and Ohmart 1977; Johnson et al. 1977). Riparian habitats contribute breeding sites, feeding areas, and migratory routes for birds. Mammal species diversity is also higher along watercourses, where some species find cover that is lacking in more open adjacent arid vegetation (Anderson, Drake, and Ohmart 1977), although small mammal densities in upland vegetation may be higher.

Reptiles, in contrast, have been little studied with respect to the importance of riparian habitats to their density and diversity. It is common to find comments in the literature about the higher density of some species in riparian sites (Lowe and Johnson 1977; Tinkle 1982; Vitt and Ohmart 1977), and researchers have performed some studies of lizard demography in riparian areas (Tinkle 1976; Tinkle and Dunham 1983; Vitt and Van Loben Sels 1976). However, quantitative studies comparing reptile density and diversity in riparian and adjacent non-riparian habitats are few. Studies on riparian ecosystems have only recently begun to address effects of management practices and habitat manipulation on riparian reptile communities (Jakle and Gatz 1985; Jones and Glinski 1985; Szaro et al. 1985).

In this study we examined the distribution of reptilian species relative to riparian habitats along the Colorado River in Grand Canyon National Park. The work was part of a larger study to determine the effects of fluctuating and flood releases from Glen Canyon Dam on plant and animal populations in and along the Colorado River. We gathered our data during constant flow levels of approximately 40,000 cubic feet per second (cfs) in June 1984, 25,000 cfs in August 1984, 35,000 cfs in June 1985, and 25,000 cfs in August 1986.

OBJECTIVES

The goal of this project was to evaluate the effects of fluctuating river levels, as controlled by Glen Canyon Dam, on the herpetofauna of the Grand Canyon. Because no information previously existed about the distribution and population ecology of the herpetofauna in Grand Canyon, the primary focus of the study was to analyze patterns of habitat use by reptile and amphibian species, and to determine the relative importance of riparian habitats to the density and diversity of those populations. Our analysis emphasized those lizard species for which we had the largest sample sizes: those species that were most readily censused within the project's time and manpower constraints. Interpretation of possible effects of fluctuating river flow levels on the herptofauna of the riparian corridor was a secondary emphasis based on indirect inferences since no fluctuating flows occurred during the study period.

METHODS

STUDY AREA. We censused sites along the Colorado River in Grand Canyon National Park beginning near Lees Ferry and extending downstream 220 miles almost to Diamond Creek. The elevation at river level dropped from approximately 945 m (3,100 ft) at Lees Ferry (River Mile [RM] 0) to approximately 427 m (1,400 ft) at the last census locality at RM 220. The upland vegetation along the river is generally Mohave desertscrub. There is, however, a gradual transition from more cold-tolerant species at the upper end of the study area to many frost-sensitive species at the lower end (Warren et al. 1982).

Two vegetation zones, more or less distinct in species composition and distribution, characterize the riparian corridor. Prior to construction of Glen Canyon Dam in 1963, floods scoured the river channel on a regular basis. The only riparian vegetation formed a belt along the high water line where flood disturbance was minimal. Since dam construction, lack of large-volume flooding has allowed plants, many of them exotics, to grow along the water's edge (Turner and Karpiscak 1980). The original riparian vegetation (called here the Old High Water Zone, or OHWZ), consisting largely of mesquite (Prosopis glandulosa) and catclaw acacia (Acacia greggii), is now perched on talus slopes and alluvial terraces several meters above the current average water level. The new riparian vegetation (called here the New High Water Zone, or NHWZ) dominated by tamarisk (Tamarix chinensis) and arrowweed (Tessaria sericea), occupies sand and cobble bars along the water's edge.

SAMPLING PROCEDURES. We used visual belt transects, modified from the Emlen (1971) bird census technique, to census the common diurnal species (Lowe and Johnson 1977). This method involved walking transects through representative areas of the target habitats and recording all individuals observed within a 4 m-wide belt. Transect length varied with size of the habitat patch, but was usually 100 to 300 m. We selected transect sites to sample variation within old and new riparian habitats and in adjacent non-riparian desertscrub. Transects were visually selected to sample homogenous stands of each habitat. We recorded the time of day at the beginning and end of each transect walk, as well as a temperature profile consisting of soil surface temperature and air temperature at 5 mm and 1.5 m above the soil surface. We also noted wind speed and other weather conditions such as cloudiness.

As each individual lizard was sighted, we recorded distance along the transect and substrate upon which it was first observed, as well as its sex and age, when possible. Substrate categories used were bare soil, litter, rock (less than 1 m in diameter), boulder (greater than 1 m in diameter), cliff face, or tree. When individuals were in a tree, we recorded tree species and height above ground.

HABITATS SAMPLED. We sampling ten habitats distributed in four zones relative to the river. The first zone was shoreline habitats within 5 m of the river shore. The second zone was NHWZ riparian vegetation greater than 5 m from the river shore. The third zone was OHWZ riparian vegetation, which always occurred at a greater distance from the shore than the NHWZ vegetation. The fourth zone was non-river habitats, both upland desertscrub and tributary riparian (Table 1).

We sampled three distinct habitats in the river shoreline zone: cobble shore, rocky shore, and vertical rock faces at the water's edge. All of these habitats had low vegetation cover, usually less than 10 percent. Cobble shores generally had numerous rocks less than 0.5 m in diameter and rounded by erosion. Larger, uneroded boulders were absent and large patches of bare sand were occasionally present. Cobble shores generally occurred at the mouths of tributary canyons, where coarse alluvium was washed into the river, forming level cobble bars.

Table 1. Location of study sites for lizard transect sampling in 1984. Number of habitats sampled in each vegetation zone is indicated for each site. Under River Mile, R and L mean right and left shore when facing downstream.

Site Name	River Mile	Shore-line	River Riparian	Non-River
Lees Ferry	-1R		1	1
Badger	8R	1		
none	16L	1		
none	20R	1		
North Canyon	20.5R	1		
none	43.5L	1		
Saddle Canyon	47R	1	3	1
Nankoweap	53R	2	3	2
Kwagunt	56R	1		
Cardenas	71L	1	4	
Cremation	86L		1	
none	94L		1	
Crystal	98R	1		
Bass	108.5R	1	2	1
Elves Chasm	116.5L	1	1	
Forster	123L		2	
Tapeats	134R	1		1
none	140L	1	1	
Kanab	143.5R	1	4	
National	166L	2	1	
Stairway	171R	1	2	
none	185R	1	3	1
Whitmore	188R		3	
Parashant	198R	1	3	1
Granite Park	209L	1	1	
Three Springs	216L	1		
220 Mi. Canyon	220R	1		
Total Transects		24	36	8
Total Transect Length (meters)		2,665	5,522	2,420

In contrast, rocky shores consisted of rock fragments varying from cobbles to boulders several meters in diameter. These shores were generally uneroded talus and rockfall debris with occasional pockets of bare sand trapped among the boulders. In contrast to the level cobble shores, rocky shores usually fell steeply to the water's edge and were commonly very rugged and irregular.

Sandy shores and heavily vegetated shores were examined, but not sampled systematically for several reasons. Dense vegetation immediately at the water's edge was uncommon. In most locations where dense cover was present near the shore, it occurred on sandy soil. Frequently, erosion of sandy soil along the river's edge kept the immediate shoreline free of dense cover even though adjacent sandy bars were thickly vegetated. Open sandy shorelines that lacked vegetation or rock cover had no reptiles and amphibians. Although such sandy shores were spot-checked repeatedly, no systematic transects were sampled.

Within the riparian NHWZ, we sampled three post-dam habitats: open tamarisk with 15-40 percent cover, dense tamarisk with 60-100 percent cover, and arrowweed with cover similar to the open tamarisk. Open tamarisk and arrowweed habitat categories were similar in structure and intergraded extensively in species composition. For that reason, they were combined for some analyses in the later part of the study. We sampled two pre-dam habitats in the OHWZ riparian vegetation: mesquite/acacia alluvial terraces and mesquite/ acacia talus slopes. Finally, we sampled two habitats in the non-river zone: desertscrub on canyon slopes generally ranging from a 15-30 percent grade, with 15-30 percent vegetation cover, and non-river riparian habitats along perennial tributary streams.

We assessed habitats in September 1983 and April 1984, then performed the census during June and August 1984. At that time, we sampled between one and five habitats per locality (Table 1) with a total of 68 transects at 27 localities. Censuses were repeated in June 1985 and in May, June, and August 1986. A total of 79 transects were sampled during each of those years.

RESULTS AND DISCUSSION

We recorded five common diurnal lizard species using the belt transect method. One lizard species (Holbrookia maculata), two toad species (Bufo punctatus and B. woodhousei), and one frog species (Hyla arenicolor), occurred in numbers too small for adequate conclusions to be drawn concerning distribution patterns. Eight snake species were observed during the course of the study. Rattlesnakes were by far the most abundant, with 11 observations of Crotalus viridis abyssus and 9 of C. mitchellii. Of the remaining snakes, Masticophis taeniatus was third most common with five sightings, and M. flagellum, Lampropeltis getulus, Pituophis melanoleucus, Sonora semiannulata, and Diadophis punctatus were observed only once or twice each. Although there was a weak trend toward more frequent snake sightings in riparian habitats, the pattern was not significant due to an insufficient sample.

SUBSTRATE PREFERENCE. Lizards showed strong species-specific patterns of substrate preference (Table 2). No two common species occurred with highest frequency on the same substrate, although up to four species were commonly observed along a single transect.

Table 2. Distribution of lizards on substrates along the Colorado River in Grand Canyon, June and August 1984. Numbers in parentheses indicate percent of individuals of each species observed on each substrate.

Species	Substrate						Total
	Litter	Bare Soil	Rock <1m	Boulder >1m	Cliff	Tree	
Uta stansburiana	2 (1.3)	70 (46.7)	71 (47.3)	2 (1.3)	1 (0.7)	4 (2.7)	150
Cnemidophorus tigris	9 (9.5)	78 (82.1)	4 (4.2)	3 (3.2)	0	1 (1.1)	95
Sceloporus magister	11 (12.5)	11 (12.5)	7 (8.0)	34 (38.6)	3 (3.4)	22 (25.0)	88
Urosaurus ornatus	3 (4.9)	1 (1.6)	9 (14.7)	16 (26.2)	27 (44.3)	5 (8.2)	61
Crotaphytus insularis	0	1 (14.3)	4 (57.1)	2 (28.6)	0	0	7
Sauromalus obesus	0	0	0	1 (100)	0	0	1
Holbrookia maculata	0	1 (100)	0	0	0	0	1
Total	25	162	95	58	40	32	403

Side-blotched lizards (Uta stansburiana) were the most common species (Table 3) as well as the smallest. They were found predominately in open sites, on rocks less than 1 m in diameter or bare soil. They were rarely more than 1 m away from the cover of rocks or small shrubs.

Western whiptail lizards (Cnemidophorus tigris), the second most abundant species (Table 3), were found most frequently on bare soil or litter. They often occurred in the same habitats with Uta, but unlike Uta, rarely perched on small rocks. Cnemidophorus was the only species commonly observed to roam up to several meters across open sand away from cover.

Desert spiny lizards (Sceloporus magister) were approximately equal in abundance to Cnemidophorus, although they were less noticeable due to more sedentary habits and a preference for cryptic vertical substrates such as large boulders and/or trees. Desert spiny lizards were most commonly on boulders larger than 1 m in diameter, usually with fractures and crevices. At sites without boulders but with trees (such as tamarisk stands on sandbars), this species also occurred on larger tree trunks. When they were observed on the ground, they were almost invariably at the base of a large tree or boulder.

Tree lizards (Urosaurus ornatus) also used vertical substrates; however, they preferred sheer, vertical rock faces on cliffs or large boulders. Cliff faces that dropped vertically into the river, usually along eddies or quiet stretches, had the highest densities of tree lizards. They often sat less than 1 m above water level, just above the splash zone, on faces with no fractures or other protection and that were up to 20-40 m from the nearest water-level alluvial soil.

We saw black collared lizards (Crotaphytus insularis) and chuckwallas (Sauromalus obesus) much less frequently than the four preceding species. These two species were also more common in desertscrub than in the riparian corridor. Collared lizards generally were observed perched on rocks or on small boulders approximately 1 m in diameter or slightly smaller. We rarely saw Chuckwallas on transects, but additional observations indicated that they preferred deeply fractured boulders and rock outcrops.

PATTERNS OF DENSITY AND HABITAT OCCUPATION. The most striking observation was the large differences in lizard densities among habitats (ANOVA with unequal sample size, $F=17.41$, Prob. <0.001; Tables 3a,b,c). Total lizard densities were highest in shoreline and open New High Water Zone riparian habitats and lowest in desertscrub, with intermediate densities in Old High Water Zone sites. Most species followed the general pattern, with highest densities in shoreline and NHWZ habitats and lowest density in desertscrub. The only exception was the collared lizard, which, although relatively rare, was seen more commonly in desertscrub than in any other habitat.

Table 3a. Lizard densities in habitats along the Colorado River in Grand Canyon, Arizona during June and August 1984. Values are mean number of individuals per hectare.

Habitat	Month	Lizard Species: Uta	Cnemidophorus	Sceloporus	Urosaurus	Crotaphytus	All Lizards
Shoreline (<5m)							
Rocky Shore	June	48	23	60	20	0	150
	Aug.	20	0	0	100	0	120
Cobble Bar	June	68	40	15	0	3	125
	Aug.	60	18	13	0	0	90
Cliff Face	June	0	0	0	858	0	858
	Aug.	0	0	0	223	0	223
River Riparian (>5m)							
(NHWZ) Open Tamarisk	June	31	101	59	14	0	206
	Aug.	53	60	60	0	0	173
Arrowweed	June	35	35	5	0	0	73
	Aug.	33	18	18	0	0	68
Dense Tamarisk	June	0	13	40	0	0	53
	Aug.	no sample					
(OHWZ) Terrace	June	30	15	15	3	1	65
	Aug.	0	0	13	25	0	38
Talus	June	28	10	15	0	0	53
	Aug.	no sample					
Non-River							
Desertscrub	June	18	8	5	0	2	30
	Aug.	5	5	0	0	5	15
Riparian	June	25	0	125	150	0	300
	Aug.	208	0	0	0	0	208
Grand Mean (All habitats)	June	35	25	23	10	0.7	93
	Aug.	30	13	13	23	1	80

Table 3b. Lizard densities in habitats along the Colorado River in Grand Canyon, Arizona during June 1985. Values are mean number of individuals per hectare.

Habitat	Lizard Species					All Lizards
	Uta	Cnemidophorus	Sceloporus	Urosaurus	Crotaphytus	
Shoreline (<5m)						
Rocky Shore	94	17	53	37	1	202
Cobble Bar	69	10	14	33	0	126
Cliff Face	0	0	200	350	0	550
River Riparian (>5m)						
(NHWZ) Open Tamarisk	36	23	27	0	0	86
Arrowweed	39	78	7	0	0	123
Dense Tamarisk	0	41	30	0	0	71
(OHWZ) Terrace	22	9	14	0	0	45
Talus	9	0	10	0	0	19
Non-River						
Desertscrub	23	4	3	0	1	31
Grand Mean (All habitats)	43	13	20	14	0.4	90

Table 3c. Lizard densities in habitats along the Colorado River in Grand Canyon, Arizona during 1986. Values are mean number of individuals per hectare.

Habitat	Lizard Species					All Lizards
	Uta	Cnemidophorus	Sceloporus	Urosaurus	Crotaphytus	
Shoreline (<5m)						
Rocky Shore	124	17	29	32	0	202
Cobble Bar	92	13	25	42	0	172
River Riparian (>5m)						
(NHWZ)						
Open Tamarisk	18	73	50	0	0	141
Arrowweed	50	75	12	0	0	137
Dense Tamarisk	0	42	69	14	0	125
(OHWZ)						
Terrace	28	4	3	0	0	35
Talus	9	0	10	0	0	19
Non-River						
Desertscrub	12	2	00	0	1	15
Grand Mean (All habitats)	43	14	14	11	0.3	82

Direct comparison of density values derived from visual transects in this study with density data available in the literature is difficult for several reasons. First (and most important), our visual census did not account for every lizard in the study site as would a mark/recapture study on a permanent grid. Visual transect estimates will therefore generally be lower than a comparable mark/recapture estimate. Second, lizard densities vary substantially between sites, and between years, seasons, or even days at a single site. Thus, any comparison of densities, regardless of the sample technique, is fraught with problems unless the sampling is performed simultaneously at all sites compared. With these problems in mind, it is still useful to compare our results with density data available in the literature.

In general, lizard densities along the Colorado River were within the range of values observed for these species in other areas (Table 4). We found Urosaurus ornatus to occur in the highest density, as was true in several other studies. Similarly, of the four most common species, Sceloporus magister, had the lowest density. Sceloporus was reported by several other authors to have lower densities as well. These results indicate that visual transect data are roughly comparable with mark/recapture data.

The average June densities of 858 lizards/ha on shoreline cliff faces, and 300 lizards/ha in non-river riparian habitats, equal or exceed lizard densities reported in the literature for any habitat. This observation is of particular interest considering the expected under-estimate of a visual census compared to mark/recapture methods. The lizard densities we observed in riparian habitats along the Colorado River were higher than those in most habitats thus far studied in the Southwest. They were up to an order of magnitude higher than densities we observed in desertscrub immediately adjacent to the river corridor.

The most likely explanation for these high densities is an increased abundance of food resources. Many shoreline sites appear to have much greater numbers of insects than non-riparian areas for two major reasons. First, debris washed up along the water's edge in eddies and backwaters is frequented by many insects. Second, many riparian plant species support a larger insect fauna than non-riparian species (Stevens 1976). The two highest local lizard densities observed anywhere along the river were both at sites along the shoreline where lizards were feeding upon insects. The highest density was observed at Cardenas where a total of eight Cnemidophorus tigris and five Sceloporus magister were observed feeding along the shoreline in an area of approximately 3 x 7 m, or a density equivalent to 6,500 lizards/ha. In spite of their close proximity to one another, no antagonistic interactions were observed between individuals of either species, and all were active in the

Table 4. Comparison of average lizard densities in Grand Canyon with those from other localities. Ranges are shown in parentheses. In some cases the ranges are from replicate sampling in adjacent sites, and in some cases from sampling in different years.

Species	Average Density (Number/ha)	Location	Source
<u>Uta</u>	140 (62-238)	Texas	Tinkle 1967
<u>stansburiana</u>	22	Ariz. desertscrub	Vitt and Van Loben Sels 1976
	7	Ariz. mesquite	Vitt and Van Loben Sels 1976
	7	Ariz. riparian	Vitt and Van Loben Sels 1976
	33 (0-208)	All habitats	This study
<u>Cnemidophorus</u>	12 (8-18)	Nevada	Turner et al. 1969
<u>tigris</u>	8 (3-15)	Texas	Degenhardt 1966
	17	Colorado	McCoy 1965
	30	Nevada	Tanner and Jorgensen 1963
	114 (45-184)	Texas	Milstead 1967
	3	Ariz. grassland	Lowe and Johnson 1977
	12	Ariz. deserscrub	Vitt and Van Loben Sels 1976
	32	Ariz. mesquite	Vitt and Van Loben Sels 1976
	32	Ariz. riparian	Vitt and Van Loben Sels 1976
	7	Ariz. dry wash	Vitt and Van Loben Sels 1976
	19 (0-78)	All habitats	This study
<u>Sceloporus</u>	15	Utah riparian	Tinkle 1976
<u>magister</u>	10	Ariz. desertscrub	Vitt and Van Loben Sels 1976
	25	Ariz. mesquite	Vitt and Van Loben Sels 1976
	25	Ariz. riparian	Vitt and Van Loben Sels 1976
	18 (0-125)	All habitats	This study
<u>Urosaurus</u>	158 (131-188)	Ariz., spring	Tinkle and Dunham 1983
<u>ornatus</u>	101 (42-161)	Ariz., summer	Tinkle and Dunham 1983
	370	Ariz. mesquite	Vitt and Van Loben Sels 1976
	185	Ariz. riparian	Vitt and Van Loben Sels 1976
	16 (0-858)	All habitats	This study
Total	6 (2-12)	Southwest deserts	Pianka 1967
Lizards	55	Ariz. riparian	Lowe and Johnson 1977
	66	Ariz. grassland	Lowe and Johnson 1977
	8	Ariz. Chihuahuan Desert	Lowe and Johnson 1977
	593	Ariz. mesquite	Vitt and Van Loben Sels 1976
	277	Ariz. riparian	Vitt and Van Loben Sels 1976
	89	Ariz. Sonoran Desert	Vitt and Van Loben Sels 1976
	12	Ariz. dry wash	Vitt and Van Loben Sels 1976
	86 (15-858)	All habitats	This study

area for an hour. The second highest density was observed on a vertical rock face at the waterline on which eight Urosaurus ornatus were observed in an area of 2 x 25 m, or 1,600/ha. Again, they were feeding on insects at the water's edge with no apparent antagonistic interactions for an extended period of time.

The distributions of several of the lizard species studied were consistent with the concept of "preferential" riparian species as used by Johnson et al. (1984) in their discussion of plant species distributions. Urosaurus, Cnemidophorus, Sceloporus, and Uta could be considered "preferential" riparian species by virtue of their higher densities in riparian habitats compared to non-riparian. As with the original application of these terms to plant distributions, it is important to note that these classifications refer only to local distribution and do not apply throughout the species' ranges.

The pattern of differences in lizard densities among habitats was stable through time as shown by comparison of data from different seasons and different years (Table 5). Correlation analysis of density data gathered in the same habitats during consecutive years indicates that differences in total lizard densities between habitats were stable year to year (1984/1985 r=0.94, n=12; 1985/1986 r=0.93, n=11).

Comparison of densities observed during the two different census periods in 1984 shows a decline from June to August (Table 2). It appears that the cooler, cloudier weather encountered during the August census resulted in lower activity levels of some species. Whiptails and desert spiny lizards both declined in observed densities by approximately one-half between the two census periods.

POPULATION RESILIENCE TO FLUCTUATING FLOWS. The observation that 1984 lizard densities were highest in the shoreline zone, and that those densities were among the highest ever observed in lizard populations in the arid Southwest, suggests that lizard densities recovered to a large degree within one season from whatever deleterious effects they experienced due to the high water of 1983. The unusually high water of that year undoubtedly eliminated the populations on many cobble bars and lower rocky shores.

In some parts of the canyon, horizontal displacement of the shoreline from normal flow levels to high water levels during 1983 was up to 100 m across wide cobble bars. Vertical displacement between normal and high shoreline locations was up to 8 m. The observation that densities on shoreline sites were back to near maximum levels within one season after the flood, and before newly hatched young could disperse, suggests that many adult lizards recolonized the previously flooded shoreline as the water level dropped.

Table 5. Variation in lizard densities in riparian and non-riparian habitats along the Colorado River between 1984 and 1986. Mean densities are individuals/ ha. Sample size indicates number of transects sampled in each habitat.

Habitat	1984			1985			1986		
	mean	S.D.	n	mean	S.D.	n	mean	S.D.	n
Shoreline									
All sites	425	1,067	26	179	143	36	186	98	21
Rock face	782	840	4	550	--	1	--	--	--
Rocky shore	144	82	11	199	119	17	203	118	10
Cobble bar	98	68	11	125	136	18	167	69	11
NHWZ									
All sites	94	74	16	91	77	15	125	82	9
Open Tamarisk	184	142	7	87	82	6	141	94	5
Arrowweed	96	77	5	124	75	4	137	124	2
Dense Tamarisk	72	75	4	71	92	5	125	119	2
OHWZ									
All sites	56	49	18	37	34	16	29	28	11
Talus	56	49	7	19	29	8	<8	--	2
Terrace	55	51	11	46	38	8	36	27	9
Non-riparian									
Desertscrub	21	22	6	32	21	12	15	11	7

A weak trend was seen in shoreline and NHWZ riparian habitats toward a continued increase in lizard densities from 1984 to 1986 (Table 5). Most habitats showed a consistent, but non-significant, increase during the three years of observation, suggesting that populations near the river are not yet completely stable following the 1983 flood. The one major exception to the pattern of increasing densities in the riparian zone during 1984 to 1986 was *Urosaurus*. Inadequate sampling of cliff faces, *Urosaurus'* preferred habitat, during 1985 and 1986 resulted in an erroneous appearance of a large decline in Urosaurus numbers. It is important to note that the opposite trend in density was seen in OHWZ habitats, with a consistent decline in density between 1984 and 1986. One possible, but unsubstantiated, interpretation of this pattern is that some individuals are migrating from the higher old zone back into the new zone habitats that were left vacant by the high water of 1983. No consistent pattern of change in density between years was observed in the desertscrub.

REPRODUCTION. Reproductive activity of lizards along the Colorado River was not evaluated directly, but indirect evidence of reproduction was inferred from the distribution of immature individuals (Table 6).

Table 6. Relative densities of juvenile lizards in riparian habitats along the Colorado River expressed as percent of adult density. For the relative juvenile densities of all species chi-square = 40.75; $p < 0.001$. The "open shrub" habitat category combines open tamarisk and arrowweed.

Habitat	Uta	Sceloporus	Cnemidophorus	Urosaurus	Crotaphytus	All Species
Shoreline						
Cobble bar	30.2	175.0	16.7	13.8	--	29.6
Rocky shore	8.9	25.8	5.6	13.0	--	12.6
Rock face	0	31.8	0	5.3	--	9.1
NHWZ						
Open shrub	30.6	20.0	13.7	0	--	20.2
Dense tamarisk	33.3	0	0	0	--	1.4
OHWZ						
Terrace	12.0	16.7	0	0	--	10.0
Talus slope	0	0	0	0	--	0
Non-riparian						
Desert scrub	0	0	0	0	20.0	4.4

The greatest number of immature lizards was observed in shoreline and riparian habitats with a mosaic of bare sand, which provides nest locations, and cover such as cobbles and small shrubs. Uta juveniles were the most common and were often seen on cobble bars and the shoreline. Tinkle's (1967) observations that the average first-year dispersal of juvenile Uta is less than 6 m suggests that these habitats are the location of higher reproductive activity than non-riparian sites. Although the young of other species are likely capable of dispersing greater distances than do Uta, they are probably found within a few tens of meters of their hatching site during the first two or three months.

One unexpected observation was that juveniles of most species were generally found in highest proportions in a habitat other than that in which the adults achieved maximum density (Chi-square = 40.8, D.F.=7, Prob. <0.001). This was particularly apparent for Sceloporus magister, in which juveniles outnumbered adults by almost two to one on cobble bars. In the case of Urosaurus, this pattern is easily explained by the fact that the preferred adult foraging areas are rock faces that lack nest sites.

CONCLUSIONS

Shoreline lizard densities along the Colorado River were found to be higher than densities in riverine riparian vegetation, which in turn were higher than densities in non-riparian desertscrub. Shoreline densities for the most common species, which are among the most common and widespread lizard species in the Southwest, were higher than any previously reported anywhere else in the Southwest. The reason for the high densities observed is probably abundant food availability on riparian plants and among debris along the water's edge.

It is possible that rapidly fluctuating river flow levels have short-term deleterious effects on shoreline lizard populations for two reasons. First, rapidly rising water could trap and destroy large numbers of individuals on alluvial bars, and second, rising water during the breeding season from May to July may inundate nest sites in shoreline and riparian-zone sand. However, lizard populations appear to be very resilient to disturbance due to high river flow levels and reestablish rapidly along the shoreline.

RECOMMENDATIONS FOR OPERATING CRITERIA

The characteristics of river flow levels that are likely to adversely affect lizard, and other reptile and amphibian, populations are seasonality and rates of fluctuation, rather than absolute magnitudes of fluctuation. The critical season for these lizard populations is late spring and summer when reproduction occurs. Egg laying occurs primarily from April through June (Tomko 1976), followed by hatching and dispersal from June through August. During this period of time, rising water levels would inundate and destroy nests, which appear to be most abundant in shoreline and NHWZ habitats. Additionally, rapid changes in water levels (more than three to four vertical feet in less than one day) would be more likely to trap and destroy populations on cobble bars and beaches than gradual flow changes.

Based on these considerations, an ideal flow scenario for riparian herptofauna would be a maximum annual river flow during late March or April, which would cause nest site selection to occur high on the shore, followed by a gradual reduction in flow through the summer without large, rapid fluctuations.

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